

ANALYSIS OF THE GLIDING BEHAVIOR OF *PTYCHOZOOON LIONATUM* (REPTILIA: GEKKONIDAE)

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ABSTRACT: The glides of the lizard, *Ptychozoon lionatum*, with lateral cutaneous expansions tied and untied were measured and timed. Analysis demonstrated that untied animals traveled farther and at lower speeds than animals with expansions tied. Glide distances for untied lizards were negatively correlated with weight/surface area and with weight/snout-vent length. It is suggested that the primary function of the lateral cutaneous expansions is to facilitate gliding.

PTYCHOZOOON is a small genus of arboreal geckos occurring in southeast Asia, the Indo-Australian Archipelago, and the Philippine Islands. The five species are characterized by extensive digital webbing; small skin flaps on the head, neck, and limbs; a strongly depressed tail with scalloped lateral membrane; and large lateral cutaneous folds or expansions from axilla to groin (Fig. 1). The latter lie close to the body during rest or normal locomotor activity, are apparently not under muscular control, and lack skeletal or muscular support. Remarks on the functional significance of these structures have been largely speculative due to the scarcity of reliable field observation and experimentation.

Cantor (1847) suggested a parachute-like function for the lateral expansions. Boulenger (1890) figured *Ptychozoon homalocephalum* [= *P. kuhli*] in "flight." However, Annandale (1905) and Barbour (1912) dismissed the "flight" hypothesis and maintained a cryptic function for the expansions. De Rooij (1915) made no mention of flight but referred to a concealing purpose. Smith (1935) suggested that the lateral expansions, though not under muscular control, might be raised by wind resistance in "flight."

Behavioral observations in nature have rarely been reported. Boulenger (1908) referred to a *P. homalocephalum* reportedly caught in flight between two trees, and Taylor (1922) recorded the capture of the type specimen of *P. intermedia* when it was disturbed in a tree and jumped to the ground. Taylor (1963) reported a *P. lionatum* that was discovered near the sum-

mit of a small dead tree and, after prodding with a bamboo pole, took "flight" and jumped a horizontal gap of about 2.5 m to another tree where it landed on the trunk about 5 m lower than its point of departure. Casual experiments by several workers (Tweedie, 1950; Tweedie, 1954; Heyer and Pongsapipatana, 1970), each conducted with a single experimental animal and with few replications, have established the gliding ability of *Ptychozoon*. Tiwari (1961) restated the assumption (Tweedie, 1950) that the webbed feet and frilled tail of *Ptychozoon* are adaptations for concealment and gliding, while lateral cutaneous expansions function solely in gliding. In this paper we quantify the gliding ability of *Ptychozoon lionatum* and establish the function of the lateral expansions.

MATERIALS AND METHODS

Eight *Ptychozoon lionatum* (6 ♀♀, 2 ♂♂) in the United States National Zoological Park collection were housed, singly or in groups of two or three, in glass terraria at 25°–32°C, and maintained on a diet of living insects. All specimens appeared healthy throughout the study period (26 May–26 June) except one animal which died of an injury not associated with the study. Specimens were individually marked with spots of nontoxic paint on the dorsum. Weights (6.1–12.5 g) and linear measurements (SVL 73–85 mm) were recorded on 26 May and 26 June.

Ventral surface area of each specimen was estimated by summing estimates of tail, feet and body ventral surface areas. Tail surface area was defined as length × width

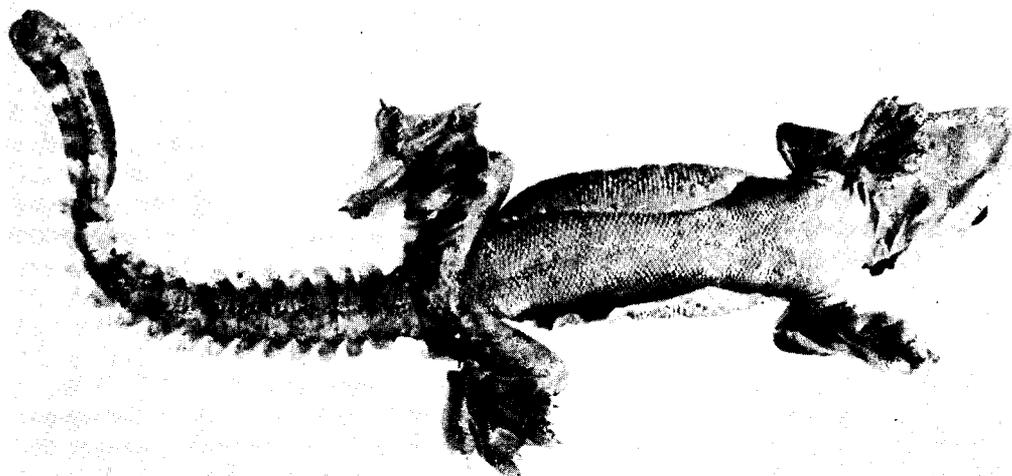


FIG. 1.—Ventral aspect of living *Ptychozoon lionatum* photographed through glass.

at midpoint vent to tip. The maximum straight-line distance across the expanded front foot was taken as the diameter of a circle; each front foot was thus $\frac{1}{2}$ of this circle and the computed area of the circle was an estimate of the surface area of the two front feet. The area of the two hindfeet was similarly estimated. Ventral body surface area was computed by visualizing the animal's trunk as a rectangle, the width being maximum width of the expanded lateral folds and the length being from the vent to a line across the gular region. Head and limb surface areas were not calculated. Ventral surface area estimates ranged from 20.69–33.38 cm².

Ten gliding trials were conducted, four on 26 May and two each on 28 May, 4 June and 26 June. A trial consisted of releasing each animal from the edge of the roof of a building 8.25 m above the ground. In five trials the lateral cutaneous folds of the animals were restrained in a natural resting position by tying two pieces of fine thread around the trunk, one posterior to the axilla and the other anterior to the groin; in the other five trials the folds were not tied. Trials were run in the late afternoon (1530–1800 h) at air temperatures

of 24.5°–28.0°C. Clear and relatively windless conditions prevailed during the trials.

The animals were released in a consistent manner by being held at arm's length away from the building. Each specimen was restrained immediately behind its head, the longitudinal axis of its body was held perpendicular to the wall of the building with the animal's snout directed outward. A person on the ground below timed the descent with a stopwatch, marked the contact point and measured the horizontal distance from contact point to a point directly below the release point. The calculated straight-line distance from release point to contact point was used as an estimate of glide distance for computation of glide rate. Calculated glide rates probably represent underestimates as the glide paths were curved and not straight.

Film records of some of the descents were made with a movie camera operated at 54 frames/second.

RESULTS

Table 1 and Fig. 2 show data for drops of *P. lionatum* with lateral folds tied and untied. The greatest horizontal distance attained was 9.35 m for individual 3 with

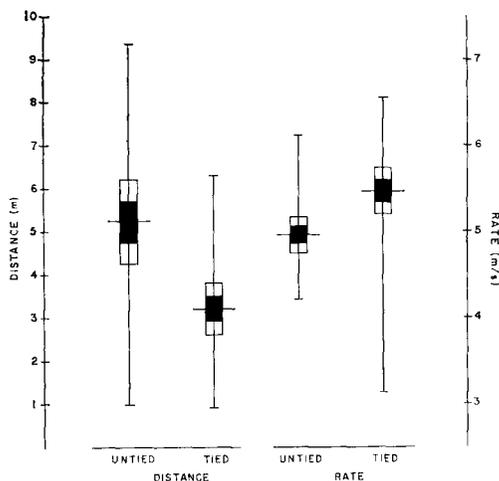


FIG. 2.—Horizontal distances traveled and glide rates for *Ptychozoon lionatum* with lateral cutaneous folds tied and untied. Vertical lines are ranges, horizontal lines are means. Rectangles represent 95% confidence limits of means and solid black rectangles indicate SE of means. $N = 25$ for each condition.

folds untied, and the shortest distance was 0.91 m for individual 5 with folds tied. The mean horizontal distance for untied animals was 5.24 m and the mean for tied animals 3.20 m. The means were compared using a t -test and showed a significant difference at the $p < .01$ level. A comparison of glide rates (Fig. 2) also disclosed a significant difference between the means at the $p < .01$ level. Geckos with folds tied generally travelled shorter distances at a higher rate than those with folds untied (Fig. 2). It is clear that animals with folds tied retained considerable gliding ability; individual 5 reached a horizontal distance of 6.30 m with folds tied (Table 1), well above the mean distance of untied descents.

Generally, horizontal distance was positively correlated with time. However, a glide with a very short horizontal distance (first untied descent of individual 4) occasionally took as long as one with $6 \times$ as great a horizontal component (untied descent of individual 5). This appeared to be the result of differing behavior during the descent.

It was hypothesized that horizontal distance would be correlated with such physical parameters as weight, SVL, and ventral surface area. Correlation coefficients were calculated between horizontal distance of untied glides and (1) weight/SVL, and (2) weight/estimated ventral surface area. Highly significant negative correlations of $r = -.57$ ($p < .01$) and $r = -.51$ ($p < .05$), respectively, were found.

Filmed descents showed that the behavior and subsequent glide path of the geckos, with or without tied lateral expansions, was similar. Three distinct types of descent were observed. In all types the animals appeared to control their body position and there were no cases of tumbling. First, and least common, was a nearly direct vertical drop without strong posturing (3 of 50 descents; 2 tied and 1 untied). Second was a nearly vertical drop with posturing during the last 5 to 7 m of the descent (13 of 50; 9 tied and 4 untied). Third, and most common, was a descent consisting of an initial vertical drop of 1.2–3.0 m with strong posturing followed by a descending arc of varying distance (34 of 50; 14 tied and 20 untied). The arc was steep at first and leveled out during the last few meters with a slight rise just before landing. Type 3 descents varied in steepness, distance and rate.

The posture assumed in all three types of descents was similar but differed in intensity. The basic posture observed in all descents was one with limbs and tail extended and belly downwards. This posture was further enhanced by stronger extension of the limbs and tail and expansion of the webbed digits. The stronger posture increased the effective ventral surface area as the appendages were spread in the same plane as the body. If not tied around the trunk, the lateral cutaneous expansions were widely spread by wind resistance, further increasing surface area. The time it took a gecko to reach the ground was a function of the type of descent and the posture assumed. Thus, as discussed previously, a descent may have

TABLE 1.—Data for 50 drops of eight *Ptychozoon lionatum* with lateral cutaneous expansions untied and tied. Rates calculated with descent distance. Values are: horizontal distance (m), descent distance (m), time (s), rate (m/s).

Individual	Untied descents	Individual	Tied descents
1	8.03-11.51-2.5-4.6	1	4.27- 9.29-1.8-5.2
	6.65-10.60-2.3-4.6		4.27- 9.29-1.8-5.2
	4.62- 9.46-1.9-5.0		4.62- 9.46-1.5-6.3
2	3.71- 9.05-1.7-5.3	2	2.74- 8.69-1.6-5.4
	5.84-10.11-2.4-4.2		4.65- 9.47-1.6-5.9
	6.35-10.41-2.4-4.3		1.07- 8.32-1.5-5.6
3	3.05- 8.80-1.8-4.9	3	4.01- 9.17-1.4-6.6
	5.11- 9.70-2.1-4.6		1.42- 8.37-1.6-5.2
	9.35-12.47-2.5-5.0		5.13- 9.71-1.8-5.4
4	2.08- 8.51-1.6-5.3	4	3.96- 9.15-1.6-5.7
	0.97- 8.31-1.7-4.9		1.88- 8.46-1.6-5.3
	1.52- 8.39-1.5-5.6		6.30-10.38-1.8-5.8
5	6.32-10.39-1.7-6.1	5	0.91- 8.30-1.4-5.9
	6.30-10.38-1.9-5.5		3.63- 9.01-1.7-5.3
	7.87-11.40-2.3-5.0		1.55- 8.39-1.4-6.0
6	6.91-10.76-2.1-5.1	6	2.84- 8.72-1.6-5.4
	2.34- 8.58-2.0-4.3		3.66- 9.03-1.7-5.3
	7.47-11.13-2.2-5.1		3.40- 8.92-1.6-5.6
7	4.72- 9.50-1.7-5.6	7	1.88- 8.46-1.5-5.6
	6.93-10.77-1.9-5.7		2.69- 8.68-1.5-5.8
	5.92-10.15-2.4-4.2		1.88- 8.46-2.7-3.1
8	3.73- 9.05-2.1-4.3	8	3.05- 8.80-1.4-6.3
	1.42- 8.37-1.7-4.9		3.38- 8.92-1.8-5.0
	5.38- 9.85-1.9-5.2		1.60- 8.40-1.8-4.7
			5.23- 9.77-1.8-5.4

been short in duration but with a considerable horizontal component, while another may have been of similar duration but with a very small horizontal component.

The horizontal direction of the descents appeared to be at random, although no quantitative records were kept. The wall of the building precluded horizontal movements in that direction, and 30 of 80 trials were terminated when animals struck the side of the building. The higher number of successful trials was probably because the animals were held with their heads pointing away from the wall prior to release.

DISCUSSION

A function of the lateral abdominal expansions of *P. lionatum* is clearly to aid in gliding flight by increasing ventral surface area. The hypothesis that they function in crypsis cannot be rejected, but appears questionable. The folds lie closely curled

around the animal's trunk when it is resting or crawling; thus situated, they do not break up the visual outline of the animal's body. The frilled tail and the small flaps of skin on head, neck and limbs appear to make *Ptychozoon* less conspicuous to a human observer and probably serve a dual function in gliding and camouflage.

The work of Tweedie with *P. kuhli* (1950, 1954) and that of Heyer and Pongsapipatana (1970) with *P. lionatum*, although limited, gave results similar to those presented in this paper. Both horizontal distances and glide rates were greater, but release points were higher. Tweedie (1954) reported orientation to wind direction during descent, and other investigators (Boulenger, 1908; Taylor, 1963) mention glides from one tree to another, implying voluntary orientation not apparent in the present study.

Oliver (1951) made an arbitrary distinction between gliding and parachuting. He

defined gliding as a retarded descent along a path deviating $> 45^\circ$ from the vertical, and parachuting as a retarded descent along a path deviating $< 45^\circ$. In the present study only two of the untied and none of the tied descents were "glides" in Oliver's sense if angle of descent is derived from a right triangle with vertices at the release point, a point on the ground directly below the release point, and the landing point. Since all animals fell vertically one to several meters before any horizontal deflection occurred, a more accurate estimate of angle of descent was obtained by assuming the glide path to have started 1.25 m below the release point. Even then only five of the untied and none of the tied descents qualified as "glides"; thus the definition may be inadequate. It is apparent that *P. lionatum* can perform a retarded vertical descent ("parachute") as well as cover considerable horizontal distances ("glide"). Separate definition of these behaviors is arbitrary, as one merges into the other. It is suggested that behavioral descriptions are more useful than definitions, which should be avoided.

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