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Substrate excavation in the Namibian web-footed gecko, *Palmatogecko rangei* Andersson 1908, and its ecological significance

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Palmatogecko rangei Andersson 1908 occupies compacted windward dune faces in the Namib sand sea. It excavates burrows in this compacted sand and employs the webbed feet to both break and shift the sand. High speed cinematography of digging sequences revealed that the manus undergoes both sand breaking and sand shoveling cycles, with the former having about half the duration of the latter and involving a smaller arc of excursion of the limb and manus. The pes is used in sand shoveling also and is able to deposit the sand masses moved by the manus further to the rear. It is herein postulated that interdigital webs in *Palmatogecko* Andersson 1908 serve primarily in these excavatory processes and that their role as «sand shoes» in spreading the weight of the animal during locomotion is relatively minimal. The webs act as mechanical shovels and contain the loosened sand as it is transported posteriorly. Although psammophilous lizards are numerous and widespread, very few exhibit webbing of the toes. Most instead possess fringes on the digits that are used in weight support and excavating. Only in very particular sets of ecological circumstances do webs appear to be effective as alternatives to digital fringing.

KEY WORDS: Namib desert, Gekkonidae, *Palmatogecko*, excavation, digital webbing.

INTRODUCTION

The gekkonid lizard *Palmatogecko rangei* Andersson 1908 is common in dune areas in the sand sea south of the Kuiseb River, as well as in coastal dunes and in the adjacent river bed areas of the Namib desert (Haacke 1976a, Stuart 1980). *Palmatogecko* Andersson 1908 occurs mostly on fine sands, although it may occupy coarse-grained sand deposits where available (Haacke 1976a). The areas occupied all have sand accumulations and rainfall of less than 125 mm per annum (Haacke 1976a). Nowhere in its distribution from the mouth of the Orange River to southern Angola is *Palmatogecko* found more than 130 km inland (Koch 1962, Haacke 1976a, Visser 1984). The frequency of fog and the presence of wind blown material within this zone provide the basis for the support of the Namib dune animal community (Louw 1972, Seely & Griffin 1986). Although climatic conditions vary seasonally, daytime temperatures below the substrate surface, at the level of *Palmatogecko* burrows, remain fairly constant year round (Lancaster et al. 1984).

Palmatogecko exhibits a number of morphological attributes associated with the sandy habitat. These features have been discussed, at least superficially, by Andersson (1908), Proctor (1928), and Haacke (1976a). They include, raised scales around the nostril, reduction of claws, cryptic colouration, enlarged extra-brillar fringes, and elongate limbs. The last feature is associated with an erect or semi-erect posture, supposedly related to increasing visibility over sand ripples (Fitzsimons 1935, Werner & Broza 1969). The feet and limbs of this gecko are unique in several aspects. In addition to being highly webbed, they exhibit the presence of paraphalangeal elements (Haacke 1976a, Russell & Bauer 1988) and the unique opposition of digit V of the pes (Proctor 1928, Haacke 1976a) which results in a digital span of 236°, greater than that of any other reptile.

Interdigital webbing is the rarest of all dune-dwelling gekkonid pedal specializations (Bauer & Russell in press). Since webs exclude all sand grains from passing between the digits they appear to be well-suited to acting as shovels during excavation, but their mode of action has been poorly documented and has been the source of considerable speculation. Andersson (1908) first assumed that the webs served as adhesive organs for climbing on stones. As observations of *Palmatogecko* in the wild became available, however, this view was abandoned in favour of the postulation that the webs served as «sand shoes» for running across the sand surface and for «diving» into the sand (Barbour 1926). Proctor (1928) proposed that the webs served as shovels during burrowing. The dual roles of «sand shoes» and «shovels», combining the views of Barbour (1926) and Proctor (1928), have been advocated ever since (Fitzsimons 1943, Haacke 1976a, Holm & Scholtz 1980).

The relative significance of these two functions was recently assessed (Bauer & Russell in press), based upon the physical properties of sand surfaces, the role of body mass and the general distribution of alternate pedal modifications (fringes, spinose scales) in other dune-dwelling geckos. It was concluded that the primary specialization of digital webbing in *Palmatogecko* is associated with digging («shovels»). Tests to evaluate the effectiveness of the webs as «sand shoes» were carried out (see Bauer & Russell in press) and demonstrated that weight-bearing is not a significant function of these structures. We herein report on the role of the webs in excavation as a test of the «shovel» hypothesis.

MATERIALS AND METHODS

Live specimens of *Palamatogecko rangei* were collected in Namibia and the South African enclave of Walvis Bay under permits issued by the Nature and Conservation Directorates of South West Africa and Cape Province, respectively. Specimens were returned alive to Calgary where they were filmed under artificial light with super-8 color reversal film at 100 fps. Temperature in the filming tank was approximately 24 °C. Animals were provided with a substrate of sand obtained from dunes just south of the Swakop River Bridge, at the site of collection of several *Palmatogecko* specimens. Digging sequences were initiated by spraying the geckos and the sand with a fine mist of water [the presence and/or lifting of naturally occurring fog is generally believed to initiate burrowing activity in both *Palmatogecko* (WERNER 1977) and *Kaokogecko* (STEYN & HAACKE 1966)]. Fims were examined using a Lafayette Instruments stop action analytical projector.

RESULTS

There are several published descriptions of digging in *Palmatogecko rangei* (WERNER 1915, PROCTOR 1928, FITZSIMONS 1943, STEYN & HAACKE 1966, HAACKE 1976a, KÜHNELT 1982). Most of these authors reported that limbs of the same side of the body were used in a repeated pattern of excavation (forelimb stroke) and shoveling away (hind limb stroke), but provided little discussion of the kinematics of the feet themselves. We filmed four extended digging sequences using three wild-caught *Palmatogecko rangei*. A total of 12 additional sequences were filmed but these involved only a few digging strokes or sequences in which stroke type was obscured due to the camera angle.

Three types of digging strokes were identified: sand loosening strokes of the manus, sand shoveling transport strokes of the manus, and sand shoveling strokes of the pes. Throughout the digging process the body was raised well above the substrate.

Manual sand loosening

Sand loosening by the manus is depicted in Fig. 1. The power stroke of this action lasts an average of 0.12 sec (range 0.09-0.20 sec, n = 81), and the recovery stroke an average of 0.14 sec (range 0.10-0.22 sec, n = 82). This stroke is typically short and results in sand surface breaking but little sand transport. It begins with one forelimb extended forward so that the tips of the digits are placed anterior to the snout. The elbow is bent at about 90° and the digits are maximally abducted (Fig. 1.0). The manus is then brought into contact with the substrate, beginning with the distal ends of the digits (Fig. 1.4). The antebrachium is drawn back as the humerus undergoes long axis rotation (counterclockwise for the left forelimb if the distal end of the humerus is viewed end on). This movement appears to impart considerable force onto the substrate and results in the fragmentation of compacted and consolidated sand. The initial phase of the power stroke may result in the manus traversing a considerable distance relatively quickly as the compacted sand gives way and the manus jerks backward (Fig. 1.4-8). The manus becomes relatively vertical as this initial phase of retraction occurs and although some degree of humeral retraction occurs, the chief movement appears to be due to humeral long axis rotation.

The first phase of the sand loosening stroke finishes when the humerus makes an

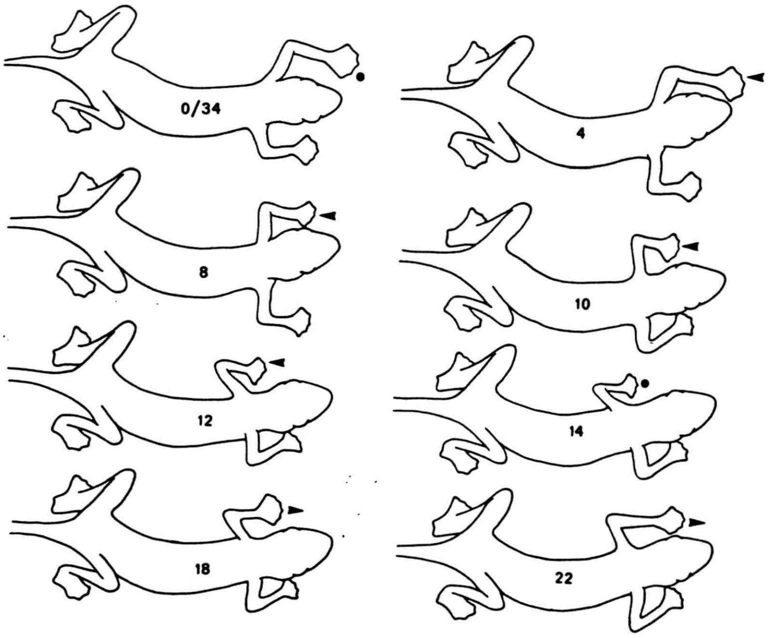

Fig. 1. — Diagramatic representation of a left manual sand loosening stroke of *Palmatogecko rangei*, filmed in dorsal view at 100 frames per second. The numbers within the outline drawings represent frame numbers. Arrows represent direction of movement, solid circles represent stationary stages where direction of movement is reversed.

angle of 90° with the body long axis (Fig. 1.10). From this point, movement of the manus across the substratum depends more on humeral retraction and less on long axis rotation, with little plantar flexion occuring. As the humerus is retracted (Fig. 1.12) the manus is dragged across the substrate, pulling loosened sand with it in the cupped web. As retraction occurs, the digits adduct and surround the loosened sand. Retraction of the humerus ceases when the manus is drawn back to a level in line with the glenoid fossa of its own limb (Fig. 1.14). As the manus reaches this point it is raised from the substrate, leaving a mass of loosened sand at the point of farthest retraction. The recovery stroke occurs with the humerus, antebrachium and manus being held horizontally, and with the digits once again being abducted (Fig. 1.18). Clockwise long axis rotation of the left humerus occurs at the beginning of the recovery stroke, restoring the original orientation of the humerus before protraction occurs. The humerus is protracted in the horizontal plane (Fig. 1.22) until the tips of the digits are again extended beyond the snout. The manus is then lowered into contact with the substratum and the cycle repeats (Fig. 1.34).

In typical digging cycle a large number of sand loosening strokes may be performed by a single manus before any sand shifting takes place. As many as 32 consecutive sand loosening strokes have been observed before a sand shifting cycle of the same forelimb intervenes. More typically, however, between seven and 11 loosening strokes occur before the accumulated loosened sand is moved away.

As a typical loosening stroke occurs, the centre of balance of the animal shifts. While the forelimb undergoing the digging cycle is protracted the weight of the body shifts to this side (Fig. 1.0, 1.4, 1.18, 1.22). Then, as a result of the resistance to the force of sand loosening during the power stroke, the body is shifted towards the contralateral forelimb (Fig. 1.8, 1.10, 1.12, 1.14). Slight pivoting of the body about the fixed feet occurs, but the latter show no signs of any movement with respect to the substrate.

Manual sand shoveling

Manual sand shoveling begins in a manner essentially similar to that described for sand loosening (above). Here again humeral long axis rotation and retraction bring the tips of the digits in line with the glenoid (Fig. 2.6, 2.11). Unlike the situation in sand loosening, however, the humerus continues to retract and the manus is plantar flexed on the crus (Fig. 2.14). The digits of the manus are abducted and the manus is cupped as it is flexed, moving the sand further back as it picks up material from previous sand loosening strokes. Here the antebrachium is still flexed on the humerus. The humerus is then further retracted so that it lies almost parallel to the body long axis (Fig. 2.17). At this time the antebrachium is extended on the humerus and the wrist begins to extend again. These movements result in a virtual straightening of the forelimb (Fig. 2.19) and a flipping backwards of the sand as it is released from the manual cup. Thus, the transfer of loosened sand from the point of initial deposition by the loosening strokes to the point from which it can be moved by the hind foot involves a launching of the sand bolus, and not merely a pushing action.

As the manus is already free of the substrate at the release of the transported sand, its recovery stroke involves protraction and long axis rotation of the humerus and extension of the antebrachium while manus remains raised (Fig. 2.21, 2.23, 2.26). The digits of the manus abduct as the forelimb continues its recovery stroke (Fig. 2.29, 2.33) and the manus again meets the substrate in a manner identical to that seen at the end of the recovery stroke in sand loosening (Fig. 2.37). As the recovery stroke results in identical positioning in both sand loosening and sand shoveling, one shoveling stroke may be followed by another or, as more frequently observed, by a resumption of a series of sand loosening strokes.

The power stroke of manual sand shoveling has a mean duration of 0.22 sec (range 0.17-0.29 sec, n = 11), and the recovery stroke has a mean duration of 0.23 sec (range 0.18-0.29 sec, n = 11). Mean duration of the entire manual sand shoveling stroke (0.45 sec) is thus considerably greater than that of the sand loosening stroke (0.26 sec).

Pedal sand shoveling

Sand shoveling strokes by the pes follow sand shoveling strokes of the ipsilateral manus and may occur immediately after the latter, some time after the latter has occurred, or simultaneously with the latter (as depicted in Fig. 3). In the latter situation the body is supported by the snout while both ipsilateral limbs are operative in excavation. From a resting position (Fig. 3.0), the pes in question is initially raised from the substrate by the flexing of the knee (Fig. 3.5). Following this the knee continues to flex as the femur is protracted and the pes begins to rotate medially on

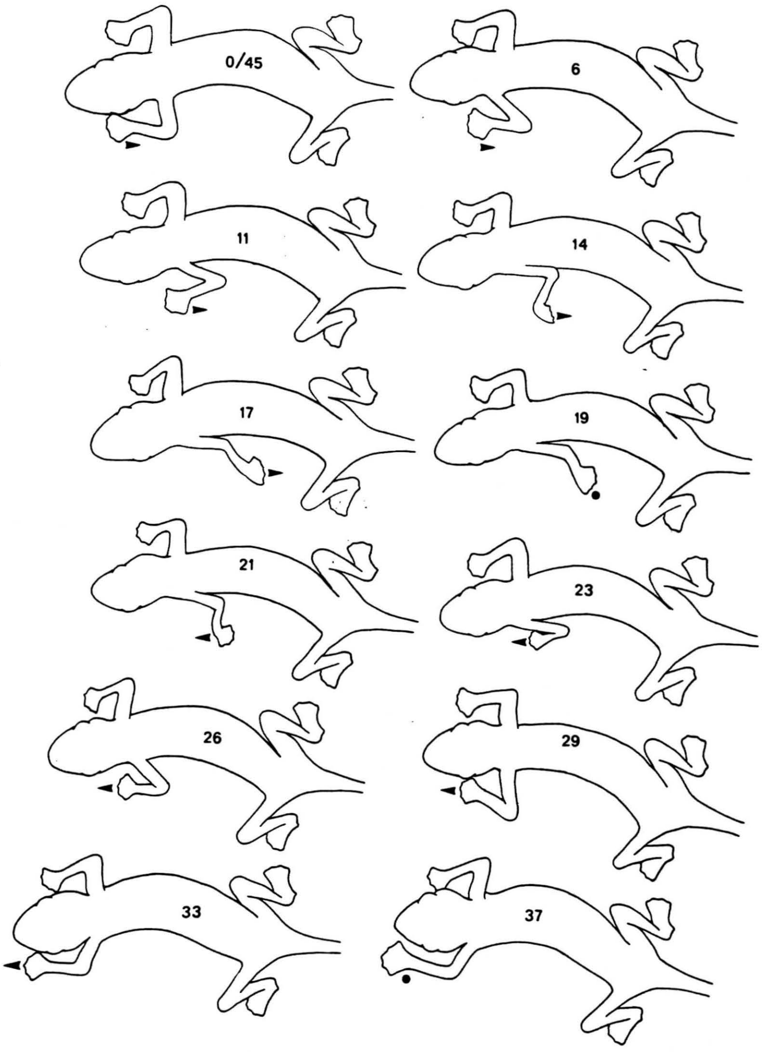

Fig. 2. — Diagramatic representation of a left manual sand shoveling stroke of *Palmatogecko rangei*, filmed in dorsal view at 100 frames per second. The labelling conventions are identical to those in Fig. 1.

the crus (Fig. 3.8, 3.11). The femur is protracted until it takes up a position approximately parallel to the body long axis (Fig. 3.14). The crus then extends on the femur as the pes is rotated further medially and the digits are abducted (Fig. 3.18). The crus continues to extend on the femur (Fig. 3.21) until the segments of the hindlimb are almost perfectly aligned (Fig. 3.21). At this point the pes makes contact with the substratum slightly in advance of the mound of sand deposited by the manual sand shoveling strokes.

Initial backward movement of the sand bolus is brought about by flexion of the crus on the femur and a lateral rotation of the pes (Fig. 3.29, 3.33). The pes cups around the sand mass, but unlike the situation seen in the manus, the pes is not lifted free of the substrate. Instead it maintains contact with the sand along the medial edge of the first digit and metatarsus. The extreme opposability of digit five provides a broad surface for sand pushing as the pes is retracted. As the pes reaches a position approximately level with the acetabulum, the femur begins to retract (Fig. 3.37, 3.41), providing the power for further posterior displacement of the transported sand. As the femur continues to retract the knee is initially flexed further (Fig. 3.41) and then begins to extend as the femur swings back beyond a position in which it is perpendicular to the body long axis (Fig. 3.45, 3.49). Extension of the crus on the pes continues as femoral retraction proceeds, until these two segments of the limb are almost aligned (Fig. 3.53). The pes, however, does not extend on the crus but remains flexed so that the displaced sand is pushed straight backward and is not directed towards the tail (Fig. 3.53). The tips of the digits of the pes thus trace a line essentially parallel to the body long axis (if treated as a straight line). At the end of a sequence of ipsilateral and contralateral manual and pedal excavating strokes, the lizard is surrounded by a rectangle of groomed sand where the loosened substrate has been shifted backwards by the combined efforts of the fore and hind limbs.

The recovery stroke begins after the hindlimb has become fully retracted (Fig. 3.53). The pes is raised from the substrate and the web collapsed by digital adduction as the recovery stroke proceeds (Fig. 3.56). The crus flexes on the femur as the latter protracts, and the pes rotates medially (Fig. 3.63, 3.80). The recovery stroke usually results in placement of the pes back into the resting position (Fig. 3.0), but on occasion a series of pedal sand shoveling strokes occurs. The longest continuous sequences observed was four consecutive strokes. Fig. 3 represents a stroke that has a longer than normal duration as the recovery stroke was interrupted at the 63rd frame and did not resume again until frame 75. The power stroke of pedal sand shoveling (from pedal contact, equivalent to Fig. 3.25, to full retraction, equivalent to Fig. 3.53) has a mean duration of 0.24 sec (range 0.22-0.26 sec, n = 8). The recovery stroke (from the beginning of protraction, equivalent to Fig. 3.56, to placement of the foot, equivalent to Fig. 3.25) has a mean duration of 0.21 sec (range 0.17-0.31 sec, n = 7). Thus, the mean duration of the manual and pedal sand shoveling cycles are identical (0.45 sec).

Interlimb coordination

The pattern of limb movements in the digging cycle was highly variable. Not enough digging trials were performed to determine which, if any, aspects of the pattern were related to individual variation and preference of the study subjects and which reflected physical aspects of the substrate. The primary variability in the stroke sequences involved the number of loosening strokes employed before a transport stroke.

While there was variance in the number of strokes employed in each bout of manual sand loosening and manual and pedal sand shoveling, the pattern of interlimb coordination was always precise. Manual sand loosening was always followed by ipsilateral manual sand shoveling. When manual and pedal sand shoveling occurred ipsilaterally and simultaneously, retraction of the manus was coupled with protraction of the pes so that a mass of sand was moved by the manus and then the pes in a continuous action. The timing of events is such that the manual and pedal sand shoveling strokes have the same mean duration, permitting precise coordination. The manual sand shoveling strokes are of shorter duration and are never carried out simultaneously with pedal sand shoveling.

The kinematics of burrowing are apparently similar in *Ptenopus* Gray 1865 (BRAIN 1962, HAACKE 1975) and *Kaokogecko* Steyn & Haacke 1966 (STEYN & HAACKE 1966). In the latter, however, digging strokes are reported to be slower and more powerful. Further, the distal portions of the toes in this species are hyperextended (dorsiflexed) during digging in order to protect the apical scansors from clogging (STEYN & HAACKE 1966). Both *Kaokogecko* and *Palmatogecko* are capable of grasping material with the hind feet, although this ability is of minor significance to the latter's shovel stroke in light of the fine-grained substrate, while in the gravel plain habitat of the former species this ability is more generally employed (STEYN & HAACKE 1966).

DISCUSSION

Observations of digging in *Palmatogecko* indicate that the webs play an active and well-defined role in this activity. Limb and foot posture, pedal movements, limb cadence and the co-ordination between front and hind limbs combine to enhance the effectiveness of the webs as sand breaking and sand shifting devices. The webbed feet of *Palmatogecko rangei* appear to be much more efficient excavating structures than the feet of other dune-dwelling geckos with fringed digits (BAUER & RUSSELL in press). The webs are able to trap sand in a continuous receptacle and move it as a unitary mass.

Palmatogecko occupies compacted windward dune faces and the webs form an unbroken excavating surface that can be brought into contact with a relatively resistant substrate, loosen it along a continuous line of contact, and shift it away in a controlled and predictable fashion. This ability is particularly important in the construction of patent burrows in the compact sand of the windward dune face. It is here that bulk sand transport is most effective. In the loose sand of the leeward face, where sand is merely displaced rather than excavated, bulk sand transport would offer little advantage. The particular morphological configuration of the feet in *Palmatogecko* appears to be suited to a very particular set of ecological circumstances. This may explain why webbing of the digits in gekkonid (and other) dune-dwelling and psammophilous lizards is relatively rare (it occurs only in the gekkonid genera *Kaokogecko* and *Stenodactylus* Philippi 1902 apart from *Palmatogecko*). If the primary role of webbing was associated with the «sand shoe» scenario one would expect it to be far more widespread as many geckos (and other psammophilous lizards) live and move on loose sand. Fringes, however, may be more significant in avoiding sinking

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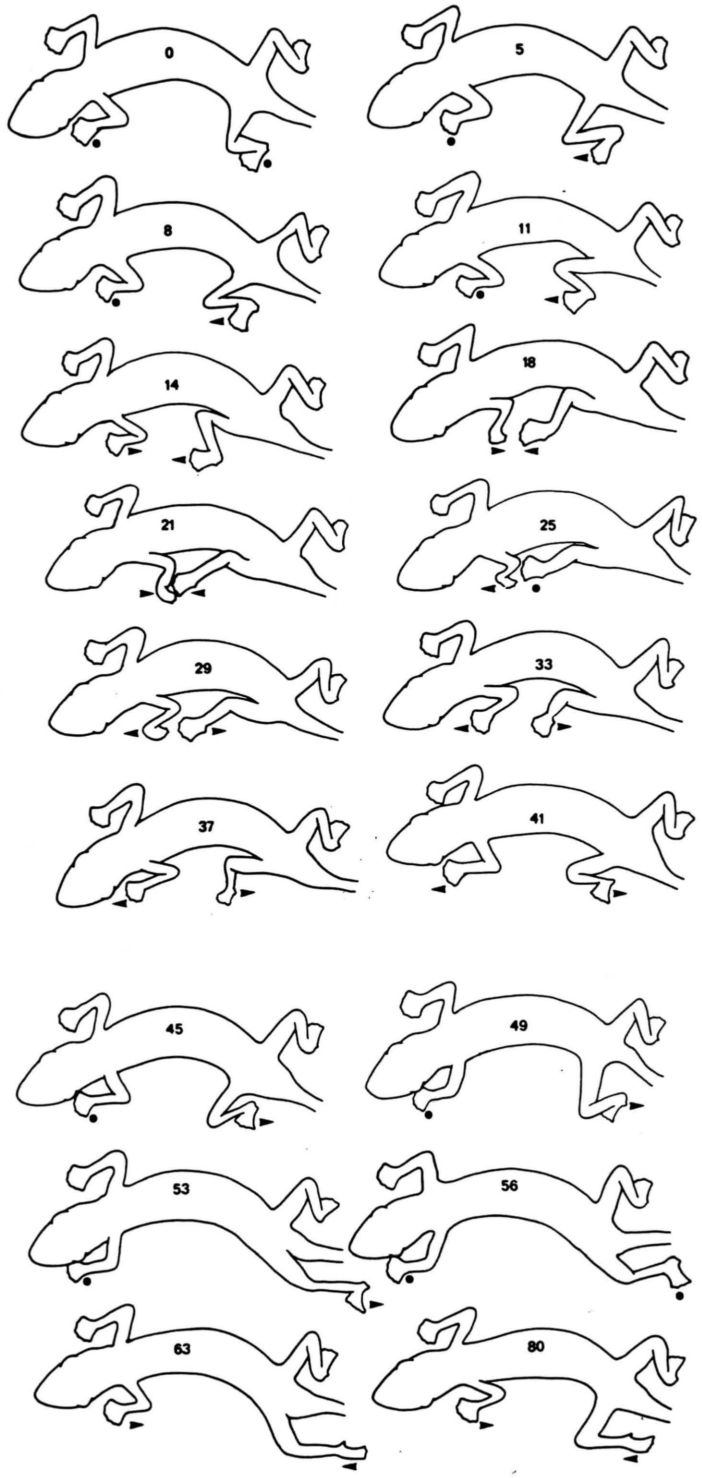
Fig. 3. — Diagramatic representation of a left pedal sand shoveling stroke of *Palmatogecko rangei,* filmed in dorsal view at 100 frames per second. The labelling conventions are identical to those of Fig. 1. Note that simultaneous left manual sand shoveling strokes also occur.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into the substrate (LUKE 1986, PIETRUSZKA 1988, BAUER & RUSSELL in press), although their primary role appears to be in increasing speed and acceleration on sand (CAROTHERS 1986). The continuity of skin between the digits when they are fully webbed restricts the freedom of movement and independence of each digit, thus reducing the overall versatility of the feet. In the case of *Palmatogecko* the webs are part of a suite of features that facilitate excavation in sand of a particular consistency and may not be viewed merely as an alternative to digital fringes.

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