Substrate Use and Locomotor Modes of the Neotropical Pygmy Squirrel *Sciurillus pusillus* (E. Geoffroy, 1803) in French Guyana

Dionisios Youlatos

Department of Zoology, School of Biology, Aristotle Univ. of Thessaloniki, Thessaloniki GR-51424, Greece

Dionisios Youlatos (2011) Substrate use and locomotor modes of the Neotropical pygmy squirrel *Sciurillus pusillus* (E. Geoffroy, 1803) in French Guyana. *Zoological Studies* **50**(6): 745-750. The Neotropical pygmy squirrel *Sciurillus pusillus* is the smallest South American squirrel. This primitive sciurid is rarely encountered and exhibits morphological and behavioral specializations related to bark gleaning and bark and/or exudate feeding. The present account reports the 1st quantitative data on substrate use and locomotor patterns of *S. pusillus* from a high terra-firme forest in French Guyana. *S. pusillus* made extensive use of medium vertical supports. The most frequent locomotor modes were claw-climbing and reversion, an orthograde airborne switching mode. Quadrupedalism was used to a lesser extent. The behavioral repertoire of *S. pusillus* was examined in light of its postcranial morphological features. Together, they suggest a large degree of vertical trunk foraging for bark and/or exudates similar to what was reported for other pygmy squirrels in Africa and Asia. More-detailed studies are required to elucidate these patterns of morphological convergence in pygmy squirrels across tropical forests worldwide. http://zoolstud.sinica.edu.tw/Journals/50.6/745.pdf

Key words: Sciuridae, French Guyana, Locomotion, Neotropical pygmy squirrel, *Sciurillus pusillus*.

The Neotropical pygmy squirrel *Sciurillus pusillus* (E. Geoffroy, 1803) is the smallest New World squirrel, weighing 38-43 g (Hayssen 2008b), and is found in terra-firme forests in the Guyanas, northern Brazil, eastern Peru, and the lower Tapajos River of Brazil (Emmons and Feer 1990, Gharaibeh and Jones 1996, Voss et al. 2001, Thorington and Hoffman 2005, Amori et al. 2010). It belongs to its own subfamily Sciurillinae, which appears to have split early in sciurid radiation, and along with *Ratufa*, may form a monophyletic sister group to all remaining squirrels (Mercer and Roth 2003, Steppan et al. 2004, Thorington and Hoffman 2005). The species is characterized by unique physiological and morphological specializations (Hayssen 2008a). Compared to other tree squirrels, it bears a small litter size of 2 (Ollala 1935, Emmons and Feer 1990, Hayssen 2008a). The skull of *S. pusillus* is unique in being longitudinally compressed posterior to the orbit, and having dilated distal maxillaries, a forward shift of the tooth row, and a reduced musculus (m.) temporalis (Anthony and Tate 1935, Moore 1959, Roth 1996). In addition, the mandible bears a diminished coronoid process and an extensive origin of the anterior part of the m. masseter pars profunda which provides high mechanical advantages for jaw retraction and protraction for bark scraping (Thorington and Darrow 1996, Velhagen and Roth 1997). Such movements are usually related to bark gnawing and exudate feeding, as is supported by anecdotal observations for this species (Emmons and Feer 1990, Heymann and Knogge 1997, Voss et al. 2001).

Similar bark scraping and gnawing and probable exudate feeding were also reported for the West African pygmy squirrel *Myosciurus pumilio* (Emmons 1980, Gharaibeh and Jones 1996).

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*To whom correspondence and reprint requests should be addressed. Tel: 30-23-10998734. Fax: 30-23-10998269.
  E-mail:dyoul@bio.auth.gr

Analogous behavior was also observed in Asian pygmy squirrels, *Exilisciurus* and *Nannosciurus*, that reportedly feed on bark, bark mosses, and insects (Payne and Francis 2005). In all pygmy squirrels, these feeding behaviors are associated with frequent bark gleaning i.e., rapid claw climbing locomotion and claw-clinging postures on medium- to large-sized trunks, as well as other vertical and steep substrates (Emmons 1980, Gharaibeh and Jones 1996, Payne and Francis 2005).

Postcranially, claw climbing and clinging impose significant biomechanical constraints to the postcranium related to the forces applied for embedding claws on a surface, exerting a propulsive force against gravity by both the fore- and hindlimbs, and stabilizing the body by counteracting any unbalancing reaction forces (Cartmill 1974, Bock and Winkler 1978, Stalheim-Smith 1989). Compared to quadrupedal squirrels, bark gleaners possess long forelimbs that lengthen the arm span and enable grasping onto larger-diameter substrates by increasing the normal component of the adductive forces of the shoulder (Cartmill 1974, Stalheim-Smith 1989, Thorington and Thorington 1989). In addition, their long forearms with a limited degree of prono-supination promote greater protraction and overall excursion of the forelimb (Thorington and Thorington 1989), and reduce involuntary rotation, assuring forearm stability during claw-clinging (Stalheim-Smith 1989, Thorington et al. 1997). Furthermore, bark gleaners possess short hindlimbs that stabilize the clinging body close to the trunk by counteracting unbalancing reaction forces (Cartmill 1974, Bock and Winkler 1978), and a short lumbar region that assures the maintenance of a rigid torso while moving vertically along or below large substrates (Thorington and Thorington 1989, Shapiro 1995).

Some of these postcranial features were also identified in Neotropical pygmy squirrels. In a comparative study with *Microsciurus* and *Sciurus*, *Sciurillus* was found to possess relatively long forelimbs and short hindlimbs, expressed as ratios of the vertebral column, a relatively short lumbar region, and elongated forearms and short tibiae, respectively expressed as ratios of the humerus and femur (Thorington and Thorington 1989). This suite of characters does not provide a mechanical advantage to fast bounding or leaping activities, but is functionally associated with frequent and efficient vertical climbing and clinging activities (Cartmill 1974, Thorington and Heany 1981, Thorington and Thorington 1989).

Similar morpho-behavioral associations are

essential for understanding the evolution and adaptive significance of morphological complexes in squirrels, and the study of basal forms, like *Sciurillus* which may have retained ancestral features, is important for elucidating the evolution of sciurid locomotion (Youlatos 1999a, Essner 2007, Youlatos et al. 2008). However, such links require detailed quantitative studies of locomotor and postural behavior and habitat use, and in this context, I report the 1st study on the locomotion and substrate use of wild *S. pusillus* in French Guyana.

MATERIALS AND METHODS

Behavioral observations of *Sciurillus pusillus* occurred during a 3-mo field study (June-Sept. 1993) at Nouragues Station, French Guyana (4°05'N, 52°40'W), where I had the opportunity to encounter solitary individuals of the species on 5 occasions. During each encounter, the animal was followed for as long as possible, and its behavior was observed with a pair of binoculars, coupled with video recordings at 24 frames/s, with a shutter speed of 1/1000 s (Sony Hi8 CCD-TR705E, Tokyo, Japan). I used focal animal instantaneous sampling to collect data on locomotion, the forest layer, substrate size, and substrate orientation every 30 s.

During data collection, I identified and recorded 4 locomotor modes: claw-climbing (up/downwards quadrupedal progression using the claws upon vertical or steeply inclined substrates), reversion (an instantaneous 180° change in direction on a vertical large substrate, involving an aerial phase with no height loss), quadrupedalism (bounding along the top of horizontal and sub-horizontal single substrates), and airborne (mainly leaping with an aerial horizontal displacement across substrates). Sampled forest layers were understory (at a height of < 15 m) and canopy (at a height of > 15 m). Substrate size categories were based on the estimated diameter (d), and were divided into fine (d < 2 cm), small (2 cm ≤ d < 5 cm), and medium (d ≥ 5 cm). Finally, substrate orientation categories involved horizontal (at an angle of 0°-22.5°), oblique (at an angle of 22.5°-67.5°), and vertical (at an angle of 67.5°-90°). Data collection resulted in a total of 570 instant records. Differences among frequencies of behaviors or substrate use were calculated using G-tests (Mehta and Patel 1995).

RESULTS

During the field study, *Sciurillus pusillus* mainly ranged in the canopy (63.6%), and primarily used medium (G = 28.9, *d.f.* = 2, *p* < 0.001) and vertical (G = 39.6, *d.f.* = 2, *p* < 0.001) arboreal substrates (Fig. 1A).

Claw-climbing was the most frequent locomotor mode (G = 77.7, *d.f.* = 3, *p* < 0.001, Fig. 1B). During upward climbing, the forelimbs were always laterally abducted, and the elbows alternated from partial to full extension. The hindlimbs were strongly flexed at the hip joint, and ranged from partial to full abduction, while the knee joint was mainly semi-flexed. When climbing down, the hindlimbs were mostly adducted and partially flexed at the hip joint. On the other hand, the forelimbs were kept abducted, and the elbow was partially extended.

Reversion represented a fair proportion of the locomotor repertoire (Fig. 1B). This unique switching mode occurred on large vertical substrates and was initiated both from a head-up and head-down clinging posture. The switch in direction was particularly rapid, lasting 0.34 s,

as indicated by a video analysis (*n* = 12), and involved an aerial phase, where fore- and hindlimbs essentially switched places, while the animal did not lose any height. Video analyses showed no particular pivotal points, although the hind foot may serve as one, and the body switch actually occurred while airborne. During body rotation, the torso was held orthograde in both the initial and terminal phases. Quadrupedalism was slightly less common than reversion and involved bouts of bounding locomotion along the top of single substrates, while airborne locomotion was moderately frequent (Fig. 1B).

DISCUSSION

The present results are preliminary but provide insights into a poorly known species. *S. pusillus* used wide vertical substrates (Fig. 1A), where it engaged in extensive claw-climbing (63.2%), while other modes such as reversion (15.7%), quadrupedalism (12.3%), and airborne (8.8%) were used to lesser degrees (Fig. 1B).

Regarding substrate use, *S. pusillus* exhibited very frequent use of wide and vertical branches. Actually, compared to other free-ranging squirrels for which similar data are available, Neotropical pygmy squirrels seem to exhibit the highest rates (Garber and Sussman 1984, Youlatos 1999a, Stafford et al. 2003, Youlatos and Samaras 2011). In a recent report, Samaras and Youlatos (2010) identified a gradient indicating that smaller squirrels tend to more frequently use larger and vertical substrates than larger squirrels. This may be related to the fact that claw-climbing and clinging onto such substrates are rendered biomechanically and physiologically costly for larger species, as they require more energy and higher forces to withstand unbalancing torques while stationary and initiating movements while vertically ascending or descending (Cartmill 1974, Bock and Winkler 1978, Stalheim-Smith 1989).

In terms of locomotion, the dominance of claw-climbing over other modes was also observed in the small-bodied arboreal squirrel *Microsciurus flaviventer* (with a body weight (BW) of 82-98 g) and the small-bodied callitrichine primate *Cebuella pygmaea* (with a BW of 150 g), with claw-climbing respectively accounting for 51% (Youlatos 1999a) and 42.7% (Youlatos 1999b 2009) of their locomotor repertoire. In contrast, larger arboreal squirrels exhibit much lower rates of vertical activities and higher rates of quadrupedalism
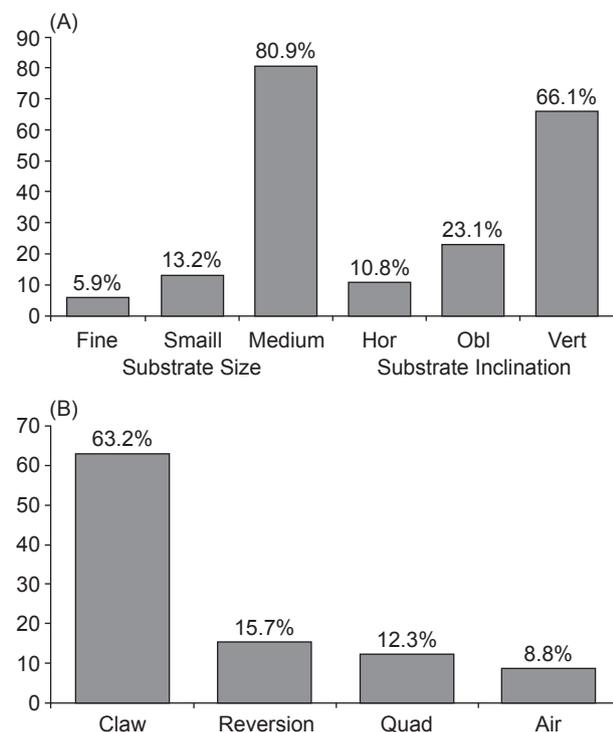
Fig. 1. Bar graphs of the percentages of use of (A) locomotor modes (CLAW, claw-clinging; QUAD, quadrupedalism; AIR, airborne) and (B) substrate size and substrate inclination (HOR, horizontal; OBL, oblique; VERT, vertical) by Neotropical pygmy squirrels in French Guyana.

(Garber and Sussman 1984, Youlatos 1999a, Stafford et al. 2001, Youlatos and Samaras 2011).

These findings indicate that small-bodied squirrels and clawed primates are primarily claw-climbers, but infrequent walkers and bounders. The occasional use of quadrupedalism in *S. pusillus* is consistent with its postcranial morphology. Efficient quadrupedal running and bounding require long hindlimbs and more particularly, long distal elements, such as tibiae that enhance the mechanical advantage and enable long and extended strides per time unit (Alexander and Maloyi 1984, Steudel and Beattie 1993, Gasc 2001, Fischer et al. 2002). In addition, a long flexible lumbar region would add to each stride length, advancing long and fast quadrupedal progression (Gasc 2001, Fischer et al. 2002). In contrast, *S. pusillus* possesses short hindlimbs (0.92), expressed as a ratio of the vertebral column length, a short tibia, as suggested by the low tibia/femur ratio (1.12), and a rather-short lumbar region (1.44), expressed as a ratio of the total column length (Thorington and Thorington 1989). The short hindlimbs and tibiae, with both ratios falling below the respective regression lines for other squirrels (Thorington and Heaney 1981, Thorington and Thorington 1989), indicate that they are not mechanically advantageous for high speeds and long strides despite the lower mass that has to be moved (Alexander and Maloyi 1984, Steudel and Beattie 1993, Gasc 2001). On the other hand, they contribute to bringing the center of gravity closer to the arboreal substrate, assuring well-balanced movements (Cartmill 1974). Finally, the rather-short lumbar region, similar to the claw-climbing *Microsciurus* (1.45; Thorington and Thorington 1989), contrasts with the longer flexible regions of more-quadrupedal sciurids (*Sciurus carolinensis* at 1.48, Thorington 1972). The combination of these characters in *S. pusillus* does not appear to favor quadrupedalism on horizontal substrates of diverse diameters, but a rather generalized and occasional use of these activities, as found in the current study.

Locomotion within and across tree crowns is not continuous, and the encountered canopy gaps are usually crossed either by leaping or by climbing down and up the trunks of adjacent trees. The current results indicate that *S. pusillus* is not a frequent leaper. Research on primates showed that leaping requires long specialized hindlimbs, and especially the distal parts (e.g., tibiae or tarsi), that provide a mechanical advantage for the output force, as well as powerful hindlimb musculature

that regulates the necessary hindlimb extension (Jouffroy and Lessertisseur 1979, Anemone 1993, Demes et al. 1998). The relatively short hindlimbs and tibiae of *S. pusillus* might not provide the necessary mechanical advantage for facilitating efficient terminal leaps and are therefore seldom used as a means to cross gaps. However, since the leaping performance differs between primates and squirrels (Essner 2002 2007), it is difficult to assess the functional importance of similar postcranial features in sciurids, especially when higher leaping rates were recorded in other species (Youlatos 1999a, Stafford et al. 2003, Youlatos et al. 2008, Youlatos and Samaras 2011). Apart from leaping, crossing between and traveling along trees can be achieved by climbing down and up trunks of neighboring trees. This would involve frequent vertical clawed locomotion on large substrates.

S. pusillus scored the highest rates of claw-climbing locomotion compared to other squirrel species with available locomotor data (Youlatos 1999a, Essner 2007, Youlatos et al. 2008, Youlatos and Samaras 2011). Extensive claw-climbing and clinging is facilitated by long forelimbs that increase the arm span, enabling a firm grasp of large substrates by powerful adduction. Moreover, long forearms provide a mechanical advantage by efficiently enhancing arm protraction, because of the limited excursion of sciurid shoulders in general (Stalheim-Smith 1989, Thorington and Thorington 1989). In addition, use of the claws further improves this condition by enabling pygmy squirrels to climb and cling onto even larger substrates, as adduction is dependent on the angle of the embedded claws and less on the actual arm span (Cartmill 1974). Similar forces during clinging and placing the arms around a substrate at each upward thrust are best applied through a stable forearm (Stalheim-Smith 1989), and in African and Asian pygmy squirrels, this is assured by the lack of m. pronator quadratus and an overdeveloped m. spinodeltoideus respectively (Thorington et al. 1997). A similar muscle arrangement would be expected in *S. pusillus*, but only future dissections will prove the veracity of this assumption. The use of these forces is facilitated by the small size of the animal which imposes fewer biomechanical and physiological restrictions (Cartmill 1974, Stalheim-Smith 1989). Large-bodied claw-climbing mammals need to exert increased forces to keep the claws embedded in the tree bark, require higher stabilizing and propulsive forces, and need more energy to maintain the balance

while clinging and bounding vertically upward or downward (Cartmill 1974, Bock and Winkler 1978, Stalheim-Smith 1989). This may partially account for the frequent claw-climbing in small arboreal and semi-terrestrial sciurids (Youlatos 1999a, Essner 2007, Youlatos et al. 2008), and other pygmy squirrels (Emmons 1980, Gharaibeh and Jones 1996, Payne and Francis 2005). Frequent vertical climbing and clinging activities in pygmy squirrels and small clawed primates are usually associated with bark gnawing and scraping to feed on bark, bark insects, mosses, and exudates (Garber 1992, Gharaibeh and Jones 1996, Payne and Francis 2005, Youlatos 2009). In effect, the mandibular morphology of *S. pusillus* is functionally adapted to extracting exudates from bark (Thorington and Darrow 1996, Velhagen and Roth 1997), a fact supported by both personal and published observations of intensive bark scraping and, very likely, exudate foraging on mimosoid trunks (Emmons and Feer 1990, Heymann and Knogge 1997).

Although only moderately used, reversion was the most distinctive locomotion mode of *S. pusillus* This is the 1st detailed report of this behavior for the species, excluding Emmons and Feer's (1990) short description (p. 176): "… characteristic habit of making almost instantaneous 180-degree switches of direction." This switch of direction seems to be part of the swift intermittent locomotor patterns of *S. pusillus* while searching, locating, and ultimately foraging on specific sites in order to scrape and gnaw for bark, exudates, or insects. This extremely rapid change in direction is feasible from a relatively stable central point. The hind foot may serve as an initial pivotal center implying ample prono-supination of the tarsal elements during the switch. Unfortunately, there are no detailed anatomical descriptions of the foot of *S. pusillus* to consider this assumption, but hind foot reversal is extensively used by other squirrels during clawed-down activities and hind-foot hanging (Jenkins and McClearn 1984). During the aerial phase, the animal switched vertically across a center of rotation alternating hand holds with foot holds. The body was initially and terminally held orthograde, facing head up or down, or vice versa. In these cases, the orthograde position and resistance to unbalancing forces while airborne are usually achieved by a relatively short lumbar region that assures spinal rigidity and overall robustness (Shapiro 1995). In *S. pusillus*, the relatively short lumbar region (Thorington and Thorington 1989) would maintain a rigid and orthograde torso

capable of withstanding rapid vertical takeoffs and landings during the initial and terminal phases of reversion. However, more detailed locomotor data are required to assess similar morpho-behavioral associations in *S. pusillus* and other pygmy squirrels.

Despite its basal phylogenetic position within sciurids, *S. pusillus* appears to be morphologically and physiologically specialized (Hayssen 2008a). The current study showed that it also exhibits a very specialized locomotor behavior, associated with frequent bark gleaning, probably related to bark and/or exudate feeding, which is reflected by specific derived postcranial features. Similar ecologies (Gharaibeh and Jones 1996, Payne and Francis 2005) and morphological features (Thorington and Thorington 1989, Thorington and Darrow 1996, Velhagen and Roth 1997) are also shared by other phylogenetically distant pygmy squirrels. It is thus very likely that these morpho-behavioral complexes are related to dwarfism and evolutionarily adaptive convergence to bark gnawing and scraping for exudates and bark moss, and bark insect feeding (Thorington and Darrow 1996, Velhagen and Roth 1997); these were also observed in exudativore marmosets (Vinyard et al. 2009, Youlatos 2009). Future research should focus on the locomotor ecology of other basal sciurids, such as the large-bodied *Ratufa*, and the phylogenetically distant African and Asian pygmy squirrels in order to elucidate similar trends of evolutionary convergence and novelty within sciurids (Essner 2007).

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