POSITIONAL BEHAVIOR OF JAPANESE GIANT FLYING SQUIRRELS (PETAURISTA LEUCOGENYS)

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Positional behavior of Japanese giant flying squirrels (Petaurista leucogenys) was studied based on 3,318 positional bouts and 2,687 instantaneous samples. Resting, feeding and foraging, locomotion, and grooming were the most common behaviors. The most common locomotor behaviors were leaping, scrambling, walking, bounding, vertical bounding, and gliding. The most common postural behaviors were quadrupedal squatting, hind-limb squatting, vertical clinging, clinging, and crouching. Compared with smaller tree squirrels, Sciurus igniventris and Microsciurus flaviventris, P. leucogenys exhibited a higher frequency of “scrambling” for foraging among terminal branches. The tree squirrels foraged on terminals but fed on larger branches. They also foraged and fed more on vertical surfaces. P. leucogenys spent the most time on small supports, whereas the smallest squirrel (M. flaviventris) spent most on the largest supports.

Key words: locomotion, musasabi, Petaurista, positional behavior, Pteromyinae

Studies of positional behavior in the wild provide a critical link between ecology, behavior, and morphology. They provide contextual information crucial to functional-adaptive analysis, a method for determining homology, and ecological morphology (Bock 1977, 1981; Szalay and Bock 1991). Further, they provide evidence for the biological roles of morphological character complexes (Bock and von Wahlert 1965; Dickinson et al. 2000; Williams et al. 2000). It is only through such studies that we can propose meaningful hypotheses about the evolution and maintenance of character complexes through natural selection.

There have been no reports of positional behavior (Prost 1965) of gliding mammals in natural environments. Existing reports concentrate mostly on gliding. Only the publications of Ando and Shiraishi (1985, 1991, 1993) and Hingston (1914) on Petaurista are more broadly oriented, but even they offer little information on positional behavior in the wild. We present the 1st such study of positional behavior in a mammal adapted for gliding. Data exist on the positional behavior of only 2 tree squirrels, Microsciurus flaviventris and Sciurus igniventris (Youlatos 1999). Comparisons of Petaurista, a flying squirrel, with these tree squirrels provided only a limited context for gliding because of different methods used in the 2 studies.

MATERIALS AND METHODS

Petaurista leucogenys was studied at Nara Park, Nara Prefecture, Japan (135°50’E, 34°41’N) from 12 May 1999 to 15 June 1999. Animals had previously been habituated to hu-
man observers by the studies of Kawamichi (1997). Data were collected on 25 days, resulting in 91.5 h of contact with animals. We recorded 3,318 positional bouts of which 1,628 were locomotor and 1,690 were postural. We also collected 2,687 instantaneous samples at 1-min intervals to document larger behavioral categories. Animals were not marked for identification, but at least 7 adult animals are represented in the data set. Although individuals were not marked, we believe sampling was fairly even among individuals as we began each night’s observations at different nest holes throughout the study and overlap among home ranges is minimal (Kawamichi et al. 1987). The forest in the study area consisted of trees like pine and cedar with straight trunks and others like maple and oak with more complex structures. Details of the study area and its ecology are given in Kawamichi (1997).

Individuals were observed by eye using binoculars and a headlamp and with a video camera (Sony Hi8, Sony Corporation of America, New York) equipped with infrared nightshot technology. We collected focal-animal data on positional bouts by eye and recorded behavior, substrate size, orientation, texture of substrate, and canopy height. We also collected instantaneous samples by eye at 1-min intervals on focal animals, noting the exact behavior, substrate size, orientation, canopy height, and texture. These behaviors were later grouped into more inclusive categories. Each observation period of bout sampling, instantaneous sampling, or video taping continued for 2 h of contact whenever possible. Sampling periods were rotated each night to provide coverage of the entire night for each sampling regimen for the course of the study. Videotapes were collected for kinematic analysis. Bout and instantaneous data were also collected from these.

Observations were conducted under protocols established in studies of primates (Fleagle 1976, 1977; Fleagle and Mittermeier 1980; Gebo and Chapman 1995; Stafford et al. 1994, 1996). The unit of observation was a positional sequence, which is composed of a series of locomotor and postural bouts. A locomotor bout occurs when an animal moves so as to displace its center of gravity by more than 1 body length. While an animal is moving, any change in gait, substrate size, or substrate orientation signals a change of locomotor bout because locomotion is likely to differ on supports of different size or orientation. Postural bouts were scored when an animal was not displacing its center of gravity by more than 1 body length (i.e., it was stationary). Displacement of the center of gravity by less than 1 body length was classified as a shift in posture.

Support size was determined in relation to the size of the animal. Therefore, the animal provided scale within each observation. This was necessary because animals interact differently with supports of different relative sizes. The mechanics of walking on a support 10 cm in diameter is quite different for different sized animals. Absolute sizes of supports were estimated based on anatomical measurements of museum specimens (Appendix 1). A support recorded as size 3 in the field was only recognized as being about the same diameter as the animal’s torso. Subsequent measurements on museum specimens revealed such supports to be about 5–20 cm in diameter.

Forest-level categories were based on structure, not on height above the ground. The canopy was the level above which branches began radiating from the main trunk and formed a generally continuous, interlocking environment. The canopy had several distinct characters among which we did not distinguish. For example, areas with high densities of oak had continuous, geometrically complex, closed canopies. Conversely, in areas with high densities of pine or cedar, the canopy was continuous at low heights and less continuous at greater heights. The subcanopy was the area between the canopy and the ground. High densities of sika deer (Cervus nippon) resulted in a browse-line at 1.5 m, below which there was little undergrowth. Substrate texture was classified as smooth (cherry, Prunus), moderately rough (oaks, Quercus and Castanopsis; maples, Acer), rough (pines, Pinus), and vertically striated (cedars, Chamaecyparis).

Behavioral and environmental categories are listed and defined in Appendix 1. Our gliding category includes the initial leap of the glide and the landing posture (usually vertical clinging). When not vocalizing or moving, P. leucogenys is quite cryptic; therefore, as with any locomotor study of an arboreal animal, behaviors that occur high in the canopy, especially postural behaviors, are likely underrepresented.

Spearman’s rank correlation ($r_s$) was used to determine the similarity of data collected visually and with the video camera. Visual and video
data that were significantly correlated \((P \leq 0.05)\) were combined. Spearman’s rank correlation could not be performed on forest-level data because we had only 3 categories and, therefore, insufficient degrees of freedom to perform this test. We combined video and visual data on forest-level use because differences between methods were only 1% for any category. Spearman’s rank correlation was also used to evaluate similarity of locomotor profiles among *M. fleviventer* and *S. igniventris* (Youlatos 1999), and *P. leucogenys*.

Data gathered by eye and from video recording were significantly correlated \((P < 0.05)\) in all but 2 cases. There was no significant correlation between data on support orientation collected by eye and from videotape under our bout sampling method \((r_s = 0.70, n = 6, P > 0.05)\). Similarly, for support orientation, the data collected by focal animal and by instantaneous sampling were not significantly correlated \((r_s = 0.54, n = 6, P > 0.10)\). Combined frequencies are reported for data collected under the same protocols when video and visual samples were correlated. Uncorrelated data are not combined. In no case was focal animal bout data and instantaneous samples combined. In following sections, numbers in parentheses show percentage of behavior for bout data and 1-min instantaneous samples (bouts, 1 min). Data are more fully presented in Appendix 1.

**RESULTS**

*Petaurista leucogenys* is primarily a canopy dweller (92%, 94%). Noncanopy observations all occurred in the subcanopy (8%, 6%). Animals were never seen on the ground during our study, although terrestrial behaviors are known to occur. Glides usually began in the canopy (96%) and ended in the subcanopy (47%).

Horizontal supports were the most frequently used (49% video bouts, 38% visual bouts, 45% 1 min). Based on bout data collected by video, vertical (19%) and diagonal (19%) supports are the next most commonly used followed by terminal branches (13%). Based on data collected by eye, vertical (22%) and terminal (21%) supports are the next most commonly used followed by diagonal supports (19%). Tree crotches and nest holes were used in less than 1% of bouts. The order differs slightly for samples based on instantaneous sampling; horizontal supports were most frequently used (45%) followed by diagonal supports (24%), terminal branches (14%), nest holes (10%), vertical supports (7%), and tree crotches (1%). Glides usually began from horizontal supports (27%), but terminal (18%) and diagonal (16%) supports were also frequently used. Landings were most often on vertical supports (47%), although terminal branches were also used (7%).

Both bout and instantaneous data show that supports, which the animal could grasp in its palm (34%, 30%) or with its fingers (27%, 27%) were most used followed by supports that approximated body diameter (23%, 24%). Larger supports (size 1, size 2) were each used less than 10% of the time. For substrate texture, trees with moderately rough and rugose bark, oaks and maples, were most commonly used (57%, 52%). Trees with vertically striated bark, cedars and cypress, were used less often (19%, 26%), followed by rough-barked trees, pines (12%, 16%), and smooth-barked trees, cherry (10%, 6%). Artificial supports (cables) were used in less than 1% of bouts. Small (size 4, size 5) supports were most often selected for launching platforms (56%), whereas large supports (size 1) were the most commonly used landing sites (37%).

Leaping was the most frequent locomotor behavior (31%, 16%). Scrambling (19%, 29%), walking (14%, 15%), vertical bounding (10%, 14%), bounding (9%, 5%), and gliding (7%, 12%) occurred at lower frequencies. Quadrupedal squatting was the most common posture (43%, 37%). Hind-limb squatting (20%, 34%), vertical clinging (10%, 3%), clinging (10%, 7%), and crouching (8%, 5%) occurred at lower frequencies. Note that rank orders change slightly between sampling regimens. Of nonpositional behaviors recorded during instantaneous sampling, resting (45%) was the most common behavior followed by
foraging and feeding (19%), locomotion (17%), and grooming (11%).

There was no significant correlation between bout data and instantaneous data for substrate orientation ($r_s = 0.54, n = 6, P > 0.10$). Locomotion ($r_s = 0.96, n = 14, P < 0.0005$), posture ($r_s = 0.85, n = 12, P < 0.001$), substrate size ($r_s = 1.00, n = 6, P < 0.01$), and substrate texture ($r_s = 1, n = 5, P < 0.05$) were significantly correlated. These results, however, mask differences between sampling methods. With bout sampling, leaping is the predominant locomotor behavior (31%), and scrambling is ranked 2nd (19%). With instantaneous sampling, scrambling is predominant (29%) and leaping ranked 2nd (16%). With bout sampling, vertical clinging ranked 3rd (10%), but with instantaneous sampling, indeterminate squatting ranks 3rd (8%). For substrate size and texture, and forest level, bout and scan samplings produced remarkably similar profiles. These data confirm theoretical predictions (Altman 1974; Martin and Bateson 1993) that different sampling regimens record behaviors at different resolutions. However, they also indicate that there can be a large degree of concordance between these methods.

**DISCUSSION**

The importance of field observations of locomotor behavior for functional–adaptive analysis is well documented (Dickinson et al. 2000) and has long been recognized by primatologists (cf. Fleagle 1976, 1977; Fleagle and Mittermeier 1980; Napier and Walker 1967; Prost 1965; Ripley 1967; Rose 1973). Likewise, laboratory or controlled-environment studies are critical (Alexander 1974; Biewener et al. 1988; Demes et al. 1999; Ishida et al. 1990; Schilling and Fischer 1999), and the theoretical foundation for such studies has been discussed (Bock 1977, 1981; Bock and von Wahlert 1965; Szalay and Bock 1991). The present study provides a quantitative description of positional behavior in *P. leucogenys* in the wild for future comparison with other glid-
iors in gliding versus arboreal taxa (Scheibe and Robins 1998; Scholey 1986). Such models overemphasize vertical climbing in flying squirrels. However, greater use of vertical supports in both tree squirrels is shown in Fig. 1b. Contrary to theoretical predictions (Cartmill 1985), the largest taxon (P. leucogenys) spent the most time on the smallest supports and the smallest taxon (M. flaviventer) spent the most time on the largest supports (Fig. 1c). This highlights that claws allow ready and easy access to vertical and planar surfaces (Cartmill 1974), indicates that there may be little correlation between body size and selection of support size within this size range, but indicates that ecology may be a much more important factor.

Stafford et al. (2002) describe the gliding behavior of P. leucogenys in detail. In this study we only provide the environmental context for gliding (Appendix I). It is clear that gliding occurs in diverse environmental settings. Smaller canopy supports are preferred for launching, whereas large subcanopy vertical supports are preferred for landing. Beyond this it is difficult to characterize a typical glide. In contrast, although there are no quantitative data, tree squirrels commonly leap from terminal branches to terminal branches when moving between trees. Seldom do they leap to vertical trunks.

There is no typical glide. Glides begin and end at different places, representing choices made by individual animals. Models of gliding behavior must account for this variability. For example, the rigidity of the launch support will affect launch velocity.

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Fig. 1.—Comparison of Petarista leucogenys with 2 species of tree squirrels, Sciurus igniventris and Microsciurus flaviventer, showing a) locomotion, b) orientation of substrate used, c) relative size of substrate used. Comparisons are based on instantaneous samples of focal animals: tree squirrel data from Youlatos (1999) based on 20-s instantaneous samples, P. leucogenys data from 1-min instantaneous samples.

D, diagonal; G, gliding; GB, gap bridging; H, horizontal; L, leaping, bounding leaps; Q, walking, bounding, transaxial bounding; S, scambling; T, terminals; V, vertical bounding, vertical climbing; VS, vertical supports; <5 cm, less than 5 cm in diameter; >5 cm, greater than 5 cm in diameter.
and the length of the glide. Perhaps more importantly, the choice of landing on a trunk as opposed to that in the canopy affects the energy expended in subsequently moving to a food source in the canopy terminal branches.

Flying squirrels (Thorington and Heaney 1981) and gliding mammals in general (Rustead and Ruff 1992; Stafford 1999) have longer limbs than their nongliding sister taxa. This relationship has been interpreted as related to increasing the surface area of the wing (Thorington and Heaney 1981 and references therein). However, it has been proposed (Simmons 1995; Simmons and Quinn 1994; Stafford 1999) that forelimb elongation in flying lemurs (order Dermoptera) and bats is related to underbranch suspensory positional behaviors. Similarly, the slow climbing of lorid primates (McArdle 1981) and the feeding postures of gibbons (Grand 1972) have been related to limb elongation in these taxa. We suggest that scrambling, associated with accessing young leaves in the terminal branches, may have been important in the evolution of elongate limbs in flying squirrels. This does not contradict the importance of gliding in the origination or maintenance of elongate limbs in flying squirrels but highlights the complex mosaic of selective pressures likely acting on these animals.

Gliding in flying squirrels is a dramatic and efficient means of locomotion. Except that Petaurista use a higher degree of scrambling, there is no clear distinction in other locomotor behaviors between the gliding, P. leucogenys, and nongliding squirrels, S. igniventris and M. flaviventer, discussed in this study. This is partly due to the variability of behaviors among tree squirrels. Differences between Petaurista and these tree squirrels appear to have more to do with their foraging and feeding behaviors than with their different means of locomotion between trees. Some of these differences are probably size related. Folivory, as observed in Petaurista, is normally associated with larger body size. Smaller animals with their higher metabolic rates require more concentrated sources of energy. These differences in foraging and feeding behaviors influence locomotion within the tree and are dominating features in the locomotor profile of the animals, probably more important than locomotion between trees. Consequently, evaluation of energetic costs of gliding compared to arboreal locomotion requires the incorporation of a wider diversity of behaviors into the models, specifically, behaviors occurring during travel within trees. We find no evidence that vertical climbing, vertical bounding, or overall use of vertical supports is more prevalent in gliding than nongliding taxa. Also, such models may need to consider different types of glides. We caution against interpreting animals with spectacular adaptations solely in the light of those adaptations.

In order to assure future comparability among studies, we suggest the use of Hunt et al. (1996), with appropriate modifications (Appendix I), as the standard for describing positional behavior of gliding mammals in future studies. Alternatively, behaviors should be described in minute detail (Prost 1965) in order to capture the maximum amount of information, as they can always be grouped later into more inclusive categories.

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APPENDIX I

Behavioral and environmental categories describing positional behavior in Petaurista leucogenys. Positional categories follow Hunt et al. (1996) and Stafford et al. (1996). Substrate orientation and forest level categories follow Stafford et al. (1996). Numbers in parentheses show number of occurrences of each behavior (bouts, 1-min instantaneous samples). For gliding behavior (n = 114), numbers in parentheses show number of launches and landings (launch, land).

Positional behavior

**Bound** (149, 9).—Asymmetrical gait; forelimbs move in unison; hind limbs move in unison contacting the substrate in close proximity. Includes bounding and halfbounding in this study.

**Bounding leap** (7, 0).—Transfer between supports characterized by period where animal is in contact with no substrate. Hind limbs provide propulsion as an immediate extension of some form of rapid quadrupedal locomotion (i.e., a running start).

**Cling** (164, 65).—Flexed-limb posture using multiple supports of any, or multiple, orientation.

**Crouch** (128, 51).—Body weight borne by all 4 cheiridia (hands and feet); hip, knee, and elbow strongly flexed; animal parallel to axis of support.

**Gap bridging** (3, 0).—Torso-pronograde gap-closing movement where manus reaches out to grasp a support and pull body across gap. Hind feet retain grip until after a secure grip is obtained with manus.

**Glide** (114, 19).—Transfer between supports characterized by an extended period where squirrel is in contact with no support and patagium generates lift forces; ratio between horizontal distance traveled and altitude lost glide ratio ≥1; glide includes a leap at the beginning of the movement and a postural category, usually vertical clinging, at end of the movement; characterized by 5 phases—launch, glide, transition, braking, landing.

**Hind-limb suspension** (1, 0).—Suspension from foot or feet with no support from forelimbs or tail; only used to transfer between supports and never observed as a postural event in P. leucogenys.

**Leap** (512, 27).—Transfer between supports characterized by period where squirrel is not in contact with substrate; hind limbs provide propulsion from a standing start; patagium may be deployed, but there are no glide or transition phases.

**Pull-up** (5, 0).—Transfer between supports where a support is grasped with forelimbs, and forelimbs retract and flex to effect transfer between supports.

**Quadrupedal suspension** (2, 0).—Inverted quadrupedal walk, run, or scramble.

**Scrambling** (316, 47).—Nonsuspensory quadrupedal locomotion lacking a regular gait; occurring on small, irregularly oriented supports at many angles.

**Ski** (17, 12).—Posture in which ischia bear most of body weight.

**Sprawl** (0, 3).—Limbs dangling as squirrel rests on ventrum.

**Squat** (68, 79).—Body weight borne by indeterminate number of cheiridia; hip, knee, and el-
bow strongly flexed; squirrel at right angle to axis of support.

**Squat, hind limb (339, 319).**—Body weight borne by hindfeet; hip and knee strongly flexed; squirrel at right angle to axis of support.

**Squat, 3 limbs (14, 22).**—Body weight borne by 3 cheiridia; hip, knee, and elbow strongly flexed; squirrel at right angle to axis of support.

**Squat, 4 limbs (719, 342).**—Body weight borne by all 4 cheiridia; hip, knee, and elbow strongly flexed; squirrel at right angle to axis of support.

**Stand (57, 3).**—Body supported on a single substrate with knee and elbow relatively extended.

**Transaxial bound (14, 4).**—Asymmetrical gait; hind limbs and forelimbs in equal contact with substrate; hind limbs overstride forelimbs, and the cheiridia are all oriented to 1 side of the support.

**Vertical bound (158, 23).**—Ascent of vertical supports with forelimbs grasping support and hind limbs gathered under the body to propel squirrel upward.

**Vertical climb (54, 5).**—Ascent or descent of vertical supports with head above rump with contralateral hind- and forelimbs providing propulsion; squirrel generally moving in same direction as long axis of support.

**Vertical climb, head down (61, 6).**—Head-first descent on vertical supports with head below rump; forelimbs moving together, and hind limbs moving together, and forelimbs often acting as a brake.

**Vertical climb, side-to-side (6, 0).**—Ascent or descent of vertical supports with head above or at same level as rump; ipsilateral hind- and forelimbs generally provide propulsion; squirrel generally moving in the same direction as the long axis of the support.

**Vertical cling (172, 31).**—Support on vertical and subvertical supports with hip and knee strongly flexed; elbow may be flexed with the forelimb held close to the body or may be extended with forelimb abducted.

**Vertical cling, head down (12, 3).**—Support on vertical and subvertical supports with head below rump and hind limbs supporting weight in tension; forelimbs may act as a brace, brake, or to support some weight in tension.

**Walk (226, 24).**—Pronograde quadrupedal progression on top of single supports; includes running.

**Forest level**

**Canopy (3,573, 1,906).**—Level above which branches begin spreading from trunks of trees, may or may not form interlocking layer.

**Subcanopy (329, 129).**—Level above the ground and below which branches begin spreading from trunks.

**Terrestrial (0, 0).**—Locomotion on the ground or upon substrates lying on the ground.

**Substrate orientation**

**Horizontal (1,791, 577).**—Substrates of 0–30° inclination.

**Diagonal (123, 305).**—Substrates of 30–60° inclination.

**Vertical (750, 95).**—Substrates of 60–90° inclination.

**Terminal (577, 177).**—Geometrically complex interlocking substrates with multiple inclinations.

**Tree crotch (10, 12).**—Joining of 2 or more branches, often of different orientation or size.

**Nest hole (0, 125).**—Cavity in trunk of a tree that squirrels were seen to emerge from at dusk or to enter at dawn.

**Substrate size categories**

1 (355, 114).—Supports too wide for squirrels to reach halfway around with forelimbs (greater than about 45 cm diameter).

2 (268, 86).—Supports that squirrels can encircle approximately halfway with forelimbs (about 20–45 cm diameter).

3 (368, 306).—Supports the same diameter as the animal’s torso (about 5–20 cm diameter).

4 (1,322, 389).—Supports that can be grasped with manus (about 1–5 cm diameter).

5 (1,019, 348).—Supports around which squirrels could curl phalanges (<1 cm diameter).

**Cable (2, 0).**—Electrical cable strung between poles, about 2.5 cm diameter.

**Gliding behavior**

**Substrate size.**—1 (3, 42), 2(1, 10), 3(10, 3), 4(40, 0), 5(21, 9), not visible (36, 50).

**Substrate orientation.**—Horizontal (31, 1), diagonal (18, 1), vertical (9, 54), terminals (20, 8), not visible (36, 50).

**Substrate texture.**—Smooth (2, 2), moderately rough (51, 27), rough (17, 13), vertically striated (31, 30), not visible (13, 42).

**Forest level.**—Canopy (110, 28), subcanopy (1, 54), terrestrial (0, 0), not visible (3, 32).