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Habitat Use and Positional Behavior of Northern Palm Squirrels (*Funambulus pennantii*) in an Urban Forest in Central Nepal

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Abstract: Urban forests impose significant challenges to the animals that inhabit them due to the altered properties of available substrates from anthropogenic interventions. To cope with these structural peculiarities, urban species exhibit behavioral adjustments to successfully exploit the urban habitat. The present study examined habitat use and positional behavior of northern palm squirrels (*Funambulus pennantii*) in the urban forests of Kathmandu, Nepal, to test such behavioral modifications. Between July and August 2018, we collected focal animal instantaneous data on the behavior, locomotor/postural mode, forest layer, tree crown part, and substrate type, size, and inclination use of four different individuals. Our results indicated a primarily arboreal species, mostly using the middle canopy layers and the intermediate and central tree parts. Moreover, tree branches and artificial substrates were commonly used that were mainly large and horizontal. Locomotion was dominated by quadrupedalism and claw climb, whereas postures by quadrupedal stand, and, to a lesser extent, sit and claw cling. Most of our initial predictions were only partly supported by our findings. This behavioral idiosyncrasy most likely reflects the adaptive flexibility of the species to human-modified habitats. In this way, northern palm squirrels apparently expanded their ecological niche and successfully persisted against anthropogenic pressures throughout their range. As urban expansion is inexorable, more research is required to understand the behavioral and ecological flexibility of animals that effectively exploit these impacted habitats.

Keywords: Asia; Kathmandu; locomotion; posture; urbanization

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1. Introduction

The arboreal environment of forest canopies is composed of complex, three dimensional networks of finite, discontinuous, and unstable available substrates, such as tree branches, large vertical trunks, pliable lianas, compliant palm fronds, etc. [1,2]. These particularities impose challenging mechanical constraints that can be successfully negotiated by the variety of morphological, locomotor, and postural adaptations that arboreal dwellers have evolved [2–4]. The diversity of locomotor and postural behaviors (=positional behavior) represent the behavioral responses of the interaction between the morphological characteristics of the animals and the structural features of their surrounding environment. This behavioral idiosyncrasy most likely reflects an adaptive flexibility that enables species to effectively exploit a diversity of habitats, including those that have been impacted by anthropic interventions.

This positional diversity is evident in the ways arboreal squirrels currently exploit the forest canopies. Squirrels are an ancestrally arboreal group [5–9], which subsequently evolved a variety of positional patterns that enabled them to successfully exploit a wide variety of forested and non-forested habitats [7–9]. Currently available data show that small-bodied arboreal squirrels tend to engage in high proportions of vertical claw climbing and clinging activities making extensive use of relatively large and vertical substrates [10–13]. However, this relation is not very clear. Semiarboreal small squirrels appear to equally use quadrupedal and clawed locomotion [12,14]. Moreover, they tend to share their activities between smaller and larger substrates, as well as between vertical and horizontal substrates [12,14]. On the other hand, larger arboreal squirrels seem to emphasize on quadrupedal walk and bound, as well as leaps, using higher proportions of small and medium substrates of mainly horizontal and oblique orientations [10,15–18]. These interactions allow us to understand how different arboreal squirrels manage to perform successfully in specific natural habitat conditions [4].

However, in recent decades, the growing expansion of urban habitats with the dominance of anthropogenic effects resulted in dramatic changes in the structure of natural habitats, such as degradation, fragmentation, pollution, important abiotic changes, and severe biotic modifications [19–23]. Therefore, it is important to study these interactions in scenarios of alteration of the natural habitat, such as urban forests, where several ecological characteristics diverged from natural ones. Urban forests are usually characterized by a discontinuous canopy, secondary growth, high dominance of pioneer species, and the presence of human structures and interventions that alter the stand structure and canopy layers [24,25]. Regarding the anthropogenic structures, they are unbranching, flat, and broader in diameter compared to trees forming a less structurally complex environment. To cope with these architectural peculiarities, studies in urban populations of vertebrates showed various behavioral changes, such as faster running, more agile climbing or leaping, higher positional diversity, or increased arboreality to avoid predators and reach alternative food sources, which function as adaptation techniques used to exploit the novel ecological characteristics of the urban habitat [26–30]. Examining the extent of these behavioral responses in different environmental settings brings important insights into the level/capability of adaptation of the species regarding its behavior [28–30]. Thus, more field studies in urban environments are required to elucidate these interrelations between ecological and behavioral differences and to better understand how locomotor and postural modes enable the exploitation of the habitats by these urban populations.

In this context, this study focuses on the positional behavior and habitat use of the northern palm squirrel *Funambulus pennantii* (Wroughton 1905) in an urban forest in Kathmandu, central Nepal. The northern palm squirrel is a diurnal, semiarboreal, small-bodied squirrel (male mean head-body length = 134.4 mm, tail length = 130 mm, body mass = 95.2 g—female mean head-body length = 155 mm, tail length = 134.6 mm, body mass = 102.9 g; [31]). The species occurs in southeastern Iran, east through Pakistan to Nepal, Bangladesh, North and central India, and occupies a wide range of habitats from subtropical–tropical dry deciduous forests and montane forests to scrublands and open plains, as well as plantations and urban areas [31–33]. In Nepal, it is mainly encountered across the forests of the Terai, as well as in parts of central Nepal, and especially in many urban forests, such as in Kathmandu [33,34] (Figure 1). Northern palm squirrels actively forage on the ground and in trees for seeds, berries, buds, flowers, nectar, tender shoots, insect larvae, insects, and, occasionally, small vertebrates [31,32,35,36]. The species play a key role in forests by dispersing seeds, pollinating plants, and providing food for birds of prey [37]. Although widespread and relatively common, habitat loss, poaching for subsistence, pet trade, and traditional medicine (butti) are major threats, and urban populations are drastically decreasing [33–35,38].

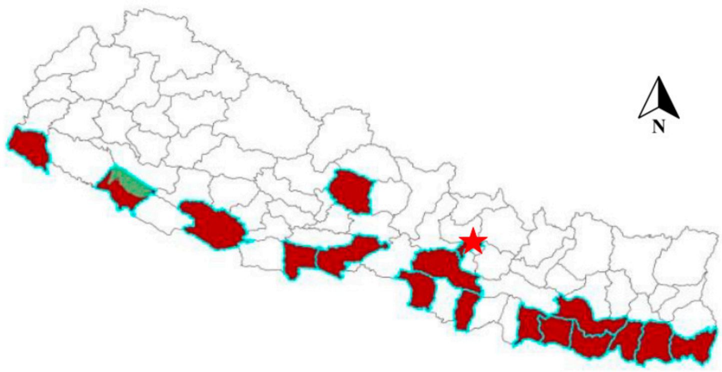

Figure 1. Distribution (deep red patches) of northern palm squirrels (*Funambulus pennantii*) in Nepal (adapted from [29]). Red asterisk indicates Kathmandu city, where the present study was conducted.

Therefore, understanding the positional capabilities of the species in relation to habitat characteristics is fundamental for elucidating its ecological niche and can eventually contribute to develop effective conservation measures [4,30]. This study represents the first quantitative analysis of the positional behavior (locomotion and postures) of northern palm squirrels. The study population comprises individuals that live in an urban forest of Kathmandu, central Nepal. Considering the small size, semiarboreal habits, and omnivorous diet of the species, we expect northern palm squirrels to (a) confine their activities to the lower parts of the forest and the central parts of trees, (b) use relatively large, more vertical arboreal substrates, and (c) considerably use clawed locomotion and postures. However, taking into consideration the urban nature of the forest, different positional behaviors (quadrupedalism and leap), different substrate types (artificial and terrestrial), and different substrate features (wide and horizontal) might be selected by the animals to cope with the more open, discontinuous forest canopy, or the many available wide and horizontal artificial structures [27]. Similar data are important for understanding the plasticity of ecological adaptations of urban squirrel populations that assure their survival and should be taken into consideration in conservation actions and will contribute to the growing literature on the behavioral adaptations of vertebrates to urbanization (e.g., [20–24,26–30]).

2. Materials and Methods

This field study complied with the guidelines for the treatment of animals in behavioral research and teaching [39] and was approved by the Central Department of Zoology, Tribhuvan University and the School of Biology, Aristotle University of Thessaloniki.

2.1. Study Area

The study was conducted in an urban forest of Kathmandu city (27.7147° N, 85.3145° E, altitude 1400 m a.s.l.) located in central Nepal (Figure 1). The study site covered a small (1.45 ha) forested area interspersed by human-made constructions and structures, such as brick walls, houses, buildings, artificial poles, wires, etc. The forested part was characterized by the presence of secondary growth trees, palms, and a dense network of lianas mostly found in the peripheries of edge habitats. The dominant plant families were the Aquifoliaceae, Ericaceae, Fagaceae, Moraceae, Rosaceae, Sapindaceae, and Theaceae. Kathmandu city is characterized by a seasonal climate with significant ranges of mean temperature (10–24 °C), mean precipitation (4.1–184.2 mm), and mean humidity (0–97%). January–March are the coldest and driest months, whereas July–August are the months with the highest temperatures, precipitation, and humidity.

To test overall utilization, preference, and/or avoidance of specific substrate categories, we quantified the presence of available substrates in the study area. For these purposes, we selected 15 different 10 m × 1 m line transects spaced by, at least, 50 m between them. The transects were selected to represent all the different habitats of the urban forest. In each transect, all available substrate type, size, and inclination categories were calculated by unit.

At the end of this substrate quantification process, we measured a total of 2186 substrates for each variable (type, size, and inclination). Regarding substrate type, the most common categories were branches (75.8%), followed by artificial substrates (11.9%), and trunks (4.6%). In terms of size, fine substrates prevailed (36.3%), followed by small (24.5%), medium (21.6%), and large (17.6%) ones. Finally, oblique substrates dominated (62.5%), followed by horizontal (22.6%) and vertical (14.9%) ones. Subsequently, preference or avoidance of these categories was estimated by Jacobs' D value $D = U - A/U + A - 2U \times A$, where U is proportion of use and A is proportion of availability. Values of the index ranged from -1, indicating strong avoidance, to +1, showing strong preference, whereas values around 0 were considered as neutral.

2.2. Study Animals and Data Collection

Field observations occurred during July–August 2018 (rainy season: maximum temperature: 28 °C, minimum temperature: 20–21 °C), precipitation (138–185 mm), and humidity (87–97%). Northern palm squirrels are diurnal and live in small groups of 2–4 individuals [31–35]. All observations occurred between 8:00 and 17:00, by walking along forest trails until a group of animals was encountered. During each encounter, the study animals were followed for as long as possible and their behavior was observed with a pair of binoculars, coupled with video recordings at 50 fps with a Sony digital video camera FDRAX33B (Sony Corporation, Tokyo, Japan). The study area was inhabited by a group of four different squirrels that were regularly encountered during the study period. We used the focal animal instantaneous sampling method for collecting data on locomotion, postures, and habitat use every 30 s [13,17,40]. Each focal individual was followed for 15 min and then, we shifted to the next available individual for another 15 min, until all four individuals or all available individuals were observed. This rotational observation was carried out throughout a full observation day. However, if any focal individual was lost out of sight before the 15 min sampling period, we also shifted to the next available individual, following the rotational observation protocol. Total fieldwork time for all four individuals was 406.4 h (mean = 101.6 ± 2.9 h per individual, range = 97.7–104.9 h), which corresponded to ~45 observation days. Moreover, during fieldwork, we paid particular attention to collect data from all individuals during all periods of the day and in all areas of the study site. The rotational protocol we used permitted a, more or less, equal temporal and spatial distribution of observations for the four studied individuals. At each focal instant, the recorded variables were: (i) behavior, (ii) locomotor/postural mode, (iii) forest layer, (iv) tree crown part, (v) substrate type, (vi) substrate size, and (vii) substrate inclination (see categories and definitions in Table 1).

Table 1. Definition and description of all the categories of the recorded variables for northern palm squirrels in Kathmandu city, Nepal (adapted from [10,11,13,14,17]).

Behavior	
Travel	Active movement between tree parts and habitat layers
Feed	Active search, manipulation, and processing of food
Rest	Non-active behaviors and sleeping
Groom	Active fur cleaning, scratching, and maintenance
Social	Social interaction with other individual(s) of the same species
Explore	Active search and investigation of the habitat
Locomotor modes	
Quadrupedalism	Symmetrical slow/fast progression (walk/run) or asymmetrical fast progression (bound) along single horizontal/moderately inclined substrates
Claw climb	Quadrupedal upward, downward, horizontal, or inverted progression using the claws along single vertical/steeply inclined substrates

Table 1. *Cont.*

Locomotor modes	
Grasp climb	Quadrupedal upward/downward progression along single small vertical/steeply inclined substrates using hand grasp
Clamber	Quadrupedal progression to various directions across over or below multiple substrates
Leap	Active gap crossing involving an airborne phase where the horizontal distance is longer (leap) or shorter (drop) than the vertical distance
Bridge	Active or passive gap crossing upward, horizontal, or downward gap without an airborne phase
Reversion	Active 180° change in direction on a vertical large substrate, involving an aerial phase with no height loss
Postural modes	
Quadrupedal stand	Stand on four straight (stand) or very flexed (crouch) limbs
Sit	Seated posture with strongly flexed hindlimbs
Bipedal stand	Stand on two flexed hind limbs
Claw cling	Upward, downward, or horizontal clawed or grasp posture keeping the body parallel to the vertical or steeply inclined substrate
Cantilever	The feet anchor the lower body close to the substrate and the rest of the body and forelimbs are extended
Hang	Suspensory posture from the feet below the substrate
Forest Layer	
Ground	Ground and related structures (e.g., rocks, etc.)
Lower layer	Lower strata of the forest, bushes, tree saplings
Middle layer	Middle strata of the forest
Upper layer	Upper strata of the forest
Tree Crown Part	
Central	Trunk, central boughs, and primary bifurcations
Intermediate	Inner parts of tree crown
Periphery	Terminal branches in tree crown periphery
Substrate Type	
Artificial	Human-made structures (walls, roofs, wires, ropes, etc.)
Trunk	Tree bole
Tree branch	Branches of trees
Other	Lianas, bamboos, palm fronds
Ground	Dirt, rocks, logs, roads, etc.
Substrate Size	
Fine	Diameter $\leq$ 2 cm
Small	2 cm < diameter $\leq$ 5 cm
Medium	5 cm < diameter $\leq$ 10 cm
Large	Diameter > 10 cm
Substrate Inclination	
Horizontal	Angle between 0 and 22.5°
Oblique	Angle between 22.5 and 67.5°
Vertical	Angle between 67.5 and 90°

2.3. Data Analysis

At the end of the study, the collected data derived from the four different observed individuals (initial mean sample = 2131.5 $\pm$ 62.5 instants, range = 2050–2200 instants, n = 4 individuals). As such, initially, the dataset of each sampled individual was considered separately. A problem in studies of positional behavior is the autocorrelation of successive sampling events because following instants of the same individuals usually lack independence [35]. Although the time lapse used (30 s) was sufficient for assuring relative independence between consecutive behavioral events, we applied the following trimming procedure to safely guarantee independence. In each dataset, we only considered every second instant (i, i + 2), deleting each intermediate one (i + 1) [17]. After trimming, the frequencies of the different categories were calculated for each individual squirrel. Subsequently, inter-individual variability of these frequencies was tested by using the non-parametric Kruskal–Wallis test, as similar data were not arranged in a natural way, violating assumptions of randomness, and departing from normality [41]. These preliminary analyses showed that there were not any statistically significant differences among the profiles of the variables between the four individuals ($p > 0.05$). As the profiles of the different individuals were similar, we opted for merging the four datasets to obtain a larger dataset. In effect, despite the study period of only two months during the rainy season, intensive field data collection resulted in a total of 4208 instants. This dataset was subsequently divided into a locomotor (total of 1029 instants) and a postural (total of 3179 instants) subset that were analyzed separately. Differences among frequencies of behaviors within single substrate categories were tested using χ^2 tests, whereas differences among frequencies of behaviors across different substrate categories were calculated using log likelihood G tests. All statistical analyses were performed using SPSS 25.0 (SPSS Inc., Chicago, IL, USA). Tests yielding p-values < 0.05 were considered statistically significant, and only those are reported in the Section 3.

Although the sampling period (rainy season of two months) and the studied individuals (four squirrels) may appear limited, the sampling effort was intense, resulting in a relatively large number of observations, covering all day hours and all the different areas of the study site for all individuals, more or less, equally. Sampling more individuals would have implied observations in other different sites and capturing potential seasonal variation would have required a longer sampling period. We were aware of these drawbacks, but we felt that the sampling effort was representative of the studied population for the specific area. Nevertheless, results should be considered as indicative, and interpretations should always be treated with caution.

3. Results

3.1. General Behavior

During the study period, feed was the dominant behavior (45.9%), followed by rest (16.0%), explore (13.4%), social activities (12.8%), and to a lesser extent, travel (9.9%) were moderately used. Groom was rarely observed (1.9%).

3.2. Forest Layer, Tree Crown Part, and Substrate Type, Size, and Inclination Use

During the field study, northern palm squirrels were basically arboreal (total: 96.9%; Table 2). The ground was seldom used and was slightly avoided (Jacob's D = −0.39). During both locomotion and postures and all behavioral contexts, the use of the middle layers of the forest was dominant. The upper layers were also considerable used, with the lowest rates observed in travel and groom (G = 105.0, $p < 0.001$; Table 2).

In total, the use of the intermediate part of tree crowns was almost shared with that of the central tree parts (Table 2). Similar proportions of tree part use were also observed during both locomotion and postures and in most behavioral contexts (Table 2). However, explore, rest, and social activities occurred mainly in the central tree parts compared to other behaviors (G = 143.5, $p < 0.001$; Table 2). The tree peripheries were frequently used only during feeding behavior (G = 31.9, $p < 0.001$; Table 2).

During all behaviors, northern palm squirrels used the tree branches at significantly higher rates than all other substrate types (G = 31.8, $p < 0.001$; Table 2). However, considering their availability, they were rather avoided (Jacob's D = −0.47). Overall, artificial substrates were considerably used (Table 2) and preferred (Jacob's D = 0.42), but their use (mainly brick walls) significantly dominated during feeding activities (G = 117.7, $p < 0.001$; Table 2). Finally, vertical trunks were, in general, moderately used and preferred (Jacob's D = 0.51), but scored significantly higher percentages during explore, rest, and social activities (G = 46.8, $p < 0.001$; Table 2).

Table 2. Percentages of forest layer, tree crown part, and substrate type, size, and inclination use during the different behaviors, locomotion, and postures by northern palm squirrels in Kathmandu city, Nepal.

	Explore	Feed	Social	Travel	Groom	Rest	Locomotion	Postures	Total
Forest Layer									
Ground	5.3	4.6	0.0	0.5	1.3	3.2	2.4	3.3	3.1
Lower layer	9.5	5.7	0.6	11.0	0.0	8.4	8.9	5.9	6.7
Middle layer	76.1	79.1	85.7	83.2	94.7	80.1	83.0	79.9	80.7
Upper layer	9.1	10.7	13.7	5.3	3.9	8.3	5.5	10.9	9.5
Tree Crown Part									
Central	54.3	21.2	47.3	37.5	17.3	44.6	39.2	36.4	37.2
Intermediate	29.1	44.7	44.8	47.4	78.7	42.5	41.2	44.3	43.4
Periphery	16.6	34.1	7.9	15.1	4.0	12.9	19.6	19.3	19.4
Substrate Type									
Artificial	9.9	47.8	2.7	6.2	6.1	5.4	13.5	29.1	25.2
Trunk	24.6	1.3	22.5	19.9	6.1	28.7	16.0	12.6	13.5
Tree branch	48.6	46.1	60.3	67.1	81.7	55.8	62.6	49.2	52.6
Other	11.9	2.4	14.5	6.2	4.9	7.8	5.6	6.8	6.5
Ground	5.1	2.5	0.0	0.7	1.2	2.3	2.3	2.3	2.3
Substrate Size									
Fine	2.6	7.4	0.0	2.1	0.7	6.2	5.8	4.5	4.9
Small	21.3	19.7	1.2	7.2	4.3	14.7	22.6	12.8	15.3
Medium	26.4	12.6	28.4	32.2	33.0	32.3	23.3	21.9	22.2
Large	49.7	60.3	70.4	58.6	62.0	46.8	48.3	60.8	57.6
Substrate Inclination									
Horizontal	31.2	71.7	48.1	42.6	32.1	35.6	34.6	58.3	52.4
Oblique	30.3	18.4	45.7	26.1	44.3	36.8	32.9	25.0	27.0
Vertical	38.5	9.9	6.2	31.3	23.6	27.7	32.5	16.7	20.6
N	*570*	*1946*	*543*	*392*	*82*	*675*	*1029*	*3179*	*4208*

Regarding substrate size, northern palm squirrels made extensive use of large substrates that were also strongly preferred (Jacob's D = 0.73); in contrast, fine substrates were seldom used (Table 2) and avoided (Jacob's D = −0.83). Large substrates were also significantly used during postures compared to locomotion ($G = 48.65$, $p < 0.001$; Table 2). In terms of behaviors, during social interactions, the use of large substrates was significantly higher than in other behaviors, such as rest, with the lowest percentage of large substrate use ($G = 481.4$, $p < 0.001$). Fine substrate use was generally infrequent, with significantly higher percentages during feed, rest, and travel ($G = 61.9$, $p < 0.001$).

In general, horizontal substrates represented the most frequently used category and were preferred (Jacob's D = 0.57). Vertical and steep substrates were used at moderate rates (Table 2) but were only slightly preferred and strongly avoided, respectively (vertical: Jacob's D = 0.21; oblique: Jacob's D = −0.63). Horizontal substrates were also primarily used during postural behavior, with a significant decrease during locomotion, where vertical substrate use was considerable ($G = 181.9$, $p < 0.001$). In terms of behavioral context, horizontal substrate use was significantly higher during feed, travel, and social activities, compared to rest, groom, and explore ($G = 446.7$, $p < 0.001$; Table 2). By contrast, vertical substrates were significantly used only during explore and, to a lesser extent, traveling ($G = 113.4$, $p < 0.001$; Table 2).

3.3. Positional Behavior

Regarding the positional profile of the species, quadrupedalism and claw climb were the most dominant modes during locomotion, followed by grasp climb at moderate rates

(Table 3; Figure 2). Clamber, bridge, and leap were infrequently used. Quadrupedalism was the primary locomotor mode in all behaviors, except social activities, where claw climb dominated (G = 15.3, $p = 0.008$; Table 3). During feeding, grasp climb was used considerably and at significantly higher percentages than in other behaviors (G = 179.7, $p < 0.001$; Table 3). During travel and social activities, leap was also used at relatively higher rates compared to other behaviors (G = 25.6, $p < 0.001$; Table 3).

Table 3. Percentages of locomotor and postural modes used during the different behaviors by northern palm squirrels in Kathmandu city, Nepal (groom and rest did not involve any locomotor modes; travel did not include any postural modes).

	Explore	Feed	Social	Travel	Groom	Rest	Total
Locomotion							
Quadrupedalism	36.4	40.3	34.2	38.3	-	-	37.9
Claw climb	26.7	17.5	38.7	21.9	-	-	23.8
Grasp climb	15.5	26.1	4.5	11.2	-	-	15.4
Clamber	6.9	7.1	6.3	9.2	-	-	7.8
Leap	4.3	5.6	10.8	13.3	-	-	8.8
Bridge	7.7	2.6	3.6	5.1	-	-	4.9
Reversion	2.3	0.7	1.8	1.0	-	-	1.4
N	*258*	*268*	*111*	*392*			*1029*
Postures							
Quadrupedal Stand	41.9	36.5	60.9	-	60.9	56.3	45.2
Sit	1.9	40.6	1.2	-	34.2	0.7	22.8
Bipedal stand	3.5	6.9	0.2	-	0.0	0.4	4.1
Claw cling	36.5	3.9	30.6	-	4.9	39.7	18.4
Cantilever	5.5	4.2	0.0	-	0.0	1.5	3.1
Hang	10.6	7.7	7.2	-	0.0	1.3	6.4
N	*312*	*1678*	*432*		*82*	*675*	*3179*

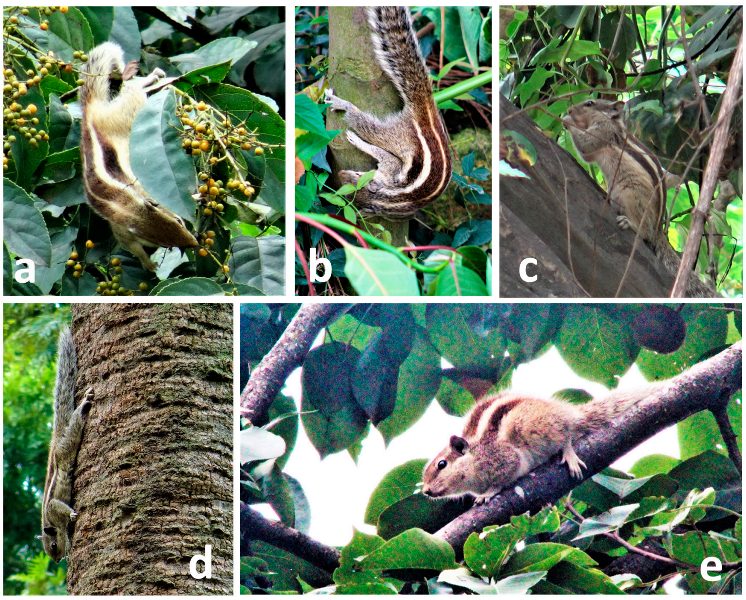

Figure 2. Main positional modes of northern pam squirrels in Kathmandu city, Nepal: (**a**) suspensory posture; (**b**) reversion; (**c**) sit; (**d**) claw climb; (**e**) quadrupedal stand.

Overall, in terms of postural behavior, quadrupedal stand dominated, followed by sit and claw cling (Table 3; Figure 2). Quadrupedal stand was the most frequent posture in almost all behaviors, apart from feed, where sit dominated (G = 714.8, $p < 0.001$; Table 3). Claw cling was used at significantly higher rates during rest, explore, and social activities than during feed and groom (G = 385.6, $p < 0.001$; Table 3). Hanging postures (mainly by suspending the body by the grasping feet) were significantly used during explore (G = 164.9, $p < 0.001$; Table 3).

4. Discussion

To our knowledge, this study represents the first quantitative analysis on habitat use and the associated general and positional behavior of northern palm squirrels (*Funambulus pennantii*). Our results indicate that the species was primarily arboreal, avoided the ground, and mostly used the middle layers of the canopy and the intermediate and central parts of tree crowns. Northern palm squirrels mainly used tree branches and preferred artificial substrates, the latter especially during feeding activities. The most used and preferred substrates were large and horizontal. Feed and rest were the most frequent behaviors during the study period. Locomotion was dominated by quadrupedalism and claw climb and, to a lesser extent, grasp climb, whereas quadrupedal stand and, to a lesser extent, sit and claw cling were the most frequent postures. These findings indicate that northern palm squirrels engaged in a diversity of locomotor and postural modes exploiting a variety of arboreal substrates. However, the profile of the species appeared to be slightly different from our initial predictions, which were based on previous studies of the positional behavior of other sciurid species in natural habitats.

Our first prediction, suggesting that small-bodied northern palm squirrels would use the lower canopy layers and the central parts of trees, was only partly supported by our findings (Table 2). Unlike similar-sized squirrels, which prefer the lower forest layers (*Microsciurus flaviventer*: [10]; *Tamiops rodolphii*: [13]), northern palm squirrels extensively used the middle layers of the canopy, during all behaviors. This profile is comparable to that of larger-bodied squirrels, which generally prefer the middle and upper forest layers (*Sciurus igniventris*: [10]; *Petaurista leucogenys*: [16]; *Sciurus vulgaris*: [36]). Regarding tree crown part use, northern palm squirrels shared their behaviors between the intermediate and central tree parts (Table 2). Analogous tree crown use profiles were encountered in other small-bodied squirrels, however, with an emphasis on central crown use (*Microsciurus flaviventer*: [10]; *Tamiops rodolphii*: [13]). In contrast, large-bodied squirrels extended their activities to tree peripheries (*Sciurus igniventris*: [10]; *Sciurus vulgaris*: [42]). The lower layers of the canopy and the inner parts of tree crowns were usually characterized by a complex network of branches and lianas, with dense foliage providing natural shelters from potential predators. As small-bodied squirrels are more susceptible to predation, the increased use of such concealed microhabitats enhances their chances of remaining unnoticed and enables safe navigation within the canopy. However, in the case of urban forests, this architecture was severely modified by anthropic interventions, and, more especially, the lower forest layers, which face extensive impact [26,27,29]. Moreover, in urban areas, the most potential predators are mainly terrestrial (humans, feral pets, etc.) hindering the use of lower forest layers and the ground of urban environments. This was also evident by the very low use and avoidance of the ground by northern palm squirrels. Thus, it is very likely that the species was forced to ascend to relatively higher forest layers and to restrict to the intermediate parts of tree crowns, in order to mitigate potential threats and assure effective forest use. Similar behavioral trends, related to increased arboreality, also characterize other urban vertebrates and facilitate the avoidance of the altered structure of human modified habitats [26,27,29,43,44].

The second prediction, indicating that small-bodied northern palm squirrels would use more large and vertical arboreal substrates, was also only partly supported by our observations. Northern palm squirrels preferred and used high proportions of large substrates (Table 2) in a manner comparable to other small-bodied squirrels (*Microsciurus flaviventer*: [10]; *Glaucomys volans*, *Tamias striatus*: [12]; *Sciurillus pusillus*: [11]; *Tamiops rodolphii*: [13]). However, in contrast to the increased use of vertical substrates by other small-bodied squirrels (*Microsciurus flaviventer*: [10]; *Eutamias sibiricus*: [14]; *Sciurillus pusillus*: [11]; 58.5% *Tamiops rodolphii*: [13]), northern palm squirrels mostly used and preferred horizontal substrates in almost all behavioral contexts, and primarily during feeding and postural behavior (Table 2). This difference was most likely related to the considerable use and preference of artificial substrates, especially during feed and postural behavior overall (Table 2). Urban forests include a variety of human-made structures (e.g., roofs, walls) that are large, flat, horizontal, and unbranching [27]. Similar substrates are readily used by squirrels as non-terrestrial crossings between forest patches, as relatively safe feeding platforms, and as vigilance perches that provide a wide scan of the environment (Figure 2). Moreover, such substrates can be easily negotiated via quadrupedal activities (see below) and require less climbing and clinging capacities, which are biomechanically and physiologically demanding [27,43–45]. In this way, northern palm squirrels manage to cope successfully to the additional challenges of the modified substrate properties of anthropogenic habitats, in a similar manner to other urban vertebrates, and overcome potential barriers that may hinder their survival [22,27,29,44]. In this way, the effective use of such substrates may further help urban populations to travel safely and efficiently, successfully exploiting many aspects of human-modified habitats [27,43–46].

The third prediction, suggesting that the small-bodied northern palm squirrels would engage more in vertical claw climbing and clinging activities, was not supported by our data (Table 3). Unlike other small-bodied arboreal squirrels, which extensively used claw climb and cling (*Microsciurus flaviventer*: [10]; *Glaucomys volans*: [12]; *Sciurillus pusillus*: [11]; *Tamiops rodolphii*: [13]), northern palm squirrels engaged in clawed activities at moderate rates (Table 3). This profile was comparable to that of similar-sized semiarboreal squirrels (e.g., *Tamias striatus*: [12]), which shared their positional repertoire between clawed and quadrupedal activities. As mentioned above, quadrupedal locomotion and postures were usually associated with the use of relatively flat and horizontal substrates. In the case of altered urban environments, these substrates can be either artificial (e.g., walls, roofs, cut logs, etc.), terrestrial (pavement, dirt, large boulders, etc.), or arboreal (primary bifurcations of main branches in the central and, to a lesser extent, intermediate parts of tree crowns). Quadrupedalism permits rapid and effective locomotion that enables the exploitation of different urban patches and successful escape from potential predators, whereas quadrupedal stand facilitates long feeding or short resting bouts while staying vigilant [26,27,43,44].

The findings of the present study on habitat use and the locomotor and postural behavior of northern palm squirrels in the urban forests of Kathmandu did not support most of our predictions that were based on previous research on arboreal squirrels in natural environments. This behavioral idiosyncrasy most likely reflects a certain adaptive flexibility that permits the efficient exploitation of many different habitats, such as the ones impacted by anthropic interventions. Analogous behavioral flexibility was observed in many vertebrates that exploited urban habitats [22,23,26–30,43–46]. Urban forests shape a different environmental setting for species, as they are characterized by a discontinuous canopy, secondary growth, high dominance of pioneer species, and the presence of human structures and interventions that alter the stand structure and canopy layers [19,24,25]. To cope with these architectural peculiarities of the Kathmandu urban forest structure, northern palm squirrels employed more quadrupedal activities to deal with wider and more horizontal, as well as artificial, substrates. Moreover, climbing activities were shared between claw climb on larger substrates and grasp climb on slenderer, steeply inclined substrates that usually abound in discontinuous canopies with forest openings [24,25]. The complex structure of the urban forest with a dense network of mixed intertwined substrates further provided a perfect microhabitat for the small-bodied squirrels which mainly used the middle forest layers and intermediate parts of trees. To safely navigate and efficiently exploit this rather complex forest structure, northern palm squirrels adopted a more variable locomotor and postural repertoire, departing from the more stereotyped positional profile of small-bodied squirrels. Similar diversity in positional modes was also reported in other vertebrates, such as lizards and birds which inhabit urban environments [27–29]. This profile was probably related to the behavioral versatility of northern palm squirrels, which use both the arboreal and other types of substrates at variable rates [31,32,36].

This behavioral versatility most likely reflects their adaptive flexibility towards habitat alterations and has apparently contributed to the efficient use of urban forests ([27]; for the Kathmandu valley (see [34,35]) and in the successful exploitation of a diversity of habitat types across its wide range [31–33,38]. In this way, northern palm squirrels seemingly expanded their ecological niche (e.g., see [4]) and managed to circumvent the altered habitat features resulting from intense anthropogenic pressures throughout their range.

The present data, indicating the behavioral flexibility of northern palm squirrels, were derived from a small number of sampled individuals over a limited period. Thus, similar assumptions should be interpreted with caution. Nevertheless, they supported the locomotor and postural variability of squirrels, which, especially when related to shifts that enable the effective exploitation of diverse habitats, was the milestone for their adaptive radiation and success [7–9,31,47,48]. Northern palm squirrels belong to the subfamily Callosciurinae, of which the most basal member, the Indian striped squirrels (*Funambulus* spp.), exhibit a comparable flexibility [8,9,32]. This early offshoot most likely adopted a more generalist behavior, exploiting both the forest canopy, as well as the undergrowth, and artificial and terrestrial substrates. These capacities most likely promoted ecological niche differentiation that may have contributed to the ecological success of callosciurines in a multitude of natural and human-modified forests in South and Southeast Asia. However, our data did not suffice for identifying whether these squirrels capitalized in pre-existing morphological, behavioral, and ecological adaptations to exploit urban areas and took advantage of specific environmental factors that urban habitats accommodate (e.g., [29,30,45]).

5. Conclusions

Urban habitats are markedly altered, creating novel, unique challenges and selection pressures for animals that exploit them [20–25]. These challenges are more significant for arboreal species because of the altered substrate properties of anthropogenic structures [27,29]. To cope with these structural peculiarities, most animals exhibit behavioral adjustments to efficiently exploit the urban habitat [20–23,26–30,43–46]. Some of these adjustments involve increased arboreality, higher diversity of locomotor and postural modes, and use of specific habitat features, such as artificial, or large and horizontal substrates [26–29,43–46]. The present data were derived from a small number of individuals during a very specific period of the year (rainy season) and should be considered only as indicative, but not conclusive, of the behavior of the species in an urban habitat. Despite these limitations, they appeared to highlight the importance of forested patches within urban habitats. Trees, along with diverse artificial substrates, increase habitat diversity, allow fragment connectivity, enable animals to avoid potential terrestrial predators, which abound in urban habitats, and facilitate safer and more efficient travel and rest within a variety of perches [20–22]. In effect, similar habitat features are responsible for advancing urban diversity and are most likely related to increased behavioral flexibility of urban populations [20,21,25]. However, our data were insufficient to identify if the observed behaviors were interrelated to the exploitation of the urban habitat or if they were important for colonizing and, subsequently, surviving in urban habitats. Relatively little is known about the role of pre-existing adaptations in the successful exploitation of urban habitats and how urban populations invest in them in order to respond flexibly to human-modified habitats [27,29,30]. We know even less about whether these behavioral changes are due to evolutionary adaptive factors or habituation to humans who abound in urban habitats [30]. Moreover, few things are known about how anthropogenic changes to habitat structure impact positional strategies and shape positional flexibility [27,43–46]. Establishing links between behavioral shifts and ecological shifts in urban species provides an important context for predicting and interpreting evolutionary adaptations. In this way, we gain insight into the behavioral challenges that urban animals encounter. For some species, urban areas may act as an important barrier, whereas for others, they may provide a novel living environment with the opportunity to exploit novel resources [22,27]. Thus, more field studies in urban environments are required to elucidate these interrelations between ecological and behavioral differences and to better understand how locomotor and postural modes enable the successful exploitation of these modified habitats. More precisely, more research is needed to effectively evaluate the positional and general behavioral repertoire of urban species in human-modified environments throughout the whole year, as well as a comparison of the behavior with populations inhabiting natural habitats. This would eventually shed light on the adaptability of generalist, behaviorally flexible species and how the urban environment can alter their behavior (see [22,26–30,43–46]).

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