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Gliding performance of the red giant gliding squirrel *Petaurista petaurista* in the tropical rainforest of Indian eastern Himalaya

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Gliding squirrels occur globally and many are of conservation concern due to habitat fragmentation and degradation. Information on their ability to cover the distance between two trees by gliding is lacking in many species which might be vital for habitat management and conservation. The aim of the study was to present the field observations on gliding behaviour of the red giant gliding squirrel *Petaurista petaurista* observed within tropical rain-forest of Namdapha National Park, Arunachal Pradesh, Indian eastern Himalaya. The data were collected on 71 glides observed at nights. The mean height of launching and landing trees were 28.5 ± 1.0 m and 16.4 ± 0.9 m, respectively. Gliding variables calculated were vertical drop (mean = 13.4 ± 1.0 m), horizontal distance (mean = 36.3 ± 2.7 m), air speed (mean = 8.9 ± 0.2 m s⁻¹), ground speed (mean = 7.9 ± 0.2 m s⁻¹), glide ratio (mean = 3.1 ± 0.2), glide angle (mean = $19.0 \pm 0.9^{\circ}$), GBH of launching tree (mean = 156.8 ± 8.5 cm) and GBH of landing tree (mean = 195.2 ± 9.5 cm). Gliding distance was categorized in four types. The highest glides in a 26-50 m glide-class (44% (n = 31)) were the most frequently observed. Gliding squirrels preferred top canopy (56%, n = 40) for distant glides. Forest structure has an influence on the gliding habits of gliding squirrels and thus our data on gliding parameters should be used when planning forest management actions.

The evolution of unique locomotory types has played a significant role in the conquest of new habitats, partitioning of resources within those habitats and ultimately in the evolution of organismal diversity (Vermeij and Dudley 2000, Vermeij 2006). The origin of flight represents one such important transition and requires the integration of a suite of morphological, physiological and behavioural features, and it might have evolved as an energy cost-effective mode of locomotion in arboreal animals because gliding between trees consumes less energy and time compared to running and flying. Also, it might be to reduce predation risk or to limit the energy consumption of dispersal (Norberg 1985, Goldingay 2000, Dudley et al. 2007, Byrnes and Spence 2011). Gliding has evolved independently in at least six groups of mammalian taxa namely Volitatia, Pteromyinae, Anomaluridae, Acrobates, Petaurus and Petauroides (Stafford et al. 2002) and among them, the most diverse and widespread are gliding squirrels (Goldingay 2000, Vernes 2001). Gliding squirrels belong to the order Rodentia and family Sciuridae and are globally represented by 44 species and are placed in 15 genera (Thorington et al. 2012). India is home to 14 species of gliding squirrels, among which nine species are found in Arunachal Pradesh (Murali and Kumar 2014). Among these nine species, the red giant gliding squirrel *Petaurista petaurista* is a widely distributed species in Indian states of Arunachal Pradesh, Assam, Jammu and Kashmir, Meghalaya, Sikkim and Uttaranchal (Srinivasulu et al. 2004, Ray et al. 2012) and globally from northern South Asia, southern China and Southeast Asia (Walston et al. 2008).

Unlike other terrestrial mammals, gliding squirrels depend on gliding locomotion and though it is an effective locomotory mode in forest, they cannot cross forest gaps beyond their gliding capacity (Asari et al. 2007, Goldingay and Taylor 2009), which makes gliding behaviour an important aspect to be studied and findings of such study could play an important role in forest management. Globally studies have examined the gliding behaviour of gliding squirrels such as Indian giant gliding squirrel Petaurista philippensis (Koli et al. 2011), Japanese giant gliding squirrels Petaurista leucogenys (Stafford et al. 2002), and northern gliding squirrel Glaucomys sabrinus (Vernes 2001). But, only a single study appears from India on the gliding behaviour of the Indian giant gliding squirrel (Koli et al. 2011). Only two studies are reported on the gliding habits of *P. petaurista* which have covered a few aspects of gliding (Barrett 1984, Scholey 1986). Not a single study represents the gliding behaviour of P. petaurista from India and thus, there is a need to better understand their preference of micro-habitat for secured gliding in the local environment. As a result, we initiated this study, to better understand the gliding behaviour of P. petaurista in tropical rainforest of Namdapha National Park, Indian eastern Himalaya, which might help in future for species conservation and park management.

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Methods

The study area

The study was carried out in Namdapha National Park (NNP; 27°23'30″–27°39'40″N, 96°15'02″–96°58'33″E; 1985 km²) which lies in the eastern Himalayan region of Arunachal Pradesh, India. The park contains some of the northernmost tropical rainforests of the world (Proctor et al. 1998). Its high habitat heterogeneity and vast altitudinal range from 200-4571 m a.s.l. boost the national park with rich floral (Nath et al. 2005) and faunal diversities (Proctor et al. 1998, Datta et al. 2003, Srinivasan et al. 2010) which include many rare, endemic and threatened species (Adhikari et al. 2003, Datta et al. 2003, Murali et al. 2012). Detailed climatic, vegetation, faunal diversity of park are reported by Ghosh (1987) and Nath et al. (2005). The present study was conducted around Deban (27°29' N, 96°23' E) and Gibbons Land (27°30'N, 96°19'E) areas within the park based on the occurrence of species. The elevation in the two sites ranged between 300-450 m a.s.l. The area is dominated by tall trees (15-50 m) like Duvanbanga grandiflora, Neolamarkiana kadamba, Biscofia javanica, Cinnamomum sp., Castonopsis sp., Ficus sp., Shorea assamica, Syzgigium cumini, Spondius axillaris and Toona ciliata.

Collection of gliding data

Gliding squirrels were initially detected by the eye-shine caused by red light of headlamps, calls and sounds due to travel in or between trees. Further, animals were observed visually, using night vision binoculars and spotlight between 19:00-04:00 h. Whenever a gliding squirrel was sighted, its behaviour was observed. A distance of 10-15 m was maintained (distance between observer and the tree in which the squirrel's activity was happening) during the process. Gliding squirrels in these areas are well habituated to humans as there are forest camps used by people around the area. Though the animals were not marked, we could distinguish at least 8-10 adult individuals. The data collected were not separated based on the sexes as it was difficult to differentiate males from females in the available field conditions. Data were collected for 4–5 days per month over a period of 12 months. We collected complete data for 71 glides. Also, data were collected opportunistically whenever the glides happened during the normal trail walks during the study period as these forest trails facilitated night observations.

For each glide, 10 variables were recorded: 1) height of launch (m), 2) height of landing (m), 3) vertical drop (m), 4) horizontal distance (m) 5) air speed (m s^{-1}), 6) ground

Table 2. Mean and range of various gliding aspects of *P. petaurista* at NNP.

		All glides $(n = 71)$		
S/No	Gliding aspects	$Mean \pm SE$	Minimum	Maximum
1	Height of launch (m)	28.5 ± 1.0	13.5	51.6
2	Height of landing (m)	16.4 ± 0.9	3.2	36.5
3	Vertical drop (m)	13.4 ± 1.0	3	43.1
4	Horizontal distance (m)	36.3 ± 2.7	7.8	104.3
5	Air speed (m s ⁻¹)	8.9 ± 0.2	5.5	13.3
6	Glide ratio	3.1 ± 0.2	0.6	11.7
7	Gliding angle(°)	19.0 ± 0.9	6	37.5
8	Ground speed (m s ⁻¹)	7.9 ± 0.2	3.1	12.3
9	GBH of the launching tree (cm)	156.8 ± 8.5	65	375
10	GBH of the landing tree (cm)	195.2 ± 9.5	90	425

speed (m s⁻¹), 7) glide ratio, 8) glide angle(°), 9) girth at breast height (GBH) of launching tree and 10) girth at breast height (GBH) of landing tree (cm) (Vernes 2001, Stafford et al. 2002, Koli et al. 2011) (Table 1). GBH of the trees were measured using measuring tapes. Heights of launch, total heights of the launching and landing trees, landing and horizontal distance were measured using a laser operated Bosch distance measurer (accuracy ± 1 m). A stopwatch was used to record the time of gliding. Vertical drop, glide ratio, direct glide distance, gliding angle, air speed and ground speed were calculated as per Stafford et al. (2002) and Koli et al. (2011). The canopy was categorised based on the glide launch by the squirrel species. Whenever the glide was launched from tree top, the canopy type was represented as top canopy and similarly, when the glide was initiated from terminal branches, the canopy was categorised as terminal canopy and any glide that initiated from middle portion of the tree was categorised as middle canopy. During the gliding episode if the squirrel gained elevation that exceeded the launching height immediately after the launch, was noted as 'S' shaped glide (Vernes 2001). Whereas in 'J' shaped glide, the elevation of squirrel rapidly dropped after the launching point. Vegetation analysis was done using point-centered quarter method and data was analysed to evaluate the tree density (Cottam and Curtis 1956). Pearson's moment correlation (r), and Kruskal–Wallis ANOVA (χ^2) tests were performed to analyse the collected field data using SPSS 16.0.

Results

The data on various glide aspects are presented in Table 2. Glides were categorized into four classes based on their

Table 1. Gliding aspects and their definition (Vernes 2001, Stafford et al. 2002, Koli et al. 2011).

S/No.	Gliding aspects	Definition		
1	Height of launch (m):	The point on tree from which the glide is initiated by the flying squirrel		
2	Height of landing (m):	The point of landing on tree at the end of glide		
3	Vertical drop (m):	Total height of landing tree minus the height of point of landing		
4	Horizontal distance (m):	Horizontally distance between the points of launching and landing		
5	Air distance (m):	Diagonal distance between the points of launching to landing		
6	Glide ratio:	Horizontal distance divided by vertical drop		
7	Gliding angle (°):	Angle between horizontal distance and air distance		
8	Air speed (m s^{-1}):	Direct glide distance divided by time taken to travel		
9	Ground speed (m s ⁻¹):	Horizontal distance between the gliding trees divided by time taken to trave		

8

Table 3. Mean gliding angle and girth at breast height (GBH) of landing tree in different horizontal distance classes of *P. petaurista*.

Horizontal glide distance class (m)	No. of glides (n)	Gliding angle (°) Mean ± SE	GBH of launching tree (cm) Mean ± SE	GBH of landing tree (cm) Mean ± SE
0–25	27	20.6 ± 1.8	167.6 ± 16.8	194.3 ± 16.6
26-50	31	17.7 ± 1.3	150.5 ± 11.5	185.9 ± 12.0
51-75	5	16.4 ± 2.6	137 ± 19.5	170 ± 7.6
76 <	8	20.4 ± 2.1	145 ± 16.7	250 ± 39.6

horizontal glide distance (glide ratios) and are presented in Table 3. Maximum number of glides were observed in 26–50 m glide class (n = 31; 43.7%) followed by 0–25 m (n = 27; 38%), 76 m and above (n = 8; 11.3%) and 51-75 m (n = 5; 7%) (Table 3). Most glides were initiated from the upper canopy (n = 40; 56.3%) followed by middle (n = 19; 26.8%) and terminal canopy (n = 12; 16.9%). There was significant difference in gliding preference among the three canopy levels (Kruskal–Wallis ANOVA $\chi^2 = 11.6$, DF = 2, p < 0.01). Airspeed to horizontal distance (r =0.40, p < 0.01) and launching height to horizontal distance (r = 0.62, n = 71n, p < 0.01) were correlated. Air speed and ground speed also showed significant correlation (r = 0.88, n = 71, p < 0.01). Air speed was slightly higher than ground speed. Gliding squirrels preferred 'S-shaped' glide paths which accounted about 78.9% (n = 56) of the total glides followed by 14.1% (n = 10) 'J-shaped' glide paths and only 7% (n = 5) of glides included 'straight' or rather 'horizontal' glides (Table 4).

Glide ratio ranged between 0.6 and 11.7. The most glide class ratio was $1 - \langle 3 \rangle$ (n = 43, 61% of glides) followed by $3 - \langle 5 \rangle$ (n = 22, 31%), $5 - \langle 7 \rangle$ (n = 4, 6%), $\geq 7 \rangle$ (n = 2, 3%) (Fig. 1). Glide angle and horizontal distance were not correlated (r = -0.117, n = 71, p < 0.01). The highest mean GBH (250 ± 39.7 cm) of the landing trees were recorded in horizontal glide distance class of ≥ 76 m and the lowest GBH (170 ± 7.6 cm) were in 51–75 m class (Table 3). The tree density was 132 trees ha⁻¹ and based on the density, species like *Syzygium cumini, Terminalia myriocarpa, Magnolia hodgsonii, Dysoxylum gobara* and *Altingia excels* were among the most dominant tree species in the forest.

Discussion

In this study, the most common horizontal glide distance of *Petaurista petaurista* was 26–50 m, followed by 0–25 m which might be due to observations made over the forest trails which had 20–40 m gaps. In contrast, the most frequent glide distance of *P. philippensis* was 11–20 m (Koli

Table 4. Gliding parameters observed based on types of glide.

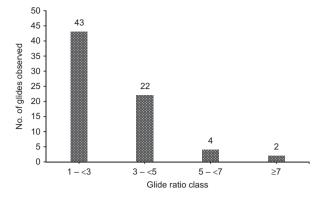


Figure 1. Number of glides observed under four different glide ratio class.

et al. 2011). Barrett (1984) reported that in unlogged forest, P. petaurista avoided trees with lianas even though they had suitable substrate for landing. Similar observations were also recorded in the present study. This may lead to a choice of longer glides to reach the preferred trees that are liana free and having a broad substrate to land. The longest glide of P. philippensis was 35 m (Koli et al. 2011), which is slightly higher than the present study. This possibly could be due to difference in forest structure, forest type and tree height. Moreover, the forest trails had 20-40 m gaps and longest glides recorded in the present study are from those areas which have huge canopy gap. However, P. petaursita can leap a long distance and the highest recorded glide distance is 150 m (Thorington and Heaney 1981). Only a single long distance glide of 104 m was observed in the present study, which was similar to a study conducted by Ando and Shiraishi (1993) where a single glide of 115 m was observed and shorter glides were much preferred. Possibly, short-distance glides do not allow enough time to attain the optimal glide ratio for a constant glide which makes the squirrels prefer moderate distances to glide (Ando and Shiraishi 1993). Other potential factors affecting glide distance are forest structure and tree height, with denser forest of smaller trees reducing the possibility for long glides.

The mean glide ratio of 3.1 ± 0.2 was observed in the present study with greater variability in their range 0.6–11.7. These values do not concur with those of other studies viz. Stafford et al. (2002) where the observed value was 1.87 for *P. leucogenys* and *P. philippensis* (2.32, Koli et al. 2011). The higher glide ratios in the present study could be due to no environmental obstacles that prevented animals from gliding (Stafford et al. 2002). Also, the canopy gap in the forest trails might have influenced the higher glide ratios as the horizontal distance of glides were higher in the forest trails. A majority of the glides that we observed were along the

	No. of	Horizontal distance (m)		Horizontal distance (m)	GBH of landing tree (cm)	
Type of glide	observations (n)	Max	Min	Mean \pm SE	Mean \pm SE	
S-shaped glide	56	93.7	9.7	31.4 ± 2.2	194.2 ± 10.4	
J-shaped glide	10	104.3	39.4	72.5 ± 7.9	213.5 ± 34.6	
Straight or horizontal glide	5	40.3	7.8	18.2 ± 6.5	169.0 ± 28.6	

Table 5. Comparison or	different gliding aspects	of gliding so	quirrels studied	globally.

Species	Sample size (n)	Maximum gliding distance (m)	Glide ratio	Air speed (m s ⁻¹)	Ground speed (m s ⁻¹)	Vertical Drop (m)	Source
Petaurista leucogenys	_	160	_	_	_	_	Imaizumi 1983
	202	115	3.5	_	-	-	Ando and Shiraishi 1993, Stafford et al. 2002
P. petaurista	-	150	1.0	15.2		7.4	Thorington and Heaney 1981, Scholey 1986
P. philippensis	100	38.5	2.3	7.0	7.0	7.5	Koli et al. 2011
Glaucomys volans	_	50	2.8	_	-	1.8	Nowak 1991, Scheibe and Robins 1998
G. sabrinus	100	90	2.0	-	-	1.9	Wells-Gosling 1985, Vernes 2001
Glaucomys sp.	100	6–20	-	-	-	_	Wells-Gosling 1985
Hylopetes lepidus	_	>135	-	_	-	_	Nowak 1991
H. alboniger		110	-	-	-	_	Krishna et al. 2013a
Pteromys volans orii	31	52.8	1.7	_	-	11.9 (M) 10.8 (F)	Ansari et al. 2007, Suzuki et al. 2012
P. petaurista	71	104.3	3.1	8.9	7.9	13.4 ± 1.0	this study
Petaurus australis	22	140	2.0		3.8 - 8.3	12.7*	Goldingay 2014
Petaurus breviceps	_	42	1.8			10.0	Jackson 2000
Petaurus gracilis	-	60	1.9			15.2	Jackson 2000
Petaurus norfolcensis	85	47	1.8			11.7*	Goldingay and Taylor 2009
Galeopterus variegatus	222	150	-	-	10.1	-	Byrnes et al. 2008

*launch and landing trees may not be on flat ground.

forest trails ranging between 20–40 m (Table 3). Also, gliding squirrels preferred 'S-shaped' glide when compared to 'J-shaped' glide paths. In S-shaped glide paths, the squirrel leaps from the tree by forcing their limbs backwards in order to gain additional elevation before entering the downward glide path and usually, such glides were observed in moderate distant glides. In the case of J-shaped glide paths, the animal dives from the perch, losing elevation rapidly, and then pulls out of the glide to a more horizontal glide angle such glides were observed for distant glides. A 'straight' or rather a 'horizontal' glide path was the least observed where the animal leaps from its perch at approximately the glide angle for most of the glide.

Air speed of *P. petaurista* was higher than the ground speed which looks similar to the observations made for *P. philippen*sis where the air speed was $(4.18-11.36 \text{ m s}^{-1})$ was slightly higher than its ground speed $(3.75-10.39 \text{ m s}^{-1})$; Koli et al. 2011). The present results (8.9 ± 0.9) diverge from Scholey (1986) who recorded mean air speed (15.1 ± 3.2) for P. petaurista and also in previous studies, the gliding speed of P. *leucogenys* were 7 and 15.1 m s⁻¹ (Ando and Shiraishi 1993) and 3.03-8.89 m s⁻¹ (Stafford et al. 2002), respectively (Table 5). All of the above mentioned studies, including the present study, are based on the assumption that launch and landing phases of the glides are of equal duration on short and long glides, and that there is no consistent difference in mid-glide speeds between short and long glides. Gliding squirrels may have increased their gliding speed by increasing their gliding angle, which in turn would reduce the glide ratio. Localized variations like that of wind speed and direction might also affect the optimal speed (Vernes 2001, Koli et al. 2011). The mean vertical drop in the present study was 13.4 ± 1.01 m, which is much higher than the vertical drop measured in the same species in the previous study (7.5 m: Scholey 1986). Also, another species of the same genus Petaurista (P. philippensis) showed 7.5 m vertical drop, which is much less than the present study. The higher mean vertical drop in the present study could be due to the difference in tree heights and the absolute tree density of the area. Gliding mammals are thought to select a landing point before take-off (Caple et al. 1983). Aerial manoeuvers such as banking and turning result in losses in altitude, so the landing point must be large enough to allow vertical variation in the point of contact (Caple et al. 1983). Thus, for longer glides, gliding mammals usually select vertical tree trunks (Caple et al. 1983). Even in the present study, we observed lesser glides where the gliding squirrels preferred landing on branches. Also, no distant glides were observed where the animal landed on lianas. But for shorter leaps, they preferred lianas as substrate to travel. Most often the landing was seen on larger tree trunks. The mean GBH of the launching and landing trees was 156.8 ± 8.50 cm (SE) and 195.2 ± 9.48 cm (SE) respectively. The GBH values of the landing tree were similar to reports by Koli et al. (2011, 224.4 ± 77.9 cm (SD)). Also, there were no observations in the present study where the landing occurred on ground.

In the current situation, gaps created in few areas of the habitat might affect the overall ecology of the gliding squirrels and essentially the gliding pattern in that particular habitat. The available literature also suggests that the gaps created between forests patches should be less than the distance traversable by gliding squirrels species (Asari et al. 2007). In the present study, it was noted that maximum numbers of glides were observed in < 50 m glide distance which can therefore be considered as the optimum traversable distance for the species in the study area. The developmental activities like road widening in the study area have created 50-75 m of canopy gap in a few areas and also many tall trees were uprooted along the roadside (Krishna et al. 2013b). Further, the biology and occurrence of gliding squirrels was found to be affected by clear-cutting of forest or forest fragmentation (Woodworth et al. 2000). It is noteworthy that

10

the disjunctions in the habitat of gliding species beyond gliding capability epitomize barriers for the movement of the species which might lead to the disruption of population processes (Lampila et al. 2009, van der Ree et al. 2010, Taylor and Goldingay 2013, Soanes et al. 2013). Thus, knowledge on gliding performance enables assessment of the ability of a gliding species to cross tree-canopy gaps (Goldingay and Taylor 2009, Kambouris et al. 2013) and this may lead to a management response such as the installation of tall wooden poles to enable, gap crossing (Goldingay et al. 2011, Taylor and Goldingay 2013). Therefore the information of gliding distance covered by the gliding squirrels is to be given importance in habitat manipulation and restoration activities whenever applicable for species conservation at local as well as at global level. Also, gliding behaviour might acts as important tool of measure in forest management, conservation and restoration activities.

In conclusion, gliding behaviour seems to be more diverse than previously assumed; local environmental factors may have a significant role in determining glide paths. Local factors like seasonal wind speed, topography, canopy cover, liana density are to be taken into account for refining the data and for obtaining accuracy. Although we recorded the majority of gliding aspects to determine the gliding ability of *P. petaurista*, other aspects like wing load, body weight, habitat composition, forest structure, distribution of food resources, anthropogenic factors, climatic factors, etc. should also be considered for a better understanding of the gliding behaviour of species in the wild.

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12