

## ECOLOGICAL STUDIES ON TWO SYMPATRIC *PETAURISTA* SPECIES IN TAIWAN

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Pei-Fen Lee, Donald R. Progulske and Yao-Sung Lin (1986) Ecological studies on two sympatric *Petaurista* species in Taiwan. *Bull. Inst. Zool., Academia Sinica* 25(2): 113-124. The study, conducted at Chitou, was to describe the general ecology and behavior of the two species of giant flying squirrel (*Petaurista petaurista* and *P. alborufus*), to determine if they debark conifer plantations, and to compare their habitats and feeding. We made observations primarily at night during 1800-2400 hrs along established trails by spotlighting the tree canopy from October 1981 to May 1983.

The two species appeared tolerant to each other while out feeding or loafing. Although sighting of singles was the norm, pairs and triples were sometimes observed. Three types of behavior: mating, feeding and following, were recognized when two or more individuals of the same species were seen at the same time. Mating behavior was observed in December, January, and June for *P. petaurista*, and in June for *P. alborufus*.

Each species has unique vocalizations. Counts revealed that *P. petaurista* celled more frequently than *P. alborufus*. Most calls were from the tree canopy but individual squirrels sometimes called from a tree cavity.

Eighteen tree cavities used for nesting were located. Nearly all cavities were built in the trees of Lauraceae and Fagaceae. Two leaf nests used by *P. petaurista* were also found.

Both species of squirrels showed strong preference for the hardwood forest. *P. alborufus* were at higher altitudes than *P. petaurista* although the ranges overlapped. Both species utilized many of the same tree species for feeding and resting. *P. petaurista* usually used lower layers of vegetation for their daily activity, while *P. alborufus* used higher layers. Seasonal abundance of food in different tree layers influenced where the squirrels would be. Two *P. petaurista* were observed feeding on bark of *Cryptomeria japonica*, a plantation tree, and when they were collected, their stomachs were nearly full of bark.

**Key words:** ecology, flying squirrel, food habit, *Petaurista alborufus*, *Petaurista petaurista*, resources partitioning.

Giant flying squirrels, all grouped taxonomically in *Petaurista*, are widely distributed in mountainous areas of East and Southeast Asia (Phillips, 1980; Honacki *et al.*, 1982). Five species are recognized (Nowak and

Paradiso, 1983); *P. leucogenys*, *P. magnificus*, *P. elegans*, *P. alborufus*, and *P. petaurista*. All species are nocturnal arboreal folivores and inhabit forests with abundant tree cavities (Eisenberg, 1978; Muul and Lim, 1978; Nowak and Paradiso, 1983; Phillips, 1980).

Extensive studies have been done on the white-cheeked giant flying squirrel (*P. leucogenys*) in Japan (Ando and Imaizumi, 1982; Ando and Shiraishi, 1983, 1984; Ando *et al.*, 1983, 1984; Baba *et al.*, 1982). However, little is known about the ecology of other members in this genus. Several investigators (Cross *et al.*, 1969; Hoogstraal and Kohls, 1965; Lien and Cross, 1968) reported their studies of parasites found in the Formosan giant flying squirrel (*P. petaurista*). Nadler and Lay (1970) published their work on chromosomal numbers of this species. Other than physical descriptions and geographic distributions, there appears to be no study or literature on the white-headed giant flying squirrel (*P. alborufus*) which resides sympatrically with *P. petaurista* in Taiwan and perhaps elsewhere.

In Taiwan *P. petaurista* are found at elevations from 300 to 2200 m while *P. alborufus* are distributed from 1100 to 3600 m. McCullough (1974) reported that *P. petaurista* is most abundant in the lower elevations of hardwood forests and that *P. alborufus* has its greatest density in high elevation virgin conifer forests. Overlap of ranges for the two petauristids in Taiwan provides an opportunity to study partitioning of their habitat resources. While partitioning of habitat by tree squirrels has been investigated (MacKinnon, 1978a; Emmons, 1980; Whitten, 1981; Glanz, 1984), only limited field studies have been made on nocturnal sciurids (Weigl, 1978).

The red-bellied tree squirrel (*Callosciurus erythraeus*) was condemned for debarking conifers extensively and thereby causing heavy loss of timber in Taiwan, particularly in plantations (Kuo, 1957; Lin and Yo, 1981; Wang and Kuo, 1980). For some time foresters have suspected that flying squirrels also cause some of the damage (Chu and Yie, 1970). In Japan, bark stripping of *Cryptomeria japonica* (Japanese fir) by *P. leucogenys* has been reported since 1942 (Udagawa, 1954).

Our study, initiated in 1981 to address

some forest management problems in Taiwan, was to: 1) describe the general ecology and behavior of *P. petaurista* and *P. alborufus*; 2) determine if the two species debark plantation conifers; and 3) compare habitat selection and feeding of these squirrels.

## STUDY AREA

Observations were made in the National Taiwan University Experimental Forest at Chitou, Nantou County. The relative humidity there is high (annual mean 90%). Rainfall occurs unevenly between April and September while other months are dry; average annual precipitation is nearly 3000 mm. The yearly mean temperature is 16.8°C with monthly variances from 10.3°C (January) to 21.0°C (July).

Chitou Forest, encompassing 2488 ha, is at the upper end of a precipitous mountain valley rimmed on the east by Phoenix Mountain (elevation 1669 m) on which our study was conducted. Since 1895 most of the forest in Chitou and adjacent areas has been converted to monoculture plantations of *Cryptomeria japonica*, *Cunninghamia konishii*, and *Chamaecyparis formosensis* but some natural hardwood forest still exists. Dominant trees in hardwood stands are *Pasania kawakamii* and *Machilus japonica* (Liu and Lio, 1975). In general, conifer plantations are at mid to low elevations on the mountains whereas the natural forest ranges upward from 1200 m. Prominent understory trees and shrubs in both types include *Morus australis*, *Debregeasia edulis*, and *Ficus erecta* but species diversity is greater in the hardwoods.

Several mountain trails have been constructed to allow access of visitors and workers to the forest. Three interconnected ones which pass 9.5 km through conifer plantations and 3.3 km through natural hardwood stands were chosen as transects for observing flying squirrels at night. These trails are 6.7, 3.6, 2.5 km in length, each with elevation change from approximately 1100 m to 1525, 1340, and 1360 m respectively.

## METHODS

We made observations on three consecutive nights each month from October 1981 to May 1983 using a different trail each night during 1800–2400 hrs., the period when squirrels were most active. Rain prevented us from making observations along one trail in December 1981 and February and March 1983. Spotlights powered by a 6-volt backpack battery and having an effective range of 60 m in open areas were used to locate squirrels. On each occasion at least two observers would walk together slowly spotlighting the forest canopy and shrub layers along both sides of the trail.

Squirrels were located mainly by reflection of the light from their eyes, sometimes by their calls, or the noise they made moving in the trees. We then used 7×30 binoculars for further observations. *P. petaurista* is dark brown with orange-red underparts whereas *P. alborufus* is mahogany red above with white belly and head. When squirrels were too distant from us (<35 m) or partly obscured to note the pelage, we used color of eyeshine to identify them. *P. petaurista* has an orange-red reflection while *P. alborufus* has a greenish one.

For each squirrel sighted, its species, location, behavior, habitat type, and perching height were recorded. The perching height was determined by telephoto lens measurement as under 5 m, 6–10 m, 11–15 m, 16–20 m, or over 20 m. As long as we were over 10 m distance from a spotlighted squirrel, the animals appeared undisturbed by our presence which gave us the opportunity to observe their behavior. Whenever possible we also identified species of the tree and type of food the squirrel was utilizing. Changes in feeding sessions were also noted. According to Heaney and Thorington's (1978) definition, a session is a squirrel feeding on one food until it either left the field of vision or began to feed on a different food. Generally we spent more than ten minutes observing each squirrel.

To characterize position and distribution of each squirrel nest we measured the height and diameter of the tree, height of the nest, and also identified the species of the nest tree.

In addition to sight observations, all calls heard in route were recorded for possible identification of breeding periods and future population estimates.

## RESULTS

### Grouping and General Behavior

During 57 observation nights 165 sightings of *P. Petaurista* and 131 of *P. alborufus* were made (a sighting being one or more squirrels in a tree). Sightings of the former included 155 singles, 7 pairs, and 3 triplets while those of the latter included 124 singles, 6 pairs, and 1 triplet. Members of different species were never seen less than 30 m apart from each other. We did not observe any aggressive encounter between either inter- or intraspecific individuals. Most squirrels were either feeding or resting. While feeding, both species would sit on a branch reaching for food with their forelegs. Usually they would not consume all the food picked, consequently, remains fell on the ground where it was often noticeable. More than 70 per cent of the sighted squirrels were more than 10 m (Table 1), and none were less than 3 m above the ground.

When two or more squirrels were seen at the same time, three types of behavior were recognized: 1) feeding, such as when the animals were actively reaching for food or chewing; 2) mating, including precopulatory movements and calling to each other and mounting; 3) following, characterized as an adult accompanied by one or two apparent offspring. Feeding was the most common behavior noted for both species in all seasons. Mating behavior of *P. petaurista* was observed in December, June and January. Mating of *P. alborufus* was only seen once in June. Young *P. petaurista* were seen following various adults in March, July,

TABLE 1  
Height distribution of observed *Petaurista* during the study

Species and Season	Height above ground (m)					Total
	0-5	6-10	11-15	16-20	20-up	
<i>P. petaurista</i>						
Fall	1	15	16	7	3	42
Winter	7	6	17	13	1	44
Spring	10	9	26	12	5	62
Summer	2	2	18	8	0	30
Total	20	32	77	40	9	178
Per cent of observation	(11%)	(18%)	(43%)	(23%)	(5%)	
<i>P. alborufus</i>						
Fall	0	7	19	16	7	49
Winter	0	2	12	8	6	28
Spring	1	2	12	21	3	39
Summer	1	5	9	4	4	23
Total	2	16	52	49	20	139
Per cent of observations	(1%)	(12%)	(37%)	(35%)	(14%)	

August, and November. Similar behavior of *P. alborufus* was noted in March only.

#### Calling

Both species of giant flying squirrels of this study have distinct vocalizations that can be distinguished by human ears. *P. petaurista* emits low pitched sounds whereas *P. alborufus* makes high pitched whistles. Counts revealed that *P. alborufus* called more frequently than *P. petaurista* (1165 vs. 159 respectively). Calls of *P. alborufus* were mostly heard from within the natural hardwood forest while calls of *P. petaurista* were equally audible in conifer plantations and the hardwoods (Table 2). This pattern is similar to the numbers of each species sighted in the

two forest types. No correlation ( $p > 0.05$ ) was found between the call count and total squirrels observed each month for either species.

However, squirrel were rarely seen while making calls. The few occasions that we witnessed the calling may provide some clues as to the function of calls. In March 1982 a *P. alborufus* called continuously from a tree cavity 25 m above ground when 2 congeners were within 25 m apart. We think that this might have been a territorial call. In late November 1982 we noticed our yearling female *P. petaurista*, which was raised by hand since the previous March and was being held in a large wire cage within the Chitou study area, called and attracted a conspecific squirrel which moved around on

TABLE 2  
Use of forest types by *Petaurista petaurista* and *P. alborufus* according to animals observed and calls heard, October 1981 to May 1983

Species	No. animals observed		No. calls heard	
	Conifer Plantations	Natural Hardwoods	Conifer Plantations	Natural Hardwoods
<i>P. petaurista</i>	75 (42%)	103 (58%)	77 (48%)	82 (52%)
<i>P. alborufus</i>	23 (17%)	116 (83%)	288 (25%)	877 (75%)

TABLE 3  
Den tree characteristics of *Petaurista Petaurista* and *P. alborufus* found in Chitou. When  $n > 1$  only mean was shown

Species	<i>n</i>	Tree height (m)	Nest height (m)	Diameter breast (cm)
<i>P. petaurista</i>				
<i>Beilschmiedia erythrophloia</i>	5	24.8	13.8	48.2
<i>Persea japonica</i>	3	25.0	17.0	30.7
<i>Machilus japonica</i>	3	24.0	17.0	52.0
<i>Pasania kawakamii</i>	2	22.5	11.0	38.0
<i>Litsea acuminata</i>	1	30.0	11.0	30.0
<i>Cyclobalanopsis glauca</i>	1	23.0	17.0	45.0
<i>Schefflera octophylla</i>	1	13.0	8.0	25.0
<i>P. alborufus</i>				
<i>Beilschmiedia erythrophloia</i>	1	20.0	25.0	60.0
<i>Machilus japonica</i>	1	30.0	25.0	80.0

the roof of the cage and in surrounding trees apparently attempting to located an entrance to the cage. On another occasion while we were observing three *P. petaurista* (one adult and two young) feeding on buds in a conifer, we heard the adult emitting a "ho-ho" sound that might be used as parent-offspring bonding.

**Nests**

From records of the local hunter assisting us in the field and from our observations, we located 16 tree cavities used by *P. petaurista* and 2 by *P. alborufus* (Table 3). The latter cavities were higher on the mountain (above 1400 m), whereas the cavities used by *P. petaurista* were sparsely distributed within the 1100-1400 m zone. All but one species of trees (*Schefflera octophylla*) in which nest cavities were found belong to Lauraceae or Fagaceae which are dominant in Chitou forest. Certain cavities showed gnawed marks which might be a sign of ownership. The last time we saw a squirrel looking out from a cavity was in March 1982 when two adult *P. alborufus* were feeding adjacent to it. In addition to natural cavities, we found two leaf dreys of *P. petaurista* (one in August 1982, the other in March 1983) each of which held a young squirrel. The dreys, hidden in

high branches of conifer trees (*Cryptomeria japonica* and *Chamaecyparis formosensis*) were blown down by strong wind. We did not find any evidence of *P. alborufus* using dreys as nests in Chitou.

**Habitat Use**

Both species of squirrels showed strong preference for the hardwood forest though this habitat type included only 26 per cent of our transects. *P. petaurista* was more evenly distributed in the study area than was *P. alborufus*; 58 per cent of *P. petaurista* vs. 83 per cent *P. alborufus* sightings were in hardwoods (Table 2). The elevation where flying squirrels were sighted also differed; *P. alborufus* were found at higher altitudes than *P. petaurista*. We detected no seasonal changes in use of the habitat types by either species ( $p > 0.05$ ).

Although both squirrel species were observed in some of the same tree species (12 species), they used them (other than for nesting) in different frequency (Table 4). *P. petaurista* were in 16 hardwoods and 4 conifer species whereas *P. alborufus* were in 15 hardwoods and 2 conifers.

Forest vegetation was assigned to life forms according to height so that we could further identify possible partitioning of the

TABLE 4  
Frequency and percentage of tree species in which *Petaurista*  
were sighted, October 1981 to May 1983

Tree species	Plant <sup>1</sup> life form	<i>P. petaurista</i>		<i>P. alborufus</i>	
		<i>n</i>	Percent	<i>n</i>	Percent
Broad-leaf Hardwood					
<i>Machilus japonica</i>	MM	40	22.5	45	32.4
<i>Pasania kawakamii</i>	MM	22	12.4	25	18.0
<i>Beilschmiedia erythrophloia</i>	MM	15	8.4	7	5.0
<i>Turpinia formosana</i>	MM	5	2.8	7	5.0
<i>Gordonia axillaris</i>	MM	4	2.2	5	3.6
<i>Cyclogalanopsis glauca</i>	MM	4	2.2	1	0.7
<i>Listea acuminta</i>	MM	2	1.1	3	2.2
<i>Elaeocarpus sylvestris</i>	MM	1	0.6	6	4.3
<i>Morus australis</i>	M	10	5.6	2	1.4
<i>Debregeasia edulis</i>	N	10	5.6	1	0.7
<i>Lagerstroemia subcostata</i>	MM	4	2.2		
<i>Ficus erecta</i>	M	5	2.8		
<i>Hibiscus taiwanensis</i>	M	3	1.7		
<i>Sinocalamus latiflorus</i>	M	2	1.1		
<i>Paulowia fortunei</i>	M	1	0.6		
<i>Acer albopurpurascens</i>	M	1	0.6		
<i>Pasania nantoensis</i>	MM			7	5.0
<i>Trochodendron aralioides</i>	MM			6	4.3
<i>Lithocarpus amygdalifolius</i>	MM			3	2.2
<i>Schefflera octophylla</i>	MM			2	1.4
<i>Villebrunea pedunculata</i>	N			3	2.2
Coniferous tree					
<i>Cryptomeria japonica</i>	MM	30	16.9	8	5.8
<i>Cunninghamia konishii</i>	MM	4	2.2	8	5.8
<i>Pinus morrisonicola</i>	MM	10	5.6		
<i>Chamaecyparis formosensis</i>	MM	5	2.8		
Total		178		139	

1. MM=megameso-phanerophyte; M=micro-phanerophyte; N=nanophanerophyte.

habitat: 1) megameso-phanerophytes (MM), canopy trees >12 m tall; 2) micro-phanerophytes (M), understory trees <12 m; 3) nano-phanerophytes (N), compose mostly of shrub species up to 3 m in height. Twenty-five species of trees were utilized by the squirrels (Table 4), but only the 12 species of trees or shrubs were used by both squirrels 10 of which are in the MM zone. However, difference in use of the vertical zones was evident. Five of the 6 hardwood tree species in which only *P. petaurista* were found are in the lower vegetation forms. The opposites was apparent

for *P. alborufus* as only one of the five species used exclusively by this squirrel was not in the canopy.

Both species of squirrels show a high degree of arboreality. The spatial distribution of squirrels sighted (Table 1) was significantly different ( $\chi^2 = 25.57, p < 0.01$ ) though an extensive overlap was found. We did not observe any squirrels on the ground. Both species were most commonly seen 11-20 m above ground (66 per cent *P. petaurista* vs. 72 per cent *P. alborufus*). More *P. petaurista* (29 per cent) than *P. alborufus* (13 per cent)

were below 10 m. The reverse was true at the higher levels as 14 per cent *P. alborufus* and 5 per cent *P. petaurista* were above 20 m.

**Food Habits**

Both squirrel species utilized a variety of foods but *P. petaurista* fed on more species(16) than *P. alborufus*(11). *Mucuna macrocarpa* and *Pasania kawakamii* are the major plants used by *P. petaurista* in Chitou; these two species

comprised 43 per cent of the total usage. Comparatively, *P. alborufus* fed mostly (74 per cent) on *Pasania kawakamii*, *Machilus japonica*, and *Cunninghamia konishii*, trees which are abundant on the study area (Table 5).

Seasonal feeding trends were noted for both squirrel species. *P. petaurista* consumed leaves of *Mucuna macrocarpa*, acorns of *Pasania kawakamii*, and seeds of *Cunninghamia konishii* and *Chamaecyparis formosensis* in fall.

TABLE 5  
Observed seasonal variation of feeding sessions by *Petaurista petaurista* and *P. alborufus*, October 1981 to May 1983

Food species	Feeding sessions				Total	Food <sup>1</sup> type
	Fall	Winter	Spring	Summer		
Food of <i>P. petaurista</i>						
<i>Mucuna macrocarpa</i>	9	19	3	1	31 (29%)	L
<i>Pasania kawakamii</i>	4	8	1	2	15 (14%)	L, Fr
<i>Pinus morrisonicola</i>	1			9	10 ( 9%)	Bu
<i>Debregeasia edulis</i>		3	6	1	10 ( 9%)	L, Fr
<i>Morus australis</i>		3	4		7 ( 7%)	L, Fr
<i>Cunninghamia konishii</i>	3			3	6 ( 6%)	S
<i>Gordonia axillaris</i>	2	2			4 ( 4%)	L, FL
<i>Ficus erecta</i>	1		2	1	4 ( 4%)	L, Fr
<i>Machilus japonica</i>	3		1		4 ( 4%)	L
<i>Turpinia formosana</i>	3				3 ( 3%)	L
<i>Chamaecyparis formosensis</i>	3				3 ( 3%)	S
<i>Cyclogalanopsis glauca</i>		1	2		3 ( 3%)	L
<i>Hibiscus taiwanensis</i>		2			2 ( 2%)	Fl
<i>Cryptomeria japonica</i>	2				2 ( 2%)	Ba
<i>Ficus pumila</i>	1				1 ( 1%)	Fr
<i>Paulowia fortunei</i>			1		1 ( 1%)	Fl
Total	32	37	20	17	106	
Food of <i>P. alborufus</i>						
<i>Pasania kawakamii</i>	8	8	5	8	29 (38%)	L, Fr
<i>Machilus japonica</i>	12	2	2	2	18 (23%)	L
<i>Cunninghamia konishii</i>	6	1		3	10 (13%)	S
<i>Elaeocarpus sylvestris</i>		3	2	1	6 ( 8%)	L
<i>Trochodendron aralioides</i>			4		4 ( 5%)	L
<i>Mucuna macrocarpa</i>	1			2	3 ( 4%)	L
<i>Gordonia axillaris</i>	1	1		1	3 ( 4%)	L, Fl
<i>Turpinia formosana</i>	1				1 ( 1%)	L
<i>Cyclogalanopsis glauca</i>		1			1 ( 1%)	L
<i>Pasania nantoensis</i>		1			1 ( 1%)	L
<i>Lithocarpus amygdalifolius</i>				1	1 ( 1%)	L
Total	29	17	13	18	77	

1. L=leaves; Fr=fruits; Bu=buds; S=seeds; Fl=flowers; Ba=bark.

After these food supplies dwindled, *P. petaurista* fed on new leaves and fruits of *Debregeasia edulis* and *Morus australis* in winter until fruits of *Ficus erecta* became available in spring. In summer the squirrel was seen eating buds of *Pinus morrisonicola*. *P. alborufus* ate almost the same food as *P. petaurista* during fall and winter but also utilized leaves of *Elaeocarpus sylvestris* in winter. In spring they exploited leaves of *Trochodendron aralioides*.

In November 1982 we saw two *P. petaurista* feed on the bark of *Cryptomeria* trees in a 30-year-old stand outside our study area. We collected fragments of bark dropped by the squirrels and noted that both the inner bark and cambium were eaten. The squirrels were in the same trees for four consecutive nights then they were collected for study. One stomach was dissected and we found 79 per cent of its content was inner bark. The remaining 21 per cent was leaves.

The composition of the overall diet of *P. petaurista* and *P. alborufus* in respect to food types (Table 6) shows that both squirrel species eat a large amount of leaves but the degree of usage of each food type was different. Our data reveal that *P. petaurista* exploits food such as buds and bark which *P. alborufus* does not. Apparently *P. alborufus* depends on more limited food resources than does its congener.

TABLE 6  
Number of feeding sessions observed from October 1981 to May 1983 on general categories of food for two species of *Petaurista*

Food type	<i>P. petaurista</i>	<i>P. alborufus</i>
Leaves	65 (61%)	55 (71%)
Seeds	9 (9%)	11 (14%)
Fruits	8 (8%)	9 (12%)
Flowers	12 (11%)	2 (3%)
Buds	10 (9%)	0
Barks	2 (2%)	0
Total feeding sessions	106	77

## DISCUSSION

On our study area *P. petaurista* inhabits both the natural hardwood forest and conifer plantation nearly equally while *P. alborufus* is found almost exclusively in hardwoods. Such distribution reflects the ecological needs of both species as well as their adaptation to the changing habitat in Taiwan. Animals such as flying squirrels living at lower elevations (below 1500 m) face selection pressure when their habitat is destroyed by developmental activities of humans. Much of the original hardwood forest which *P. petaurista* formerly occupied has either been destroyed or replaced by monoculture conifer plantations mostly at mid to lower elevations. This squirrel species has adapted successfully to the new artificial habitat. Since *P. alborufus* normally live at higher elevations where forest change was less severe, they were not so adversely affected. In other geographical areas *Petaurista* species have responded to human induced changes, even to the point where existing species have been replaced by others. For example, in Malaysia *P. petaurista* reportedly replaces *P. elegans* where the primary forests are cut and *P. elegans* replaces *P. petaurista* at high elevations as well as in deep forests (Muul and Lim, 1978). Sympatry occurs when one congener exploits resources of the common habitat divergently enough to avoid competition by the other (MacKinnon, 1978b). In our observations the coexisting *Petaurista* squirrels show divergences in habitat usage, spatial distribution, and dietary specializations. This is similar to diurnal squirrels in Southeast Asia according to MacKinnon (1978a), and Whitten (1981), in Africa as reported by Emmons (1980), and in Neotropical Panama (Glanz, 1984).

The vocal repertoire of each squirrel species is distinctly different, therefore calls can be used as an indicator of the presence of either species. Since most of the flying squirrels of our study were solitary, vocalization might be the communication signals among inter- and intra-specific individuals



during nighttime. These calls seem to function at least for indicating territories and for mating in *P. alborufus* and for mating and parent-offspring bonding in *P. petaurista*. *P. alborufus* calls more frequently than *P. petaurista*; this may relate to their habitat partitioning. The calls may be a means whereby the two species avoid direct competition with one another, as Smith (1981) pointed out for other animals, and combined with other behavior and feeding habits, allows both to partition themselves temporally and spatially in their common habitat. Judging from the high density of both species in the hardwood forest (1.6 squirrels sighted per kilometer of trails for *P. petaurista* and 1.8 for *P. alborufus*; 20-month mean of this study), it would be advantageous for *P. alborufus* to call frequently to defend its resources against *P. petaurista*. Further study is needed to test these hypotheses.

Tree cavities can provide flying squirrels with desirable breeding and hiding sites during daytime (Mull, 1968), thus the quantity of suitable cavity trees may be a factor limiting distribution and population density of flying squirrels (MacKinnon, 1978a). Muul (1968), in his study of American flying squirrels, proposed that the southward spread of *Glaucomys sabrinus* is prevented by competitive interaction with *G. volans* because the latter breeds earlier and would use up the limited number of tree cavities. We discovered that both petauristids in Taiwan use tree cavities for nests and that *P. petaurista* builds leaf dreys in conifer plantations when natural cavities are unavailable to them. This behavior enables *P. petaurista* to be superior in adapting to the new artificial habitat and also enable them to exploit the conifer plantations in a sympatric area when population of their congener in the hardwoods are at carrying capacity.

Both *Petaurista* species in our study are strictly arboreal but with different degrees of usage of spatial distribution and plant life form. *P. petaurista* uses more micro-phanero-

phyte and nano-phanerophyte than *P. alborufus* does for resting and feeding. These differences may partly because of the difference in body sizes. Adult *P. petaurista* were slightly smaller in average body weight than *P. alborufus* (1285 g vs. 1479 g, where  $n=46$  for *P. petaurista* and  $n=45$  for *P. alborufus*, unpublished data). Efficiency of movement in a tree is seriously impaired when an arboreal folivorous mammal becomes too large (Eisenberg, 1978). If the body weight of an arboreal species becomes too great, access to the more slender twigs could not occur (Clutton-Brock and Heavey, 1983).

Seasonal abundance of food in different tree layers influenced where the squirrels would be. The descent by *P. petaurista* to the 0-5 m height in late winter and spring was likely a response to the abundant new leaves and fruits on lower trees and shrubs. Likewise, the shift to upper canopy trees (especially *Machilus japonica* and *Trochodendron aralioides*) of *P. alborufus* during the same seasons was due to the new food supply.

Our data on food habits of both *Petaurista* species is based only on night observations therefore might be somewhat misleading without analysis of stomach contents (Emmons, 1980). However, our evidence of squirrels feeding in certain species of trees (including differences in usage of tree parts) suggests preferences of the two squirrels are different. We have documented that *P. petaurista* feed on bark of *Cryptomeria* trees. Barks similar to that collected in November 1982 when two *P. petaurista* were observed stripping were found under other stripped *Cryptomeria* in February-April 1983 (Lee, 1983). Bark has been reported as food of many species of tree squirrels, e.g. *Sciurus variegatoides*, *S. granatensis* (Glanz, 1984; Heaney and Thorington, 1978), *S. aureogaster* (Brown and McGuire, 1974), *Paraxerus cepapi* (Viljon, 1977), *Sundasciurus tenuis*, *Callosciurus prevostii*, *C. motatus*, *C. melanogaster* (MacKinnon, 1978a; Whitten, 1981), and *C. erythraeus*

(Chou *et al.*, 1985; Lin and Lee, 1985). Since *P. petaurista* has adapted to living in secondary growth forests and plantations, it is not surprising that they utilize tender underbark of the softwood trees. We did not find any evidence that *P. alborufus* debark the conifer. In allopatric areas where this squirrel species is found and where plantations of exotic conifer trees exist, it is possible that the squirrels will damage some trees.

An animal's niche includes many factors such as habitat preferences, food habits, activity patterns, and reproductive strategy. In our study, focus was directed to the first two relating to both species of giant flying squirrels in the sympatric area. We conclude from this study that *P. petaurista* can use a broader resource and, conversely, that *P. alborufus* is more limited to the natural hardwood forest. However, our findings are only a subset of the n-dimensional niche of both species. To understand ecological separation of these two petauristids, activity patterns, spatial movements, and reproduction should be investigated.

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## 臺灣兩種同地共存鼯鼠 (*Petaurista*) 之生態學研究

李培芬 蒲唐納 林曜松

本研究之目的在於瞭解臺灣產大赤鼯鼠 (*Petaurista petaurista*) 和白面鼯鼠 (*P. alborufus*) 之基本生態和行爲，判定其是否會爲害林木，並比較這兩種鼯鼠在棲所和食物需求上的差異。從 1981 年 10 月至 1983 年 5 月在溪頭觀察鼯鼠，觀察時間集中於 1800-2400 時。

大赤鼯鼠和白面鼯鼠在外覓食和活動時，似能忍受對方之存在。兩種鼯鼠大都單獨活動，但偶亦有成對或三隻以上同時出現的情形。當兩隻以上之鼯鼠一起出現時，曾發現其有交配、攝食和跟隨等三種行爲。大赤鼯鼠之交配行爲發生於 1, 6, 12 月，而白面鼯鼠之交配行爲可於 6 月發現。

兩種鼯鼠均有其獨特的叫聲，由叫聲數顯示，白面鼯鼠使用聲音之頻度要高於大赤鼯鼠。鼯鼠的叫聲大都是在樹上活動時所發出，但偶亦有在樹洞內使用叫聲之情況。

在溪頭共發現 18 個樹洞被鼯鼠當作巢穴，樹洞所在之樹種大都屬於樟科和殼斗科。另在針葉造林地內發現兩個由大赤鼯鼠所築之樹葉巢。

兩種鼯鼠均以原始林爲主要棲所。白面鼯鼠比大赤鼯鼠更常出現於高海拔地區，但兩種鼯鼠活動之海拔高度有重疊。牠們在攝食和休息時，亦會利用相同的樹種，大赤鼯鼠常在較低的植物層內活動，而白面鼯鼠則傾向於利用較高的樹冠層。由於兩種鼯鼠之食物呈季節性變化，因而影響了牠們在樹上出現的位置。觀察中曾發現兩隻大赤鼯鼠啃咬柳杉 (*Cryptomeria japonica*)，其胃內含大量的樹皮內層組織。