

Temporal and spatial patterns of seed dispersal of *Musa acuminata* by *Cynopterus sphinx*

ZHANHUI TANG^{1,2}, LIANXI SHENG^{1,6}, XUNFENG MA¹, MIN CAO², STUART PARSONS³, JIE MA⁴,
and SHUYI ZHANG⁵

¹Department of Environmental Science and Engineering, North East Normal University, Changchun 130024, China

²Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China

³School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

⁴Department of Physiological Science, University of California, Los Angeles 90095, USA

⁵School of Life Science, East China Normal University, Shanghai 600026, China

⁶Corresponding author: E-mail: Shenglx@nenu.edu.cn

The foraging behavior of greater short-nosed fruit bats (*Cynopterus sphinx*) on wild banana (*Musa acuminata*) and subsequent dispersal of seeds were studied in the Tropical Rainforest Conservation Area, Xishuangbanna Tropical Botanical Garden, Yunnan province, by direct observation of marked fruits, mist netting, and seed collection. The mean number (\pm SE) of individual *C. sphinx* captured by mist net were $2.2 \pm 0.33/\text{day}$ and $1.4 \pm 0.32/\text{day}$ in the rainy season (September to October) and dry season (November to December), respectively; the difference was not significant. The number of seed pellets expelled was $9.0 \pm 1.12/\text{day}$ and $7.2 \pm 1.37/\text{day}$ in the rainy and dry seasons respectively; again the difference was not significant. The removal curves for marked fruit were similar for 10 focal trees. Fruits were consumed heavily within two weeks after ripening and all the marked fruit were removed within one month. The difference in seed dispersal was significant between different feeding roosts indicating that patterns of seed dispersal may not be uniform. We found the seeds of *M. acuminata* can be dispersed by *C. sphinx* to a distance of about 200 m, and *C. sphinx* can be considered as an effective seed disperser of *M. acuminata*.

Key words: *Cynopterus sphinx*, *Musa acuminata*, feeding, seed dispersal, China

INTRODUCTION

Frugivorous bats in forests feed mostly on fruits and nectar (Fleming, 1993; Banack, 1998; Tan *et al.*, 1998). Previous studies have showed that fruit-eating bats play an important role in seed dispersal (Heithaus *et al.*, 1975; Fleming, 1981; Fleming and Heithaus, 1981; Cox *et al.*, 1991; Estrada *et al.*, 1993) and interchange of seeds among different forest patches, a process necessary for recruitment in

fragmented and/or disturbed habitats (Galletti and Morellato, 1994; Whittaker and Jones, 1994).

Even though frugivorous bats have attracted the attention of researchers for many years, little is known about their feeding behavior; when and where the bats disperse seeds may affect germination or seedling survival (Corlett, 1998; Godínez-Alvarez and Valiente-Banuet, 2000; Elangovan *et al.*, 2001). For example, the greater short-nosed fruit bat, *Cynopterus sphinx* (body

mass 40–70 g), is common in Xishuangbanna Tropical Botanical Garden, Yunnan province yet no study has documented its foraging behavior in this area. Wild bananas, *Musa acuminata*, are very common in the local area. Seeds germinate easily after dispersal and the seedling can produce fruit after a few years. This species has been identified as important for regrowth of modified forests (Shi *et al.*, 2002).

Cynopterus sphinx feeds heavily on the bananas of *M. acuminata* in Xishuangbanna and can carry the bananas several hundred meters before they consume them. However, little is known about when (time of night or season) they feed on bananas or where they are taken for consumption. Such information has important implications for the maintenance, spread and regrowth of wild banana forests. The aims of this study were to investigate the temporal and spatial characteristics of the feeding behavior of *C. sphinx*, and to investigate the role of this species as a disperser of *M. acuminata* seeds.

MATERIALS AND METHODS

Study Area

This study was carried out in a protected area of seasonal rainforest ($21^{\circ}55'N$, $101^{\circ}16'E$, and 550 m in altitude) within Xishuangbanna Tropical Botanical Garden (XTBG), Yunnan province, China. The area encompasses 90 hectares occupied mostly by *Pometia tomentosa* and *Terminalia myriocarpa* (Zhang and Cao, 1995). A small river runs through the garden and a wild banana forest (*M. acuminata*) of around 2,000 m² lies on its northern side. Average annual rainfall is approximately 1,500 mm, with 80% falling in the wet season (May–October) and 20% in the dry season (November–April). The average annual temperature is 22°C (Cao and Zhang, 1997).

Individual Captures

Bats were captured using five mist nets (10 × 2.5 m each) set up approximately 30–50 m from the boundary of the wild banana forest. We checked

the mist nets every 30 minutes from 19:00 to 24:00. Captured bats were released after a copper ring was fitted around the neck. Captures were made over 400 net-hours.

Seed Collection and Seedling Investigation

To investigate quantity of seed dispersed to different sites and in different seasons, we searched systematically for feeding roosts around the wild banana forest and located four. The directions to and characteristics of the roosts are: (i) Feeding roost 1 — 40 m south of the boundary of the wild banana forest. The area around the roost was well protected and the vegetation was dominated by *Carallia lanceaefolia*, *Caryota urens*, *Cinnamomum mollifolium*, *Knema cinerea* and *Oroxylum indicum*. There was almost no disturbance around the area and vegetative cover was more than 95%; (ii) Feeding roost 2 — 150 m west of the boundary of the wild banana forest where the vegetative cover was 70%. The following plants dominated the area: *Mayodendron igneum*, *Syzygium oblatum*, *Erythrina indica* and *Caryodaphnopsis tonkinensis*. A brook goes through this area and little disturbance was evident; (iii) Feeding roost 3 — 200 m southwest of the boundary of the wild banana forest, near a narrow trail. Vegetative cover was about 45% and consisted mainly of *Mesua ferrea* and *Syzygium szemaoense*. Herbaceous plants were replaced by economic plants such as *Semnostachya menglaensis* and *Amomum* spp.; (iv) Feeding roost 4 — 50 m south of the boundary of the wild banana forest, 200 m from feeding roost 1. Vegetative cover was 50% and there was some disturbance from the activity of tourists. The vegetation consisted mainly of *Millettia leptobotrys*, *Erythrina stricta*, *Anthocephalus chinensis* and *Mesua ferrea*.

We recorded the numbers and position of seed pellets spat out by the bats found under the four feeding roosts 10 times every month (2–3 times each week) at 06:00 from September to December 2004. To collect seed pellets we placed three traps (1 × 1 m each) made from plastic cloth under the feeding roosts. To prevent consumption or removal of pellets by terrestrial vertebrates traps were set 1 m above the ground.

We investigated the distribution of seedling and mature *M. acuminata* within a radius of 10 m around each feeding roost. As a control, we also sampled within a 10 m radius of 4 randomly selected non-feeding roost trees. Non-feeding roost trees were located at least 50 m away from each of the four feeding roosts and the habitat around them was the same as their corresponding feeding roosts.

Estimating Fruit Consumption

To quantify the number of bananas removed by bats, we investigated 10 infructescences in each of 10 different wild banana trees from 1 May to 8 July, 2005. Iron sheeting (height about 1.5 m) was used to enclose the focal trees to prevent rodents from consuming the bananas when they began to ripen. Thus, only bats and birds could forage on the fruits. During this study we did not observe bananas being consumed by bats during the day. Therefore, we assumed the fruit removed during the night was due to bats, and during the day was due to birds. We checked the number of bananas removed from the infructescences daily at 07:00 and 18:00 until all were consumed.

Statistical Analysis

We recorded the numbers of individuals captured every 1 h. The data from September and October were combined and categorized as rainy season and those from November and December as dry season. Quantity of seed pellets dispersed and numbers of individual bats captured were then compared across seasons. One-sample Kolmogorov-Smirnov tests were used to determine whether data were normally distributed and Levene's tests were used to confirm homogeneity of variances. One-way ANOVA was used to determine the effect of feeding roost on quantity of seeds dispersed. Two independent-sample Kolmogorov-Smirnov tests were employed to determine whether there were differences in quantity of seeds dispersed between seasons by *C. sphinx* and numbers of individual bats captured between seasons. Differences were considered significant if $P < 0.05$. Summary statistics presented in the text are means ± 1 SE with sample sizes given in parentheses unless otherwise noted.

RESULTS

Captures

Between September and December 2004, 36 individuals of *C. sphinx* were captured and no bats were recaptured. The mean number of individuals captured between 19:00 and 20:00 was 0.5 ± 0.13 , ($n = 16$), followed by 0.4 ± 0.13 ($n = 16$) between 20:00 and 21:00, and 0.4 ± 0.16 ($n = 16$) between 21:00 and 22:00. The number then increased to 0.7 ± 0.22 ($n = 16$)

between 22:00 and 23:00 and subsequently decreased to 0.3 ± 0.11 ($n = 16$) between 23:00 and 00:00.

In the rainy and dry seasons, captures averaged 2.2 ± 0.33 ($n = 8$) and 1.4 ± 0.32 ($n = 8$) individuals per day, respectively. There was no significantly difference between these two seasons ($Z = 0.949$, $P > 0.05$).

Removal Rate of Fruits

Bats removed most bananas within two weeks of ripening, and all were removed within one month. On average, 1.8 ± 0.12 ($n = 10$) bananas were removed per tree each day (Fig. 1). Bats removed most of the fruits of the 10 banana trees observed during night ($79.1 \pm 2.76\%$) with the remainder removed by birds during the day ($20.9 \pm 2.76\%$).

Temporal Pattern of Seed Dispersal

Cynopterus sphinx fed on the pulp of fruit, with seeds spat out in the form of seed pellets. The average number of seeds in a pellet was 2.9 ± 0.24 ($n = 53$). In rainy and dry seasons, there were on average 9.0 ± 1.12 and 7.2 ± 1.37 seed pellets (in both cases $n = 20$) collected across the four roosts per day, and no significant difference was found between the two seasons ($Z = 0.632$, $P > 0.05$).

Spatial Pattern of Seed Dispersal

There were significant differences in the number of seed pellets between the four feeding roost ($F = 4.6$, $d.f. = 3$, $P \leq 0.05$). Feeding roost 2 received the most seed pellets (3.5 ± 0.64) followed by feeding roost 3 (2.3 ± 0.53), feeding roots 4 (1.2 ± 0.47) and feeding roost 1 (1.1 ± 0.40 ; for all cases $n = 40$).

The average distance of feeding roosts from the edge of the *M. acuminata* forest

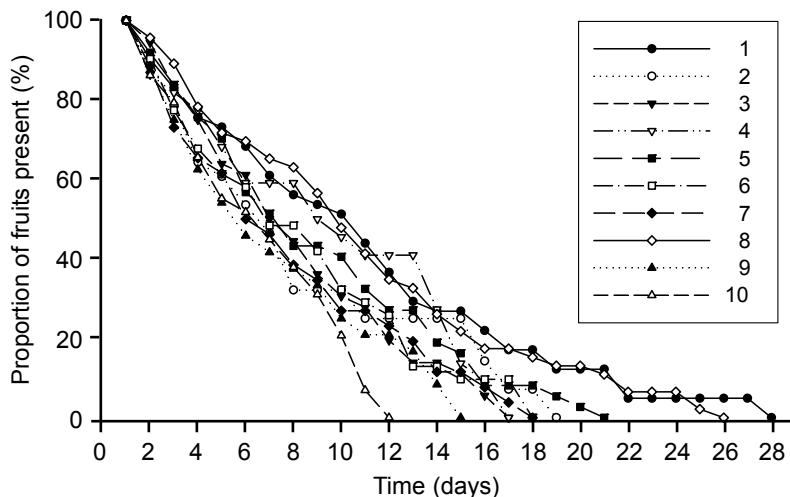


FIG. 1. Remove curves for marked fruits of 10 *M. acuminata* individuals

was 84.3 ± 24.30 m ($n = 4$). Assuming fruits could have been taken from non-focal trees further inside the *M. acuminata* forest, the actual distance of fruit transportation was likely further. In our study, the furthest feeding roost was 169.0 m from boundary of the banana forest, so the distance of seeds carried can be further than this.

Seedlings Distribution Around Feeding Roost

We found two *M. acuminata* seedlings around feeding roost 1 and one mature tree around roost 4. No seedlings or adults were found around feeding roosts 2 or 3. There were no seedlings or mature trees around the four non-roost control trees.

DISCUSSION

Musa acuminata produces fruit throughout the year. Judging from seed pellets and pericarps discarded by bats, these animals feed only on ripe fruit. However, rodents feed on unripe fruit of *M. acuminata* in this area (Z. Tang, personal observation). It is probable that the preference for ripe fruit by

bats optimizes their foraging strategy, as levels of carbohydrate and water are higher in ripe fruit (Herrera, 1987; Corlett, 1996). Carrying ripe or unripe fruit from parent trees to feeding roost requires equivalent energy as they are similar in size, but ripe fruit better meets the carbohydrate and water requirements of the bats (Ruby *et al.*, 2000). Moreover, it was more difficult for bats to pluck unripe fruit because its stalk is more firmly inserted into the parent plant, resulting in greater energy expended and time spent exposed to predators during its removal. In addition, unlike dispersers such as rodents that consume fruit on the parent trees (Ma *et al.*, 2003; Xiao *et al.*, 2004), *C. sphinx* regularly carried the fruit to feeding roosts where they were consumed. In Xishuangbanna, another fruit bat, *Rousettus leschenaulti*, coexists with *C. sphinx*. However, we captured no *R. leschenaulti* around the banana forest during our study.

Our previous observations (Tang *et al.*, 2005) and captures of bats indicate foraging activity of *C. sphinx* on *M. acuminata* peaks first before 20:00, and then at 22:30. Similarly, two peaks of nightly activity were observed when *C. sphinx* fed on *Terminalia*

catappa and *Vitis vinifera* (Elangovan *et al.*, 1999; Srinivasulu and Srinivasulu, 2002). However, the timing of this peak of nightly activity may vary according to plant species. For example, an activity peak occurred at 21:00 when *C. sphinx* fed on *Annona squamosa*, *Polyalthia pendula* and *P. longifolia*, at 22:00 when they fed on *Coccinia indica* and at 23:00 when they fed in *Achras sapota* (Elangovan *et al.*, 1999). A peak in visits to flowers of *Musa paradisiaca* by *C. sphinx* occurred at 20:00 and at 21:00 for flowers of *Bassia latifolia* (Elangovan *et al.*, 2000). Fleming (1988) suggested that patterns of nightly activity of some neotropical species is influenced by either food quality or quantity. Singaravelan and Marimuthu (2006) reported that the total number of *C. sphinx* visited to *Muntingia calabura* was significantly greater than to seven other fruit species, including commercial fruits. The results reported for *C. sphinx* when feeding on different species also indicated that the abundance of fruit influences the foraging activity of these bats (Elangovan *et al.*, 1999). In our study, the patterns of foraging activity of *C. sphinx* may be influenced by quantity of *M. acuminata* fruits which are only available in small numbers on one night. Foraging activity begins early in the night presumably making it possible for bats to exploit available resources while avoiding interference competition from conspecifics.

We found no significant difference in the number of seeds dispersed between the rainy and dry seasons. *Musa acuminata* is possibly a stable food resource for *C. sphinx*, although their diet is broad, and other dietary items probably vary in availability from season to season. The number of seed pellets collected at our four sample sites was significantly different, which indicated that *C. sphinx* exhibited a preference for specific feeding roosts. Feeding roost 3, 200 m from the southwest margin of the

M. acuminata forest, had the second highest number of seed pellets collected. The site bordered a road no more than 1 m wide, which indicates that *C. sphinx* can disperse seeds to modified habitats. Feeding roost 3 was also near a creek, which is a good habitat for seed germination and establishment of *M. acuminata* seedlings.

We did not test for difference between the distribution of seedlings and mature trees around feeding roost and control trees because of our small sample size. However, the pattern of the data indicates that seeds can germinate to seedlings under feeding roosts and that bats play an important role in the transport of seeds. Old World fruit bats (family Pteropodidae) are strong flyers, and so potent dispersers of seeds of many plant species (Fujita and Tuttle, 1991; Webb and Tidemann, 1996). The distance that seeds are dispersed depends on many biotic and/or abiotic factors such as the size of individual bats, speed of flight, pattern of activity, etc. Small species of pteropodids can fly 38 km in search of food over a whole night (Start and Marshall, 1976), and large species can range even more widely (Hall, 1983). Fruit bats can disperse seeds from several to 250 m away from parent tree (Phua and Corlett, 1989; Bhat, 1994), and our results (about 200 m) are consistent with this conclusion. Thomas (1988) studied flying foxes in Madagascar and showed that they could carry seeds up to several kilometers. There are fewer vertebrates in forests gap and degraded habitats, but fruit bats can reach these habitats easily and disperse seeds that are important to forest regeneration, especially in forest fragments (Thomas, 1982; Swystun *et al.*, 2001). *Cynopterus sphinx* is distributed widely in Xishuangbanna, and occurs in different habitat types. As a medium sized species, these bats can fly over diverse habitats and disperse large numbers of seeds including those of *M. acuminata*.

ACKNOWLEDGEMENTS

This research was financed by the Laboratory for Tropical Rain Forest Ecosystem Research and Management (TRERM), Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, the National Geographic Society (Grant No: 7806-05) and a special grant from East China Normal University to S. Y. Zhang. We thank the directors of the protected area in XTBG for permission to work in forest and the staff for their hospitality and support.

LITERATURE CITED

- BANACK, S. A. 1998. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology*, 79: 1949–1967.
- BHAT, H. R. 1994. Observations on the food and feeding behaviour of *Cynopterus sphinx* Vahl (Chiroptera, Pteropodidae) at Pune, India. *Mammalia*, 58: 363–370.
- CAO, M., and J. H. ZHANG. 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodiversity and Conservation*, 6: 995–1006.
- CORLETT, R. T. 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *Journal of Tropical Ecology*, 12: 819–833.
- CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73: 413–448.
- COX, P. A., T. ELMQVIST, E. D. PIERNON, and W. E. RAINY. 1991. Flying foxes as strong interactors in South Pacific Island ecosystems: a conservation hypothesis. *Conservation Biology*, 5: 448–454.
- ELANGOVAN, V., G. MARIMUTHU, and T. H. KUNZ. 1999. Temporal patterns of individual and group foraging behaviour in the short-nosed fruit bat, *Cynopterus sphinx*, in south India. *Journal of Tropical Ecology*, 15: 681–687.
- ELANGOVAN, V., G. MARIMUTHU, and T. H. KUNZ. 2000. Nectar feeding behavior of the short-nosed fruit bat, *Cynopterus sphinx* (Pteropodidae). *Acta Chiropterologica*, 2: 1–5.
- ELANGOVAN, V., G. MARIMUTHU, and T. H. KUNZ. 2001. Temporal patterns of resource use by the short-nosed fruit bat, *Cynopterus sphinx* (Megachiroptera: Pteropodidae). *Journal of Mammalogy*, 82: 161–165.
- ESTRADA, A., R. COATES-ESTRADA, and D. MERRITT, JR. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography*, 16: 309–318.
- FLEMING, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalgo* (Piperaceae), a bat-dispersed tropical shrub. *Oecologia*, 51: 42–46.
- FLEMING, T. H. 1988. The short-tailed fruit bat: a study in plant-animal interactions. University of Chicago Press, Chicago, Illinois, 365 pp.
- FLEMING, T. H. 1993. Plant-visiting bats. *American Scientist*, 81: 460–467.
- FLEMING, T. H., and E. R. HEITHAUS. 1981. Frugivorous bat, seed shadows, and the structure of tropical forests. *Biotropica*, 13: 45–53.
- FUJITA, M. S., and M. D. TUTTLE. 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology*, 5: 455–463.
- GALETTI, M., and L. P. C. MORELLATO. 1994. Diet of the large fruit-eating bat *Artibeus lituratus* in a forest fragment in Brasil. *Mammalia*, 58: 661–665.
- GODÍNEZ-ALVAREZ, H., and A. VALIENTE-BANUET. 2000. Fruit-feeding behavior of the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds. *Biotropica*, 32: 552–556.
- HALL, L. S. 1983. Black flying fox. Pp. 280–281, in Australian Museum: complete book of Australian mammals (R. STRAHAN, ed.). Angus and Robertson Publishers, Sydney, 530 pp.
- HEITHAUS, E. R., T. H. FLEMING, and P. A. OPLER. 1975. Patterns of foraging and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, 56: 841–854.
- HERRERA, C. M. 1987. Vertebrate dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs*, 57: 305–331.
- MA, J., Q. F. LI, R. Y. SUN, and D. Z. LIU. 2003. Composition of rodent community structure and the reproductive characteristics of the dominant species (*Apodemus peninsulae*) in the Dongling Mountain. *Acta Zoologica Sinica*, 49: 262–265.
- PHUA, P. B., and R. T. CORLETT. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). *Malayan Nature Journal*, 42: 251–256.
- RUBY, J., P. T. NATHAN, J. BALASINGH, and T. H. KUNZ. 2000. Chemical composition of fruits and leaves eaten by the short-nosed fruit bat *Cynopterus sphinx*. *Journal of Chemical Ecology*, 26: 2825–2841.
- SHI, J. P., G. M. ZHANG, K. J. BAI, and J. W. TANG. 2002. The effects of human disturbance on biomass and plant diversity of *Musa acuminata*

- community. Journal of Wuhan Botanical Research, 20: 119–123.
- SINGARAVELAN, N., and G. MARIMUTHU. 2006. *Muntingia calabura* — an attractive food plant of *Cynopterus sphinx* — deserves planting to lessen orchard damage. Acta Chiropterologica, 8: 239–245.
- SRINIVASULU, C., and B. SRINIVASULU. 2002. Greater short-nosed fruit bat (*Cynopterus sphinx*) foraging and damage in vineyards in India. Acta Chiropterologica, 4: 167–171.
- START, A. N., and A. G. MARSHALL. 1976. Nectarivorous bats as pollinators of trees in West Malaysia. Pp. 141–150, in Tropical trees: variation, breeding and conservation (J. BURLEY and B. T. STYLES, eds.). Academic Press, London, 243 pp.
- SWYSTUN, M. B., J. M. PSYLLAKIS, and R. M. BRIGHAM. 2001. The influence of residual tree patch isolation on habitat use by bats in central British Columbia. Acta Chiropterologica, 3: 197–201.
- TAN, K. H., A. ZUBAID, and T. H. KUNZ. 1998. Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. Journal of Tropical Ecology, 14: 299–307.
- TANG, Z. H., M. CAO, L. X. SHENG, B. LIANG, and S. Y. ZHANG. 2005. Fruit consumption and seed dispersal of wild banana *Musa acuminata* by short-nosed fruit bat *Cynopterus sphinx*. Acta Zoologica Sinica, 51: 608–615.
- THOMAS, D. W. 1982. The ecology of an African savanna fruit bat community: resource partitioning and role in seed dispersal. Ph.D. Thesis, University of Aberdeen, Aberdeen, 205 pp.
- THOMAS, D. W. 1988. Analysis of diet of plant-visiting bats. Pp. 211–220, in Ecological and behavioral methods for the study of bats (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.
- WEBB, N. J., and C. R. TIDEMANN. 1996. Mobility of Australian flying-foxes, *Pteropus* spp. (Megachiroptera): evidence from genetic variation. Proceedings of the Royal Society of London, 263B: 497–502.
- WHITTAKER, R. J., and S. H. JONES. 1994. The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. Journal of Biogeography, 21: 245–258.
- XIAO, Z. S., Z. B. ZHANG, Y. S. WANG, and J. R. CHENG. 2004. Acorn predation and removal of *Querus serrata* in a shrubland in Dujiangyan Region, China. Acta Zoologica Sinica, 50: 535–540.
- ZHANG, J. H., and M. CAO. 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. Biological Conservation, 73: 229–238.

Received 12 September 2006, accepted 16 February 2007