BIOTROPICA 33(4): 718–722 2001

Fruit Characteristics and *Muntiacus muntijak vaginalis* (Muntjac) Visits to Individual Plants of *Choerospondias axillaris*[1]

Key words: Choerospondias axillaris; *fruit characteristics;* Muntiacus muntijak vaginalis; *seed dispersal; selective visitation; tropical rain forest; Xishuangbanna.*

THE INFLUENCE OF FRUIT MORPHOLOGY AND NUTRIENT CONTENT on frugivore food selection has been discussed by several authors (McKey 1975, Snow 1981, Howe & Smallwood 1982, Janson 1983, Debussche & Isenmann 1989, Willson *et al.* 1989). In many studies, frugivore selection was significantly correlated with fruit characteristics such as size (Wheelwright 1985, Alcantara *et al.* 2000), dry pulp mass (Johnson *et al.* 1985), pulp to fruit ratio (Howe & Vande Kerckhove 1980, Piper 1986), fruit color (Willson & Melampy 1983, Wheelwright & Janson 1985, Willson *et al.* 1989), and insect infestation (Herrera 1984). Other studies have contradicted these observations (Chabot & Hicks 1982; Manasse & Howe 1983; Herrera 1985, 1987, 1995; Levey 1988). Many investigations were based on indirect statistical inference and have focused on interspecific comparisons. Comparatively few studies are available on the relationship of dispersers' selection to morphological and nutritional fruit features of individuals from a single species.

Choerospondias axillaris (Roxb.) Burtt *et* Hill (Anacardiaceae) is a typical pioneer tree species with a relatively large seed (17.5 × 14.3 mm). The plant depends on frugivores for seed dispersal and there are very few seedlings under the canopy of adult trees. We observed that the muntjac (*Muntiacus muntijak vaginalis* [Boddaert]) is the most important disperser of *C. axillaris.* The whole fruit is eaten; then the stone is regurgitated at a different location after several hours of rumination. The possibility of selective visits to different individuals by a frugivorous mammal may influence plant gene frequency and its evolution. The species may have evolved certain traits to enhance the attraction of frugivores to secure the dispersal of their seeds away from mother trees. This paper addresses the following questions regarding the interactions between muntjacs and morphological and nutritional aspects of fruits from a single species. First, since the muntjac is the major disperser of *C. axillaris* seeds, what kind of rewards do muntjacs receive from the fruits? Second, do muntjacs selectively visit individual trees and what are the factors influencing their selection?

Our study was conducted within Mengla National Natural Reserve of Xishuangbanna, Yunnan province, China (21°24'–21°53'N, 101°22'–101°50'E), in an area of seasonal humid tropical climate. Average rainfall is *ca* 1500 mm/yr with the rainy season starting in early May and ending in early October. The greatest rainfall is in August. Annual average temperature is *ca* 21.0°C. The total area is 929 km^2 and the elevation ranges from 630 to 1500 m.

We randomly located and labeled 30 mature trees (DBH [diameter at breast height] >20cm) before fruiting time at the edge of the Mengla National Natural Reserve at an elevation of 1050 to 1150 m. The minimum distance between trees was *ca* 40 m, while maximum distance was *ca* 2000 m. Observation started on 1 June 1999 and ended on 14 September 1999. This covered the entire fruit ripening period of the 19 individuals that fruited. Every four days, two of the authors who were experienced in the identification of animals tracks checked the 19 trees and recorded the presence or absence of fresh muntjac tracks under each tree.

Freshly fallen fruit were collected on 19 July 1999 from the ground under these 19 individuals for analysis of nutrient content (18 individuals for mineral elements and 17 for main nutrient analyses) and morphological description (18 individuals). Ten fruits were measured for fruit weight, fruit size, and other morphological data. Methods used to analyze moisture content, total sugar, titratable acid, vitamin C, soluble tannin, crude fiber, starch, and crude fat were the same as in Chen *et al.* (1999). Fresh pulp samples were collected from fruits of individual trees and dried at less than 40°C and then brought to Kunming Biological Geochemistry Laboratory of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, for analysis. The methodologies used for mineral element content analysis are

[1] Received 18 November 1999; revision accepted 15 August 2000.

TABLE 1. *Average values and inter-tree variation for morphological characters and nutrient composition of* Choerospondias axillaris. N = *number of trees, CV = coefficient of variation (= 100 × SD/x̄).*

Items	*N*	x̄ ± SD	CV
Fruit length (mm)	18	26.4 ± 1.38	5.2
Fruit diameter (mm)	18	20.3 ± 1.25	6.1
Fruit shape index (H/D)	18	1.3 ± 0.02	1.3
Fruit weight (g)	18	9.5 ± 1.11	11.8
Stone weight (g)	18	2.5 ± 0.48	19.1
Edible part percentage in wet weight (%)	18	73.5 ± 3.57	1.4
Pulp in dry weight:stone weight	18	2.4 ± 0.47	19.5
Moisture of pulp (%)	18	83.8 ± 1.18	1.4
Total sugar (%)	17	3.0 ± 1.36	45.2
Titratable acid (%)	17	1.7 ± 0.67	39.4
Starch (%)	17	2.1 ± 0.28	13.8
Vitamin C (mg/100 g)	17	18.6 ± 10.06	54.0
Protein (%)	17	2.7 ± 0.95	35.1
Soluble tannin (%)	17	0.9 ± 0.27	28.3
Crude fiber (%)	17	1.9 ± 0.35	18.3
Crude fat (%)	17	0.6 ± 0.19	32.2
N (%)[1]	18	0.7 ± 0.16	22.6
P (%)[1]	18	0.1 ± 0.04	33.0
K (%)[1]	18	1.6 ± 0.45	27.2
Ca (%)[1]	18	0.7 ± 1.22	163.8
Mg (%)[1]	18	0.2 ± 0.16	69.2
Fe (%)[1]	18	0.2 ± 0.21	100.0
Na (ug/g)[1]	18	130.6 ± 86.66	66.4
Zn (ug/g)[1]	18	28.3 ± 19.47	68.7
Cu (ug/g)[1]	18	30.9 ± 8.40	27.2

[1] Percent (or ug/g) dry weight of pulp including pericarp; others are wet weight of pulp with pericarp.

summarized as follows: For analysis of nitrogen (N), phosphorus (P), potassium (K), and sodium (Na), samples were digested with H_2SO_4–H_2O_2. The total N was determined by diffusion, and protein was estimated as total N × 6.25. Total P was determined by the molybdenum blue colorimetric method. K and Na were determined by atomic absorption spectrum photometry (AAS, GBC Scientific Equipment Pty. Ltd., City, Australia; type: 932). For analysis of calcium (Ca), magnesium (Mg), zinc (Zn), copper (Cu), and iron (Fe), samples were dry-ashed and then soluted with 1:1 HCl. The concentration in the solution was determined by AAS as above.

BIOMstat 3.2 software was used for statistical analyses (Sokal & Rohlf 1995). We used nonparametric correlation analyses (Spearman's coefficient of rank corelation) to relate animal visitation frequency to morphological characteristics and nutritional content of fruit pulp. The Mann-Whitney *U*-test was used to compare the mean values of muntjac visitation frequency to different fruit color groups.

Averages and inter-tree variability of *C. axillaris* morphological characters are summarized in Table 1. Of the morphological characters, fruit weight, stone weight, and the ratio of pulp (dry weight) to stone weight had high inter-tree variation. Their coefficients of variation (CV) were 11.8, 19.1, and 19.5 percent, respectively. Fruit appearance, such as fruit height, fruit diameter, and fruit shape index (fruit height/fruit diam.), had relatively low inter-tree variation. The CVs were 5.2, 6.1, and 1.3 percent, respectively. There were two fruit colors: yellow (including pale yellow) and yellowish green (or olive-green). Among the 18 individuals recorded, 13 had yellow fruits and 5 individuals had yellowish green fruits.

The major nutrients had relatively high inter-tree variation with CVs varying from 13.8 to 54.0 percent (N = 18). The ranking of inter-tree CVs for the different nutrients was as follows: vitamin C > total sugar > titratable acid > protein > crude fat > soluble tannin > crude fiber > starch (Table 1). The mean values and CVs of mineral contents are also presented in Table 1. The CVs for Ca, Fe, Mg, Zn, and Na had relative high values, with CVs being 163.8, 100.0, 69.2, 68.7, and 66.4 percent, respectively; the CVs for P, K, Cu, and N were relatively low, with CVs of 33.0, 27.2, 27.2, and 22.6 percent, respectively.

TABLE 2. *Comparison of nutrient content in* Choerospondias axillaris *fruits to published values for other tree species.*

Species	Nutrient content of dry pulp ($\bar{x}$ ± SD)				Reference
	Protein (%)	Crude fat (%)	Calcium (%)	Ca:P	
Choerospondias axillaris	16.6	3.7	0.7	7.0:1	
Indonesian fig (20 spp.)			1.2 ± 0.33	3.7:1	O'Brien *et al.* (1998)
Indonesian non-fig fruit (36 spp.)			0.5 ± 0.37	1.1:1	O'Brien *et al.* (1998)
For 22 species from Illinois, U.S.A.*	5.1 ± 2.24	7.9 ± 12.92	0.4 ± 0.44		Data computed from Johnson *et al.* (1985)
For 28 tree species from the Iberian Peninsula, Spain**	4.1 ± 2.17	8.3 ± 15.08	0.2 ± 0.15	3.2:1	Data computed from Herrera (1987)

* Data from 20 species for calcium and protein contents respectively; 19 species data for fat content.
** Data from 20 species for calcium and Ca:P.

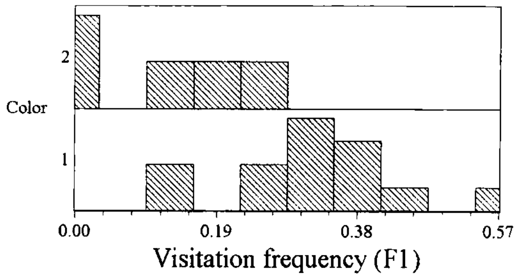

FIGURE 1. Animals' visitation frequency (F_1) to individuals with different fruit colors (color$_1$: yellow; color$_2$: yellowish green; Mann-Whitney *U*-test: $N_1 = 13$, $N_2 = 5$, $P = 0.0024 << 0.01$). F_1 is the number of times that tracks were recorded per total number of observations.

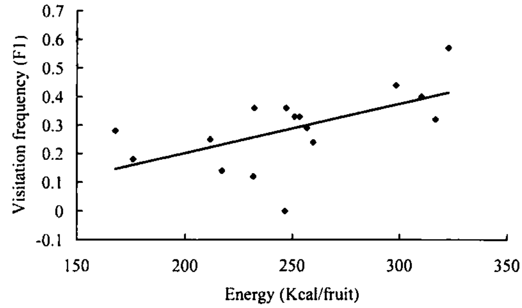

FIGURE 2. Correlation of animals' visitation frequency to richness of energy per fruit. F_1 is the number of times that tracks were recorded per total number of observations. Energy per fruit is measured by: pulp weight per fruit × (4 × % protein + 4 × % starch + 4 × % total sugar + 9 × % crude fat).

The concentration of protein and fat in fruits probably are the most important nutrients for frugivorus dispersers (McKey 1975, Herrera 1981). Comparatively, the fruits of *C. axillaris* have a very rich protein content. Protein content, 16.6 percent of the dry weight of fruit pulp with pericarp, was obviously higher than other fruits (Table 2). O'Brien *et al.* (1998) suggested that high Ca to P ratio may cause figs to be especially important to maintain an adequate balance of Ca among fruit-eating animals because it is essential to bone growth. Fruits of *C. axillaris* also had relatively high Ca content (0.7%) and Ca to P ratios (Ca:P = 7.0) compared to other fruits (Table 2). Avian dispersers may get Ca and other mineral nutrients from other sources such as insects and vertebrates (Herrera 1987); however, the herbivorous muntjac may depend on Ca-rich fruits of plants such as *C. axillaris* for their Ca supply. Being protein-rich and Ca-rich, the fruit of *C. axillaris* offers a good nutritional reward to its muntjac disperser.

To understand the selective visits of muntjac to certain individual trees, we collected two types of data to measure muntjac visitation frequency to different individuals. The measure F_1 is the number of times that tracks were recorded per total number of observations. The measure F_2 is the number of times that tracks were recorded during the period when all individuals had fruit (10 June–28 July). Statistical calculation showed that F_1 was significantly correlated with F_2 ($r = 0.941$, $N = 18$, $P << 0.01$).

This study showed that muntjacs may be sensitive to fruit color. Trees with yellow fruit ($N = 13$) had significantly higher visitation frequency than those with yellowish green fruit ($N = 5$; Fig. 1; Mann-Whitney *U*-test: $P = 0.0024 << 0.01$). Willson *et al.* (1989) pointed out that fruit color could be a signal of some sort, either for attraction of fruit consumers or indication of fruit quality. The fact that muntjacs selectively visited fruit trees with different colors may be due to their visual sensitivity.

The results strongly suggest that muntjacs may selectively visit individual trees with more energetically rewarding fruits. Several data have been used as the indicators of fruit nutrition or energy in the literature, such as dry pulp in crude lipid and protein combined (Herrera 1981) or pulp dry mass per fruit (Johnson *et al.* 1985). Here, we measured the richness of energy per fruit (RE) by the formulation: energy richness (kcal) = pulp weight per fruit × (4 × % protein + 4 × % starch + 4 × % total sugar + 9 × % crude fat. We measured one gram of protein, starch, total sugar, and fat as 4, 4, 4, and 9 kcal of energy, respectively (Wang 1999). The results showed that muntjac visitation frequency was highly and significantly correlated with energy richness per fruit ($N = 16$, $r = 0.6200$, $P = 0.0082 < 0.01$) (Fig. 2). No significant correlation was found between animal visitation frequency and either specific nutrients or other morphological characters.

Choerospondias axillaris produces fruit from June to September, a critical period for female muntjacs as they usually give birth during that period (Yang 1993). The muntjac is an important dispersal agent for several large-seeded woody plants in this area, such as *Phyllanthus emblica* (Euphorbiaceae; ripe season January–March), *Elaeocarpus prunifolioides* (Elaeocarpaceae; April–May), *Melia azedarach* (Meliaceae; September–December), *Canarium album* (Burseraceae; November), *Spondias pinnata* (Anacardiaceae; November–December; authors' obs.). Our study suggests that the muntjac and *C. axillaris*, both of which showed the likelihood of receiving mutual benefits, may be one of the key species pairs in humid tropical rain forest in the study area.

This study was supported by a grant from the Life Science Special Fund of CAS, Ministry of Finance of China (NO: Stz98-1-08). Our appreciation and thanks are extended to Ms. Fu Yun and Prof. Dr. Kun-Fang Cao of the Xishuangbanna Tropical Botanical Garden for their assistance in nutrient analysis and statistical consultation, respectively, and to M. Fuentes for his constructive comments on a previous version of this paper. Finally, we would like to thank Dr. Kendrick Marr for his help in improving the language.

ALCANTARA, J. M., P. J. REY, A. M. SANCHEZ-LAFUENTE, AND F. VALERA. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant–seed disperser interaction. Oikos 88: 362–370.

CHABOT, B. F., AND D. J. HICKS. 1982. The ecology of leaf life spans. Annu. Rev. Ecol. Syst. 13: 229–259.

CHEN, J., Y.-C. SU, G.-Q. CHEN, AND W.-D. WANG. 1999. Ethnobotanical studies on wild edible fruits in southern Yunnan: Folk names, nutritional value and uses. Econ. Bot. 53: 2–14.

DEBUSSCHE, M., AND P. ISENMANN. 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. Oikos 56: 327–338.

HERRERA, C. M. 1981. Are tropical fruits more rewarding to dispersers than temperate ones? Am. Nat. 118: 896–907.

———. 1984. Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of *Berberis hispanica*. Oikos 42: 166–170.

———. 1985. Determinants of plant–animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132–141.

———. 1987. Vertebrate-dispersed plants of the Iberian peninsula: A study of fruit characteristics. Ecol. Monogr. 57: 305–331.

———. 1995. Plant–vertebrate seed dispersal systems in the Mediterranean: Ecological, evolutionary, and historical determinants. Annu. Rev. Ecol. Syst. 26: 705–727.

HOWE, H. F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13: 201–228.

———, AND G. A. VANDE KERCKHOVE. 1980. Nutmeg dispersal by tropical birds. Science 210: 925–927.

JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. Science 219: 187–189.

JOHNSON, R. A., M. F. WILLSON, J. N. THOMPSON, AND R. I. BERTIN. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66: 819–827.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecol. Monogr. 58: 251–269.

MANASSE, R. S., AND H. F. HOWE. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. Oecologia 59: 185–190.

MCKEY, D. 1975. The ecology of coevolved seed dispersal systems. *In* L. E. Gilbert and P. H. Raven (Eds.). Coevolution of animals and plants, pp. 159–191. University of Texas Press, Austin, Texas.

O'BRIEN, T. G., M. F. KINNAIRD, E. S. DIERENFELD, N. L. CONKLIN-BRITTAIN, R. W. WRANGHAM, AND S. C. SILVER. 1998. What's so special about figs? Nature 392: 668.

PIPER, J. K. 1986. Seasonality of fruit characters and seed removal by birds. Oikos 46: 303–310.

SNOW, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13: 1–14.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research, 3rd edition. W. H. Freeman, New York, New York.

WANG, G. Y. 1999. Tables of food composition. People's Health Press, Beijing, China. (in Chinese).

WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808–818.

———, AND C. H. JANSON. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. Am. Nat. 126: 777–799.

WILLSON, M. F., A. K. IRVINE, AND N. G. WALSH. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. Biotropica 21: 133–147.

———, AND M. N. MELAMPY. 1983. The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41: 27–31.

YANG, D. 1993. Fauna of Xishuangbanna. Yunnan University Press, Kunming, Yunnan, China. (in Chinese).

Jin Chen[2], X.-B. Deng, Z.-L. Bai, Qing Yang, G.-Q. Chen, Yong Liu, and **Z.-Q. Liu**

Xishuangbanna Tropical Botanical Garden
The Chinese Academy of Sciences
Mengla, Yunnan province 666300
People's Republic of China

[2] E-mail: biotrans@bn.yn.cninfo.net