Research paper

Differences in Foraging Ecology between Generalized and Specialized Frugivorous Birds in the Fushan Experimental Forest, Northeastern Taiwan

Chao-Chieh Chen,[1] Lien-Siang Chou[2,3]

【Summary】

In order to distinguish differences in foraging between generalized and specialized frugivores, we studied the foraging ecology of 3 commonly seen fruit-eating birds (Gray-cheeked Fulvetta *Alcippe morrisonia morrisonia*, Black Bulbul *Hypsipetes madagascariensis nigerrimus*, and Black-browed Barbet *Megalaima oorti nuchalis*) in Fushan Experimental Forest, northeastern Taiwan. From June 1997 to May 1998, the foraging behaviors, species of fruit eaten, and habitat characteristics of these 3 species were recorded monthly. Habitat variables included vegetation level, vegetation density, foraging height, plant height, and diameter at breast height (dbh) of the fruiting plant. In terms of foraging behavior, gleaning and reaching were used frequently by all 3 species to obtain fruit; however, the Black-browed Barbet used much more reaching than gleaning. On the other hand, the Black Bulbul also used sallying to snatch fruit, and the Gray-cheeked Fulvetta was seen to hang at times. The Black-browed Barbet and Black Bulbul predominantly foraged high in the canopy (> 70% of the time) for drupes and berries, while the Gray-cheeked Fulvetta spent more time foraging in the understory (52.3%) and consumed a greater diversity of fruit types than the other 2 species. In addition, the Black-browed Barbet and Black Bulbul concentrated their foraging in large fruiting trees, whereas the Gray-cheeked Fulvetta took fruit mainly from smaller and thinner trees or bushes. As a result, the Gray-cheeked Fulvetta, a generalized frugivore, not only exhibited greater niche breadth in terms of fruit type and vegetation level, but also expressed a wider variation in foraging habitat use than did the specialized frugivores, the Black Bulbul and Black-browed Barbet. This study showed that specialized frugivores use a far more select set of fruits, fruiting plants, and habitats than do generalized frugivores.

Key words: Black Bulbul, foraging behavior, fruit type, Gray-cheeked Fulvetta, habitat use, Black-browed Barbet.

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研究報告

福山試驗林廣食性食果性鳥類與專一性食果性鳥類在攝食生態上的差異

陳炤杰[1)] 周蓮香[2,3)]

摘 要

我們研究福山試驗林內三種常見食果性鳥類(繡眼畫眉*Alcippe morrisonia morrisonia*，紅嘴黑鵯*Hypsipetes madagascariensis nigerrimus*及五色鳥*Megalaima oorti nuchalis*)的攝食生態，以驗證廣食性食果性鳥類與專一性食果性鳥類在攝食生態上是否有明顯的差異。從1997年6月到1998年5月，每個月3~10天到福山試驗林從事鳥類攝食生態的觀察，記錄鳥種、攝食行為、取食果實種類、利用棲地環境等資料。在攝食行為上，三種鳥類主要使用啄食(gleaning)和伸展(reaching)取食果實，不過五色鳥用伸展遠比啄食多，而紅嘴黑鵯也利用飛啄(sallying)以攫取果實。另外，五色鳥和紅嘴黑鵯主要在樹冠層的喬木上取食核果跟漿果；而繡眼畫眉則較常出現在底層較小棵的喬木或灌木上，取食的果實類別也比前兩者更龐雜而多樣。廣食性食果性鳥類，如繡眼畫眉，不僅利用較多樣的果實種類，在攝食生態上也展現較大的區位寬度(niche breadth)，與專一性食果性鳥類，如五色鳥和紅嘴黑鵯，確實呈現顯著的差異。

關鍵詞：紅嘴黑鵯、攝食行為、果實類別、繡眼畫眉、棲地利用、五色鳥。

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INTRODUCTION

In a forest community, avian frugivores usually occupy an important role, and they may be specialized or generalized in their exploitation of fruit. Several studies (Snow 1971, McKey 1975, Howe and Estabrook 1977) have pointed out that specialized frugivores use different kinds of fruits than generalized frugivores. Snow (1971) proposed that avian frugivores can basically be divided into generalists and specialists, which coincides with the nutritional quality of the fruits they eat. McKey (1975) further hypothesized that some plants produce nutritious fruits to adapt to the consumption of certain reliable, specialized frugivores that provide a good service of seed dispersal; other plants offer superabundant but nutritionally limited fruits to attract a variety of generalized frugivores that are less reliable in terms of seed dispersal. However, such a paradigm remains largely understudied because these hypotheses are too comprehensive to test and require integrated efforts from both ornithologists and plant ecologists (Howe 1993).

Some studies have been conducted to test these hypotheses, but most were in tropical (e.g., Wheelwright 1983, 1985, Loiselle and Blake 1993) and temperate zones (e.g., Herrera 1984, 1998, Johnson et al. 1985, Snow and Snow 1988), but little is known from subtropical areas. In a previous paper (Chen and Chou 1999), we described the diet of 14

species of forest birds based on a year-round observation in the Fushan Experimental Forest of Taiwan, a subtropical island. We found that 3 commonly seen fruit-eating birds, the Gray-cheeked Fulvetta *Alcippe morrisonia morrisonia* (Timaliidae), the Black Bulbul *Hypsipetes madagascariensis nigerrimus* (Pycnonotidae), and the Black-browed Barbet *Megalaima oorti nuchalis* (Capitonidae) (Feinstein et al. 2007), together accounted for 78% of frugivory observations, but each used different assemblages of fruits. In particular, fruit occupied 94% of all items eaten by the Black Bulbul (n = 138), 90% by the Black-browed Barbet (n = 51), but only 38% by the Gray-cheeked Fulvetta (n = 632). When examined using those characters associated with specialization and generalization of frugivorous birds enumerated by Howe (1993), the Black Bulbul and Black-browed Barbet can be considered specialized frugivores because fruit makes up at least 90% of their diet, and both species eat fruit year round. On the other hand, the Gray-cheeked Fulvetta appears to be a generalized frugivore that takes fruit only to a moderate degree and predominantly during the non-breeding season. In this paper, we extend the comparison between generalized and specialized frugivores beyond fruit species used, to also examine foraging behavior and habitat use.

METHODS

This study was conducted in the Fushan Experimental Forest (24°34'N, 121°34'E), at an elevation of about 600~800 m in northeastern Taiwan. The Fushan Experimental Forest is a research site of the Taiwan Forestry Research Institute. It is a humid, subtropical forest, the canopy of which is dominated by trees of the Lauraceae and Fagaceae, while plants of the Myrsinaceae, Melastomataceae, and Rubiaceae dominate the understory. A detailed description of the study site can be found in King and Hsia (1997).

In this paper, we focus on the frugivory of the Gray-cheeked Fulvetta, Black Bulbul, and Black-browed Barbet. The first author conducted fieldwork for 3~10 d mo^{-1} from June 1997 to May 1998. Most foraging data were collected during the morning hours, between 06:00 and 10:00, and some within 2 h before dusk; both are periods of high foraging activity. Foraging birds were observed with binoculars from a system of 5 trails, about 15 km in total length, which run from the administrative center in different directions and lead through 3 major parts of the study site: the botanical garden, an administration area, and natural forests. Trails were surveyed approximately twice per month. When a bird of these 3 species was detected, the observer followed it closely with binoculars until a foraging behavior, whether on fruit or arthropods, was clearly observed. Then data on bird species, foraging behavior, fruit species eaten, and habitat characteristics of the foraging site were recorded. The classification of foraging behavior followed Remsen and Robinson (1990). Gleaning is the collection of food items from a nearby substrate without full extension of the legs or neck. Reaching requires full extension of the legs or neck. Birds can also use hanging by suspending the body by the feet to reach food that cannot be reached from any other perched position. These 3 foraging behaviors are near-perch maneuvers, in which target food item can be reached from a bird's perch (Remsen and Robinson 1990). Contrary to the 3 near-perch maneuvers, sallying is an aerial maneuver in which a bird flies from a perch to snatch fruit. For each incident of frugivory, the fruit species was recorded and the fruit type was determined later using the *Flora of Taiwan* (Li

et al. 1975-1979) or by consulting botanists familiar with the plants at Fushan. Habitat variables, including vegetation level, vegetation density, foraging height, plant height, and diameter at breast height (dbh) of the fruiting plant were measured at the foraging location. We divided the vegetation into 3 levels: canopy, subcanopy, and understory. Vegetation density, modified from Remsen and Robinson (1990), was estimated as the percentage of a 1-m sphere, centered on the foraging location, occupied by vegetation. The vegetation density was estimated at intervals of 10%. Foraging height and plant height were estimated to the nearest meter, and dbh was estimated to the nearest centimeter.

For each bird species, we used foraging niche breadth, $[B] = 1/\sum P^2$ (Levins 1968), to describe the diversity of the 3 categorical variables (foraging behavior, vegetation level, and fruit type) and the coefficient of variation (CV) to describe the extent of variation of the 4 numerical variables (vegetation density, foraging height, plant height, and dbh). An analysis of variance (ANOVA) with Duncan's test (SAS Institute 1989) was performed for each numerical variable to determine if the 3 species took fruit from localities with different microhabitats. The significance level was 0.05 for all statistical tests, and all values reported below in the "Results" section are the mean ± SE.

RESULTS

All 3 bird species primarily used gleaning and reaching, which are near-perch maneuvers, to obtain fruit (Fig. 1). However, the extent to which these 2 behaviors were used differed among the bird species. Gleaning was the most commonly used foraging behavior by the Gray-cheeked Fulvetta (42.4%) and Black Bulbul (36.2%), but reaching (54.3%) was used even more than gleaning by the Black-browed Barbet. On the other hand, sallying, an aerial maneuver, was used quite often by the Black Bulbul (32.3%).

In terms of vegetation level, the Black-browed Barbet and Black Bulbul predominantly took fruit from the canopy (78.3 and 70.8%, respectively), while the Gray-cheeked Fulvetta often ate fruit in the understory

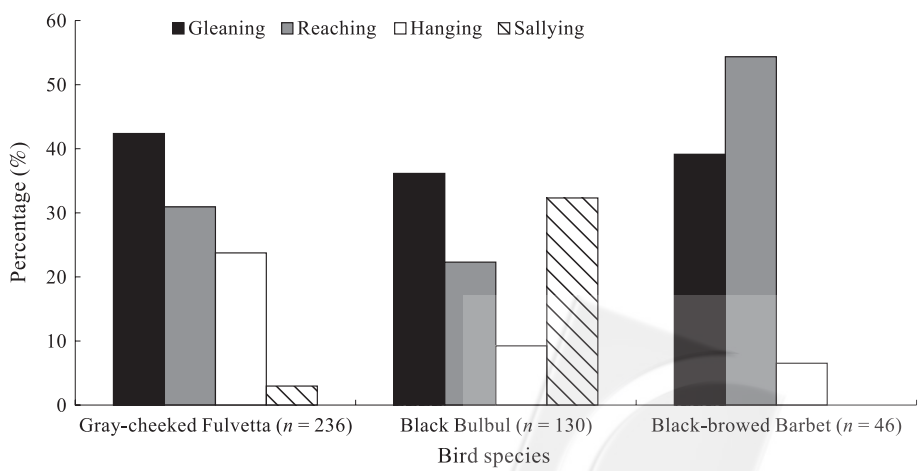

Fig. 1. Percentages of foraging behaviors used by the Gray-cheeked Fulvetta, Black Bulbul, and Black-browed Barbet in eating fruit in the Fushan Experimental Forest, northeastern Taiwan.

(52.3%), and to a lesser degree in the subcanopy (27.0%) and canopy (20.7%; Fig. 2). Regarding fruit type, the Black-browed Barbet and Black Bulbul mainly consumed drupes (73.9 and 63.8%, respectively) and berries, while the Gray-cheeked Fulvetta used a greater diversity of fruit types, including drupes (e.g., *Persea zuihoensis*), berries (e.g., *Maesa tenera*), achenes (e.g., *Villebrunea pedunculata*), caryopses (e.g., *Miscanthus floridulus*), capsules (e.g., *Glochidion acuminatum*), and aggregate fruits (e.g., *Rubus taiwanianus*) (Fig. 3). In terms of vegetation level and fruit type, the Gray-cheeked Fulvetta showed

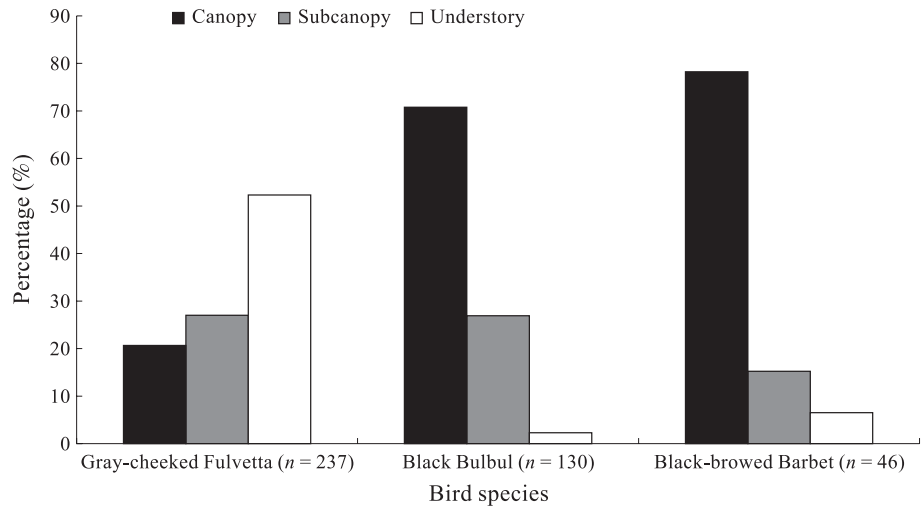

Fig. 2. Percentages of fruit taken from each of the 3 vegetation levels by the Gray-cheeked Fulvetta, Black Bulbul, and Black-browed Barbet in the Fushan Experimental Forest, northeastern Taiwan.

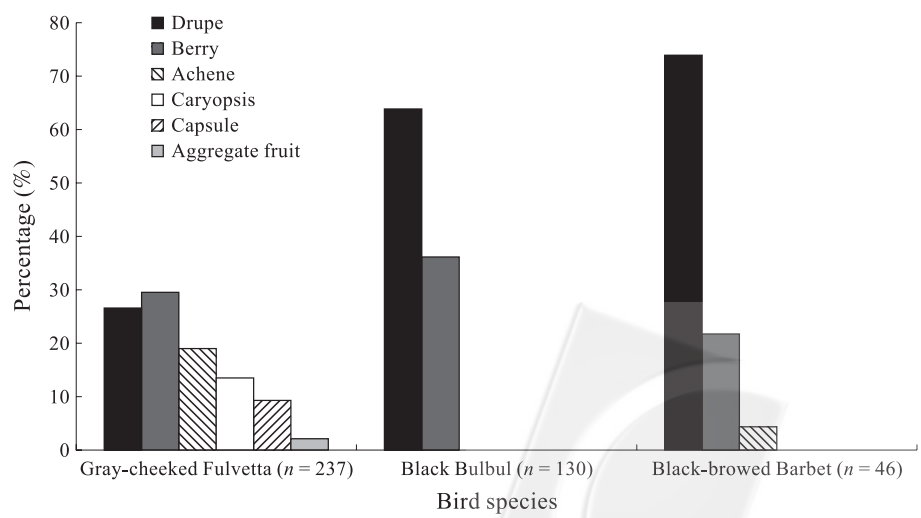

Fig. 3. Percentages of fruit types eaten by the Gray-cheeked Fulvetta, Black Bulbul and Black-browed Barbet in the Fushan Experimental Forest, northeastern Taiwan.

the greatest foraging niche breadth (Table 1). The Gray-cheeked Fulvetta also had the greatest coefficient of variation of the 4 numerical variables (vegetation density, foraging height, plant height, and dbh; Table 1). Moreover, the Black Bulbul had equal or greater coefficients of variation for the 4 numerical habitat variables compared to the Black-browed Barbet.

Comparing the means of each of the 4 numerical habitat variables (ANOVA), the 3 species significantly differed in all variables (Table 2). The Black Bulbul and Black-

Table 1. Diversity and variation indices for foraging variables of 3 commonly seen frugivorous birds in the Fushan Experimental Forest, northeastern Taiwan

Foraging variable	Gray-cheeked Fulvetta	Black Bulbul	Black-browed Barbet
Categorical variable (*B*)[1)]			
Foraging behavior	3.01	3.41	2.21
Vegetation level	2.57	1.74	1.56
Fruit type	4.52	1.86	1.68
Numerical variable (CV)[2)]			
Vegetation density	0.40	0.30	0.30
Foraging height	0.70	0.44	0.38
Plant height	0.67	0.37	0.30
Plant dbh	1.16	0.83	0.74

[1)] *B*, foraging niche breadth.
[2)] CV, coefficient of variation.

Table 2. Habitat characteristics of foraging locations used by 3 commonly seen frugivorous birds in the Fushan Experimental Forest, northeastern Taiwan

Habitat variable Bird species	*n*	Mean±SE	Duncan's test[1)]	*F*[2)]	*p*
Vegetation density (%)					
Gray-cheeked Fulvetta	236	39.4±1.0	A		
Black Bulbul	130	34.8±0.9	B		
Black-browed Barbet	46	41.0±1.8	A	5.8	0.003
Foraging height (m)					
Gray-cheeked Fulvetta	236	3.5±0.2	B		
Black Bulbul	130	7.3±0.3	A		
Black-browed Barbet	46	7.6±0.4	A	98.1	0.0001
Plant height (m)					
Gray-cheeked Fulvetta	237	4.6±0.2	B		
Black Bulbul	130	9.2±0.3	A		
Black-browed Barbet	46	9.3±0.4	A	109.1	0.0001
Plant diameter at breast height (cm)					
Gray-cheeked Fulvetta	222	5.2±0.4	B		
Black Bulbul	127	14.8±1.1	A		
Black-browed Barbet	45	14.0±1.5	A	52.0	0.0001

[1)] Different letters indicate a significant difference between means.
[2)] ANOVA.

browed Barbet foraged significantly higher than the Gray-cheeked Fulvetta. Both species foraged on fruiting plants of similar height and dbh, typically large trees, such as species of the Lauraceae, whereas the Gray-cheeked Fulvetta foraged in much smaller fruiting plants, mostly bushes, such as *Maesa tenera*, *Villebrunea pedunculata*, *Melastoma candidum*, and *Polygonum chinense*. In terms of vegetation density, the Black Bulbul took fruit from significantly less-dense habitat than did the Gray-cheeked Fulvetta and Black-browed Barbet.

DISCUSSION

This study showed that the 2 specialized frugivores, the Black Bulbul and Black-browed Barbet, concentrated their foraging on 2 fruit types, drupes and berries, and mostly from large trees, such as species of the Lauraceae. This result agrees with the statement by Herrera (1987) and Snow and Snow (1988) that drupes and berries are the 2 main fruit types that are dispersed by specialized frugivorous birds. In contrast, the Gray-cheeked Fulvetta, a generalized frugivore, consumed a much greater array of fruit types from smaller trees and bushes. In fact, the Gray-cheeked Fulvetta has been recorded eating 34 species of fruits, while the Black Bulbul and Black-browed Barbet only consume 9 and 15 species, respectively (Chen and Chou 1999). The number of species alone might not be appropriate to evaluate the specialization of a frugivore, since many different fruiting species can all belong to the same fruit type (Sherry 1990). In short, our results are consistent with the conceptual theory predicting that generalized frugivores use more different types of fruits than do specialized frugivores and the latter show greater specialization in frugivory (Snow 1971, McKey 1975, Howe 1993).

Besides fruits, the Gray-cheeked Fulvetta also had the greatest foraging niche breadth in terms of vegetation level. In addition, the Gray-cheeked Fulvetta showed the greatest coefficients of variation for all habitat variables (vegetation density, foraging height, plant height, and dbh; Table 1). Our results indicated that specialized and generalized frugivores not only used different types of fruit, but also exhibited significant differences in habitat use while feeding on fruit. Howe (1993) indicated that generalized frugivores use fruit opportunistically to complement their insect diets. In the wild, Gray-cheeked Fulvettas usually take fruit as it is encountered when they are searching for insects. This foraging pattern would cause the Gray-cheeked Fulvetta to use a much wider range of habitats since insect prey are usually spread out all over the vegetation. In fact, the range of heights within which the Gray-cheeked Fulvetta took fruit overlaps considerably with that when hunting for insects (Chen CC, unpublished data). As a result, the Gray-cheeked Fulvetta, as a generalist, displayed a much greater niche breadth in habitat use in terms of frugivory than did the Black Bulbul and Black-browed Barbet. In contrast, the 2 specialized frugivores confined their foraging to the distribution of their target fruit, and consequently had low niche breadths in habitat use.

The difference in foraging strategies between specialized and generalized frugivores should be accompanied by morphological adaptations. Moermond and Denslow (1985) pointed out that morphological and behavioral characteristics of frugivorous birds affect their selection of fruit, and may result in differential use of microhabitats. Bill size and structure limit the sizes and types of fruit that frugivorous birds can consume (Herrera 1984, 1985, Wheelwright 1985, Jordano 1987), and

consequently influence the foraging behaviors of frugivores (Jordano 1992). For example, long bills, like those of toucans (Ramphastidae) and barbets (Capitonidae), are excellent for reaching fruit from perches (Moermond and Denslow 1985). The coevolution of these frugivores with their target fruits may explain why the Black-browed Barbet in this study used more reaching than the other 2 species (Fig. 1). Moermond and Denslow (1985) also reasoned that species that predominantly use aerial maneuvers would be more selective and use fewer fruit species than birds that mostly use near-perch maneuvers, because sallying for fruit is energetically more costly than taking fruit from perches. In Costa Rica, *Pharomachrus mocinno*, a trogon that picks fruit while flying, consumes only 43 fruit species, while *Aulacorhynchus prasinus*, a toucan that collects fruit mainly by reaching eats 96 fruit species (Wheelwright 1983). Of the 2 specialized frugivores in our study, the Black Bulbul, which used aerial maneuvers to some extent, consumed only 9 fruit species, whereas the Black-browed Barbet, which mainly used reaching and gleaning, ate 15 fruit species within the 1-yr study period (Chen and Chou 1999). Furthermore, some foraging behaviors may constrain a bird to exploit a certain set of fruits (Moermond and Denslow 1985, Moermond 1990) in certain habitats. For example, species that use aerial maneuvers tend to forage in areas where the vegetation density is lower, because a relatively large amount of open space is required for aerial maneuvers (Chen 1996). This might explain the habitat characteristic of using low vegetation density by the Black Bulbul, since it had the highest proportion of aerial maneuvers among the 3 species.

The generalist-specialist dichotomy as hypothesized by Snow (1971) and McKey (1975) might not perfectly exist in nature. Instead, it could be a diffuse coevolution as proposed by several other researchers (Herrera 1982, Wheelwright and Orians 1982, Fleming et al. 1993). From this study, we found that specialized frugivores indeed express a narrower foraging niche compared to generalized frugivores. This implies that specialized frugivores are more dependent on those fruits they eat and might develop a much closer relationship with their fruits than would generalized frugivores.

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