Research paper

Seasonal Variation in the Foraging Behaviors of the Grey-cheeked Fulvetta due to Diet Changes in the Fushan Experimental Forest, Northeastern Taiwan

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【Summary】

A seasonal change in the diet of the Grey-cheeked Fulvetta (*Alcippe morrisonia*) was found in a previous study. In this study, we investigated seasonal variations in the foraging behavior of the Grey-cheeked Fulvetta between breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan. Attack behaviors, food types, and habitat characteristics of foraging locations of the Grey-cheeked Fulvetta were recorded throughout a complete annual cycle. The results showed that seasonal variations of all aspects of foraging parameters were significant, including attack behavior, food type, vegetation level, perch size, and the phenology of plants used by the Grey-cheeked Fulvetta. During the breeding season, the Grey-cheeked Fulvetta made significantly more-diverse foraging maneuvers for insects, and more often foraged in the subcaopy of larger trees and in areas with sparser vegetation. On the contrary, the Grey-cheeked Fulvetta applied more leg-powered maneuvers for more plant matter at the outer parts of smaller trees or shrubs in the understory during the non-breeding season. The patterns of resource use paralleled phenological changes in the plant species, with more new leaves on trees upon which the Grey-cheeked Fulvetta foraged in the breeding season, and more fruit on trees in the non-breeding season. In conclusion, seasonal variations in foraging behaviors of the Grey-cheeked Fulvetta were significant and mainly attributed to diet changes between the breeding and non-breeding seasons. This study is in accordance with the changing-availability hypothesis and can provide empirical evidence for adaptive evolution of birds' foraging strategies.

Key words: *Alcippe morrisonia*, diet, fruit, habitat, phenology.

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研究報告

福山試驗林繡眼畫眉覓食行為之季節變化

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摘 要

本研究探討繡眼畫眉(*Alcippe morrisonia*)食性之季節變化是否會導致覓食行為的改變。我們比較林業試驗所福山試驗林繡眼畫眉在繁殖季與非繁殖季覓食行為及棲地利用之差異。結果發現攝食行為、食物類別、利用植層、棲枝大小及利用植株之物候等在繁殖季與非繁殖季間都具有顯著差異。繡眼畫眉在繁殖季使用較多樣化的攝食行為，取食較多節肢動物，較常在亞冠層，較高大的樹，但枝葉密度較稀疏處覓食。相對地，繡眼畫眉在非繁殖季時則使用較多以腳為動力的攝食行為，吃較多的植物性食物，且在較低矮的樹或灌叢外層覓食。另外，繡眼畫眉覓食行為上的季節變化也跟整個福山森林植物的物候變化吻合，繁殖季時利用較多具新葉的植株，而非繁殖季則偏向在結果的樹上覓食。整體來說，繡眼畫眉在繁殖季與非繁殖季在覓食行為上表現出顯著差異，而這樣的差異很可能導因於不同季節中環境可供繡眼畫眉利用的食物類別差異所致。本研究結果符合changing-availability假說，也可提供為動物在攝食策略上適應演化的實際例證。

關鍵詞：*Alcippe morrisonia*、食性、果實、棲地、植物物候。

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INTRODUCTION

Seasonal variation is an important aspect of the foraging ecology of birds (Austin 1976, Smith et al. 1978, Brennan and Morrison 1990, Ford et al. 1990, Padilla et al. 2009). Seasonal changes in foraging behavior of birds were found across species (Baker and Baker 1973, Austin 1976, Morrison 1980, Bilcke 1984, Miles 1990, Murakami 2002, Whelan and Maina 2005) and habitats (Alatalo 1980, Ford et al. 1990, Lundguist and Manuwal 1990, Jedlicka 2006, Lorenz and Sullivan 2009). However, most studies were conducted in temperate regions where trees lose most of their foliage during wintertime (Willson 1970) and thus comparisons are quite obvious. Ford et al. (1990) compared seasonal changes in foraging behaviors of 3 passerines in evergreen eucalypt woodlands in Australia, and they also found clear differences in foraging behaviors of these species between seasons, especially 2 species which frequently forage on the ground in winter. That study suggested that seasonal changes in foraging behaviors of birds may be greatly affected by the abundance and distribution of food resources (Ford et al. 1990, Murakami 2002).

Some studies indicated that birds may consume food in proportion to its availability (changing-availability hypothesis), and thus increase fruit consumption in fall and winter when insects are scarce (Morton 1973, Thompson and Willson 1979, Wheelwright 1988). Seasonal changes in foraging behaviors of birds attributable to fluctuations in food resources between different seasons are straightforward (Wolda 1978, Morrison and With 1987, Poulin et al. 1992); however, such

relationships are seldom tested with field data (e.g., Herrera 1982, Kirkwood and Robertson 1997). Recently, Pechacek (2006) reported that seasonal variations in foraging behaviors of the Eurasian Three-toed Woodpecker (*Picoides tridactylus*) were clearly related to changes in the diet composition in different seasons.

Seasonal changes in the diet composition of the Grey-cheeked Fulvetta in northern Taiwan were clearly illustrated through a gut content analysis by Chou et al. (1998). The Grey-cheeked Fulvetta predominantly eats insect prey in the breeding season (spring and summer, March to August), but dramatically shifts to plant matter in the non-breeding season (fall and winter, September to January). Chen and Chou (1999) further confirmed such a seasonal variation in food consumption by the Grey-cheeked Fulvetta through foraging observations. In addition, Chen and Chou (2008) identified that the Grey-cheeked Fulvetta is a generalized frugivore, which takes food opportunistically and may forage more or less according to the abundance of food resources available. In this paper, we further tested if the foraging ecology of the Grey-cheeked Fulvetta differs between breeding and non-breeding seasons. In particular, we examined the impacts of diet changes on foraging behaviors of the Grey-cheeked Fulvetta across seasons.

METHODS

Study area

This study was conducted in the Fushan Experimental Forest (24°34'N, 121°34'E), a research site of the Taiwan Forestry Research Institute. The study areas were located at an elevation of about 600~800 m, northeastern Taiwan. Fushan's annual average temperature is 18.5℃, and the yearly average precipitation is up to 4000 mm (Fushan Experimental Forest 2010). Fushan Experimental Forest is a humid, subtropical forest. The canopy is dominated by trees of the Lauraceae and Fagaceae families, especially *Castanopsis carlesii*, *Machilus thunbergii*, *Engelhardtia roxburghiana*, *Meliosma squimulata*, and *Litsea acuminata*. Plants of the Myrsinaceae (e.g., *Maesa tenera*), Melastomataceae (e.g., *Melastoma candidum*), and Rubiaceae (*Lasianthus fordii*) are common in the understory. Epiphytes such as *Asplenium antiquum* Makino, *Pseudodrynaria coronans* (Mett.) Ching, *Aeschynanthus acuminatus* Wall., and *Hoya carnosa* (L. f.) R. Br. are also very common at Fushan, possibly due to the forest's high humidity. A detailed description of the study site can be found in King and Hsia (1997).

Birds were observed with binoculars from a system of 5 trails which radiate from the administrative center and run in different directions through 3 major parts of the study site: a botanical garden, an administration area, and natural forests. The total length of the trails that we surveyed monthly was about 15 km.

Recording method

The first author conducted fieldwork for 3~10 d mo^{-1} from June 1997 to May 1998, a complete annual cycle. Most foraging data were collected during the morning hours, between 06:00 and 10:00, with some additional data collected in the late afternoon. When a Grey-cheeked Fulvetta was detected, the observer followed it closely with binoculars until an attack behavior could be clearly identified. Then data on the attack behavior, food type (plant matters or arthropods), and habitat characteristics of the foraging site were recorded. Habitat variables, including vegetation level, vegetation density, perch size (diameter), position in the crown, foraging

height, plant height, diameter at breast height (dbh), and phenology of the plant, were measured at the foraging location.

The classification of attack behaviors followed Remsen and Robinson (1990). Gleaning is the collection of food items from a nearby substrate without full extension of the legs or neck, whereas 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. Gleaning, reaching, and hanging are leg-powered maneuvers, which birds use to attack prey along a perch, and thus Remsen and Robinson (1990) classified them as near-perch maneuvers. On the other hand, sallying is a wing-powered maneuver, or aerial maneuver, which directs the bird's attack at a flying insect or food item that cannot be eaten by near-perch maneuvers. Concerning habitat variables, we divided the forest into 3 levels: canopy, subcanopy, and understory. The 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 foliage. The vegetation density was estimated at intervals of 10%. Perch size was estimated as < 1 or > 1 cm, and the position in the crown was separated into the inner or outer half of the crown horizontally. The phenology of the plant used was noted when the plant bore new leaves, flowers, or fruit. Foraging height and plant height were estimated to the nearest meter, and dbh was estimated to the nearest centimeter.

In this analysis, we compared the foraging data of the Grey-cheeked Fulvetta between the breeding (March to June) and non-breeding seasons (October to January). Chi-squared tests (SAS Institute 1989) were applied for attack behavior, food type, vegetation level, perch size, crown position, and phenology between the breeding and non-breeding seasons. A *t*-test (SAS Institute 1989) was performed for each of the 4 numerical variables (vegetation density, foraging height, plant height, and dbh) to determine if the Grey-cheeked Fulvetta took food from different microhabitats between the breeding and non-breeding seasons. The significance level was set at 0.05 for all statistical tests, and all values below are reported as the mean ±SE.

RESULTS

In terms of seasonal variation, more wing-powered maneuvers (sallying) were used in the breeding season than in the non-breeding season; in contrast, more leg-powered maneuvers (gleaning, reaching, and hanging) were applied in the non-breeding season than in the breeding season (χ^2 = 35.60, $p < 0.0001$; Fig. 1). Overall, the Grey-

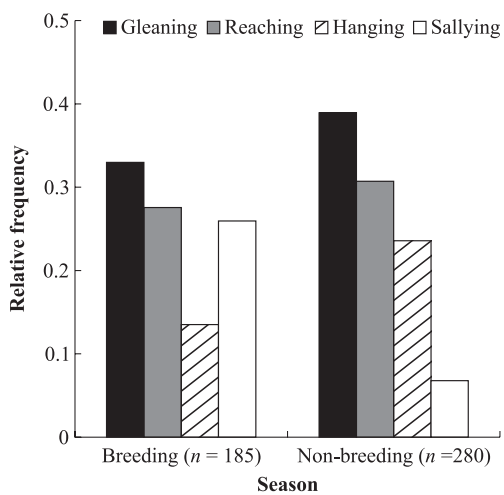

Fig. 1. Relative frequencies of foraging behaviors used by the Grey-cheeked Fulvetta between breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998.

cheeked Fulvetta used significantly more leg-powered maneuvers than wing-powered maneuvers to obtain food in both the breeding and non-breeding seasons ($\chi^2 = 31.63$, $p < 0.0001$).

Concerning food type, significantly more insects (about 80%) were taken in the breeding season than in the non-breeding season (Fig. 2), and vice versa for plant matter. Seasonal variation in food type use was conspicuous ($\chi^2 = 82.64$, $p < 0.0001$) for the Grey-cheeked Fulvetta. In addition, a significant association was found between attack behaviors and food type use. Wing-powered maneuvers were highly associated with insectivorous prey, whereas leg-powered maneuvers were applied more frequently by the Grey-cheeked Fulvetta while taking plant matter ($\chi^2 = 40.22$, $p < 0.0001$). A scatterplot of the proportion of insectivorous prey and proportion of wing-powered maneuvers was best fitted by an exponential equation (Fig. 3).

In terms of the vegetation level, the Grey-cheeked Fulvetta foraged more often in the subcanopy (46.7%; Fig. 4) in the breeding season, whereas it shifted to the understory (40.1%) in the non-breeding season. A significant difference was found in vegetation level use between seasons ($\chi^2 = 43.43$, $p < 0.0001$; Fig. 4). Nevertheless, the Grey-cheeked Fulvetta took food from the canopy at similar

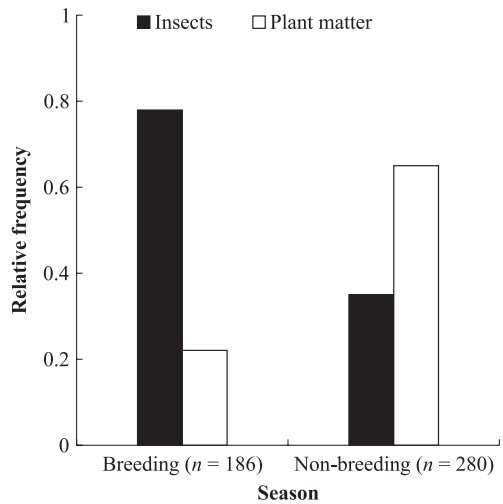

Fig. 2. Relative frequencies of food types used by the Grey-cheeked Fulvetta between breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998.

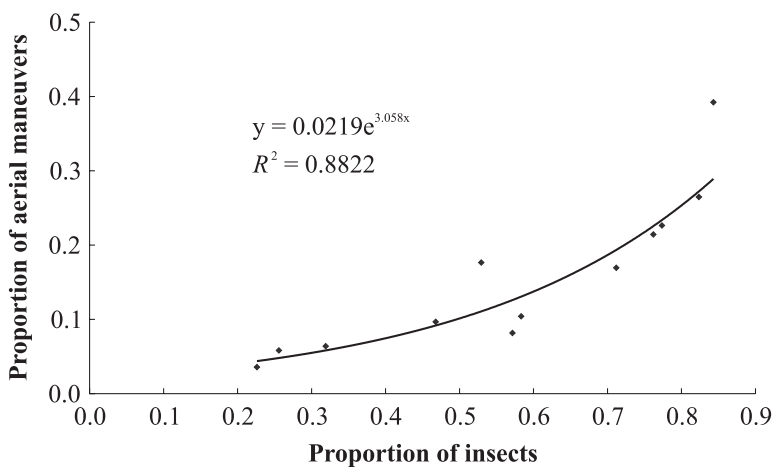

Fig. 3. Relationship between the proportion of insect prey eaten and the proportion of aerial maneuvers used by the Grey-cheeked Fulvetta in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998 (n = 12 mo).

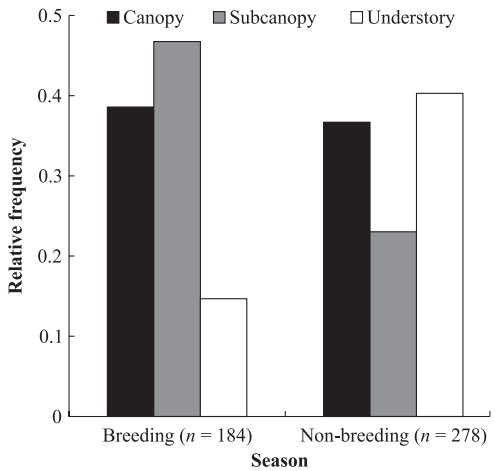

Fig. 4. Relative frequencies of the vegetation levels used by the Grey-cheeked Fulvetta between the breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998.

frequencies in both the breeding and non-breeding seasons (38.6 and 36.8%, respectively).

The Grey-cheeked Fulvetta mainly foraged in the outer parts of the tree crown in both the breeding and non-breeding seasons (66.3 and 76.7%, respectively). A seasonal variation was detected because the Grey-cheeked Fulvetta foraged more in inner parts in the breeding season than in the non-breeding season ($\chi^2 = 6.13$, $p < 0.05$; Fig. 5).

The Grey-cheeked Fulvetta mostly foraged on perches with a diameter of < 1 cm in both the breeding and non-breeding seasons (72.8 and 90.3%, respectively). However, a significant difference was found in perch size use by the Grey-cheeked Fulvetta between the breeding and non-breeding seasons ($\chi^2 = 24.13$, $p < 0.0001$; Fig. 6). That is because more perches of < 1 cm in diameter were used in the non-breeding season than in the breeding season.

Concerning phenology, the Grey-cheeked Fulvetta foraged on plants bearing more new leaves in the breeding season than in the non-breeding season ($\chi^2 = 52.15$, $p < 0.0001$; Fig.

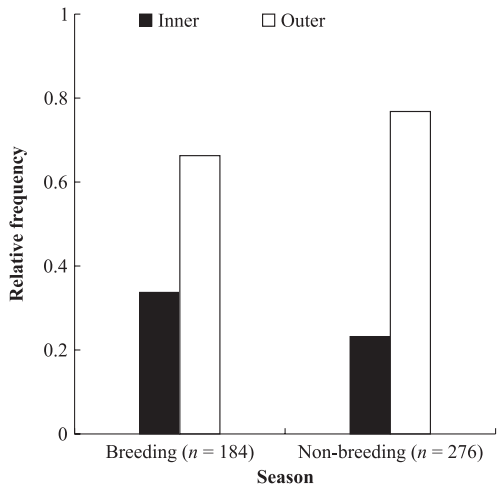

Fig. 5. Relative frequencies of the horizontal positions of plants used by the Grey-cheeked Fulvetta between the breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998.

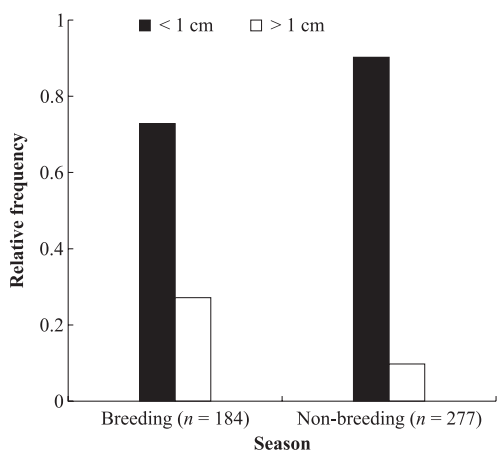

Fig. 6. Relative frequencies of perch sizes (diameter) used by the Grey-cheeked Fulvetta between the breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998.

7). In contrast, the Grey-cheeked Fulvetta foraged more on trees containing fruits in the non-breeding season than in the breeding season (χ^2 = 53.43, p < 0.0001; Fig. 7). Nevertheless, no difference was found in the frequency of the occurrence of flowers on plants used between the breeding and non-breeding seasons.

Comparing the means of each of the 4 numerical habitat variables (vegetation density, foraging height, plant height, and dbh; Table 1), the Grey-cheeked Fulvetta showed significant differences in all variables between the breeding and non-breeding seasons (t-test, p < 0.005 for all). The Grey-cheeked Fulvetta took food from significantly denser habitats in the non-breeding season than in the breeding season. On the other hand, the Grey-cheeked Fulvetta foraged at lower locations and used trees of smaller size (both height and dbh) in the non-breeding season than in the breeding season.

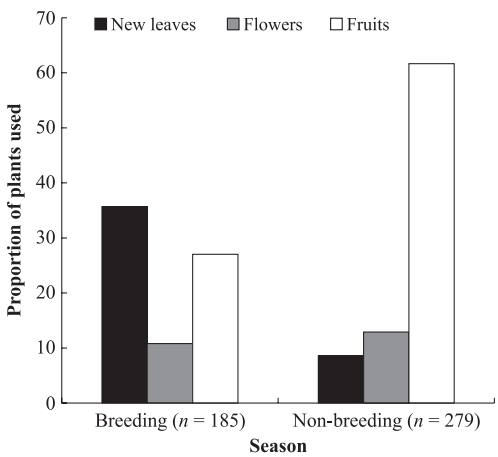

Fig. 7. Phenology of plants used by the Grey-cheeked Fulvetta between the breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998.

DISCUSSION

Compared to the non-breeding season, the Grey-cheeked Fulvetta uses several fold more aerial maneuvers (sallying) in the breeding season. Aerial maneuvers are highly associated with insect-catching, and thus such a shift in foraging techniques can be attributed to the high proportion (ca. 80%) of insect prey taken in the breeding season. Apparently, Grey-cheeked Fulvettas adjust their foraging techniques to their main prey type in different seasons. In Germany, Pechacek (2006) found that Eurasian Three-toed Woodpeckers change foraging behavior according to seasonal changes in food availability. The woodpecker takes mostly bark beetles outside the breeding season, but preys mainly on wood-boring longhorn beetle larvae during the breeding season (Pechacek and Kristin 2004). Consequently, seasonal variations in foraging behaviors of birds may result from changes in the availability of food resources across different seasons (Wolda 1978, Herrera 1982,

Table 1. Comparison of foraging habitat measurements (mean±SE) of the Grey-cheeked Fulvetta between breeding and non-breeding seasons in the Fushan Experimental Forest, northeastern Taiwan from June 1997 to May 1998

Habitat variable	Breeding	n	Non-breeding	n	t[1)]
Vegetation density (%)	29.1±1.1	184	44.8±1.6	280	-4.73***
Height (m)	4.64±0.20	184	3.90±0.14	280	3.10**
Plant height (m)	7.32±0.27	185	5.64±0.21	276	5.00***
dbh (cm)	10.0±0.6	178	6.7±0.4	264	4.70***

[1)] t statistic, probability: * p < 0.05; ** p < 0.01; *** p < 0.001.

Ford et al. 1990, Murakami 2002, Pechacek 2006).

Foraging flexibility may ensure that birds have a diversity of food items, thus enhancing their survival rate during critical periods of the year (Martin and Karr 1990, Tebbich et al. 2004). The Grey-cheeked Fulvetta is not stereotyped in foraging techniques but adopts different kinds of foraging methods to exploit the most-abundant food available in different seasons. Foraging flexibility may even make the Grey-cheeked Fulvetta competitive in resource exploitation and dispersal ability (Greenberg 1990), and eventually may have resulted in its extensive geographic distribution (Collar and Robson 2007, Zou et al. 2007) and dominant status over many other forest species (Yen 1990, Chou et al. 1998).

High energy demands during breeding will inevitably influence food choice, habitat selection, and even foraging behaviors of birds (Karasov 1996, Bujoczek and Ciach 2009). Whelan and Maina (2005) found that bark-foraging birds select different habitats in which to forage between the breeding and non-breeding season; they especially prefer larger-diameter trees in the breeding season. Grey-cheeked Fulvettas predominantly feed insects to their nestlings (Lin 1996), and such a demand will definitely motivate adults to forage in habitats with more insects in the breeding season.

The selection of vegetation level and plant characteristics by the Grey-cheeked Fulvetta indicates a divergence in food type usage in different seasons. During the breeding season, the Grey-cheeked Fulvetta used larger trees and foraged mainly in the subcanopy and canopy levels, in the outer parts of crowns and from < 1-cm twigs with new leaves. These characteristics of the vegetation are all related to the insect prey of a perch gleaner. New leaves contain fewer tannins and are more palatable and nutritious for insects (Feeny 1970), and thus the peak of insect abundance usually coincides with leaf flushing (Lowman 1982). In contrast, the Grey-cheeked Fulvetta foraged mostly in smaller trees and in the understory level, in outer parts of the crown, and from < 1-cm twigs covered with fruit in the non-breeding season. These measurements imply the consumption of many fruits from shrubs in the non-breeding season. Chen and Chou (1999) showed that the Grey-cheeked Fulvetta eats fruit from 34 plant species, mostly from small fruiting plants and bushes, such as *Maesa tenera*, *Villebrunea pedunculata*, *Melastoma candidum*, and *Polygonum chinense*.

Seasonal variations become conspicuous from tropical zones to temperate regions. Although Fushan is an evergreen forest, the difference in average monthly temperatures between summer and winter can reach 10℃ (Central Weather Bureau 2010), and seasonal variations are considered clear. The coldest day in January has a temperature closer to 5℃, and insects become scarcer on such winter days (Wang 2008). This change represents a challenge that the Grey-cheeked Fulvetta has to cope with. Nevertheless, fruiting is common after the breeding season in temperate zones (Morton 1973, Stiles 1980) and even at subtropical Fushan (Lin et al. 1997). At Fushan, plants progress naturally from more new leaves in spring to more fruit in fall (Lin et al. 1997), and this basic trend in fruit availability across seasons will definitely affect the foraging behavior of birds. The Grey-cheeked Fulvetta consumed more insects in the breeding season, but more plant matter in the non-breeding season. This result supports the changing-availability hypothesis which states that birds may consume food in proportion to its availability in different seasons (Morton 1973, Thompson and Willson 1979, Wheel-

wright 1988).

The Grey-cheeked Fulvetta was considered to be an opportunistic frugivore by Chen and Chou (2008), and Howe (1993) indicated that generalized frugivores use fruit opportunistically to complement their insect diets. The Grey-cheeked Fulvetta takes fruit opportunistically while searching for insects and only eats a moderate amount of fruit compared to other fruit specialists (Chen and Chou 1999, 2008). This foraging pattern of a mixed-food type inevitably means that the Grey-cheeked Fulvetta covers a much-wider range of habitats in the non-breeding than breeding season.

In conclusion, seasonal variations in the foraging ecology of the Grey-cheeked Fulvetta were significant and were mainly attributed to diet changes, with more insects being consumed in the breeding season and more plant matter in the non-breeding season. The seasonal variations in foraging behaviors of the Grey-cheeked Fulvetta have clearly evolved to adapt to variations in arthropod food and plant phenology. This study provides clear evidence to show that the foraging strategy of birds can flexibly shift according to food availability and breeding needs (Murakami 2002). For future studies, we would suggest collecting data on insect abundances and plant phenology across seasons and vegetation levels to examine on a finer scale the influence of food variations on the foraging behaviors of the Grey-cheeked Fulvetta.

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