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SEASONAL CHANGE OF FLOWER USE BY THE SLATY FLOWERPIERCER (*DIGLOSSA PLUMBEA*)

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ABSTRACT.—I observed a pair of Slaty Flowerpiercers (*Diglossa plumbea*) in highland Costa Rica during 1996 and quantified their flower use in three distinct months. The total number of open flowers in the territory declined from dry to wet season, and the composition of flower species changed. The pair changed their flower use from dry to wet season, exploiting more abundant flower species in each season. Previous studies have shown that the change of flower abundance and composition affected hummingbird abundance in this area because they leave the area when their favorite flower species become scarcer. The Slaty Flowerpiercers, in contrast, maintained the same territory, shifting flower use in response to seasonal changes in flower abundance and composition. My observations suggest that the unique feeding method of flowerpiercers as "nectar thieves" allows them to use flowers more flexibly and to remain resident on the same territory throughout the year.

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The Slaty Flowerpiercer (*Diglossa plumbea*) is a small, nectarivorous passerine endemic to the highlands of Costa Rica and western Panama (A.O.U. 1983, Sibley and Monroe 1990, Hackett 1995). It is usually found at forest edges and gaps, and shrubby clearings, where flowering plants are abundant (Ridgely 1989, Stiles and Skutch 1989). Flowerpiercers have been considered to be nectar thieves rather than legitimate pollinators, because they pierce and extract nectar from the base of the corolla without pollinating [Skutch 1954, Moynihan 1963; however, Graves (1982) reported pollination of *Tristerix longebracteatus* (Loranthaceae) by *Diglossa brunneiventris* and *D. humeralis* in Peru].

A nectarivorous bird community in highland southern Costa Rica has been studied in detail because of its simplicity (Wolf 1969, Wolf and Stiles 1970, Colwell 1973, Wolf et al. 1976). Most of these studies have focused on hummingbirds, and the Slaty Flowerpiercer has been mentioned only as a "parasite" of this hummingbird community (Colwell 1973, Colwell et al. 1974, Wolf et al. 1976); use of flowers by the flowerpiercer has not been quantified. The ecology of the Slaty Flowerpiercer differs from that of hummingbirds in two ways suggesting that its flower use differs from that of hummingbirds: the absence of coevolution with flower species because of the presumed lack of pollination, and little restriction in flower use because of its unique feeding method.

STUDY AREA AND METHODS

I observed a marked pair of Slaty Flowerpiercers on the Cerro de la Muerte, prov. San José, Costa Rica (09° 33′ N, 83° 43′ W). I visited the area at least once a month throughout 1996 and quantified their flower use in three months: January, February and August. The dry season of this area starts in December and lasts until April (average rainfall less than 100 mm/month); the other months receive relatively high precipitation (average rainfall 200–500 mm/month; Wolf 1976). In January, the pair had two fledglings whom they actively fed with nectar and insects. I considered that these three months would represent three different conditions under which the Slaty Flowerpiercers might behave differently: dry and breeding (January), dry and non-breeding (February), and wet and non-breeding (August). The study area is composed of shrubby secondary growth along a local road used for maintenance of electric towers, but behind the second growth is montane oak forest. The observed pair maintained the territory of 150 × 40 m throughout the study. The territory was delimited on the north and south sides by the secondary oak forest, and defended on the east and west sides against other marked conspecific pairs. The territory boundary as delineated by movements of the marked individuals and agonistic interaction with neighbors stayed unchanged during my observations. To quantify flower use, I followed each individual as long as possible and counted the number of visits to each flowering shrub that I had previously marked and identified. I observed each member of the pair for 24–26 hours in each month; total 150 hours for three months. The number of all the open flowers in the territory was counted in each month. I used the nectar concentrations and production rates of flower species that appeared in Wolf and coworkers (1976), but also

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TABLE 1. Number of open flowers found in the territory of one pair of Slaty Flowerpiercers on the Cerro de la Muerte, Costa Rica, in 1996.

Family	Flower species	Month			Nectar production (J/h)
		Jan	Feb	Aug	
Polygalaceae	*Monnina xalapensis*	5945	4519	563	1.88
Campanulaceae	*Centropogon valerii*	364	534	95	9.94[a]
	C. costaricae	331	460	391	4.85
	C. talamancensis	191	168	361	8.89[a]
Ericaceae	*Macleania rupestris*	7	54	318	<1.74[a]
	Cavendishia craciffolia	6	0	206	11.47
	Gaultheria erecta	—	1036	18	1.05–1.39[a]
Onagraceae	*Fuchsia microphylla*	428	511	149	0.70–1.05[a]
Scrophulariaceae	*Digitalis purpurea*	0	0	39	—
Loranthaceae	*Gaiadendron punctatum*	400	20	0	2.79[a]
Alstroemeriaceae	*Bomarea* sp.	52	191	—	—
Rosaceae	*Rubus* sp.	15	—	—	1.39–1.74[a]
	Total	7739	7493	2140	

[a] Values are from Wolf and coworkers (1976).

measured some additional species (see Table 1). All the statistical tests employed SYSTAT (Wilkinson 1990) except the analyses of frequencies; likelihood ratio G-test and G-test of independence to analyze the seasonal change of flower abundance; flower composition, and flower use were performed following Sokal and Rohlf (1995).

RESULTS AND DISCUSSION

Change of flower abundance.—The number of open flowers in the territory changed drastically from dry season (January and February) to wet season (August; likelihood ratio test: $G = 3935$, 2 df, $P < 0.001$; Table 1). The composition of flower species also changed from dry to wet season (test of independence: $G = 4296$, 16 df, $P < 0.001$; Table 1). In the dry season, *M. xalapensis* represented 60–77% of all open flowers. *Fuchsia microphylla, Centropogon valerii,* and *Centropogon costaricae* followed this species in abundance, with 396–470 open flowers each (each 5–6% of all flowers). From dry to wet season, *M. xalapensis, F. microphylla,* and *C. valerii* declined in abundance, while two species of Ericaceae, *Macleania rupestris* and *Cavendishia craciffolia* increased. In the wet season, *M. xalapensis* still represented 26% of all open flowers, although the number decreased by 90% from the dry season. *Centropogon costaricae, Centropogon talamancensis, M. rupestris,* and *Cavendishia craciffolia* followed in abundance with 206–391 open flowers each (each 10–18% of all flowers).

Change of flower use.—The male and the female changed their flower use in similar ways (Fig. 1). In the dry season, *C. valerii* and *M. xalapensis* were visited most frequently by both the male and the female (58.2–71.7 % of all visits, combined). In the wet season, use of these flowers declined significantly (Test of independence using sum of *C. valerii* and *M. xalapensis* against the rest of flower species; male: $G = 74$; female: $G = 87$; both: 2 df, $P < 0.001$) with their decrease in availability, and two other flower species became important in their diet (24.2–25.8 % of all visits, combined): *M. rupestris* and *C. craciffolia,* both of which had few flowers in the dry season but flowered abundantly in the wet season (Table 1). These changes of flower use coincide with the changes of each flower species in abundance.

The flower abundance of each species varied in a different way over the year, thus changing the overall species composition and the number of available flowers (Table 1). Previous studies have shown that seasonal change in flower abundance and composition affect abundance of four hummingbird species found in the area (Wolf et al. 1976). Hummingbirds have evolved bill morphology and body size consistent with a particular set of flowers (Colwell 1973, Wolf et al. 1976), and thus they leave the area when their favorite flowers decrease in abundance (Wolf 1969, Colwell 1973, Wolf et al. 1976). These changes in

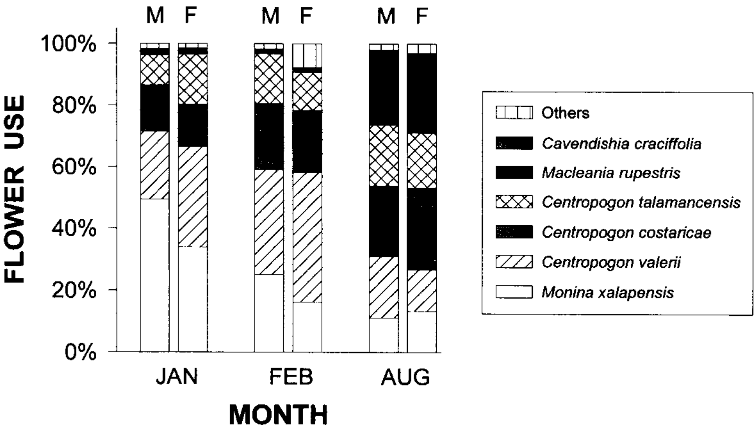

FIG. 1. Seasonal change of flower use of the male and female Slaty Flowerpiercers (*Diglossa plumbea*) on the Cerro de la Muerte, Costa Rica, in 1996. (male: n = 374 in January, n = 500 in February, n = 147 in August; female: n = 147 in January, n = 357 in February, n = 265 in August)

flower abundance and composition do not appear to cause seasonal movement in Slaty Flowerpiercers, which remained on the same territory throughout the year, adjusting their diet to the changing resource. Presumably, the lack of coevolution with certain flower species and its unique foraging method permit the Slaty Flowerpiercer to use flowers more flexibly than hummingbirds.

Flower preference.—To measure flower preference, I used the forage ratio: the quotient of the proportion of flower use divided by the proportion of flower abundance (Krebs 1989:393). If the Slaty Flowerpiercer did not demonstrate preference for certain flowers and used all flower species proportionally to their availability, then the forage ratios should be nearly one. The forage ratios of 7 flower species revealed a striking difference in preference among flower species (Table 2; Friedman's test, male: F = 10.7; female: F = 11.5; both: 4 df, $P < 0.05$). The male and female demonstrated very similar forage ratios for each flower species (Spearman's rank correlation: r_s = 0.87, n = 28, $P < 0.001$). The forage ratios did not change significantly among months (Friedman's test, male: F = 3.9; female: F = 3.1; both: 2 df, $P > 0.05$). *Centropogon valerii* was the most preferred flower species for both sexes in all three

TABLE 2. Forage ratio for twelve flower species for the male and female Slaty Flowerpiercers on the Cerro de la Muerte, Costa Rica, in 1996.[a]

	Male				Female			
Flower species	Jan	Feb	Aug	$\bar{x}$ ±SD	Jan	Feb	Aug	$\bar{x}$ ±SD
Monnina xalapensis	0.64	0.41	0.43	0.49 ±0.13	0.44	0.27	0.52	0.41 ±0.13
Centropogon valerii	4.68	4.65	4.48	4.60 ±0.11	6.88	5.90	3.06	5.28 ±1.98
C. costaricae	3.47	3.41	1.25	2.71 ±1.27	3.15	3.31	1.48	2.65 ±1.02
C. talamancensis	3.87	7.04	1.18	4.03 ±2.94	6.56	5.48	1.07	4.37 ±2.91
Macleania rupestris	—	—	0.82	0.82	—	—	0.77	0.77
Cavendishia craciffolia	—	—	1.24	1.24	—	—	1.53	1.53
Gaultheria erecta	—	0.04	—	0.04	—	0.22	—	0.22
Fuchsia microphylla	0.10	0.06	0.10	0.08 ±0.02	0.24	0.24	0.00	0.16 ±0.14
Digitalis purpurea	—	—	0.73	0.73	—	—	0.00	0.00
Gaiadendron punctatum	0.21	—	—	0.21	0.00	—	—	0.00
Bomarea sp.	0.00	0.00	—	0.00	0.00	0.00	—	0.00
Rubus sp.	0.00	—	—	0.00	0.00	—	—	0.00

[a] Forage ratios differed among flower species (Friedman's test, male: F = 10.7; female: F = 11.5; both: 4 df, $P < 0.05$), but not among months (Friedman's test with five flower species which had data for all three months, male: F = 3.9; female: F = 3.1; both: 2 df, $P > 0.05$).

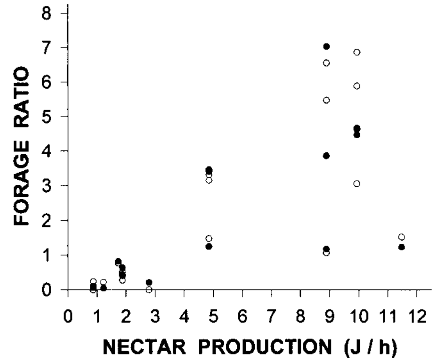

FIG. 2. Flower preference of the Slaty Flowerpiercer (*Diglossa plumbea*): forage ratio versus nectar production for each flower species on the Cerro de la Muerte, Costa Rica, in 1996. (●: male, ○: female; Spearman's rank correlation: $r_s = 0.82$, $n = 38$, $P < 0.001$)

months except February when the male preferred *C. talamancensis* (Table 2). The forage ratios were positively correlated with calorie production rates of each flower species (Spearman's rank correlation: $r_s = 0.82$, n = 38, $P < 0.001$; Fig. 2).

It is not surprising that the forage ratios for each flower species did not differ between two Slaty Flowerpiercers and were not affected by flower abundance. To maximize foraging efficiency, they chose some nectar rich flower species from the wide range of available flower species. I have not considered other factors that could also affect the forage ratio, such as the distance to the nearest flower patches, the number of flowers available per flower patch, and intensity of interaction with competitors (Wolf et al. 1975, Gill and Wolf 1979). Interaction with more aggressive, territorial hummingbirds such as the Fiery-throated Hummingbird (*Panterpe insignis*) or the Green Violet-ear (*Colibri thalassinus*) could decrease the foraging efficiency of the Slaty Flowerpiercer, because these hummingbirds defend the flower patch against the Slaty Flowerpiercer (Lyon and Chadek 1971, Colwell et al. 1974, pers. obs.). In August, Fiery-throated Hummingbirds were numerous in the study area and the surroundings; they established territories around the shrubs of *C. craciffolia* and *M. rupestris*. The interaction between the Slaty Flowerpiercer and the hummingbirds, measured by the frequency of physical attacks and approach per unit time, increased drastically during August compared to January and February when few Fiery-throated Hummingbirds were in the study area (Naoki, unpubl. data). Perhaps this explains why the forage ratio for *C. craciffolia* is low despite its high nectar production.

In summary, this pair of the Slaty Flowerpiercers shifted their foraging in response to seasonal changes in flower abundance and composition. Because my data set is based on one pair of birds and on one year, conclusions are necessarily tentative. Nevertheless, these data suggest that the morphological and behavioral adaptations of flowerpiercers which allow them to use almost any flowers also allow them to remain resident on the same territory through the year, unlike pollinating hummingbirds which move seasonally in response to flower availability.

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