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REPRODUCTION, HABITAT USE, AND NATURAL HISTORY OF THE BLACK-AND-YELLOW SILKY-FLYCATCHER (*PHAINOPTILA MELANOXANTHA*), AN ENDEMIC BIRD OF THE WESTERN PANAMA-COSTA RICAN HIGHLANDS

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Resumen. – Reproducción, uso de habitat e historia natural del Capulinero negro y amarillo (*Phainoptila melanoxantha*), una especie endémica de las tierras altas de Costa Rica y oeste de Panamá. – Estudiamos la abundancia relativa, distribución geográfica, dieta y reproducción del Capulinero negro y amarillo (*Phainoptila melanoxantha*), una especie endémica a las tierras altas de Costa Rica y oeste de Panamá. A lo largo de su ámbito de distribución, el Capulinero negro y amarillo habita principalmente los bosques montano alto, subalpino y enano. La abundancia de esta especie es mayor en los bosques subalpino y enano. En el bosque montano alto esta ave puede llegar a ser abundante en claros naturales y áreas de crecimiento secundario con abundantes frutos carnosos. La dieta del Capulinero negro y amarillo consiste exclusivamente de frutos. Esta especie se alimenta de una gran variedad de especies (36 géneros de semillas fueron registrados en 58 contenidos estomacales). El número de géneros de semillas consumidos es aparentemente mayor en la Cordillera de Talamanca (región sur de Costa Rica y oeste de Panamá). Este patrón es posiblemente causado por la mayor riqueza de especies de plantas en esta cordillera. La reproducción del Capulinero negro y amarillo ocurre principalmente de Marzo a finales de Mayo, antes de la estación lluviosa en las tierras altas de Costa Rica. El ajuste de la época reproductiva del Capulinero negro y amarillo con la estación lluviosa probablemente asegura un suministro de frutos suficiente para polluelos y volantones.

Abstract. – We studied relative abundance, geographical distribution, habitat use, diet, and reproduction of the Black-and-yellow Silky-flycatcher (*Phainoptila melanoxantha*), an endemic species of the highlands of Costa Rica and western Panamá. Black-and-yellow Silky-flycatchers occupy mainly upper montane, subalpine, and elfin forests throughout its geographical distribution. The abundance of this species is greater in subalpine and elfin forests; in upper montane forest Black-and-yellow Silky-flycatchers become abundant only when fleshy fruits are abundant in natural gaps and second growth areas. The diet of this bird consists exclusively of fruits. It feeds on a large variety of fruits (36 seed genera from 58 stomach contents) and the number of seed genera consumed is apparently greater in the Talamanca mountain range (southern region of Costa Rica and western Panamá). This pattern is likely caused by the larger plant richness present in the Talamancas. Reproduction of the Black-and-yellow Silky-flycatcher occurs mainly from March through May, before the rainy season on the highlands of Costa Rica. Reproduction timing in Black-and-yellow Silky-flycatchers likely assures fruits available for nestlings and independent fledglings. *Acceptd 10 October 2001.*

Key words: *Phainoptila melanoxantha,* Black-and-yellow Silky-flycatcher, local distribution, habitat use, diet composition, breeding biology, highlands, Costa Rica, Panamá.

INTRODUCTION

Knowledge on the biology and natural history of tropical birds is essential for understanding relationships among species, ecological packing, niche partitioning, patterns of migration, and structure of communities (Diamond 1975, Fjeldså 1985, Haffer & Fitzpatrick 1985, Remsen 1985, Stiles 1985a). Unfortunately, very little is known about the natural history of the great majority of tropical bird species. Despite the long legacy of ornithological studies in southern Central America, birds of Costa Rican and western Panamá highlands are no exception to this knowledge gap. The latter region contains the highest degree of endemism in Central America (Slud 1964, Stiles 1983, Hernández-Baños *et al.* 1995, Watson & Peterson 1999). Of 72 highland resident species (species present at 2600 m or higher in the Talamanca mountains, *sensu* Wolf 1976) reported for this region in Middle America, 50% (36 species) are endemic to these high elevations (Slud 1964, Wolf 1976, Stiles 1983).

The Black-and-yellow Silky-flycatcher is one of the 36 endemic species that inhabits the highlands in Costa Rica and western Panamá. Throughout its geographical distribution, populations of this species show a clear dichotomy in plumage color; each morph is associated to particular mountain ranges (Barrantes & Sánchez 2000). This geographical discontinuity has led to the separation of *Phainoptila*, a monotypic genus, into two subspecies: *P. m. melanoxantha*, which occurs from the Central Valley in Costa Rica to western Panamá, and *P. m. parkeri*, which inhabits the northern mountains in Costa Rica (Barrantes & Sánchez 2000). The Black-and-yellow Silky-flycatcher differs markedly from other members of the family Bombycillidae (Slud 1964, Stiles & Skutch 1986). For example, external appearance and behaviour of *Phainoptila* are very atypical (Stiles & Skutch 1989). Species of the other two related genera (*Phainopepla* and *Ptilogonys*) are crested and possess a uniform plumage, characteristics absent in Black-and-yellow Silky-flycatchers. Also, *Phainopepla* and *Ptilogonys* species forage on the wing, capturing insects and plucking fruits, whereas Black-and-yellow Silky-flycatchers pick berries from a perch (cf. Stiles & Skutch 1989). Other basic aspects of Black-and-yellow Silky-flycatcher's biology and natural history are essentially unknown. This lack of information has been attributed to the secretive habits and soft calls of this bird (Skutch 1965). Here, we describe habitat use, diet, and reproductive behavior of this species in Costa Rica.

METHODS

Abundance and habitat use. We visited 16 highland sites throughout the four main mountain ranges in Costa Rica (Talamanca, Central Volcanic, Tilarán, and Guanacaste) between 2 to 6 times each over a period of 26 months (December 1996–January 1999) (Fig. 1). During each visit, we observed individuals of Black-and-yellow Silky-flycatchers and estimated habitat use and relative abundance in highland forests above 2300 m in Talamanca, 2000 m in Central Volcanic, and 1300 m in Tilarán and Guanacaste mountains. In each mountain range we covered areas within lower montane, upper montane, and subalpine (or elfin) forests (see Gómez 1986, Kappelle 1996). The lower limit of the study areas varied between mountain ranges in order to cover appropriate vegetation types as these shifted up and down in altitude with topography and size of the mountains. During each visit, we spent a similar proportion of time in lower montane forest, upper montane forest, and subalpine or elfin forest. In Tilarán, Guanacaste, and most part of the Central Volcanic mountain ranges, elfin forest occurs above the upper montane forest zone replacing the

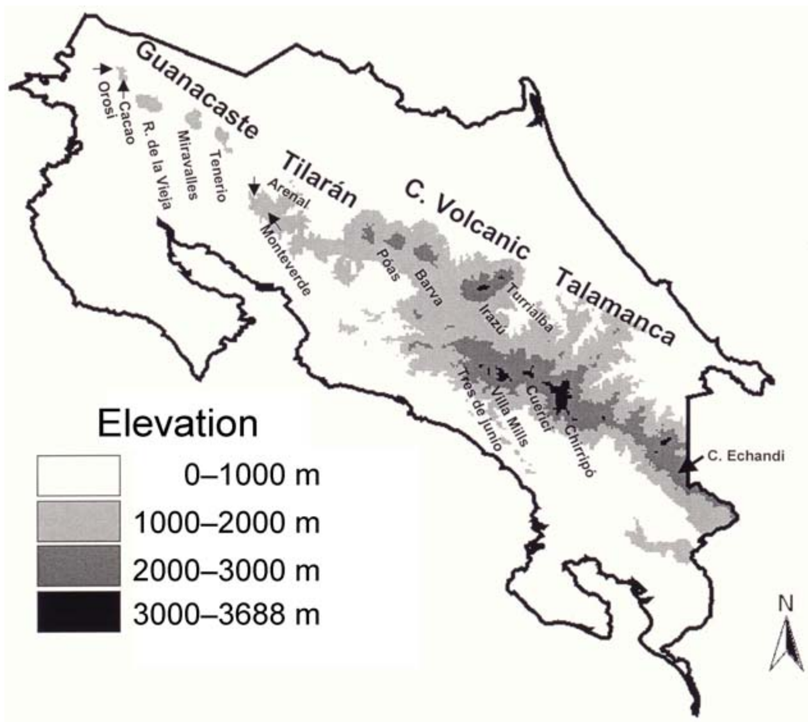

FIG. 1. Map of Costa Rica showing main mountain ranges (Talamanca, Central Volcanic, Tilarán, and Guanacaste) and localities visited during this study.

subalpine forest. Considering the differences in vegetation structure, composition, and dominance among these forests, we regard each one as a different habitat for Black-and-yellow Silky-flycatchers.

Lower montane forest is a 2-strata forest with an intermediate height canopy (25–30m), relatively dense understory, and low species dominance (Hartshorn 1983). Trees are stout and often twisted with compact umbrella-like crowns; buttresses are uncommon. Upper montane forest has a similar canopy height (except *Quercus* that may reach 40 m), and is dominated by species in the Myrtaceae and Fagaceae families. The undergrowth is dense with many individuals from the Rubiaceae, Melastomataceae, and *Chusquea* (Poaceae) (Hartshorn 1983). Subalpine forests occur in the Talamanca mountains and on the Irazú volcano (Central Volcanic mountain range) from 2900 to 3300 m, between upper mountane forest and páramo (Kappelle 1996). Plant families such as Ericaceae, Winteraceae, Rosaceae, Araliaceae, Clusiaceae, Caprifoliaceae, Myrsinaceae and Cunoniaceae are common in the subalpine forest zone (Gómez 1986). Vegetation composition of subalpine and elfin forests is similar, although the structure, particularly the height of the trees, differs between them. Elfin forests are found on exposed peaks and ridges of all mountains but Talamanca and Irazú volcano. These forests are distinguished by their low stature and the exuberant bryophytes that cloak the tree trunks and limbs (Lawton 1980). Elfin forests are composed of

TABLE 1. Relative abundance per forest type (habitat) of Black-and-yellow Silky-flycatchers in 16 sites in the mountain ranges of Costa Rica. Localities are distributed throughout most of the geographical distribution of the species.

Localities	Latitud-Longitud	n[1]	Forest types		
			Lower montane	Upper montane	Subalpine
Talamanca					
Cerro Echandi *	09°01'N, 82°49'W	5	Absent	Abundant	Common
Cerro Chirripó	09°30'N, 83°30'W	6	Absent	Rare	Rare
Cerro Cuericí	09°34'N, 83°38'W	3	Absent	Rare	Rare
Villa Mills *	09°33'N, 83°43'W	8	Absent	Absent	Rare
Reserva Tres de Junio *	09°36'N, 83°49'W	8	Absent	Common	Abundant
Central Volcanic					
Irazú Volcano	09°59'N, 83°52'W	5	Absent	Absent	Rare
Turrialba Volcano *	10°01'N, 84°46'W	4	Absent	Abundant	Abundant
Barva Volcano *	10°08'N, 84°06'W	6	Absent	Uncommon	Abundant
Poás Volcano	10°11'N, 84°13'W	3	Absent	Uncommon	Common
Tilarán					
Monteverde *	10°19'N, 84°47'W	6	Absent	Rare	Abundant
Guanacaste					
Arenal Volcano	10°27'N, 84°42'W	2	Absent	Absent	Absent
Tenorio Volcano	10°40'N, 85°00'W	2	Absent	Absent	Rare
Miravalles Volcano *	10°44'N, 85°09'W	8	Absent	Rare	Abundant
Rincón de la Vieja Volcano	10°49'N, 85°19'W	6	Absent	Rare	Rare
Cacao Volcano*	10°56'N, 85°27'W	5	Absent	Absent	Uncommon
Orosí Volcano	10°58'N, 85°28'W	1	Absent	Absent	Rare

[1]Number of visits to each locality.
*Represent localities where specimens were collected.

dense growths of gnarled trees, generally 2- to 10-m tall. Tree crowns in these forests are tightly packed into a single even canopy layer. The understory is dominated mainly by treelets and bushes of Melastomataceae (*Miconia* spp), Rubiaceae (*Psychotria* spp), Araliaceae (*Schefflera* sp), Ericaceae, and Myrsinaceae (*Myrsine* spp). The ground is covered by a mat of bryophytes from which *Heliconia* spp, *Anthurium* spp, bromeliads, palms, and other herbs emerge (Stiles 1985b). The dominant canopy species vary from one location to another. For example, *Shefflera* sp is the dominant species in the Tilarán mountains (e.g., Monteverde, Lawton 1980) and on Cacao Volcano in Guanacaste mountains (GB, pers. observ.), whereas on the Miravalles massif, Guanacaste mountains, *Clusia* sp and *Schefflera* sp dominate the canopy (Stiles 1985b, GB, pers. observ.).

To estimate the relative abundance of *Phainoptila*, we used abundance categories based on the daily number of observations (Stiles 1980). Categories included: abundant (> 10 individuals recorded in 6 h), common (5–10 individuals recorded in 6 h), uncommon (1–4 individuals recorded in 6 h), and rare (1 individual recorded in two days). This method was selected over transects or point counts, because this species has a very secretive behavior and soft calls that make it difficult to detect while conducting transects or point counts.

We evaluated habitat use by Black-and-yellow Silky-flycatchers within 16 study areas based on observed abundance in each forest type. During the initial two visits to each of the 16 study areas, we spent roughly equal time in each forest type searching for Black-and-yellow Silky-flycatchers. We evaluated habitat use within each study area based on observed abundance within each forest type. During later visits, we focused activities in study areas and in forest types that were found to contain more individuals of Black-and-yellow Silky-flycatchers (Table 1)

To estimate potential available habitat within each of the four mountain ranges, we first determined the elevation (i.e., forest type) at which *Phainoptila* became rare. For example, in the Talamancas, the center of abundance of Black-and-yellow Silky-flycatchers is around 2700–2800 m and birds become rare below 2400 m in elevation. Corresponding levels where Black-and-yellow Silky-flycatchers become rare are 2400 m in Talamanca mountains, 2000 m in Central Volcanic and 1400 m in Tilarán and Guanacaste mountains (Table 1). The area of potential habitat in each mountain range was then calculated using Geographic Information System software (ArcView, ESRI™) on a digital elevation map of Costa Rica (1:200,000; Lambert projection), and included areas above the lower limit to the summit of the four mountain ranges. Potential habitat available is slightly overestimated in the Talamancas, because of the presence of páramo at the highest elevations; Black-and-yellow Silky-flycatchers are not found in páramo.

Diet. We quantified diet of Black-and-yellow Silky-flycatchers based on direct observations of foraging birds and stomach contents from birds collected for a genetic study. Fifty eight specimens were collected from seven study areas: Cerro Echandi, Villa Mills, and Reserva Tres de Junio in the Talamanca mountains; Turrialba and Barva volcanos in the Central Volcanic mountains; Monteverde in the Tilarán mountains; and Miravalles and Cacao volcanos in the Guanacaste mountains. From these specimens, we identified the digestive tract contents (stomach contents hereafter). As these birds feed almost exclusively upon fruits, seeds contained in their stomachs were identified to the lowest level possible, mostly to genus level. Seeds of different genera found in stomach contents were described using accumulation curves for each mountain range, and slopes were compared using the method described by Zar (1984: 292–302). We also calculated overlap in diet (seed genera) between mountain ranges using Pianka's index for niche overlap (Pianka 1973). The same index was used to calculate overlap of fleshy-fruited plants (genera) between mountain ranges, using the plant data base of the Instituto Nacional de Biodiversidad (INBio) of Costa Rica. These data allowed us to evaluate whether diet overlap of Black-and-yellow Silky-flycatchers among mountain ranges is correlated with the overlap of plant species potentially eaten by this bird.

We also used information in the plant data base at INBio to evaluate changes in species richness of plants potentially eaten by Black-and-yellow Silky-flycatchers among mountain ranges. Although this is the most complete database for plants in Costa Rica, sampling efforts have not been homogeneous across highland forests in all mountain ranges (J. Gonzales, pers. com.). For example, plants in the Tilarán mountains have been the most intensively sampled, while the Central Volcanic range has been the most understudied. We analyzed the data at the genus level, to reduce the errors due to differential sampling effort. We compared, using a two-way ANOVA without repetition (model I), the number of plant genera found within families across mountain ranges

TABLE 2. Estimated area (hectares) of habitat available for Black-and-yellow Silky-flycatchers in the four main Costa Rican mountain ranges.

Talamanca[1]		Central Volcanic		Tilarán		Gunacaste	
Echandi	5,380	Irazú	15,860	Monteverde	11,970	Arenal	31
Chirripó	148,370	Turrialba	10,500			Tenorio	750
		Barva	5,800			Miravalles	2000
		Poás	5,545			R. Vieja	2900
						Cacao	100
						Orosi	40
Total	153,750		37,705		11,970		5,820

[1]Cuerici, Villa Mills, and Tres de Junio habitat are included into totals for Chirripó as habitat was continuous.

for plants that are potentially eaten by Black-and-yellow Silky-flycatchers; main effects in the model were mountain range and plant family.

Reproduction. We evaluated the reproductive activity of Black-and-yellow Silky-flycatchers using gonad size. Reproductive males were adult individuals having testes volume of 200 mm^3 or more, while reproductive females had follicles of 7 mm^3 or more. Limits for reproductively active gonad size were established based on comparisons with cloacal protuberance for males and brood patch in females for birds of similar size (i.e., *Turdus* spp) using information from museum specimens (Museo de Zoología, Universidad de Costa Rica). We selected this method because it likely is more accurate than using development of brood patch or size of cloacal protuberance alone. Moreover, brood patch in female Black-and-yellow Silky-flycatchers are not as well developed as in other birds (e.g., *Turdus* spp).

RESULTS AND DISCUSSION

Altitudinal distribution. The area of forest potentially occupied by Black-and-yellow Silky-flycatches includes primarily subalpine (or elfin) and upper montane forests and decreases in area from the Talamancas to Guanacaste (Table 2). The Talamancas account for 73% of the total habitat available (153,750 ha), Central Volcanic 18%, Tilarán 6%, and Guanacaste 3% (Table 2). Upper montane and subalpine forests occupy a continuous band throughout the whole summit of the Talamanca mountains. The Central Volcanic mountains present a different scenario. Forests occupied by Black-and-yellow Silky-flycatchers in this mountain range are dissected by two mountain passes: La Palma (at 1400m a.s.l.) between the massifs Irazú-Turrialba and Barva, and El Desengaño (at 1550 m a.s.l.) between the Barva and Poás volcanos. These depressions likely restrict, or even eliminate, movement of birds between volcanos. In the Tilarán mountains, the distribution of potential habitat is continuous along the highest peaks (e.g., La Ventana and Cerro Amigos within Monteverde Cloud Forest Reserve). The distribution of upper montane and elfin forests, and consequently the distribution of Black-and-yellow Silky-flycatchers on Guanacaste mountains, is restricted to the summit of the volcanos, with the exception of the Arenal volcano, which is mostly devoid of vegetation at the summit due to its intense volcanic activity. The Guanacaste mountain range constitutes a chain of

TABLE 3. Dates of major eruptive events of Costa Rican volcanos based on Alavarado-Induni (2000).

Volcanoes	Dates of major activities
Turrialba	1450 bC, 800 bC, 50, 650, 1866
Irazú	1723, 1775, 1847, 1963
Barva	8050 years ago
Poás	1834, 1860, 1880, 1888, 1895, 1899, 1903, 1910, 1914, 1925, 1929, 1932, 1953
Arenal	Since 1968
Tenorio	No information
Miravalles	c. 1600
Rincon de la Vieja	1860, 1863, 1912, 1922, 1966, 1970, 1983, 1991, 1992, 1995, 1998
Orosi	c. 6000 years ago

six volcanoes separated by foothills at about 500 m in altitude. Here, the distribution of Black-and-yellow Silky-flycatchers likely consists of discrete populations restricted to the isolated mountaintops.

Abundance and habitat use. The relative abundance of Black-and-yellow Silky-flycatchers varies greatly throughout its geographical distribution (Table 1). For example, Black-and-yellow Silky-flycatchers are rare or uncommon at all locations of Guanacaste mountains, with the exception of the population on Miravalles volcano. In contrast, Black-and-yellow Silky-flycatchers are abundant or common at most localities of the Central Volcanic mountains (Table 1). The source of this variation in abundance is not completely clear. Local factors, such as vegetation structure, volcanic activity, and area of available habitat may explain, in part, patterns of abundance for the Black-and-yellow Silky-flycatcher (Tables 1 and 2).

The abundance of Black-and-yellow Silky-flycatchers also showed large variation among forest types (Table 1). This bird uses subalpine/elfin forests intensively, and upper montane forest to a lesser degree. However, Black-and-yellow Silky-flycatchers are absent in lower montane forests (Table 1). Forest preference is likely partially explained by differences in abundance of fleshy-fruiting plants among high elevation forests (Kappelle 1996). Subalpine and elfin forests are dominated by bird-dispersed plants (e.g., Araliaceae, Melastomataceae, Rubiaceae, Ericaceae), while montane forests are dominated by non-fleshy fruit species (e.g., *Chusquea* spp, Poaceae; *Quercus* spp, Fagaceae; Kappelle 1996). However, natural gaps and advanced second growth areas in upper montane forests also contain abundant fleshy-fruited plant species and are likely important foraging areas for Black-and-yellow Silky-flycatchers. Such areas contain vegetation similar to subalpine forest (Kappelle 1996). The high concentration of fruits in natural gaps and second growth areas largely determine the presence of Black-and-yellow Silky-flycatchers in upper montane forests (GB, pers. observ.), sometimes below its center of abundance.

The relative abundance of Black-and-yellow Silky-flycatchers across study sites is likely related to three factors: area of potential habitat available, recent anthropogenic activity, and volcanic activity. For example, in the Talamanca mountains, Black-and-yellow Silky-flycatchers are abundant at both Cerro Echandi and Reserva Tres de Junio. These two sites contain large extensions of subalpine forests and second-growth areas due to past windstorms (southern part of the Talamancas) and past deforestation (Reserva Tres de Junio). Yet, at Villa Mills and Cuerecí, areas of both regeneration and subalpine forest are common, but Black-and-yellow Silky-flycatchers are scarce at these localities (Table 1). Therefore, the presence of potential habitat alone does not explain differences in abundance of Black-and-yellow Silky-flycatchers among localities. We know no reason why Cuerici and Villa Mills sites with apparently good available habitat and food resources, contain so few Black-and-yellow Silky-flycatcher individuals.

Volcanic activity is another factor that likely influences abundance of Black-and-yellow Silky-flycatchers on some massifs (see Table 3). This bird is totally absent from the Arenal volcano (Guanacaste mountain range), which has been active since 1968. Such activity has destroyed the vegetation on practically the whole massif and thus there is little or no habitat available for this species. Black-and-yellow Silky-flycatchers are rare at Irazú volcano (Central Volcanic mountain range). Irazú erupted in 1963 destroying all high vegetation on the volcano and likely reducing greatly, or eliminating, the Irazú population of Black-and-yellow Silky-flycatchers (see Table 3). The relatively high abundance of this species on the Turrialba volcano, which has been inactive since 1866 (Alvarado-Induni 2000) and only separated from the Irazú massif by 10 km, supports the notion that volcanic activity can impact abundance of Black-and-yellow Silky-flycatchers. Black-and-yellow Silky-flycatcher populations on Rincón de la Vieja volcano have also been affected by volcanic catastrophes. The activity of this volcano has increased during the last four decades (Table 3), and the elfin and high montane forests have been partially or completely destroyed several times since then. On the other hand, Poás volcano, which has been active since at least 1834 (Table 3), holds a relatively large population of Black-and-yellow Silky-flycatchers. The relatively high abundance of Black-and-yellow Silky-flycatchesr in this massif is likely explained by the connectivity that exists between Poás and Barva populations and the pattern of forest destruction produced by the activity of the Poás volcano. Despite the existence of a mountain pass (El Desengaño) between Barva and Poás volcanos, this depression is insufficient to prevent bird movement between these populations (GB, pers. observ.). The architecture of the crater of the Poás volcano, and the forest structure around the crater, suggest that the intense activity of this volcano has mostly affected the forest on the Pacific slope, leaving almost intact elfin and upper montane forests on the Atlantic slope. The recurrent destruction of the west slope forest in the Poás volcano has been registered since 1925 (Alavarado-Induni 2000). Additionally, the rapid colonization of pioneer elfin forest vegetation after eruptions (GB, pers. observ.) lessens the effect of volcanic catastrophes on population size, as habitat rapidly becomes available through regeneration.

The area of habitat (upper montane and elfin forests) available is a factor that likely affects abundance of Black-and-yellow Silky-flycatchers. For example, the low abundance of Black-and-yellow Silky-flycatchers on the inactive Cacao and Orosi volcanos (Table 1) is likely a consequence of the small area (100 ha) of elfin and upper montane forests on these massifs. Although no information on volcanic activity exists for Tenorio volcano, indicating no recent activity, the relatively small amount of habitat available also probably explains the low population size of Black-and-yellow Silky-flycatchers at this site.

Overall, volcanic activity directly and indirectly affects Black-and-yellow Silky-flycatcher populations, when intense volcanic activity destroys part (or all) of the vegetation used by Black-and-yellow Silky-flycatchers and partly (or completely) eliminates local populations. Other factors such as fruit avail-

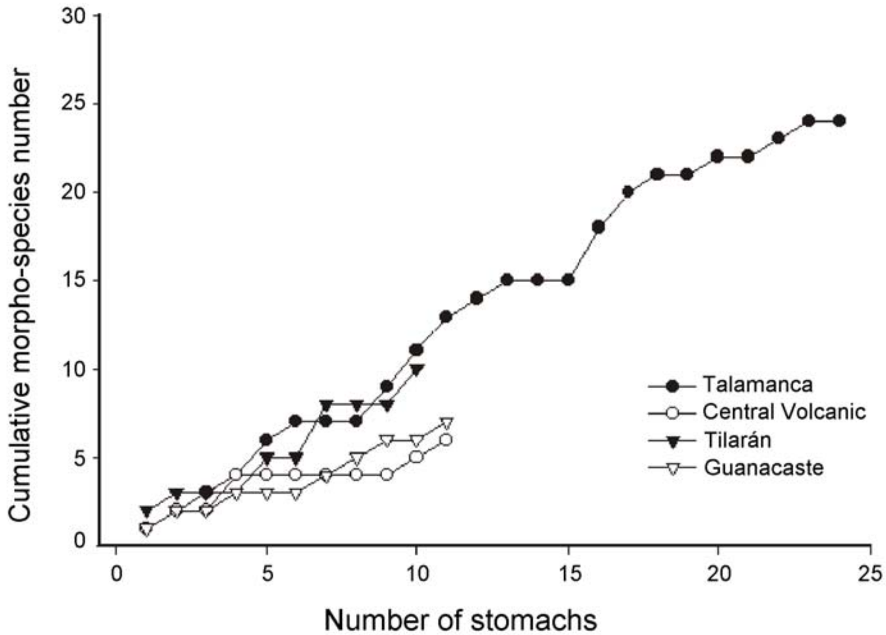

FIG. 2. Cumulative curves of seed morpho-species eaten by Black-and-yellow Silky-flycatchers in four mountain ranges (Talamanca, Central Volcanic, Tilarán, and Guanacaste).

ability and area of subalpine, elfin, and upper montane forests, also play a significant role in determining local abundance of Black-and-yellow Silky-flycatchers throughout its geographical distribution.

Diet composition. The Black-and-yellow Silky-flycatcher is an obligate frugivore that even feeds fruits to its fledglings (GB, pers. observ.). We identified 36 genera of fruits from 58 stomach contents (Table 4); only two stomachs contained insect parts. Thus, Black-and-yellow Silky-flycatchers consume a relatively large number of fruit species. Black-and-yellow Silky-flycatchers were further observed to feed on 18 fruit species, 16 of which were also present in stomach samples (Table 4). The number of seed species present in the stomach samples varied little among localities and at least half of the stomachs contained seeds of only one species (Table 5).

The number of seed genera consumed by Black-and-yellow Silky-flycatchers overall was greater in the Talamancas than elsewhere (Fig. 2). The slopes of cumulative curves of seed genera consumed by birds (Talamanca = 1.02, Central Volacanic = 0.36, Tialrán = 0.75, and Guanacaste = 0.55) differ significantly among sites ($F = 8.55$, df = 3, 32, $P < 0.001$) (Zar 1984: 300–302). We also found significant difference when the two most similar slopes (Central Volcanic vs Guanacaste) were compared ($t = -2.18$, df = 16, $P < 0.05$). The comparison between Central Volcanic and Guanacaste slopes indicated significant differences among slopes of all mountain ranges (Fig. 2). However, there is no evidence that the curves are leveling off on any mountain range, indicating that the number of fruit genera consumed is underestimated at all sites.

TABLE 4. Fruit genera or species identified from stomach contents of 58 specimens of the Black-and-yellow Silky-flycatcher. Number of specimens in which a given plant species was found is included.

Fruit genera or species	Talamanca (25)[1]	Central Volcanic (11)	Tilarán (10)	Guanacaste (11)
Alstroemeriaceae				
Bomarea sp		1		
Aquifoliaceae				
Ilex sp				6
Araceae				
sp 1	1			
sp 2	1			
Araliaceae				
Dendropanax sp	1	6		
Oreopanax sp		1	2	
Schefflera robusta	4*	+	3*	1*
Arecaceae				
Geonoma sp				1*
Asteraceae				
Clibadium sp		+	1*	
Boraginaceae				
Tournefortia sp		1*		
Caprifoliaceae				
Viburnum sp	1*			
Chloranthaceae				
Hedyosmum sp	1	1		
Clusiaceae				
Clusia estenofila			5*	
Ericaceae				
Vaccinium consanguineum	1*			
Erythroxylaceae				
Erythroxylum sp			6	2
Euphorbiaceae				
Hyeronima sp			1	
Fabaceae				
sp 1	1			
Loranthaceae				
Gaiadendron punctatum	2*	+		
Psittacanthus sp		+		
Myricaceae				
Myrica sp	1*			
Myrsinaceae				
Ardisia sp	1*			
Myrsine pittieri	7*	1		
Polygonaceae				
Muehlenbeckia sp	2*			
Rosaceae				
Hesperomeles sp	1			

TABLE 4. Continuation.

Fruit genera or species	Talamanca (25)[1]	Central Volcanic (11)	Tilarán (10)	Guanacaste (11)
Rubiaceae				
Guettarda poasana			1*	3*
Psychotria sp	7	9	1*	
Sapindaceae				
Cupania sp			1	
Smilacaceae				
Smilax sp	1			
Solanaceae				
Cestrum sp	1*			
Solanum sp			+	
sp 1				
Symplocaceae				
Symplocos sp	1		1	
Thymelaeaceae				
Dapnopsis sp	1			
Winteraceae				
Drimys winteri	4*			
Undetermined				
sp 1	1			
sp 2				1
sp 3	1			
sp 4	1			

[1]Number of stomachs analysed.
*indicates plants on which birds were observed consuming fruits but not recorded in stomach contents.
+indicates plants on which birds were observed consuming fruits and also present in stomach contents.

Composition of the fruit genera eaten by Black-and-yellow Silky-flycatchers also varied among mountain ranges. In general, overlap in diet was highest between birds of the Talamanca and Central Volcanic ranges, and lowest between birds of the Talamanca and Guanacaste mountains Table 6). Differences in diet overlap across mountain ranges may be explained by differences in plant composition at those sites. A significant positive correlation was found between diet overlap values (Pianka's index) and overlap of fleshy-fruiting genera occurring among mountain ranges ($r = 0.62$, $n = 6$, $P < 0.05$).

Our estimation of the number of fruits consumed by the Black-and-yellow Silky-flycatcher throughout its geographical range in this study, however, is biased by sampling procedures and sample sizes. Due to logistical constraints, sites were visited at different times of the year (although repeated visits did occur). Consequently, apparent differences in diet among sites are likely influenced by temporal and spatial variations in phenological patterns, as well as fruit availability (Frankie *et al.* 1974, Opler *et al.* 1980, Loiselle & Blake 1991), and thus diet overlap values must certainly be underestimated. In addition, our sample sizes are small for all mountain ranges (Fig. 2). Continued sampling would probably

TABLE 5. Presence and abundance of seed genera or species obtained from stomach contents of Black-and-yellow Silky-flycatchers from Talamanca, Central Volcanic, Tilarán, and Guanacaste mountains. Standard deviations are given in parentheses.

Cordillera	Sample size	Range of seed species/indiv.	Average seed species/indiv.	Average seed number/indiv.	Percentage of samples with one seed species
Talamanca	25	1-4	1.8 (1.0)	37 (36)	44
Central	11	1-3	1.8 (0.78)	36 (23)	36
Tilarán	10	1-4	2.1 (1.1)	55 (27)	40
Guanacaste	12	1-2	1.2 (0.45)	15 (11)	75

TABLE 6. Overlap in plant (genera) composition in diet of Black-and-yellow Silky-flycatchers (above diagonal) and fleshy-fruiting plants (below diagonal) between mountain ranges. Overlap values were calculated using Pianka's index for niche overlap (Pianka 1973).

	Talamanca	Central Volcanic	Tilarán	Guanacaste
Talamanca		0.56	0.25	0.04
Central Volcanic	0.81		0.11	0.00
Tilarán	0.76	0.78		0.28
Guanacaste	0.61	0.68	0.66	

result in more fruit species being recorded at all sites (Fig. 2).

Another factor that may also influence fruit selection by Black-and-yellow Silky-flycatchers is the variation in plant species richness among mountain ranges (Lawton & Dryer 1980, Kappelle 1996, INBio data base). Mountain ranges differ significantly in richness of highland plant genera (Table 7). In addition, ANOVA results indicated that plant families differed in number of genera. This is not a surprising result and family was included in the ANOVA as a second source of variation. In general, results show that the Talamanca and Tilarán mountains contain more plant genera per family than either the Central Volcanic or Guanacaste mountains (Fig. 3). The Tilarán mountains have been intensively sampled by botanists, while the Central Volcanic is relatively undersampled (J. Gonzáles, pers. com.). Consequently, differences in sampling effort likely confound the geographical pattern of highland plant species richness. We expect that a gradient of decreasing plant species richness occurs from Talamanca to Guanacaste mountain, mirroring the reduction in area of highland forests (Fig 2). Nonetheless, Talamanca and Tilarán birds did contain more seed species than those birds in Central Volcanic and Guanacaste, thus matching results of plant richness.

Reproduction. Breeding activity of Black-and-yellow Silky-flycatchers is poorly known (Skutch 1965). The secretive behavior of this species makes courtship behavior difficult to study and nests difficult to find. Only two cup-shaped nests were found in this study; one in April and one in May (nest structure was described by Stiles & Skutch 1989). The first one was under construction in Miravalles volcano (Guanacaste) and the second was found in Villa Mills (Talamanca) with two eggs. Nests were found in elfin and subalpine

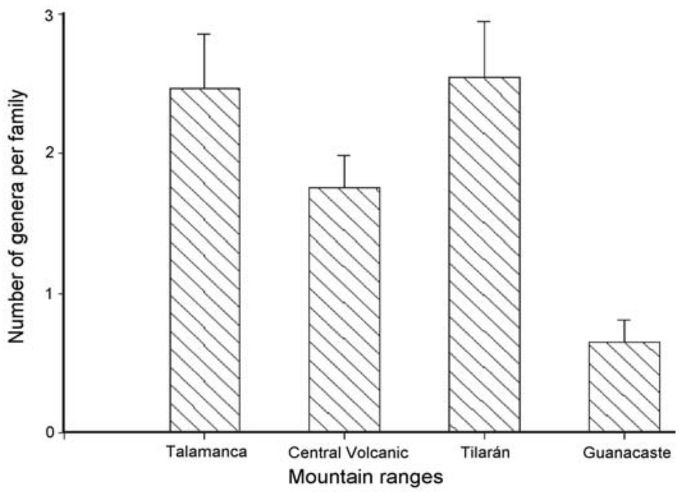

FIG. 3. Average and standard error of genera per family of fleshy-fruiting plants, potentially eaten by Black-and-yellow Silky-flycatchers in Talamanca, Central Volcanic, Tilarán, and Guanacaste mountains.

forests respectively, within 2 m above the ground. Considering the scarce information available on the reproduction of Black-and-yellow Silky-flycatchers, we evaluated its reproductive activity using gonad size, testes volume for males and largest follicle volume for females; data were available for January, March, April, May, June, July, September, and December. The data for all mountain ranges show that breeding activity in males was concentrated between March and July (males with testes volume of 200 mm^3 were considered reproductive) (Fig. 4). The timing of reproductive activity in males was similar

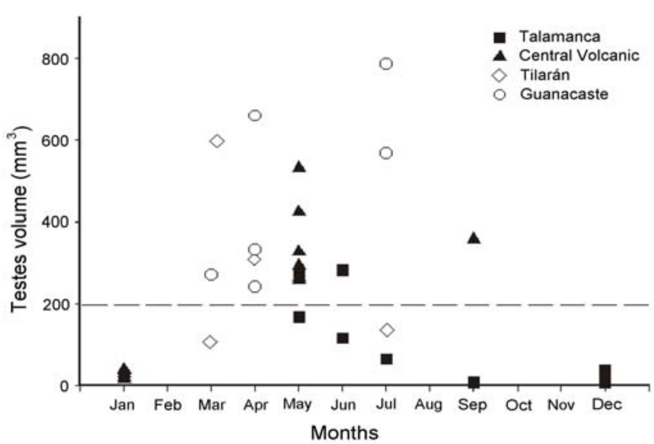

FIG. 4. Testes volume (mm^3) of Black-and-yellow Silky-flycatchers for Talamanca, Central Volcanic, Tilarán, and Guanacaste mountain ranges in Costa Rica. Reproductive individuals are distributed above dashed line.

TABLE 7. Summary of a two-way analysis of variance (without repetition) comparing number of genera per family among mountain ranges.

Effect	Variance	df	F	*P*
Mountain	36.94	3	22.65	< 0.001
ranges Family	14.13	47	8.66	< 0.001
Error	1.63	141		

throughout all cordilleras (from March to July; Fig. 4). Some outliers in July and September may represent a second attempt at reproduction, which is frequent in tropical birds when the first brood has failed due to predation or storms (Skutch 1976, Janzen 1978, Oniki 1979).

Reproduction in females presents a similar scenario (females with follicle volume of 7 mm^3 were considered reproductive). Like males, the reproductive period in females varied little among mountain ranges (Fig. 5). In general, the peak of reproduction in Black-and-yellow Silky-flycatchers occurs between March and May (fledglings were observed in June), a period which coincides with the onset of the rainy season in the highlands (Stiles 1983). Adjustment of reproduction with the rainy season is a common pattern in tropical birds, especially in relatively seasonal environments such as highland forests (Marchant 1960, Stiles 1983). This fine-tuning between breeding and rainfall may assure Black-and-yellow Silky-flycatchers a sufficient quantity of resources, particularly fruits, for raising offspring, or for independent fledglings (Fogden 1972, Wheelwright 1983, Stiles 1983, Loiselle & Blake 1991). Black-and-yellow Silky-flycatchers feed very young fledgelings with fruits and nestlings probably are also fed

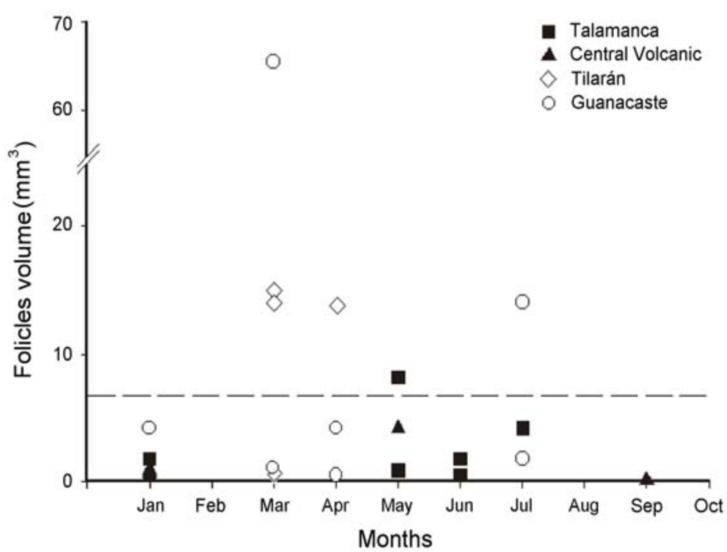

FIG. 5. Volume (mm^3) of largest folicule of Black-and-yellow Silky-flycatchers from Talamanca, Central Volcanic, Tilarán, and Guanacaste mountains. Reproductive individuals are distributed above dashed line.

fruits by adults. Iinsect parts were not found in stomach contents of reproductive females or males.

CONCLUSION

Black-and-yellow Silky-flycatchers are restricted to mainly subalpine/elfin and upper montane forests from western Panamá to the Guanacaste mountain range in Costa Rica. The abundance of this highland bird varies throughout its geographical distribution. Local abundance of Black-and-yellow Silky-flycatchers is apparently affected by area available of potential habitat (subalpine/elfin and upper montane forests) and volcanic activity. Particularly, intensity and frequency of volcanic catastrophes have likely had a significant impact on the relative abundance of Black-and-yellow Silky-flycatchers in the Central Volcanic and Guanacaste mountains, since abundance is low (or species is absent) on those massifs that have had frequent catastrophes. This highland bird is an obligate frugivore that reproduces between March and May, with little variation among mountain ranges. The peak of reproduction coincides with the onset of the rainy season. This pattern of reproduction timing may assure Black-and-yellow Silky-flycatchers a sufficient quantity of fruits for raising the offspring or for independent fledglings.

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