Wilson Bull., 92(2), 1980, pp. 229–244

NICHE RELATIONSHIPS BETWEEN TURQUOISE-BROWED AND BLUE-CROWNED MOTMOTS IN THE YUCATÁN PENINSULA, MEXICO

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As part of an overall comparison of the ecology and behavior of the Turquoise-browed (*Eumomota superciliosa*) and Blue-crowned (*Momotus momota*) motmots in the Yucatán Peninsula (Orejuela 1975, 1977), I investigated niche relationships between the species. In that region the Turquoise-browed Motmot generally occupies the drier sites with lower vegetation in the periphery, whereas the Blue-crowned Motmot occupies the wetter and higher forests of the central core (Ridgway 1914, Paynter 1955, Klaas 1968, Orejuela 1977). Where the habitats merge or interdigitate there is overlap of the distributions. In recent years there has been a dramatic reduction in the high forest that is the preferred habitat of *M. momota* (Pennington and Sarukhan 1968), presumably allowing the expansion of *E. superciliosa* and increasing the areas of sympatry. This situation permitted study of niche-parameters in areas of both joint and exclusive occurrence of the respective species.

Various aspects of behavior and ecology of the 2 motmots have been dealt with elsewhere (Orejuela 1977). Among these, it is pertinent here to mention that, whereas *E. superciliosa* nests colonially in large, steep banks, *M. momota* nests solitarily in small, concealed banks.

In this study I examined use, by each species, of 3 different categories of resources: space, food, and time, on the assumption that interactions between species and important differences in niches would likely involve use of 1 or more of these (Pianka 1969, Schoener 1974).

STUDY AREAS AND METHODS

Habitat occurrence.—One aspect of spatial relationships is habitat occupation. To study characteristics of habitats, I examined vegetation in 2 areas in southern Campeche, 1 in the vicinity of Escárcega (18°37′N, 90°44′W) occupied preferentially by *E. superciliosa*, and the other in the Mayan ruins of Chicanná near Xpujil (18°30′N, 89°26′W) where *M. momota* occurs alone.

I selected 6 plots for vegetation sampling in each area, to encompass the variety of forest types in areas adjacent to the motmot nesting banks. In sampling the vegetation from 27 June to 2 July 1974, I generally followed the method of James and Shugart (1970), but used square quadrats, 10 m × 10 m. Variables measured were: (1) percent canopy cover = the proportion of an area covered by leaves viewed from below; in each quadrat, 20 vertical sightings were taken along 2 transects; at each sighting, I estimated the percent of the vegetation visible through a 30-cm tube held 0.5 m overhead; (2) canopy height = the height of the tallest trees within the quadrat; (3) density = the number of individual trees by species within the quadrat; (4) basal area = area covered by tree trunks within the quadrat, based on diameter-breast-height measurements of all trees greater than 2 cm dbh; and (5) number of shrubs and vines, counted on 2 perpendicular strips 2 m × 10 m within the quadrat.

Use of habitats.—To study habitat-related behavior, I observed birds in areas adjacent to the nesting banks. The frequency of performance of the behavioral activities in 4 different structural levels of the vegetation was estimated.

Interspecific behavioral interactions.—I made observations in 3 jointly occupied sites near Escárcega, 1 west and 2 east of town. The site west of town was characterized by a small patch of forest with trees averaging 15 m high in the area adjacent to a nesting bank. A larger patch of suitable habitat was located about 500 m away. The 2 patches of suitable habitat were connected by a strip of secondary forest about 6–10 m high. This corridor was the preferred foraging habitat of several *E. superciliosa*, while *M. momota* foraged mostly in the habitat adjacent to the nesting bank.

Diets.—A quantitative analysis of diets was done by stomach analysis. Twenty-seven *E. superciliosa* and 13 *M. momota* were collected in the rainy season in 1973. One hundred *E. superciliosa* and 32 *M. momota* were collected at approximately weekly intervals from late February to the end of July 1974.

Stomachs were preserved in 10% neutral buffered formalin; contents were flushed into Petri dishes and significant parts, such as heads, wings and legs were separated for indentification, counting and volume determinations. Estimates of volume of food items were obtained from comparisons of length or width measurements of significant fragments with measurements of these characters in a standard reference collection of insects of known volumes. Volumes of reference items were determined by the amount of water displaced in a graduated cylinder or in a 2-ml syringe. Data were converted to percentages of total numbers and total volume for better comparison. Identification of food items was carried to the family level.

SPATIAL RELATIONSHIPS

Table 1 shows major differences between those habitats where *E. superciliosa* and *M. momota*, respectively, were found at high densities. Low, open canopy and dense understory (many shrubs and vines) accompanied the high densities of *E. superciliosa*. These forests lost 60–80% of the leaves during the dry season. Conversely, high, dense canopy and open understory favored high densities of *M. momota*. Only 20–40% leaf drop occurred in the dry season in these forests.

The tree species diversity calculated from density values with the information theoretical measure (Shannon 1949) was slightly higher in habitats favored by *E. superciliosa* (H = 1.44) than in those favored by *M. momota* (H = 1.36). Most of the difference was accountable to greater tree species richness (51 species in habitats favored by *E. superciliosa*, and 40 species in habitats of *M. momota*). The overlap (Horn 1966) of tree species was 0.13. There were 21 species in common between habitats of high density of *E. superciliosa* and habitats of high density of *M. momota*.

Three of the plots selected for vegetation sampling, near Escárcega, were used exclusively by *E. superciliosa*, while the other 3 were used by both *E. superciliosa* and *M. momota*. There were considerable differences

TABLE 1

CHARACTERISTICS OF HABITATS WHERE *E. SUPERCILIOSA* AND *M. MOMOTA* OCCURRED AT HIGH DENSITIES

Variable	*M. momota*		*E. superciliosa*
Canopy cover ($\bar{x}$ [range]) (%)	73 (62–88)		58 (35–79)
Canopy height (m) ($\bar{x}$ [range])	21 (16–25)		14 (8–22)
Number of shrubs and vines ($\bar{x}$ [range])	66 (39–91)		80 (30–133)
Leaf drop (%)	20–40		60–80
Number of tree species	40		51
Tree species diversity[1]			
% numbers	1.36		1.44
% basal area	1.10		1.16
Tree species overlap[2]			
% numbers		0.23	
% basal area		0.13	
Most important tree species[3]			
Manilkara zapota	35	*Lysiloma bahamensis*	34
Unknown A	20	*Blephardium mexicanum*	19
Gliricidia sepium	18	*Dyospyrus spectabilis*	18
Unknown B	15	unknown C	12
Drypetes latirifolia	11	*Bursera simaruba*	9
Brosimum alicastrum	9	*Vitex gaumeri*	9
Talisia olivaeformis	8	*Cecropia peltata*	7
Bursera simaruba	8	*Cochlospermum vitifolium*	5
Ehretia tunifolia	5	*Metopium brownei*	4

[1] Based on Shannon's (1949) information theoretical measure.

[2] Based on Horn's (1966) overlap index.

[3] Importance value = relative density + relative basal area.

between these sets of habitats (Table 2). *E. superciliosa* habitats showed a significantly lower canopy cover ($t = 5.63$, df = 118, $P < 0.05$), lower canopy height ($t = 6.78$, df = 12, $P < 0.05$), and higher number of shrubs and vines ($t = 5.27$, df = 4, $P < 0.05$), than habitats where both species occurred. Canopy height in jointly occupied habitats was intermediate between exclusive habitats of *E. superciliosa* and *M. momota.* Of 51 different tree species in the 2 sets of habitats, 10 were present in both types of habitats. The tree species overlap (Horn 1966), calculated from species densities, was 0.33.

E. superciliosa appeared more flexible in habitat requirements than *M.*

TABLE 2
HABITAT CHARACTERISTICS OF AREAS OCCUPIED EXCLUSIVELY BY *E. SUPERCILIOSA* AND AREAS OCCUPIED BY BOTH *E. SUPERCILIOSA* AND *M. MOMOTA* IN THE VICINITY OF ESCÁRCEGA, CAMPECHE

Variable	*E. superciliosa/ M. momota*		*E. superciliosa*
Percent canopy cover ($\bar{x}$ [range])	75 (72–79)		42 (35–81)
Canopy height (m) ($\bar{x}$ [range])	17 (10–22)		11 (8–13)
Number of shrubs and vines ($\bar{x}$ [range])	45 (30–58)		114 (99–133)
Tree species diversity[1]			
% numbers	1.22		1.25
% basal area	1.03		1.04
Tree species overlap[2]			
% numbers		0.33	
% basal area		0.50	
Most important tree species[3]			
Lysiloma bahamensis	36	*Blephardium mexicanum*	34
Dyospyrus spectabilis	35	*Lysiloma bahamensis*	33
Unknown C	20	*Cecropia peltata*	14
Vitex gaumeri	17	*Bursera simaruba*	10
Metopium brownei	7	*Cochlospermum vitifolium*	9
Chrysophila argentea	7		

[1] Based on Shannon's (1949) information theoretical measure.
[2] Based on Horn's (1966) overlap index.
[3] Importance value = relative density + relative basal area.

momota. The former species was able to occupy low, partly deciduous forests with many shrubs and vines, as well as medium-stature, partly deciduous forests with few shrubs and vines. *M. momota* only occupied forests with few shrubs and vines, and preferred forests of medium-to-high height.

Use of habitats.—Table 3 shows differences in 3 main types of behavioral use of habitats. It appeared that *E. superciliosa* performed calling, preening and foraging at approximately the same level in the habitat; all were most frequent at tree level 1. *E. superciliosa* foraged considerably in forest-edge situations and a great portion of the food was obtained on the wing. *M. momota,* on the other hand, generally foraged in levels of the

TABLE 3
FREQUENCY OF BEHAVIORAL ACTIVITIES OF *E. SUPERCILIOSA* AND *M. MOMOTA* ACCORDING TO HABITAT STRUCTURE

	Ground		Shrub (1–5 m)		Tree level 1 (5–15 m)		Tree level 2 (15–25 m)	
Level	*E.s.*	*M.m.*	*E.s.*	*M.m.*	*E.s.*	*M.m.*	*E.s.*	*M.m.*
Behavior								
Feeding	xx[1]	xxx	xx	xx	xxx	x	—	x
Calling	—	—	xx	—	xxx	xx	x	xxx
Preening	—	—	xx	x	xxx	xx	x	xxx

[1] One, 2 and 3 x's represent rare, common and frequent performance, respectively.

vegetation different from levels where it preened and called. Foraging was common at tree levels 1 and 2. *M. momota* foraged mostly inside the forest.

Interspecific behavioral interactions.—At the nesting bank west of town, I witnessed many cases of interspecific hostility. *M. momota* repeatedly displaced and sometimes chased *E. superciliosa* whenever individuals of either of 2 pairs of this species approached the nest bank where the former had a nest. By this means, the *M. momota* eventually obtained exclusive rights to a bank 6 m wide.

The nesting banks in the sites east of Escárcega were rather large (15 m wide) and well-concealed. Adjacent to the nesting banks were large, semicircular open areas (50–75 m radius) bordered by forests 10–15 m high. Opposite the nesting banks there were large patches of tall forest (15–25 m). The lower forests were generally used by *E. superciliosa* and the taller forests by *M. momota*, although crossovers frequently took place. I observed very little interspecific aggression at these sites. Neither species seemed to react aggressively to the presence of the other, even when 1 species gave its species-specific call in the vicinity of a member of the other species.

The situation described in the sites east of town resembled what Cody (1974) labeled partial interspecific territoriality. It appeared that whenever there were sufficient suitable habitat patches and large, concealed nesting banks, the socially dominant *M. momota* reduced its aggression toward *E. superciliosa*. However, when the patches were too small or too far apart from each other or from the nesting banks, and/or the nesting banks were small and fairly open, interspecific aggression occurred. *M. momota*, in such situations, also displayed aggression toward Great Kiskadee (*Pitangus sulphuratus*), Social (*Myiozetetes similis*) and Boat-billed (*Megarhynchus pitangua*) flycatchers.

TROPHIC RELATIONSHIPS

When closely related species of birds overlap in distribution, competition for food is usually reduced by differences in prey size (Hespenheide 1966, Ashmole 1968, Ohlendorff 1974), different kinds of prey (Lack 1945, Holmes and Pitelka 1968, Baker and Baker 1973), and/or differences in foraging behavior (MacArthur 1958, Orians and Horn 1969, Snow and Snow 1971, Morse 1973).

Although abundance of prey populations was not measured, both motmot species were found to be principally opportunistic insectivores. Insects accounted for 93.7% by volume of the diet of *E. superciliosa* and 84.2% of *M. momota*; gastropods, arachnids, chilopods and plant reproductive parts were also consumed.

An overall comparison of the diets of *E. superciliosa* and *M. momota* revealed several major differences (Table 4). The contribution of hymenopterans and lepidopterans to the diet of *E. superciliosa* was considerable (26.1% of the total diet), whereas in *M. momota* these 2 taxa comprised only 4.2% of the total consumption. The percentages of coleopterans were 39.5% for *E. superciliosa* and 51.9% for *M. momota. E. superciliosa* consumed a substantially higher proportion of actively flying insects and a lower proportion of ground arthropods than *M. momota*. As an index of the breadth of the food niche I used the Shannon (1949) information theoretical measure. Prey diversity by volume was higher for *E. superciliosa* ($H = 1.3$) than for *M. momota* ($H = 1.0$). The richness factor of the diversity measure was higher for *E. superciliosa* (53 families) than for *M. momota* (37 families). Certain families might have been under represented because of the smaller sample size of *M. momota.*

The degree of specialization was calculated from the formula $R = 1 - H/Hmax$ (Horn 1968). In this formula, H is Shannon's diversity measure and Hmax equals log of N (N = the number of categories). *M. momota* showed a greater degree of specialization ($R = 0.39$) than *E. superciliosa* ($R = 0.27$), when volume data were used. Overlap measurements based on families of prey taxa indicated an interspecific food overlap of 70%, based on Horn (1966).

There were marked seasonal changes in diets (Table 5, Fig. 1). Mean prey volume of *E. superciliosa* during the dry season was 0.3 ml. During the wet season, *E. superciliosa* took significantly larger prey ($\bar{x} = 0.4$ ml) ($t = 3.17$, df = 316, $P < 0.05$). Particularly significant was the contribution of prey of volumes 0.5–1.0 ml. *M. momota* also consumed significantly larger prey in the wet season (0.6–1.2 ml; $t = 4.0$, df = 79, $P < 0.05$). There was a decrease in the diversity of prey taken during the wet season in both species.

TABLE 4

OVERALL COMPARISON OF THE DIET OF *E. SUPERCILIOSA* AND *M. MOMOTA*: NUMBER AND VOLUME OF FOOD ITEMS IN EACH FOOD CATEGORY

	Momotus momota			*Eumomota superciliosa*		
Taxonomic group	No.	% no.	% vol.	No.	% no.	% vol.
Gastropoda	15	9.5	0.9	12	2.0	0.6
Chilopoda	4	2.5	0.8	2	0.3	0.3
Diplopoda	4	2.5	3.8	—	—	—
Scorpionida	2	1.3	0.4	—	—	—
Araneida	7	4.4	1.6	4	0.7	1.2
Amaurobiidae	—	—	—	2	0.3	0.2
Dysteridae	1	0.6	0.1	—	—	—
Thomicidae	—	—	—	1	0.2	0.1
Lycosidae	5	3.2	1.1	—	—	—
?	1	0.6	0.4	1	0.2	0.9
Collembola	—	—	—	1	0.2	0.1
Odonata	—	—	—	2	0.4	0.2
Aeshnidae	—	—	—	1	0.2	0.1
?	—	—	—	1	0.2	0.1
Orthoptera	36	22.8	15.4	38	6.4	15.0
Acrididae	8	5.1	2.7	30	5.1	9.9
Tettigoniidae	8	5.1	8.7	1	0.2	0.5
Gryllidae	15	9.5	2.5	5	0.8	4.2
Mantidae	1	0.6	0.7	—	—	—
Phasmatidae	1	0.6	0.3	—	—	—
Blattidae	2	1.3	0.3	—	—	—
?	1	0.6	0.2	2	0.3	0.4
Mallophaga	—	—	—	2	0.3	0.1
Hemiptera	7	4.3	2.1	49	8.4	3.1
Gelastocoridae	—	—	—	1	0.2	0.1
Corizidae	1	0.6	0.6	—	—	—
Reduviidae	1	0.6	0.2	1	0.2	0.1
Largidae	—	—	—	1	0.2	0.1
Pyrrhocoridae	—	—	—	13	2.2	1.1
Coreidae	1	0.6	0.4	9	1.5	0.7
Pentatomidae	4	2.5	0.9	23	3.9	0.9
?	—	—	—	1	0.2	0.1
Homoptera						
Cicadidae	9	5.7	10.0	26	4.4	9.7
Coleoptera	57	36.0	51.8	241	40.3	39.7
Cicindelidae	—	—	—	5	0.8	0.4
Carabidae	8	5.1	4.7	8	1.3	1.9
Leiodidae	—	—	—	2	0.3	0.3

TABLE 4
CONTINUED

	Momotus momota				*Eumomota superciliosa*		
Taxonomic group	No.	% no.	% vol.		No.	% no.	% vol.
Silphidae	—	—	—		2	0.3	0.1
Cantharidae	1	0.6	0.4		2	0.3	0.1
Cleridae	—	—	—		2	0.3	0.1
Buprestidae	1	0.6	0.2		19	3.2	5.4
Nitidulidae	—	—	—		1	0.2	0.1
Tenebrionidae	1	0.6	0.7		5	0.8	0.7
Passalidae	—	—	—		5	0.8	2.4
Scarabaeidae	38	24.1	44.4		98	16.5	21.4
Trogidae	—	—	—		1	0.2	0.1
Cerambycidae	1	0.6	0.3		22	3.7	2.6
Chrysomelidae	—	—	—		8	1.3	0.6
Curculionidae	3	1.9	0.6		52	8.8	2.8
?	4	2.5	0.5		9	1.5	0.7
Lepidoptera	10	6.3	3.7		35	6.0	9.2
Papilionidae	3	1.9	1.1		14	2.4	2.7
Pieridae	—	—	—		—	—	—
Liparidae	3	1.9	1.1		—	—	—
Sphingidae	—	—	—		4	0.7	2.1
?	4	2.5	1.5		17	2.9	4.4
Diptera							
Asilidae	—	—	—		2	0.3	0.1
Hymenoptera	6	3.7	0.5		176	29.6	15.2
Braconidae	—	—	—		2	0.3	0.1
Chalcididae	—	—	—		1	0.2	0.1
Chrysididae	—	—	—		1	0.2	0.1
Mutillidae	—	—	—		12	2.0	2.7
Scoliidae	1	0.6	0.2		—	—	—
Formicidae	3	1.9	0.1		19	3.2	0.6
Vespidae	—	—	—		10	1.7	1.0
Sphecidae	—	—	—		2	0.3	0.1
Apidae	1	0.6	0.1		128	21.5	10.4
?	1	0.6	0.1		1	0.2	0.1
Reptilia	1	0.6	0.1		3	0.5	0.9
Monocotyledonea			0.1				—
Dicotyledonea			8.5				3.4
Total no. items	158				593		
Food diversity (no.)[1]		1.3				1.3	
Food overlap (no.)[2]				0.7			
Food diversity (vol.)[3]			1.0				1.3
Food overlap (vol.)[4]				0.7			

[1] Based on Shannon's (1949) information theoretical measure, and using number data.

[2] Based on Horn's (1966) overlap index, and using number data.

[3] Based on Shannon's (1949) information theoretical measure, and using volume data.

[4] Based on Horn's (1966) overlap index, and using volume data.

TABLE 5

COMPARISON OF SIZES OF PREY TAKEN BY *E. SUPERCILIOSA* AND *M. MOMOTA* IN THE YUCATÁN PENINSULA

	Size class of prey (cm)						
Species	≤0.24	0.25–0.50	0.51–0.75	0.76–1.00	1.01–1.50	1.51–2.00	>2.00
			Dry season				
E. superciliosa	75.2[1]	8.7	6.6	5.6	3.8	—	—
M. momota	33.3	32.0	2.7	10.7	18.7	2.7	—
			Wet season				
E. superciliosa	35.8	17.3	34.7	9.8	2.3	—	—
M. momota	19.3	25.0	11.4	5.7	18.2	12.5	8.0
			Overall				
E. superciliosa	53.6	13.4	22.0	7.9	3.0	—	—
M. momota	25.8	28.2	7.4	8.0	18.4	8.0	4.3

[1] Percent of number of items.

In the dry season there was smaller contribution of coleopterans to the diet of both motmots. During the dry season, the small contribution of coleopterans in *E. superciliosa* was compensated for by large proportions of orthopterans, hymenopterans (*Apis* spp.) and homopterans. The reduction in coleopterans in *M. momota* was compensated for by increased orthopterans and homopterans (mainly cicadas). In the wet season, large coleopterans (Scarabaeidae and Passalidae) and lepidopteran larvae were consumed by *E. superciliosa. M. momota* also increased intake of coleopterans (Scarabaeidae, Tenebrionidae), lepidopteran larvae and fleshy fruits. Greater detail on dietary composition is given by Orejuela (1975).

In the change from dry to wet season, there were reductions in orthopterans, homopterans and hemipterans in the diet of *M. momota,* and in hymenopterans in the diet of *E. superciliosa.* Large numbers of coleopterans were taken by both species in the wet season. The most significant differences in diet preference were observed during the dry season. At this time, both species broadened the spectrum of prey consumed.

Trophic morphology and behavior.—The interplay between morphology and behavior of a species imposes certain constraints on the kind and size of prey taken. Table 6 indicates differences in morphology and behavior between *E. superciliosa* and *M. momota.* These differences in trophic adaptations underlie dietary differences discussed above.

Body size differences were correlated with prey size. *E. superciliosa* consumed significantly smaller prey ($\bar{x}$ = 0.4 ml) than *M. momota* ($\bar{x}$ = 0.9

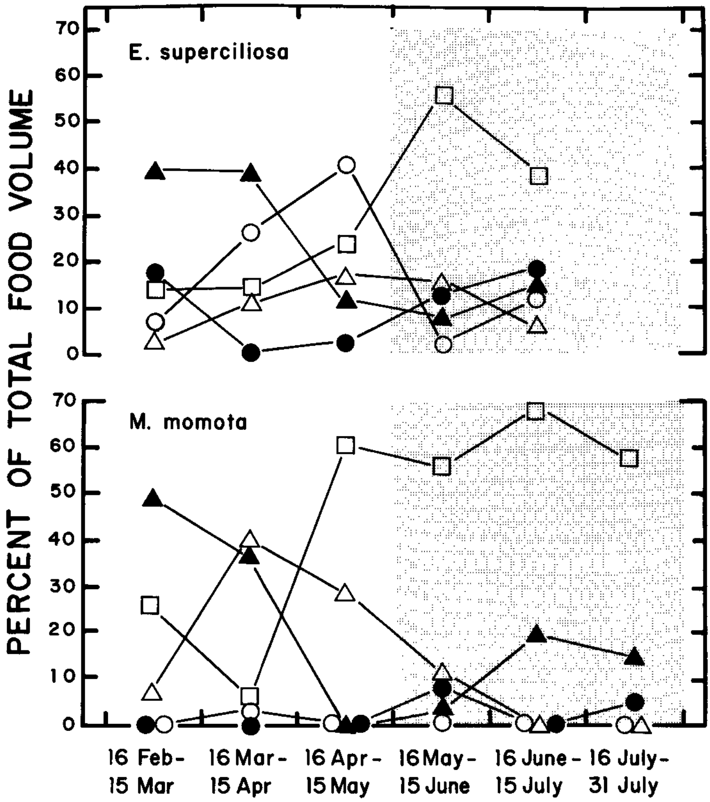

FIG. 1. Changes through time in the proportion of the most important food items in the diets of *E. superciliosa* and *M. momota*. Squares = Coleoptera, open circles = Hymenoptera, solid circles = Lepidoptera, open triangles = Hemiptera-Homoptera and solid triangles = Orthoptera. Stippled area indicates wet season.

ml) ($t = 5.51$, df = 345, $P < 0.05$). Differences in bill shape were also correlated with prey differences. Ashmole (1968) stated that long, light bills are particularly useful to species which capture active flying insects. The bill of *E. superciliosa* is long and light; it is also flat, wide and finely serrated. The diet of *E. superciliosa* showed a substantial amount of actively flying insects such as hymenopterans. The short, deep, narrow and deeply serrated bill of *M. momota* seems particularly suited for handling large insects, crushing mollusks and crushing seeds.

Differences in bill shapes have probably resulted from intense selection during the dry season when food was most likely to have been limiting. During the rainy season, both motmot species used the most abundant

TABLE 6

MORPHOLOGICAL AND BEHAVIORAL COMPONENTS OF THE FEEDING ADAPTATIONS OF *E. SUPERCILIOSA* AND *M. MOMOTA*

Components	*E. superciliosa*	*M. momota*
Morphological		
Body weight (g)	63.9 (N = 150)	110.4 (N = 45)
Bill shape[1]		
length (mm)	32.2	29.3
depth (mm)	10.0	11.8
width (mm)	11.5	9.4
serrations (no.)	45.7	10.9
depth/length	0.3	0.4
Central rectrix		
length (mm)	199	227
barbless section	long	short
Behavioral		
Sociality	colonial: group forager	territorial: solitary forager (pairs)
Flight pattern	short flights; flaps and glides; many flycatchings; maneuverable	long, straight flights; only flaps; few flycatchings; direct flight
Foraging tactic	sit-and-wait	widely foraging

[1] Measurements taken at nostril level.

and energy-rich prey (large coleopterans) irrespective of the divergent specializations of their bills.

"Sit-and-wait" and "widely foraging" (Pianka 1966) were the 2 important tactics used by motmots in capturing prey. *E. superciliosa* preferred the sit-and-wait tactic. The predator waited on a perch until a moving prey came close. A fast flycatching sally or short pursuit with a quick bill-snapping secured the prey. This foraging pattern undoubtedly furnished many small items to the diet. Its advantage lies in the economy of pursuit time and the small handling cost (Schoener 1971). *M. momota* favored a more widely foraging tactic. By means of rapid and direct flight, several patches were exploited in brief periods. The cost of this method lies in the search for suitable prey (Schoener 1971). For *M. momota* the energy return per large prey item presumably balances the high cost of searching and handling prey. This tactic was probably costly during the dry season when insect abundance was low, but very rewarding in the wet season.

TEMPORAL RELATIONSHIPS

The time of activity of motmots varied both daily and seasonally. During the dry season, both species confined their activities to the cooler times of the day: early morning and late afternoon. During the rainy season, temperatures were milder and more food was available; both motmots extended their activity periods to nearly all times of the day, although there was a tendency for greater activity during the morning.

Energetic consideration probably influenced the time of activity. *E. superciliosa* excavated their nest burrows in March, prior to the hottest months (April and May). In March, excavating activities were often performed during hot hours, but generally most work took place later in the afternoon. Skutch (1964) mentioned that "*M. momota* excavated during mid-day hours, in the rainy season when the climate was milder." The incubating parents spent the hottest hours inside the nest-tunnel, where the temperature was about 10°C cooler than ambient temperature. During the hottest hours, *E. superciliosa* sought cover under brushy areas, and *M. momota* sought shade under the tree canopy.

Activity periods were estimated from systematic observations. *M. momota* started its activity period before daylight and it was still actively foraging in the evening. It called until approximately 19:15. At this time, *E. superciliosa* was already roosting. The apparently small temporal separation of activities may have been an important factor in the differential use of resources between the motmot species. During the non-overlap period, *M. momota* may have had exclusive "rights" to many cicadas, millipedes and spiders, which constitute a significant portion of its diet.

DISCUSSION

Changes in resource use.—E. superciliosa and *M. momota* differed in their response to the seasonal changes by using different numbers of prey categories. A "food generalist" is a species using several prey categories with considerable frequency, whereas a "food specialist" is one using fewer prey categories (Morse 1971). There is strong selection for generalized diets in areas with considerable environmental fluctuations because of the unpredictability of resources (Orians 1972). Resource predictability varies both seasonally and between habitats. In Yucatán, resource uncertainty was highest during the dry season and in low partly deciduous forest types. Diets were more generalized in both species in the dry than in the wet season and in *E. superciliosa*, the inhabitant of the drier sites, than in *M. momota*. The greater relative food specialization of *M. momota* during the wet season might be due in part to its slightly greater body size. It is easier for a larger species to meet its energy demands during the favorable season by selecting fewer, but large items (Schoener 1971).

Variability of resources and the social system.—Gregarious and solitary existence are the 2 extremes of the range of social systems. The degree of sociality is influenced by seasonal fluctuations in food abundance, environmental predictability and availability of nesting sites (Crook 1965, Horn 1968, Brown and Orians 1970).

Brereton's (1970) study of parrots showed a tendency of solitary species to inhabit uniform, moist environments, while in arid regions there was a preponderance of gregarious species. There was a similar relationship between social system and environment in the 2 motmots: *M. momota,* the solitary species, lives in the more uniform, more moist environment, and the gregarious *E. superciliosa* inhabits the more unpredictable and drier habitats (Orejuela 1977).

The gregarious habit of *E. superciliosa* is enhanced by the selection of large, steep, and often high banks for nesting. Their nest-holes are naturally protected against most predators and the alarm signals of colony members may serve as an additional protection. Kruuk (1964) suggested that higher synchronization of breeding activities within a colony may decrease exposure time to predators. This may be the case with *E. superciliosa.* The general concealment of nests of *M. momota* may be the strategy by which solitary birds evade predators.

Interaction of niche parameters.—The totality of resources of an area may be partitioned in several ways. MacArthur and Levins (1964) suggested 2 general methods of niche specificity: (1) spatial separation through behavioral interaction; and (2) differences in resources because of structural specializations. The 2 motmots differed in both methods of niche specificity, and differences in use of space and food operated together to decrease the ecological overlap between the species. An idea of the overall interspecific niche overlap between *E. superciliosa* and *M. momota* was obtained by multiplying the mean interspecific niche overlap values for the 3 niche dimensions considered. Percent overlap values from 4 independent habitat measures (tree species diversity, canopy cover, canopy height and number of shrubs and vines) gave a mean spatial interspecific overlap value of 0.57. Percent overlap values from 6 measurements of trophic parameters (including numbers and sizes of prey during wet vs dry seasons as well as taxonomic composition of prey) gave a mean overlap value of 0.62. Temporal interspecific overlap was 0.95. Multiplication of the mean overlap values for the 3 dimensions gave a value of 0.33. There may be other independent dimensions that would tend to reduce interspecific overlap or increase the effective ecological distance between the competitors.

Because of differences in population sizes and in niche breadths between *E. superciliosa* and *M. momota,* the overlap affects them differently. Pianka (1969) suggested that interspecific competition should be more deleterious for the species with the smaller population size or with the narrower niche. Of the 2 species of motmots, *M. momota* had a smaller population size and narrower niche breadth in important dimensions (range of habitat types and diversity of diet) and thus might be expected to be at a disadvantage, even though it exhibits behavioral dominance over *E. superciliosa.*

Effect of man.—In the Yucatán Peninsula, extensive deforestation programs are being enacted, and the removal of already reduced tall forest (20-30 m) is an accelerating process, especially in the southern half of the peninsula. Agricultural and ranching zones are being carved out of the forest and a complete system of roads is under construction. The roads connecting the periphery with the newly opened central core of the peninsula provide avenues of invasion for opportunistic, colonizer species. Thus, the rapidly increasing demands for tolerance of habitat modification may first reduce, then even reverse, the competitive superiority of *M. momota* exhibited in interspecific hostile interactions. It is possible that *E. superciliosa* may restrict *M. momota* to a narrower range of habitats where they are together. If habitat modification goes even further, *E. superciliosa* may replace *M. momota* locally. A combination of factors may be involved in the habitat restriction and/or replacement: increased numbers of *E. superciliosa* because of increased availability of nesting banks, and the proliferation of low partly deciduous forest types; reduction of patches of medium-to-high partly deciduous forest in areas of overlap; increased predation on *M. momota* because of exposure of nesting areas; and exploitation competition by *E. superciliosa.* The last factor may operate similarly to the situation described by Stocker (1972) for voles (*Microtus* spp.). The subordinate species is present in much greater densities than the dominant species, and it may exploit the resources to the detriment of the dominant species, even if the dominant occasionally excludes subordinates.

SUMMARY

The motmots, *Momotus momota* and *Eumomota superciliosa*, were studied for possible competitive relationships in southern Campeche, Mexico, during parts of 1973 and 1974. Geographical and ecological distributions, nesting habits, food composition and feeding behavior were examined in each species.

The preferred habitats of *M. momota* were characterized by medium to high partly deciduous forest whereas *E. superciliosa* occupied fairly open forests of low partly deciduous aspect. The species displayed differences in the occupation of nesting habitats. *M. momota* nested solitarily in small nesting banks, while *E. superciliosa* formed nesting colonies in large steep banks. There were several cases of interspecific aggression at the nesting banks. At 1 site *M. momota* excluded *E. superciliosa*, but in another place both species nested in

the same bank. The diets of the motmots differed in kinds of prey, amounts of the same prey type, prey size, foraging behavior and, to a lesser extent, in time of foraging. *M. momota* foraged mostly on the ground where it generally obtained fewer but larger prey. *E. superciliosa* preferred small actively flying insects during the dry season and larger prey in the rainy season.

The accelerated habitat modification in the Yucatán Peninsula may affect *M. momota* more adversely than *E. superciliosa,* because of the former's greater habitat specificity, greater food specialization and smaller population density. *E. superciliosa* may even profit from man's activities; it can nest in exposed road banks and its preferred habitats are low, secondary forests which are proliferating rapidly.

ACKNOWLEDGMENTS

I extend special thanks to Dr. Ralph J. Raitt for providing advice and encouragement throughout the study. In addition, I wish to thank Señor Raul Narváez of Zoh Laguna, Señor Oscar Cedeño of Escárcega and Señor Felipe Osorio of Chicanná. I am grateful to my wife Kristin for her help with the fieldwork.

Financial assistance was provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and by the Society of the Sigma Xi through a Grant-in-Aid of Research.

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