NICHE DIVISION AND FORAGING TECHNIQUES OF FLYCATCHERS AT SIRENA, CORCOVADO, COSTA RICA

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Abstract (A.S.)

We studied the foraging and perch heights of three co-occurring species of flycatchers: gray-capped flycatchers (Myiozetetes granadensis), social flycatchers (M. similis) and tropical kingbird (Tyrannus melancholicus). The individuals in our study seemed to divide the resources spatially and temporally.

In the morning, Tropical Kingbirds foraged and perched in the taller trees. Gray-capped flycatchers foraged and perched nearer to the ground. Social flycatchers were absent. In the afternoon, the gray-capped flycatchers foraged and perched high and the social flycatchers used the lower areas. Kingbirds were absent in the afternoon.

In addition the tropical kingbird foraged more often over the canopy and the other two species foraged almost exclusively over the field.

Introduction (E.G.)

Three species of closely related flycatchers all coexist in the same types of habitats at the Sirena Station in Corcovado National Park, Costa Rica. Gray-capped flycatchers (Myiozetetes granadensis), social flycatchers (Myiozetetes similis), and tropical kingbirds (Tyrannus melancholicus) are frequently found foraging together and sharing the same perches in the fields and clearings surrounding the Sirena Station. Flying insects and berries are the primary food supplies of all three species. Sallying out from perches to catch aerial prey, hovering while gleaning insects off vegetation (hover-gleaning), and hovering to pluck berries are the foraging techniques of all these species (Stiles and Skutch, 1989). These facts seem to indicate that three species of birds are occupying the same space, and using the same techniques to obtain a common food resource.

However, the competitive exclusion principle states that no two species can occupy the exact same niche and coexist. When they do , it is predicted that one species will have some competitive advantage over the other, and over time the inferior species will be forced out of the niche. We hypothesized that more subtle divisions of the apparently shared niche exist between these three flycatcher species, thus enabling them to coexist. Differences in foraging behavior might be an important factor influencing niche division. Although food types and basic foraging techniques are the same among the species, it is likely that the heights at which birds forage, the time they forage, and the amount of time

they utilize different foraging tactics may differ. Since the competitive exclusion principle states that coexisting species won't occupy the exact same niche, we predicted we would observe significant differences in foraging techniques. We also hypothesized that inter-specific interactions during foraging play a role in this niche definition.

Methods (E.G.)

Our study plot was the approximately $160m^2$ area of the field and surrounding forest edge at the NE end of the airstrip at the Sirena Station, Corcovado National Park. Two sets of data were collected, between 14:30 and 17:30 on 22 January, and between 08:30 and 11:30 on 23 January. Two field observers monitored bird activity while a third recorded the observations. Information collected included the species being monitored, other species present, time of day, perch height, number and height of sallies and hover gleans, location of sallies (over canopy or field), and all interspecific interactions. Birds were monitored for the extent of time they remained in view and were foraging. When birds of more than one species were in view, a bird from each species was monitored. Occasionally the assistance of a third field observer, Tony Leukering, was employed so we could monitor three birds simultaneously.

For analysis; all foraging maneuvers for birds of the same species were pooled. Perch heights were tallied and analyzed for each sally from a perch. Mann-Whitney U-tests were used to compare mean perch heights and sally heights for the following: the gray-capped flycatcher between morning and afternoon, between gray-capped and social flycatchers in the PM, and between tropical kingbird and gray-capped flycatchers in the AM. G-tests were performed on contingency tables comparing the number of sallies over canopy vs. field, and number of sallies vs. hovergleans for all three species.

Had time permitted, we would like to have compared overall sally and perch height data (both AM-PM) between all species. We limited our tests based on the fact that social flycatcher presence was minimal in the morning, and tropical kingbird presence was minimal in the afternoon.

Results (A.S.)

The average sally and perch heights for Tropical Kingbirds (TK), Gray-capped flycatchers (GC) and Social Flycatchers (S) are summarized in Table 1. Tropical Kingbirds were found in the study area almost exclusively in the morning. A Tropical Kingbird was present for only five minutes in the afternoon. Socials occurred almost exclusively in the afternoon and were present for only 23 minutes in the morning. Since

we had such a small sample size for TK in the afternoon, and S in the morning, we did not consider these in our statistical analysis of the data.

The GC occurred during both morning and afternoon, but the perch height was significantly lower in the morning ($U_s = 876.5$, $n = 42$, $n_2 = 25$, $p < .001$). The average sally height also lower in the morning ($U_s = 1007.5$, $n = 44$, $n_2 = 31$, $p < .001$).

In the morning TK and GC were present. KB had a higher average perch height than GC ($U_s = 651.0$, $n = 31$, $n_2 = 21$, $p < .01$). The average sally height was also higher for KB than for GC ($U_s = 559.5$, $n = 27$, $n_2 = 24$, $p < .001$).

During the afternoon S and GC were present. S had a lower average perch height ($U_s = 965.0$, $n = 44$, $n_2 = 25$, $p < .01$), and also a lower average sally height ($U_s = 810.0$, $n = 41$, $n_2 = 25$, $p < .001$).

In addition to the spatial division by height, we also examined the areas over which the 3 species sallied. A G-test showed a significant difference in sally areas ($G = 33.07$, $n = 142$, $p < .001$): kingbirds foraged significantly more than did either S or GC over the canopy (Table 2).

We also noted two different types of prey capture. All birds captured insects in the air (sally) and also plucked them off vegetation without landing (hover glean) (Table 3). There were no significant differences among the species in the use of such foraging techniques ($G = 2.16$, $n = 146$, $p > .05$).

The sally heights for the three species are shown over time in Fig. 1. This shows the spatial and temporal divisions of resources between the three species.

Discussion (A.M.)

Our results indicate differences in the way three species of flycatchers, the tropical kingbird, the gray-capped flycatcher and the social flycatcher, utilize the area studied. Perch heights and sally heights among the species varied spatially and temporally during the period of our observations.

These observations are consistent with the theory that no two species can occupy the same niche, and that there must be some degree of separation and resource allocation among coexisting species. Although limitations of our study restrict us from drawing conclusions as to why the flycatchers disperse themselves in the way they do, our results give rise to several speculations.

It is likely that the tropical kingbird displaces the gray-capped flycatcher from the higher perches in the morning hours. In the afternoon, when the kingbird was absent from the area, the gray-capped's average perch rate increased from 2.5m to 7.0m and sally height increased from 5.1m to 8.1m. At one point in the morning when a gray-capped moved up to a 6m perch, it was soon displaced by a kingbird which chased it out of the

perch. The gray-capped then took a perch at 2m.

During the 23 minute period when two socials were present in the morning the kingbird chased them both out of 6m perches. No encounters were observed when the kingbird was displaced by either a gray-capped or a social. Thus it appears that the kingbird may play a dominant role in the interactions of the three species.

Kingbirds are known to frequent exposed, elevated perches (Stiles and Skutch, 1989) and the results from our study show that the kingbird we observed made 40% more sallies over the canopy (instead of the open field) than did the gray-capped or the socials. Therefore, even though we cannot determine whether one perch is better than another in terms of foraging efficiency, we can assume that the kingbird prefers high perches where it can survey the canopy.

Although there were no observed interactions between the gray-capped and social flycatchers, we suspect a similar hierarchy exists. Active displacements indicate the tropical kingbirds are dominant over gray-capped and social flycatchers. Their respective weights are 40g (tropical kingbird), 30g (gray-capped) and 27g (social) (Stiles and Skutch, 1989). Animal strength and size are frequently correlated with dominance. In addition, it was noted that during the twenty-three minutes in the morning when socials occupied perches, gray-cappeds were absent. It is possible the socials would not have entered the study area had the gray-cappeds been occupying the lower perches. Though we have no hard evidence, we speculate on the basis of these two observations that social flycatchers are subordinate to the gray-capped.

Although it seems feasible that some perches are better than others and that there is dominance and displacement among the three species studied such conclusions would require the support of further studies. Such studies could examine foraging efficiency at different perches which could provide evidence for superior and inferior perches. In order to assess temporal changes it would be preferable to study the birds over a longer period of time. Our study was limited to just one morning and one afternoon, therefore comparisons relying on time of day are minimally supported. Furthermore, it was difficult to watch all of the birds in the area at a given time. Although we were often confident that we were aware of all individuals in the area there is a likelihood that there were times when study species were present that were not taken note of.

It is impossible to make species-wide generalizations on data from just a few individuals in one small location, therefore the strength of our conclusions is limited to the individuals of the study.

Foraging behavior among the three species was the focus of our study. In observing differences in foraging behavior we found possible explanations for the coexistence of the three species. However, other aspects of the bird behavior and their niches would also have led to explanations. Locations of nesting sties could be important

in niche definition if food is not a limiting resource. Another possible explanation is predation. For example, kingbirds would be superior competitors but preferential predation on kingbirds could keep their numbers down. Their low numbers would therefore prevent them from excluding other species.

Despite these other possibilities the evidence from this study indicates that foraging behavior is a factor in niche partitioning among the flycatchers studied. Strong trends were observed that show resource allocation through hierarchies and foraging preferences of the individuals studied. Spatial partitioning of resources was observed and such partitioning may be what allows these three species to co-exist.

Table 1 Average perch and sally heights for tropical kingbirds (TK), gray capped flycatchers (GC) and social flycatchers (S) at Sirena, Corcovado from 0830 to 1115 and 1520 to (83).

	TK	GC	GC	S
Average perch height	0830-1115	0830-1115	1520-1831	1520-1831
	7.35m	4.50m	7.03m	2.38m
(n)	(31)	(28)	(40)	(47)
Average Sally height (n)	9.77m	3.00m	8.15m	3.54m
	(31)	(28)	(40)	(47)

TK=Tropical Kingbird
GC=Gray Capped Flycatcher
S=Social Flycatcher

Table 2 Sally Area Types for Tropical Kingbirds (TK), Greg Capped Flycatchers (GC) and Social Flycatchers (S) at Sirena, Corcovado from 0830 to 1115 and 1520 to 1831.

	TK	GC	S
Sally over Canopy (n)	61%	10%	9%
	(19)	(7)	(9)
Sally over Field (n)	39%	90%	91%
	(12)	(61)	(39)

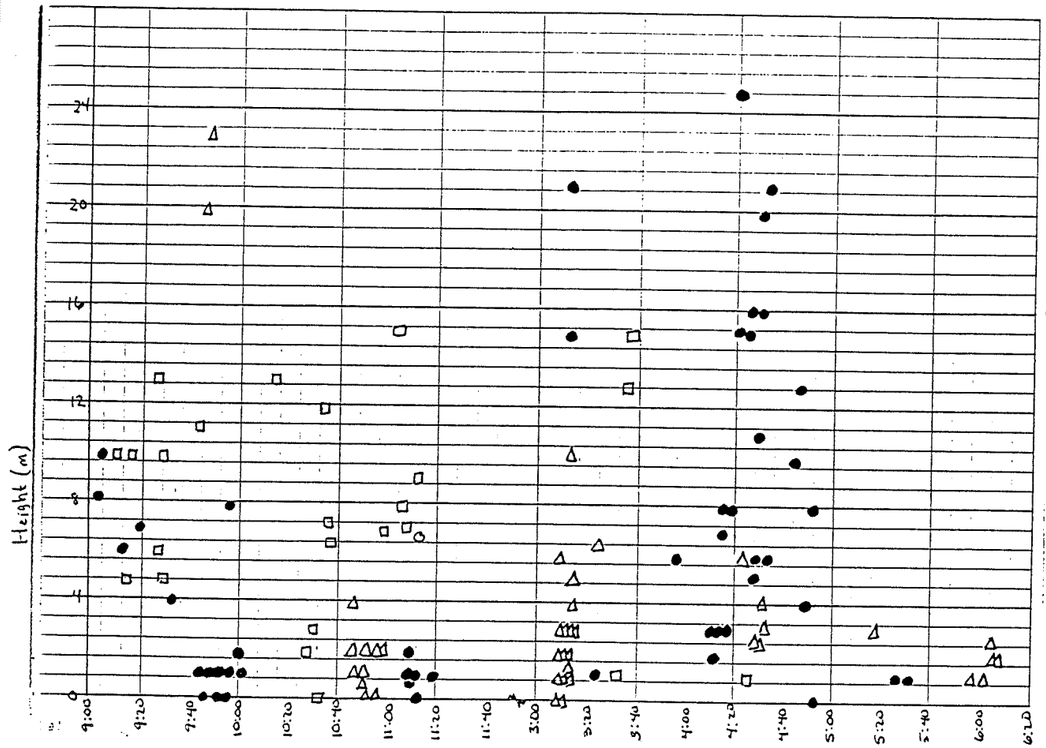
(n) = total number of observations

Table 3 Percent Sallies and Hover Gleans made by Tropical Kingbirds (TK), Greg Capped Flycatchers (GC) and Social Flycatchers (S) at Sirena, Corcovado from 0830 to 1115 and 1520 to 1831.

	TK	GC	S
Hover Gleans	23%	7%	11%
(n)	(7)	(5)	(5)
Sallies 77%	93%	89%	
(n)	(24)	(63)	(42)

(n) = total number of observations

Figure 1 Sally heights over time for Tropical Kingbirds (□), Social Flycatchers (△), and Grey-capped flycatchers (●) at Sirena Field Station, Corcovado, Costa Rica.



Literature Cited

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