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FORAGING BEHAVIOR OF THE VARIEGATED FLYCATCHER (*Empidonomus varius*) AT TWO NORTH AMERICAN VAGRANCY SITES IN THE CONTEXT OF FORAGING IN ITS NATIVE RANGE

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Abstract.—Only two vagrant Variegated Flycatchers (*Empidonomus varius*), a South American tyrannid that has an austral migrant population, are presently known from Florida. The first occurred in June 2013 in St. Johns County, and the most recent in October 2015 in Broward County. Little is known about most aspects of the species' biology. Observations on foraging behavior of the species in Florida in one case added detail and some new information on the relationship of search and aerial prey captures on foliage to the structure of a favored tree crown that appeared to complement and facilitate the manner of foraging. Search and prey-capture behavior in Florida was generally consistent with the limited information available in the literature on foraging in its native range. The species is an aerial sallying forager, taking flying insects in open air and stationary prey on foliage. It also consumes fleshy fruits, which may vary in importance depending on season in South America. Similarly, one individual in Florida combined frugivory with insectivory. The primary tactic for capturing prey on foliage and in the air, and in taking fruit *in situ*, appears to be a sally-stall maneuver. Detailed descriptive and quantitative work on variation of intraspecific foraging behavior is often scarce in the avian literature, but such detail is needed to support comparative analyses that seek to understand the evolution of foraging radiations in groups of related birds.

Variegated Flycatchers (*Empidonomus varius*) are austral migrants in the southern portion of their range in South America. The birds from this population (*E. v. varius*), which breed in northern Argentina, Uruguay, Paraguay, and southern Brazil, migrate as far north as western Amazonia and northeastern South America east to western Venezuela, and rarely Trinidad (Ridgely and Tudor 1994, ffrench 1973), to spend the austral winter. On rare occasions migrants mis-orient and move northward in error (in their austral spring) from their winter range, or overshoot their usual wintering destinations (in their austral fall), and end up in the United States or Canada in the

boreal fall or spring, respectively. Since 1977, six known individuals (Maine, early November [Abbott and Finch 1978]; Ontario, October to early November [Houle and Houle 1993, James 1991]; Tennessee, mid-May [Nicholson and Stedman 1988]; Washington state, early September [Denny 2009, Mlodinow and Irons 2009; Merrill and Bartels 2015]; and most recently, two in Florida [see below] in 2013 and 2015), have occurred far north of their normal breeding or wintering ranges in South America. Plumage coloration and pattern suggested the two Florida birds were likely representative of the nominate, migrant population that normally winters only on the continent of South America in northern tropical regions. The distinguishing features of *E. v. varius* present in both of the Florida individuals were dusky-brown feathers dorsally (in contrast, to paler brownish-gray or brownish in *E. v. rufinus*) and well streaked underparts on breast, upper abdomen, flanks, and under tail coverts (in contrast to reduced streaking, sometimes nearly obsolete, in *rufinus*) (Hilty 2003, Mobley 2004).

Empidonomus varius is the only member of its genus. Although not surprising, little is known about the ecology and behavior of the species in most of its broad range. The best information is a single study on a resident population (*rufinus*) in northeastern Brazil (Cintra 1997). Otherwise, bits of information mostly lacking detail appear in lists of species that summarize data from community-level studies (e.g., Las-Casas et al. 2012, Lasky and Keitt 2012, Malizia et al. 2005) or in regional treatments of local avifaunas (e.g., Aleixo and Galetti 1997, Pacheco et al. 2014). Other pieces of information come from studies on trophic ecology and adaptive radiation of tyrannid flycatchers in the Neotropics (Fitzpatrick 1980, 1981, 1985, Ohlson et al. 2008) and from one brief life history account (Mobley 2004). I spent about four hours observing the most recent vagrant occurrence of a Variegated Flycatcher in Florida, and was struck by its apparent dedicated focus on two trees, a fig (*Ficus*) and an adjoining Gumbo Limbo (*Bursera simaruba*; Burseraceae). Most trees in the neighborhood were mature Live Oaks (*Quercus virginiana*), which during my watches appeared to be ignored. Other field observers noted the bird occasionally visiting the oaks, apparently for brief periods of time. One observer, who watched the flycatcher on multiple days during its stay, referred to the fig as its "favorite tree" (L. Wegman, in litt. to Russ Titus, 6 November 2015).

My goals here are to (1) describe the foraging behavior that I observed in the 2015 vagrant at a site in south-eastern Florida, (2) characterize the apparent functional relationships between this bird and the architecture of the large fig (apparently the native Florida and northern neotropical strangler fig, *F. aurea*; Moraceae) and adjoining Gumbo Limbo, (3) add information on hawking behavior that was important to the 2013 bird in northeastern Florida, and (4) assess the

extent to which the limited observations in vagrant locations in Florida are representative of foraging behavior reported in its native range.

METHODS

My observations on foraging behavior reported here were opportunistic. Although I maintained a timely field record of my observations, and photographed the bird, the fruit source, and the trees, I made little effort to quantify my observations given the short time that I spent with the bird and distractions from other birders present. Observations focused on what appeared to be self-evident patterns of behavior that were performed repeatedly during the time that I was present on late-afternoon, 28 October, and mid-morning, 29 October 2015. I corresponded with three other observers (Rangel Diaz, Russ Titus, and Lee Wegman) to evaluate the extent their general observations on the bird's tree use corresponded or differed from mine. I relate my observations to the little information available in the published literature on the migratory population, as well as information on insectivory in a resident, tropical subspecies (*M. v. rufinus*) (Cintra 1997). Because my observations are based on a single individual, they are best described as anecdotal. I also illustrate (Fig. 1) and describe one foraging observation on the 2013 individual recorded on videotape during its single-day stopover. Here, I use the term "foraging" to refer to behaviors related to finding, capturing, and handling food. Moreover, I describe food capture maneuvers as specifically as possible to record details of behavior that may be useful to others who wish to undertake taxon com-

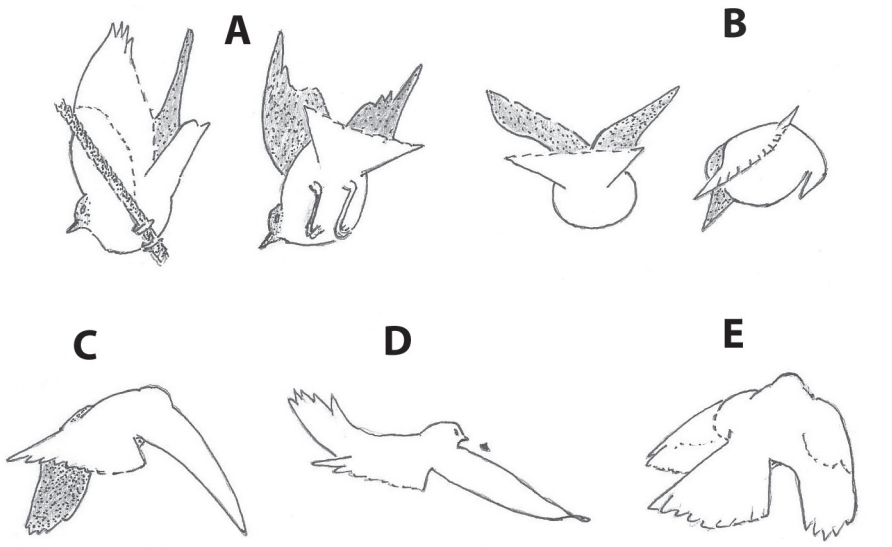

Figure 1. Representative tracings from video-frames of Florida's first vagrant of *Empidonomus varius* (St. Johns County, 2013; see Greenlaw 2015) performing a complete hawking maneuver. Stages are labelled A (flight initiation from powerline, left, and attack commencement, right); B (approach flight and maneuver adjustment by basal tail torsion, right); C (final approach, angle of attack increases); D (final approach, prey visible in front of head); E (braking and semi-stall as insect captured). See text for further comments.

parisons of tyrannids at the species or genus level. In most cases here I follow Remsen and Robinson's (1990) classification of aerial foraging maneuvers by arboreal birds to attack prey, but I depart by employing the term "hawk" or "hawking" to refer to the specialized form of aerial sallying to capture flying insects. The term "hawking behavior" is widely used and understood in the avian foraging literature. I use it because it avoids the ambiguity arising from an application of Remsen and Robinson's classification system stemming from maneuver categories (e.g., sally-stall, sally-hover, sally-strike) that apply to capturing insects in the air column and to taking arthropods found on fixed arboreal substrates (leaves, branches). In recent practice, authors using the classification segregate information on maneuver and substrate categories, and ignore relationships that can exist between the two aspects of trophic behavior (e.g., Gabriel and Pizo 2005, Martinez and Robinson 2016). Hawking behavior is sufficiently specialized that it deserves its own terminology (Fitzpatrick 1980, Robinson and Holmes 1982) in recognition of the special relationships between variation in aerial maneuver tactics that allow a flying bird to capture flying insects in three-dimensional space. More detail must be encouraged in the published literature on the foraging behavior of birds for which far too little is known in most species.

Observations

Florida records of Variegated Flycatcher.—Only two documented records of a Variegated Flycatcher exist for Florida. Both were verified by the Florida Ornithological Society Records Committee (Greenlaw 2015; A. Kratter, August 2016, ms. in preparation). The first was found by Diana Doyle on 5 June 2013 along Guana River Road at the entrance to Guana Tolomato Matanzas National Estuarine Research Reserve, St. Johns County (Greenlaw 2015). The habitat used by the bird was a semiopen area along a narrow road corridor bordered by scrub trees, and a disturbed mosaic of parking lots, buildings, and other patches of vegetation near water. It spent much or most of its time in intermittent, light rain hawking flying insects from a roadside powerline. A short video made by Doyle captured the perched bird scanning from the wire and performing a successful hawking maneuver (see below). The flycatcher was observed by several other birders. It remained for one day and was not seen again. The second individual (Fig. 2) was discovered by Russ Titus on 24 October 2015 in Evergreen Cemetery, Fort Lauderdale, Broward County. The vegetation consisted of an open, parklike stand of large, mature, and smaller sub-mature Live Oaks, several scattered strangler figs, and at least one Gumbo Limbo. Below the open canopy of trees, ground cover was mowed turf-grass lawn around the memorial stones and scattered, decorative shrubs. The bird remained until 31 October and then disappeared. While it was there, it was observed daily by numerous birders.

2013 observations.—As noted, the 2013 bird spent nearly all its foraging time hawking insects along the semiopen road corridor with screening trees on each side of the road. The detailed observations on its foraging behavior stem from two videoclips, one of which recorded a complete hawking maneuver. To my knowledge, nobody has characterized

Figure 2. Florida's second vagrant of *E. varius* (Broward County, 2015; FOSRC accepted, August 2016) perched in typical "sit-and-wait" fashion on a branch in a large fig (*Ficus aureus*) under layer of canopy foliage in semiopen upper crown. Perches offered vistas of leaf undersurfaces, which were watched for stationary prey. Captures were by sallies to foliage.

the movements of any passerine during a hawking maneuver based on an analysis of a taped record. Apart from the "sit-and-wait" (Huey and Pianka 1981) scanning session (at least 25 sec) before the launch, the sallying maneuver examined here was documented in full from its initiation on a powerline to capture of an insect. The perched, watchful phase involved abrupt, short rotations of the head, each alternating with a brief pause and rapid peering in its facing direction. Mostly the bird scanned to the front and sides to about 90°, but occasionally it turned its head to peer over its shoulder to the rear. The entire hawking maneuver from launch to capture lasted about two seconds, so the insect was fairly close to the bird. The small insect was visible on the tape and appeared to be heavy-bodied and short-winged. Earlier, a similar type of insect flew quickly on a parabolic course close over the perched bird's head, but the flycatcher appeared to ignore it or perhaps did not notice it.

As the bird leaned forward on its perch to initiate its aerial attack, it raised both wings fully over its back (Fig. 1A, left), and leaped into the air (Fig. 1A, right). Its momentum initially carried the bird below the

level of the powerline, but it quickly recovered and flew in the direction of its prey as it adjusted its course to the insect's changing position. Flight adjustment was inferred from variation in rotational positions of the spread-tail (Fig. 1B) early during its approach flight. As the bird closed on its prey, its angle of attack (body alignment relative to horizontal) increased (Fig. 1C) slightly, and its head started to elevate. Final closing attack (Fig. 1D) shows the insect close to the bird's head; the angle of attack of the flycatcher at this point is more exaggerated, with its head raised and its stereoscopic vision focused on its prey. The attack (Fig. 1E) came with a braking semi-stall maneuver, body angled upwards and wrists held up, and wings flared and cupped forward. The flared outer primaries exhibited strong, open wing slots during the capture. The bird apparently captured its prey successfully (the insect was not seen again flying past the bird), and immediately it banked and swerved right toward trees at the roadside.

2015 observations.—Observations of the 2015 bird revealed insectivory and frugivory. I observed hawking behavior on flying insects by the 2015 bird on 28 October, but not the next day during my watch. It spent time on exposed, small dead branches protruding above the live crown of the large Gumbo Limbo where the air column was visible 360° around the bird. Similarly, hawking also was observed by R. Diaz (in litt., 14 December 2015) on only one of his two visits. However, evidently it spent more time on 26 October "flycatching" in the air (L. Wegman to R. Titus, in litt.) than I encountered later in its stopover. My fieldnotes record estimated distances to prey of two hawking attacks, one about 3 m and a second about 10 m; both flights were flown horizontally from the perch. Both involved a terminal "sally-stall" capture maneuver (Remsen and Robinson 1990) similar to that illustrated in Fig. 1. In both instances, the bird returned to the same bare branches in the Gumbo Limbo to begin another period of watchfulness.

I saw frugivory on both days I observed the 2015 bird. Two other informants also mentioned watching the behavior on other days. The behavior was intermittent and lasted only long enough to snatch several fruits one at a time from the same small crop of ripe berries on an adventitious Virginia Creeper vine (*Parthenocissus quinquefolia*) about 4 m high on the upper, gnarled trunk of the fig where major limbs diverged. In each case, the flycatcher descended from higher perches in the crown, where it spent most of its foraging time, to a perch near the fruit source. From there it sallied about 3-4 m in a direct, horizontal flight followed by a partial, braking stall in front of the cluster when it grabbed a fruit, and returned to the same perch. The sally for fruit resembled a version of its hawking maneuvers. Fruits were simply swallowed whole without any preparation. On the two days I observed the bird, I watched it regurgitate and drop seeds as it sat on perches. Each creeper fruit is a fleshy berry

4-6 mm in diameter usually with two to three seeds. The fig itself had few fruits (one small cluster observed) and none of them was ripe.

Most of the bird's foraging activity involved sally-capture maneuvers at foliage from perches in the upper crown of a solitary fig in an open stand of mixed-age oaks. In a couple cases, I was not sure whether the prey substrate was a leaf or the air space near leaves. The fig was about 15 m tall (ca. 45-50 ft) and its broad, dome-like crown at least as wide. The bird perched in a fairly erect posture (45°-50° oblique) on open, horizontal or low-angled, upper interior branches below the semiopen, peripheral foliage layer, and scanned leaves and twigs near and far from its position (Fig. 2). Scan distances were judged from its attack behavior when it launched outward sally flights. Most sallies were outward maneuvers (n = 14) that ended (usually) with capture attacks on or (possibly) near foliage substrates. In two well-observed cases, the sally attacks were directed at foliage and employed a brief stall-strike or snatch maneuver similar to those observed in the videoclip of hawking and in plucking fruit on the wing (above). In one other well-observed case involving a maneuver directed at foliage overhead, the sally terminated in a brief stall-glean attack directed at the underside of a leaf. This sally was initiated steeply upwards and ended at a leaf cluster about 0.5-0.6 m above its perch, followed by a return to the same perch. In contrast, the outward, low-angled sallies at foliage varied from about four to six meters in length across a portion of the upper crown-spread. My notes on several sally maneuvers do not distinguish between the possibility of sally-strike on the way by, sally-stall, or sally-hover (flying in place) alternative capture attacks. In other cases, I was unable to see the attack substrate clearly from my position on the ground. In all outward sallies, the capture maneuvers carried the sallier away from its launch perch in the fig to a perch in another part of the crown. The sallying attacks were preceded by a variable "sit-and-wait" interval accompanied by scanning. It chiefly inspected foliage around and above its head in a series of sequential, rapid-peering scans preceded by short head rotations laterally from front to sides, or over its shoulder (Fig. 2). I did not witness visits to other trees in the vicinity, but, R. Diaz (in litt.) saw the bird leave on a long excursion, and thought it visited another fig in the cemetery. He also photographed it in a large oak perched on an interior branch below a relatively dense, peripheral foliage layer in a position similar to those chosen in the focal fig. L. Wegman (in litt.) reported seeing the flycatcher in another fig to the east, and perhaps in oaks, but it always returned to the first fig and the Gumbo Limbo. On the last day before the bird disappeared (31 October), a report on a birding listserv suggested the flycatcher may have been investigating other parts of the park-like cemetery. The status of the small fruit source in the fig just before its departure is unknown.

Discussion

Foraging behavior: vagrancy sites versus native range.—Here, I assume the behaviors of the two individuals in uncharacteristic geographic locations in Florida remain informative about foraging in the species. Species-typical behaviors, though flexible to a degree, are believed to be adaptive under the view that variation in these behaviors can affect the fitness of individuals. Increasingly, evidence supports the view that different search and food-capture tactics practiced by birds, each associated with a suite of morphological adaptations, allow effective exploitation of different food-type or patch-type resources present in different structural situations in habitats (e.g., Fitzpatrick 1980, 1985; Robinson and Holmes 1982; Schluter 1982; Moermond and Denslow 1985).

An issue arises concerning limited behavioral observations of a few individuals in out-of-range locations as to how representative the behaviors may be. Thus, the foraging behavior of a couple vagrant individuals in Florida need to be placed in the context of what may be known about this behavior in its native range. An observer can expect that in unfamiliar habitats an arboreal bird will exhibit flexibility in its use of unfamiliar plant species, but that it may be constrained by phylogeny and morphology during foraging to respond to similar vegetative structural features in similar ways and to perform similar search and prey capture tactics.

Except for details on insectivore foraging modes in Cintra (1997; see below), most published information is of a general nature. Remarks on foraging often are categorical, and refer to food type or trophic guild membership classifications offered in community or regional avifaunal studies. Categories applied to *E. varius* range in one population or another from frugivore, insects and fruits, primarily insectivore, insectivore, to omnivore (e.g., Haverschmidt 1968, Davis 1993, Malizia et al. 2005, Parrini and Pacheco 2011, Las-Casas et al. 2012, Laskey and Keitt 2012, Pacheco et al. 2014). These categories are only broadly informative. Four studies provided a general description of foraging modes or specific elements in the diet. Ridgely and Tudor (1989) noted that *E. varius* eats small fruits and sallies for insects in the air and on foliage, but they provided no details and spoke of the species as a whole. Another source reported that a single *E. varius* was observed catching swarming termites in the air (Vasconcelos et al. 2015). Parrini and Pacheco (2011) noted that *E. varius* and other species in southern Brazil ate soft fruits produced by the tree *Alchornea triplinervia* (Euphorbiaceae). Migrant *E. varius* commonly harvested fruits from this tree species before departure, and from a congeneric relative on its return. Most fruit were taken on the wing (92%, $n = 25$ cases), while only 2 cases involved taking fruit while perched. These authors reported that *E. varius* tended to alternate fruit capture

with insectivory, as I observed. Finally, in the only life history review of the species, Mobley (2004) describes food and foraging as "insects, also small fruits" and "hawks flying insects and sallies to hover-glean items from foliage." I cannot confirm "hover-gleaning," but I follow Moermond and Denslow (1985), and Remsen and Robinson (1990), in distinguishing a transitory stall maneuver (momentary, fluttering hesitation in flight) from flying in place for more than just a moment (true hovering). Florida birds appeared to practice the former behavior, but another observer may characterize the same behavior as "hovering." One student of tropical birds (Hilty 2003) described its foraging behavior in Colombia, where the migratory population often winters, as "sallies to air or flutters and hovers in front of foliage for insects and small fruit." Overall, my observations agree with most of what has been reported on foraging in Variegated Flycatchers. The species appears to be a frequent aerial forager that combines taking arthropods (mainly insects) and soft fruits in a modestly diverse diet. Observations on the Florida vagrants, albeit tentative, suggest that it uses similar capture tactics (sallying) to take insects on leaves and in the air, and small, soft fruits *in situ* from arboreal sources (also see Parrini and Pacheco 2011). Whether transitory stall-sallying is a frequent capture maneuver elsewhere remains to be seen, but I suspect it is considering its use in different contexts in Florida. If so, then the behavior may provide some understanding of a notable primary feather notch in *Empidonomus* not shared by its clade relatives (*Myiodynastes*, *Legatus*) that otherwise have similar plumage appearances; the modification is shared with two of its closest generic relatives in the same clade (*Griseotyrannus*, *Tyrannus*) (Ohlson et al. 2008, Mobley 2004). The emargination or notching on the inner webs of outermost primaries produces broad-based slots (Fig. 1E) that serve in other species to enhance lift at slow air speeds and to reduce stall-speeds (Savile 1957)—perhaps a useful feature during sallying capture maneuvers in the present case. Yet, as a generalist aerial forager, *Empidonomus* is intermediate in other ecomorphological structures related to foraging between *Legatus*, a frugivore specialist, and *Tyrannus* hawking specialists (Fitzpatrick 1985:466).

A single quantitative study (Cintra 1997) of foraging behavior in a tropical assemblage of semi-openland tyrannids in Pará, Brazil, included information on foraging tactics and vertical tree use of *E. varius* in a savanna habitat near Santarém. I assume that the population of *E. varius* there was the resident subspecies. Four modes of insectivory were recorded for *E. varius*, among which hawking was observed about 70% of the time, while sallying to foliage, characterized as "outward hover," "upward hover," and "upward strike" (terminology, Fitzpatrick 1980), constituted <15% each to complete the relative frequency in the sample of observations. Two of these capture modes involve "hovering;" in contrast, birds performing upward strikes take prey from an overhead leaf by a

rapid, flying approach, and snapping or "striking" the immobile prey on the way by without hovering (Fitzpatrick 1980, Cintra 1997). In Florida, I did not witness an upward strike, but I did see what some observers in the literature may call "hovering" at the target site. For both outward hover and upward hover Cintra (1997), true hovering may be more likely after an upward sally than after an outward sally (Fitzpatrick 1980:45). But, Cintra described his "outward hover" as featuring a "brief hovering" maneuver, which suggests the possibility of a fluttering stall at the end of the sally. Remsen and Robinson (1990) remarked that many reports of hovering captures in the literature may be examples of "sally-stalling." A cautionary remark is in order on Cintra's (1997) study, which as noted focused on a resident population of *E. varius*. Some people suspect that the migrant and resident populations may represent separate species (Hilty 2003, Mobley 2004). In any event, within the range of search and capture modes expressed in *E. varius* populations, one might expect variation in frequencies of use of these modes depending on geography, season, and resource availability among other potential factors. For example, it is possible that hawking may be less frequent in migrant populations and frugivory more important (Hilty 2003) than in resident populations in the Amazonian tropics.

Behavioral relationship to habitat structure.—My observations also implicated an apparent relationship between the foraging behavior of the 2015 bird and the structure of the two trees where it devoted most of its foraging effort. The apparent complementary match between behavior and tree structure evoked the impression of a definite functional connection between bird and trees. This impression, which I term "form/function" matching to habitat structure (Ricklefs 2000), is well supported by a body of work in the avian literature on foraging ecology concerning the importance to foraging birds of vertical and horizontal structure within habitats, plant species composition, foliage distribution, and foliage arrangement on twigs (e.g., MacArthur and MacArthur 1961, James 1971, Robinson and Holmes 1982, 1984, Whelan 1989, Parrish 1995). Such habitat-behavior relationships may be important in habitat selection (e.g., James 1971) and are associated with ecomorphological adaptations (such as beak size and shape) that can constrain behavior and also promote efficiency in finding, capturing, and processing food (e.g., Fitzpatrick 1985, Moermond and Howe 1988). Often sallying to arboreal substrates depends on spotting mid-distant to distant, stationary prey on the underside of leaves in moderately or well-lighted conditions from relatively open perches ("open-perch searchers;" Robinson and Holmes 1982). The distribution of the foliage in the focal fig reflected the condition of many broad-leaved forest trees that are mature, namely leaves chiefly occur in a continuous or semi-continuous shell around the periphery of the crown. This foliage distribution-type is described as "monolayered", in

contrast to younger trees in which foliage can be distributed through the crown volume from periphery to near the tree bole (multilayered) (Horn 1971). The focal fig, as in other monolayered trees, provided open, small branches near and below the foliage layer, which were suitable perches offering relatively unobstructed vistas of foliage near and moderately far from its vantage. No protruding twigs were present on the outside periphery of the canopy of the focal fig, so when it chose to hawk for flying prey in the air column beyond or above the trees, it moved to the adjoining Gumbo Limbo where it found several such perches. When it interrupted its other activities to pluck a few berries, it moved lower in the fig to a perch near the fruit source that provided open, horizontal flight access. The direct, unhesitant sallies to fruit clusters on the vine suggested the bird chose a cluster, perhaps even a particular berry, from its perch before it launched its foray. In contrast to the behavior of the flycatcher, a Northern Parula (*Parula americana*) entered clusters of peripheral foliage in the fig and searched leaves and twigs from the inside by active perch-shifting, each followed by brief scans; two prey attacks involved forward gleans from standing positions at near foliage.

The perch-height distribution measured by Cintra (1997) in savanna habitat in northeastern Brazil also appeared to express a relationship between perch use and foraging behavior. The puzzle in the distribution is the almost complete absence of perch use at the 90% level in trees in comparison to 100% and 60-80% levels. The most parsimonious explanation for this usage gap is that it reflected perch requirements of hawking (tops of crown in this species) and sallying to foliage (perches below the peripheral foliage canopy in the more open crown interior). Cintra's observations also describe the pattern of perch use in tree profiles by the 2015 Florida bird during perch sallying to foliage (fig, mostly 70-80% relative height) and hawking (Gumbo Limbo, 100%).

In summary, descriptions of foraging behavior of *E. varius* in South America encompass the behavior observed in Florida. The species is a semi-openland, sit-and-wait forager that specializes in sallying attacks on prey in open air and on foliage, and on taking small fruit. It was notable that the focal tree one individual used most often over a period of several days appeared to match the distance-search behavior of perch-to-foliage sallying to an overhead, umbrella-like foliage distribution above a network of open branches, which the bird used to locate potential prey. In contrast, hawking positions were from open peripheral perches at the top of an adjoining tree that permitted full view of the air column.

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