

SEARCH STRATEGIES OF TYRANT FLYCATCHERS

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Abstract. Aspects of searching behaviour among free-living South American flycatchers (Aves: Tyrannidae) are compared quantitatively. Flycatchers forage with stationary searching periods, followed either by an attempted prey capture (sally) or a 'give-up' flight to a new perch. Search times are proportional to body size within each of three categories of foraging behaviour: aerial hawking, sally-gleaning, and perch-gleaning. Over the family as a whole, search times are directly proportional to the size of the visual field scanned during the search. Intraspecific variations in search times are caused by local variations in prey density or visual complexity of the habitat. Between foraging modes, differences in searching and movement patterns are related to prey dispersion characteristics. Aerial hawkers regularly return to favoured perches, but foliage gleaners, which reduce the resources surrounding a perch by sallying only once, rarely return to a perch. In contrast to aerial hawkers, foliage gleaners appear to follow an organized scanning procedure on each perch, by searching nearby surfaces before they examine more distant prey substrates. Throughout the family, the median flight distance after a perch is abandoned is approximately twice the median search radius. Comparisons of search time distributions preceding sallies with those preceding give-up flights suggest that there is no single, optimal give-up time in a given habitat. Foliage-gleaning species appear to assess the amount of search time each perch warrants, presumably based on the degree of complexity of the search area. They either sally at prey before that time, or give-up when the allotted time has elapsed.

A growing body of experimental and field evidence supports theoretical predictions about how animals should forage so as to maximize their net rate of energy intake. As indicated in a review by Pyke et al. (1977), optimal foraging theories have described four categories of choices that a foraging animal faces: prey choice (optimal diet and meal size), habitat choice (optimal patch use), duration of foraging bouts in a patch, and movement patterns within the habitat. Studies of foraging strategies have examined all of these categories rather carefully through experimentally controlled behavioural studies (see Zach & Falls 1976a, b, c; Pyke et al. 1977; reviews in Krebs & Davies 1978). Studies of free-living animals have largely dealt with questions of optimal prey and habitat choice (e.g. Davies 1977; Goss-Custard 1977). In this paper I analyse field data on overall searching and movement patterns in a group of insectivorous bird species.

As discussed in detail elsewhere (Fitzpatrick 1980) nearly all tyrant flycatchers (Aves: Tyrannidae) use modifications of one characteristic foraging pattern: prey items are located during a stationary and measureable searching period on each perch. Prey capture normally occurs during a flight (= 'sally') from the perch to snatch insects either from the air (Aerial Hawkercatchers) or off some substrate (Sally-Gleaners). A few species specialize in picking prey from nearby surfaces without sallying (Perch-Gleaners). Following each prey

capture, the bird may either return to its most recent perch or else move some measurable distance to a new perch. Frequently, individual perches are abandoned before prey is spotted, resulting in a 'give-up' flight to a new perch. In the analyses to follow I quantify these habits based on data originally obtained for a separate study on flycatcher adaptive radiation. The patterns that emerged suggest strategic factors that influence search time, perch-to-perch movement patterns, and giving-up times (sensu Krebs et al. 1974) within free-foraging flycatchers. Critical tests of the hypotheses generated herein await more detailed behavioural and environmental measurements not presently available.

Methods

Data reported here were gathered during 18 months of field observation, between 1974 and 1977, in Peru, Venezuela, and Brazil (see Fitzpatrick (1980) for details of study sites). I accumulated quantitative samples of foraging behaviour for about 90 tyrannid species, representing all major phylogenetic lineages in the family (Traylor 1977). Data were recorded only from individuals I judged to be actively foraging, primarily during morning and late afternoon activity peaks. Notes were dictated into a portable tape recorder for later transcription. I followed easily observable species for varying periods, usually 15 min to 1 h. Rare species, and those in which habitat

density prohibited ad libitum observations, were followed whenever discovered, until they disappeared from sight.

Search times were measured with sweep-second-hand watches, or were counted by using an audible timer that clicked at 1-s intervals. In all cases, a search period began when a bird landed on a perch, and ended when it left the perch either to sally after prey or to move to a new perch. If a bird returned to its former perch after a sally, a new search period began with its landing. Handling time was not included in the search period. Sallys were classified according to the prey substrate (air, leaf undersurface, water, etc.) and flight behaviour, as detailed in Fitzpatrick (1980). Sally distances and give-up flight distances were estimated in feet. I did not distinguish between successful and unsuccessful sallys, as prey items could be seen only rarely.

Body weights were obtained primarily from mist-net captures in Peru and Venezuela. For species I never captured, I used weights listed in French (1976) and Weske (1972) and those recorded on specimen labels in the American Museum of Natural History (New York), Field Museum of Natural History (Chicago), and Louisiana State Museum of Zoology (Baton Rouge).

Results

Data on foraging behaviour are presented here in three sections, each followed by a brief interpretation of the observed patterns. In the first section I describe the typical configuration of search time distributions. Interspecific differences in absolute search time values are shown to reflect an underlying continuum in searching radii within the entire family. In the second section, fine-grained aspects of searching behaviour and movement patterns are compared and shown to be consistent with strategies that would maximize net energy intake. Finally, the question of giving-up times is addressed by comparing the distributions of successful search times with those followed by give-ups among five species with widely differing search behaviour. The results are consistent with the preceding in suggesting that individuals assess each perch independently, and give-up after varying search periods that depend upon the visual characteristics surrounding each perch.

Search Times

Search time distribution. A foraging flycatcher stops on successive perches to scan its surround-

ings for prey. Within individuals and species, the duration of these search periods varies considerably from perch to perch, and by timing many such search periods, a frequency distribution of 'search times' can be generated for any individual or species under investigation. Figure 1 shows examples of these distributions for a variety of species.

Various absolute measures of these search time distributions can be used for making inter-specific comparisons. As discussed below, inter-specific differences in absolute search times appear to reflect differences in prey densities or visual field characteristics. The important point is that despite great differences between the absolute search times of various flycatcher species, the overall distributions of all species show the same general, skewed-right configuration. They resemble log-normal distributions, with a rapid rise to modal value followed by a gradual decline. Similar distributions have been shown among other avian predators (e.g. Davies 1977). As demonstrated in Fig. 2, the median search time value for any flycatcher species is a virtually perfect predictor of the species' overall search time distribution. In the comparisons below, therefore, I use these median values as indices for each species' absolute search times.

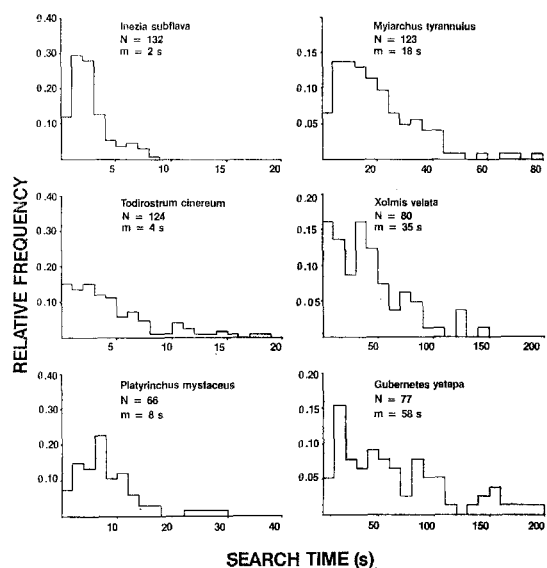


Fig. 1. Search time distributions of six flycatcher species with median search times (m) ranging from 2 to 58 s. Sample sizes (N) show the number of search periods individually timed among various individuals of each species to generate these distributions.

Comparative patterns in search times. A prediction made by MacArthur (1972) and others regarding optimal predatory behaviour is that search time should be directly proportional to body size among predators of similar type. To test this, median search times of 76 South American flycatcher species are plotted against their body weights in Fig. 3. Four broad categories of foraging behaviour are identified in Fig. 3. These are: Aerial Hawkers, species whose prey is taken largely or entirely from the air during a sally from an exposed perch; Sally-Gleaners, species that glean prey from vegetation during a sally off a perch; Perch-Gleaners, species that glean prey from vegetation without sallying; and Near-Ground Generalists, species that use many prey capture techniques but orient most sallies toward the ground. Perch-to-Ground specialists show many characteristics of Aerial Hawking species (see Fitzpatrick 1980) and are included with them in this analysis.

Regression analyses performed on each of three major behavioural categories show that within each ecological unit, search time varies directly with body size, but between-group differences in behaviour are apparent. On the average, among similar-sized flycatchers, Perch-Gleaners search one-third as long as Sally-

Gleaners, while Aerial Hawkers (and Perch-to-Ground Specialists) search about an order of magnitude longer than do Perch-Gleaners. Near-Ground Generalists cut across this spectrum and are discussed separately below.

To test for possible effects of visual field characteristics upon searching behaviour, the same median search times as those plotted in Fig. 3 are plotted directly against median sally distance for each species in Fig. 4. Sally distances show right-skewed distributions similar to search times (Fitzpatrick 1980), and the median value is used here as an index of size of the search radius in each species. Not only are search times directly proportional to search radii, but the relationship holds between all species regardless of foraging modes (again excepting Near-Ground Generalists). Furthermore, the apparently different searching strategies suggested in Fig. 3 now emerge as contiguous regions along one log-linear relationship, suggesting that physical restrictions in the visual field strongly influence the temporal search patterns of foraging birds.

If the above interpretation is accurate, one might expect that visually complex surroundings would require more search time per perch than visually simple ones. A field test for this prediction exists in Amazonian Peru where two resident flycatchers habitually forage along the

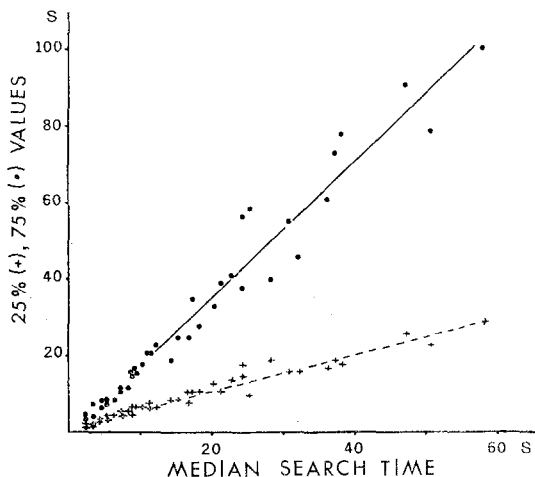


Fig. 2. Twenty-five per cent and 75% values, plotted against their respective median (50%) values, for search time distributions of 50 flycatcher species. Nearly perfect correlations between these dispersion measures exist because all distributions have essentially the same shape. Median values therefore represent accurate indices of overall distributions for purposes of interspecific comparisons.

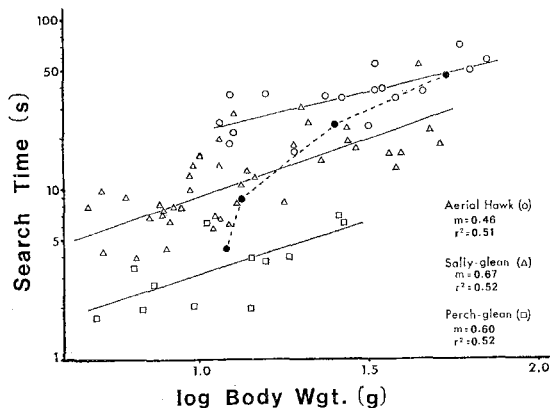


Fig. 3. Median search times plotted against body weights (both on logarithmic axes) for 76 tyrannid species. Four major foraging mode categories are identified: Perch-to-Ground Specialists are included with Aerial Hawkers (open circles; see text); Sally-Gleaners (open triangles); Perch-gleaners (open squares); Near-Ground Generalists (closed circles). Linear regression lines show increasing search times with body weight within each of three common foraging categories. Slope (m) and regression coefficient (r^2) are shown for each regression.

edges of small, meandering rivers. *Ochthoeca littoralis* perches primarily among river-washed roots and rubble on steep banks, where it gleans and hawks insect prey with short sallies. *Muscisaxicola fluvialilis* forages with short, pipit-like runs on bare sand beaches. Occasionally, each species moves into the habitat normally favoured by the other. Thus *Ochthoeca* wanders onto open ground and hops after prey along mudcracks or open sand. Especially in late dry season, *Muscisaxicola* periodically runs into elevated beach habitats to glean prey within a rich, early successional growth of a leafy composite (*Tessaria* sp.) a metre or more high. As shown in Fig. 5, both species spend significantly less time at each perch when surrounded by the simple visual field

of an open sand beach, even though one of them is a specialist in a more closed, complex habitat. Assuming that prey densities are comparable between these adjacent habitats, this pattern again points to the visual field as an important factor in the searching strategies of avian predators. It should also be noted that neither species becomes as efficient a predator in the habitat normally occupied by the other, suggesting that search-image stereotypy may be involved in this kind of micro-habitat segregation among similar species.

Prey size and search times. The effects of prey size on search times can be observed directly among the four Near-Ground Generalists (closed circles in Figs 3 and 4). In Amazonian Peru these species use a variety of capture techniques but always hunt within 1 or 2 m of the ground, usually near water. They therefore represent a set

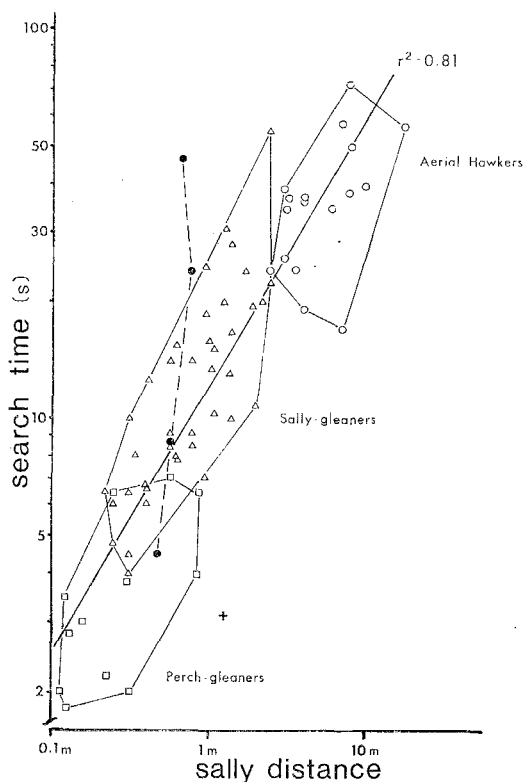


Fig. 4. Median search times of 76 tyrannids plotted against their respective median sally distances on log-arithmetic axes. Across foraging modes, search times are strongly related to the size of the area searched. Among Near-Ground Generalists (closed circles) search time directly reflects prey size (see text). Symbols as in Fig. 3, with isolated '+' showing aberrant species (*Myiobius barbatus*) whose peculiar foraging style sets it apart from the rest of the family (Fitzpatrick 1980).

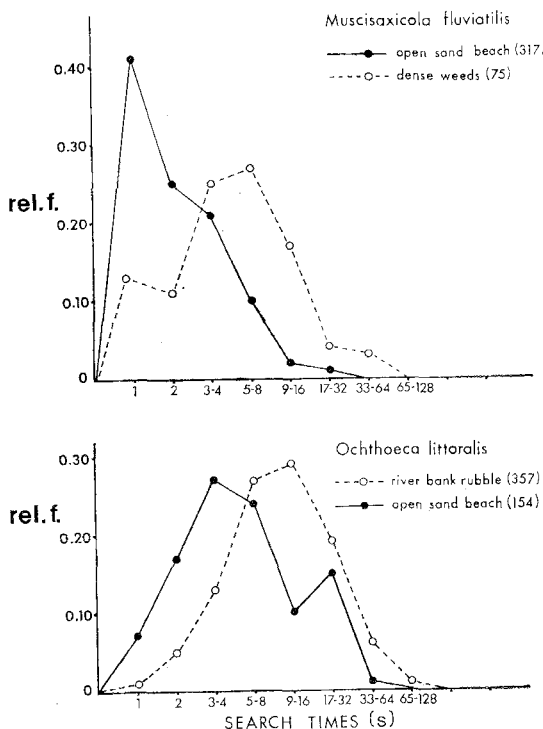


Fig. 5. Search time distributions of two river-edge flycatchers in two types of habitat. Distributions are plotted along a logarithmically increasing scale to illustrate their approximately log-normal configuration. Search times of both species are shorter in visually simple, open sand surroundings. Capture rates were similar in both habitats, indicating comparable prey densities. Sample sizes of search times are shown in parentheses.

of species whose sally distances are perforce equal (see Fig. 4). The largest species, *Pitangus sulphuratus* (weighing 53 g), commonly feeds on minnows, large aquatic nymphs, terrestrial arthropods, and even small lizards. *Pitangus lictor* (25 g) takes spiders, small dragonflies, surface-dwelling insects, and other medium-sized arthropods. The two smaller species *Ochthoeca* (formerly *Ochthornis*) *littoralis* (14 g) and *Fluvicola pica* (12 g) prey on small insects that abound at water margins. These conspicuous differences in prey size correspond closely to the birds' relative body sizes, and result in dramatically different search times (compare Figs 3 and 4) because of the decreasing abundance of the larger prey (Schoener & Janzen 1968).

Discussion. Many authors have shown with simple theoretical models that in an environment containing a continuum of prey sizes, the search times of similarly foraging predators should be proportional to the size of prey they are adapted for capturing (Schoener 1969, 1971; MacArthur 1972). This prediction assumes smaller prey to be more abundant than larger prey, and follows because search times should be inversely proportional to prey abundance. Thus, among predators of similar type, the larger species, adapted for relatively larger and less common prey, would be expected to search for longer periods than do the smaller species. Indeed, as predicted by the models, flycatchers of similar type show significant positive relationships between search time and body weight (Fig. 3). However, the parallel, evenly separated regressions in Fig. 3 suggest significant, qualitative differences in searching strategies between the three major categories of flycatcher predators. Specifically, among similar-sized species some characteristically search up to 10 times longer at the average perch than do others. Two possible explanations for the parallel regressions in Fig. 3 are plausible. First, if levels of prey abundance differ by quantum amounts between the foraging modes, similar-sized species should show proportionate differences in search times depending on their foraging mode. If these prey-abundance differences hold uniformly throughout the size classes fed upon by flycatchers, this would result in three search time regressions of similar slope. However, this would not necessarily account for the similar distances separating the regressions. Moreover, insects of the type eaten by flycatchers are known to show continuous distributions in size and abundance (e.g. Schoener & Janzen 1968; Hespenheide 1971).

Alternatively, the three seemingly separate regressions might represent three segments of a continuous function that joins all three foraging modes, in which Sally-Gleaners fall as intermediates between Perch-Gleaners and Aerial Hawkers. The parameter most likely to vary continuously among all species regardless of foraging mode is the size of the visual field scanned during the search. A bird that searches for prey a few centimetres away has a smaller area in which to search than does a bird that will sally up to a few metres within the vegetation. Both, in turn, search a smaller area than those that sally after prey at any distance in open, unobstructed habitat. Smaller fields of view require less time to search than larger ones. Moreover, the rate at which mobile prey enters into the visual field also depends at least approximately on the size of the field. Therefore, efficient predators with smaller visual fields should be forced to move from perch to perch faster than those with larger fields, in order to maximize their prey-encounter rates. Figure 4 demonstrates this to be a remarkably close relationship among free-foraging flycatchers. Obligate Perch-Gleaners move rapidly through their habitat and pause to search only briefly on each perch. Sally-Gleaners, searching within a sphere of vegetation, pause for search periods that vary with the density of foliage determining their fields of view. Aerial Hawkers, with wide fields of unrestricted view, simply remain motionless until prey appears, only rarely moving from perch to perch.

Within a given species, individuals often encounter variations in habitat characteristics, including local changes in prey density or patch-to-patch differences in visual field characteristics. These local differences do cause slight individual variation within species' overall search-time distributions. In the flycatchers I studied, however, all such changes took the form of small shifts up or down, but never away from, the search-time-versus-sally-distance regression shown in Fig. 4. Thus, foraging bouts in which an individual's sallies were longer or shorter than the normal range for its species were accompanied by correspondingly longer or shorter search times (Fitzpatrick 1978). I interpret this pattern of intraspecific variation as further evidence for the overriding importance of visual field characteristics in determining search time distributions.

Movement Patterns

Returning after sallying. After completing a sally, an individual flycatcher may either return

to the same perch or move to a new one. In this regard, the behaviour of an optimal forager should vary according to its prey dispersion characteristics. Species that deplete a local area by sallying once from a perch create an area of 'resource depression' (Charnov et al. 1976) around the perch. In contrast, species that search for randomly appearing and quickly replenished prey, such as aerial insects, are less likely to cause local depletion by sallying once from a perch. Figure 6 supports the contention that Sally-Gleaning tyrannid species represent the former category, while Aerial Hawkers represent the latter. Three species that frequently glean prey from nearby surfaces show a key characteristic of resource depression: significantly longer search times accompany repeated use of the same perch. Among Aerial Hawkers, no such increase is apparent even after many sallies from

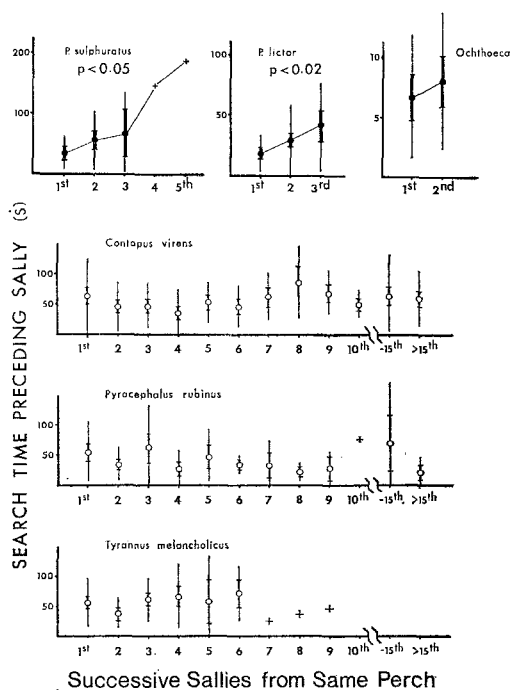


Fig. 6. Mean search times preceding successive prey captures from the same perch for six flycatchers. Upper three species are Near-Ground Generalists, predominantly Sally-Gleaners, and lower three are obligate Aerial Hawkers. The latter show no prey depletion at a perch, but positive slopes among the gleaners suggest resource depression (Spearman rank correlation; P -values show level of significance of increase in search times). Error bars show \pm one standard error (thick bars) and one standard deviation (thin bars) about mean values.

the same perch. Indeed, the flycatchers as a group demonstrate this strategic adjustment to prey dispersion characteristics. Among all species studied, the tendency to return to the same perch after a sally is strongly related to their reliance upon aerial prey (Fig. 7). Obligate Aerial Hawkers may return repeatedly to certain favoured perches, often using a few such sites throughout the day for weeks on end. This behaviour also is strongly correlated with a set of morphological adaptations and home range characteristics (Fitzpatrick 1978, and in preparation).

Return-to-perch tendency at a given perch should be inversely related to the time required to find the prey item just captured, if individuals are sensitive to between-perch variations in prey density. A short search time preceding a capture reflects some likelihood that a local concentration has been encountered; hence the bird should return to the perch. This behaviour does occur among Aerial Hawking Tyrannidae, as exemplified by one species in Fig. 8. Near-Ground Generalists are also sensitive to local prey concentrations, but to a lesser degree (Fig. 8). High return-to-perch rates characterize these species only within the first few seconds on a perch, after which they drop to a constant, low rate. This comparison suggests that local concentrations of prey may be more prevalent, or more accessible from single perches, for Aerial Hawkers than they are for gleaning species that move regularly along a path in search of stationary prey.

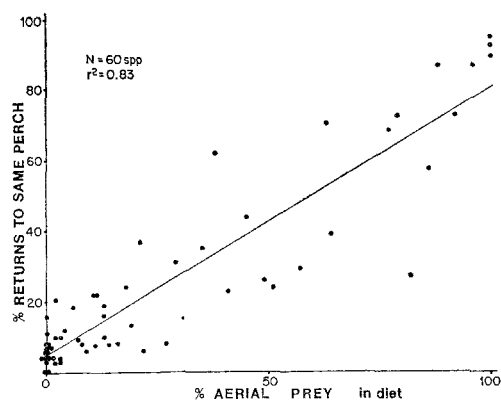


Fig. 7. Percentage of sallies that were followed by a return to the same perch among 60 flycatchers, plotted against percentage of Aerial Hawking in the foraging manoeuvres recorded for each species. Line shows linear regression through the points.

Flight distance after giving-up. After electing to abandon a perch that has produced no prey, how far should an optimally foraging individual move before landing on the next perch? Clearly, in a uniform habitat it should fly at least far enough to leave the field of view already searched, but not so far as to waste energy passing through unsearched surroundings. Thus 'give-up flight' distances should be proportional to the field of view, and in most kinds of habitats the predicted flight distance is twice the radius searched from the average perch. Of course, variability in the habitat will cause distances to be distributed over a range of values in the same fashion as sally distances. However, the prediction can be tested by plotting median distance of give-up flights against median sally distance for each species. Figure 9 shows this comparison among the 50 species for which I have adequate data on both measures. The solid line shows flight distance values exactly twice their sally distance, and its agreement with the observed values is remarkably close. The actual regression ($r^2 = 0.91$) indicates that open-country hawking species (long sallies) move

slightly more than twice their sally distance, while gleaners in dense foliage (short sallies) move only about as far as they sally. This again demonstrates the importance of visual field restrictions in determining the exact foraging behaviour of each species. Those that hunt in dense foliage have more potential perches, and can be less certain that their full search radius is free of prey, than species with unrestricted visibility on exposed, isolated perches.

Searching distance. To minimize the time and energy spent in capturing prey, nearby prey items should be preferred over more distant ones. Thus an optimally foraging flycatcher might be expected to show an organized search strategy in which, at each perch, attention is focussed first on nearby surfaces and is directed at progressively more distant ones during the search period. There exists some evidence that this strategy does characterize the Sally-Gleaning tyrannids. Figure 10 shows that three Near-Ground Generalists, predominantly gleaners with differing absolute search times, all sally significantly earlier at nearby prey. More distant items appear to be seen, or at least chosen, only after the proximal prey substrates have been searched unsuccessful-

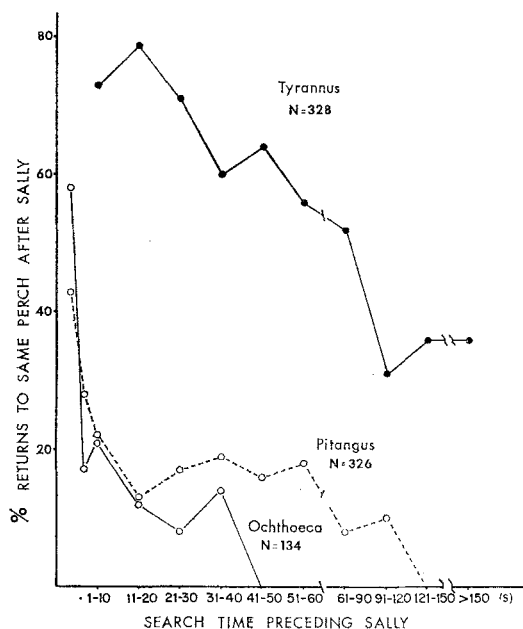


Fig. 8. Variation in return-to-perch tendency according to search time preceding the sally. *Tyrannus melancholicus* is an obligate Aerial Hawker; *Pitangus lictor* and *Ochthoeca littoralis* are Near-Ground Generalists (see text). Return-to-perch frequencies are shown for search times of 1 to 3 s, 4 to 6 s, and 7 to 10 s for the generalists, while these are lumped into 1 to 10 s for *Tyrannus*.

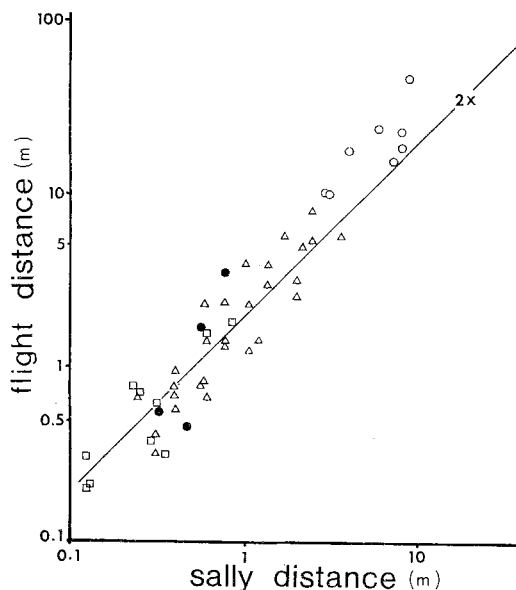


Fig. 9. Median flight distances after giving-up, plotted against median sally distances on logarithmic axes, for 50 tyrannid species. Symbols as in Figs 3 and 4. Solid line shows predicted values if species fly exactly twice their sallying distance.

fully. Furthermore, Fig. 10 also shows that Aerial Hawking species do not exhibit this tendency. On the average they sally at some rate that is proportional to the appearance rate of their flying prey, irrespective of the distance required to capture it. Figure 10 provides further evidence that differences between searching strategies of Gleaners and Aerial Hawkers are intimately tied to the nature of their prey distributions.

Discussion. Data presented in this section support certain specific predictions about energy expenditure in movement patterns of flycatchers. These predictions arise from the general notion that predators should act efficiently, (1) to reduce energetic costs while foraging, while (2) maximizing the rate at which prey is discovered. Energetic costs are reduced by flying the predicted distance to a new perch after giving up and, among Gleaners, by searching nearby areas before more distant ones. Prey appearance rates are enhanced by (1) choosing new perches over previously used ones (Gleaners), or using the same, previously successful perches (Hawkers), where these are appropriate responses to overall

prey dispersion and replenishment characteristics, and (2) responding to local concentrations of prey by re-using perches at which prey capture occurred soon after landing. Similar results to some of these are reported by Davies (1977) in *Muscicapa striata*, an Old World analogue of Aerial Hawking tyrannid flycatchers.

Giving-Up Times

In the first section I compared search times of various species to show how foraging mode differences affect the overall search time distributions. These distributions grouped searches preceding a sally ('successful searches') together with those preceding a 'give-up flight' to a new perch ('unsuccessful searches'). There is, however, no a priori reason for expecting these two seemingly independent events to show the same distribution of search times preceding them. Successful search periods presumably reflect the time a predator takes to spy and pursue a prey item from various perches, while unsuccessful search periods reflect the time a predator is willing to search in vain before choosing a new perch. One might expect an optimal predator to 'give-up' after some roughly fixed length of time, beyond which its chances of success on the perch begin to decline. Especially among gleaning species, which scan nearby substrates for stationary prey, the intuitive prediction (analogous to that modelled by Charnov (1976)) is that the tendency to give-up should increase sharply at the point where the entire searching radius has been examined without success. It seems surprising, therefore, that among all the species for which I have sufficient data, successful and unsuccessful search time distributions are virtually identical. Figure 11 shows some examples, plotted in two different ways.

These graphs reveal several important characteristics of flycatcher foraging behaviour:

(1) The search time distributions that seemed log-normal (Fig. 11, right-hand graphs; see also Fig. 1) may be better interpreted another way. If, in the habitat as a whole, departures from perches actually occur at random times, independent of the time already spent on the perch, the resulting 'waiting time' distributions would graph as a perfect exponential decay. When plotted on logarithmic survivorship paper (plotting the log of the remaining proportion of birds still on perches against increasing time), such an exponential decay function is a straight line with a negative slope. These 'survivorship' plots are shown for four species in Fig. 11 (left-hand

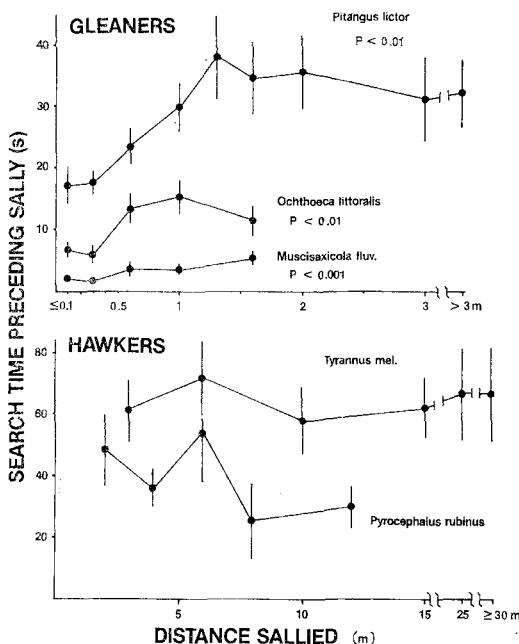


Fig. 10. Mean search times associated with sallies of different prey lengths. Species that search solid substrates for prey (upper three) show significant tendencies to select nearby prey items before more distant ones (Spearman rank correlations); not so among Aerial Hawkiers (lower pair). Error bars show \pm one standard error.

graphs), with search times preceding sallies plotted separately from those that preceded 'give-ups'. These graphs show that except for a brief, initially shallow decline, the tendency to sally after prey or to give-up at a perch indeed appears to be independent of the time spent on the perch. Put another way, each species shows a constant departure rate, at least up to the times at which 'noise' caused by small sample sizes

makes the graphs difficult to interpret. Given that this pattern holds over most of the search times for each species, I interpret the initially low frequency of very short search times (see Fig. 1; Fig. 11, right) as evidence for a 'set-up' period on each perch. Apparently, immediately after landing on a perch, these birds take a few seconds to settle and gauge their surroundings before they begin active searching.

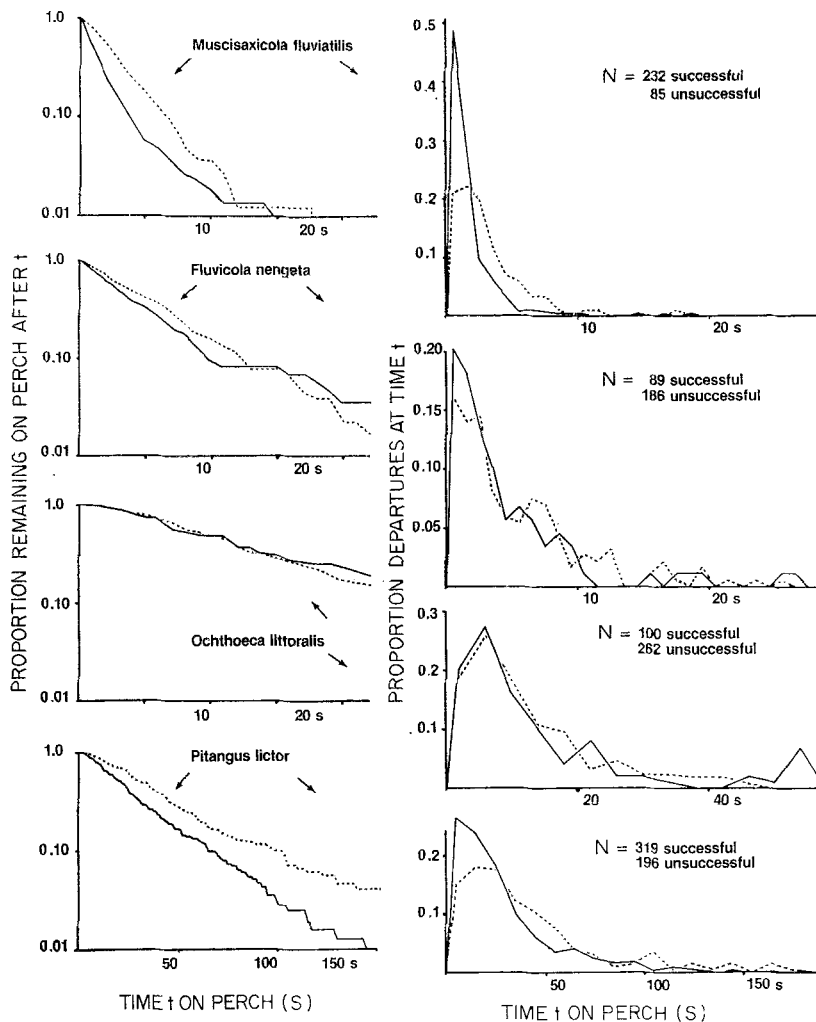


Fig. 11. Distributions of search times preceding sallies (=successful searches), and give-ups (=unsuccessful searches) for four species, plotted in two fashions. Left-hand graphs are semi-logarithmic 'perch survivorship' plots, showing proportions of individuals remaining on a perch at time t , preceding either a sally (solid line) or a give-up (dashed line). Right-hand graphs, comparable to Fig. 1, show proportions of actual sallies (solid lines) and give-ups (dashed lines) occurring at time t . Sample sizes (N) represent total number of search periods observed in each category.

(2) Interspecific differences in absolute search times, discussed in earlier sections using the median measure, are directly reflected in differing slopes in the Fig. 11 (left) 'perch survivorship' plots. Species with long search times have low departure rates, while those with short search times have much higher ones. For the samples of search times preceding sallies, these departure rates represent the perceived average appearance rate of suitable prey items. This gives us a quantitative measure by which the productivity of various habitats could be ascertained for any given species.

(3) The 'perch survivorship' plots for unsuccessful perches also indicate random departures, with a constant mean rate that is, for each species, just slightly lower than the appearance rate of its prey items. An important observation from the graphs in Fig. 11 is that many (in some cases, most) perches are abandoned relatively early despite the fact that the average appearance rate of prey items in the habitat as a whole stays constant for a long time thereafter. As an example, calculating the instantaneous probability of capture (or 'hazard rate function') for *Ochthoeca littoralis* shows that the individual bird has a roughly constant, 0.025 per second probability of capturing an insect on the average perch, until about 30 s of search time has elapsed (Fig. 12; in calculating 'capture' probabilities, each sally is assumed to represent a capture. The interpretation is unchanged even if some fraction of the sallies are unsuccessful, which would simply lower the absolute values at all points along the probability curve). Any optimal-decision model based only on this curve, and assuming that each

perch is treated as an average one, would predict few departures until the instantaneous capture rate declines (contrary to Fitzpatrick 1978). However, as shown in Fig. 12, most *O. littoralis* actually give up after only 2 to 10 s. Indeed, only 8% of the total sample remained long enough to demonstrate the shape of the curve.

Discussion. The graphs in Figs 11 and 12 argue against there being a single optimal giving-up time for a foraging flycatcher. The most satisfactory hypothesis explaining the apparent paradox is that perches vary along some continuous, random distribution of complexity or attractiveness, and that the flycatcher can assess each perch independently after landing. The 'perch survivorship' curves (Fig. 11) reflect an average over the range of perch types chosen by each species. Suppose that an individual flycatcher, after landing on a perch, can assess how much time a thorough search of the surroundings will take. It should search only that long. If a prey item is spotted while the search proceeds, the bird sallies. If the allotted time elapses, it 'gives-up'. Thus, for perches of equal complexity, successful search periods will always be shorter than unsuccessful ones. Using this strategy, and given a random distribution of perch types within the habitat, the predicted 'perch survivorship' plots for successful and unsuccessful perches would match those shown in Fig. 11.

If there were no variance in perch characteristics, or if foraging birds could not perceive the variance and adjust their behaviour accordingly, then the birds would have to be treating all perches the same way. If, under these circumstances, prey appeared at a constant rate irrespective of the time the predator had already spent on a perch (as suggested in Fig. 11), then an optimally foraging individual would never give up at a perch. Its likelihood of success, and thus its net energy intake, would not change by flying to a new perch, and the flight would only waste energy. The observation that most give-ups occur early and that giving-up occurs at a constant rate, which closely tracks the success rate, provides evidence that some perch assessment must be occurring each time a bird lands on a new one.

It must be pointed out that effective field tests distinguishing between the above hypothesis and its alternative (that giving-up tendency is related to instantaneously changing probabilities of capture) require enormous samples of accurately timed search periods. The critical portions of both successful and unsuccessful search time

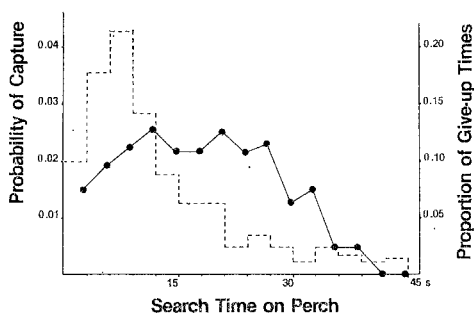


Fig. 12. Instantaneous capture probability with increasing time at each perch (solid line) for *Ochthoeca littoralis*, compared to its observed distribution of give-up times (dashed histogram). Probability curve is obtained by dividing the number of captures (=sallies) occurring at time t by the number of times an *Ochthoeca* was observed to wait at least t seconds on a perch.

distributions lie toward the tail of the distributions. The critical questions involve the degree and direction of change in instantaneous capture and give-up probabilities, parameters in which subtle changes in each curve dramatically affect the shape of the other. Calculating instantaneous probabilities of capture and of giving-up become subject to extreme sampling error at the higher search times, even with the sample sizes shown in Fig. 11. In the absence of necessary sample sizes, no such critical comparisons can be made at present.

General Discussion

The tyrant flycatchers represent a monophyletic radiation into a number of distinct modes of insectivorous foraging behaviour, elsewhere defined in terms of their differential use of various stereotyped prey capture techniques (Fitzpatrick 1980). Most of these foraging modes are convergent upon those used by a number of Old World bird families (see Keast 1972). In the Tyrannidae, and presumably among its Old World analogues as well, foraging mode and microhabitat specializations appear to be co-adapted. Thus Aerial Hawkers forage in open, unobstructed situations, Sally-Gleaners use open perches in leafy microhabitats, Perch-Gleaners hunt in dense vegetation, and so on. The results presented here demonstrate some of the subtle behavioural aspects of this co-evolving radiation. In large part, perch-by-perch decisions during hunting by these birds are affected by two important variables: visual field complexity and prey dispersion characteristics. These two variables, which are intimately associated with overall foraging mode differences, combine to determine minute-by-minute movement patterns within each species.

The results support some theoretical predictions for optimal foragers. Among predators of similar foraging mode, search times increase with body size. Assuming the latter to be an index of prey size (Hespenheide 1971, 1975), this is consistent with one of the first and most elegant predictions regarding 'consumer choice' (MacArthur 1972). MacArthur (pages 67–68) also commented upon some predicted effects of visual field characteristics on searching behaviour, but this relationship has received little attention until now. The degree to which individual species re-use the same perch depends, as predicted, upon the dispersion and replenishment rate of their prey. This finding supports the qualitative predictions of Charnov et al. (1976) regarding resource

depression and its ecological implications. Finally, more general models about minimizing energy expenditure per prey (reviewed in Pyke et al. 1977) are supported by the evidence that tyrannids habitually fly twice their search radius after giving-up (Fig. 9), and that nearby prey items are chosen before more distant ones (Fig. 10).

In the case of giving-up times the data are less supportive of simple optimality models, although my method of observation prohibited a precise analysis of this complex problem (see Krebs et al. 1974; Charnov 1976). In previous models, optimal 'giving-up' times are predicted to depend upon instantaneous comparisons to overall capture rates within a given habitat patch. In my interpretation of tyrannid foraging each perch represents a new 'patch', which either yields a prey item or is abandoned after some unsuccessful search period. Instead of there being some apparently optimal giving-up time for a given species and habitat, the birds give-up over a distribution of times that closely approximates their distribution of successful search times. The most parsimonious explanation for this pattern is that each perch is judged independently upon landing. If it is easily searched to completion in a short time, the bird gives-up quickly. Perches with more complex visual surroundings are given more time. Indeed, this hypothesis is consistent with other results of this study which demonstrate more clearly the importance of visual surroundings on search time. Critical tests of the hypothesis will require more detailed and voluminous measurements of search time variation, and of its relation to perch quality and prey density.

It is worth noting that some of the search strategy differences characterizing birds of different foraging mode are associated with large-scale differences in morphology and home range characteristics. Some of these are discussed in Fitzpatrick (1978) and will be elaborated in subsequent papers. Perhaps the most intriguing possibility, which has yet to be explored at all, is that of internal physiological and anatomical adaptations to different hunting styles. It is apparent that specialized Aerial Hawkers, for example, are visually tuned to picking out microscopic motion of aerial prey while staring for long periods against a solid, well-lighted background. This contrasts with the short-term myopia that characterizes active Sally- or Perch-Gleaning species in dense vegetation. The extent to which these differing habits among closely related species carry with them retinal or neuromuscular adaptations might shed additional light on the

adaptive interplay between structure and behaviour in birds.

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