FEEDING-TIME MINIMIZATION AND THE TERRITORIAL BEHAVIOR OF THE WILLOW FLYCATCHER (*EMPIDONAX TRAILLII*)

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ABSTRACT.—We studied breeding male Willow Flycatchers (*Empidonax traillii*) to test a model of optimal territorial behavior for feeding-time minimizers proposed by Hixon (1980). Specific predictions were that feeding time, defense time, and territory size should decrease with increasing food availability and increase with increased pressure from both conspecific and heterospecific competitors.

The constant reproductive output of 4 and 3 eggs for first and second clutches, respectively, and the large component of uncommitted (sitting) time (62.6 ± 3.2%) over the breeding season confirmed that the Willow Flycatcher conformed to a time-minimization strategy. Data analyzed over three stages of the breeding cycle, and over all stages, however, showed that only 5 of the 36 possible relationships were significant as predicted by the model. In general, food availability and competitor pressure were not important influences on the territorial behavior of these birds. Variations in territory size could not be attributed to constraints on feeding time, but correlated closely with the energetic requirements of all birds occupying the territory.

We believe that breeding insectivorous passerines, including Willow Flycatchers, maintain a large component of uncommitted time, as well as a larger than necessary territory, to minimize the impact of short-term variations in competitor pressure and food supply. Such birds need not conform to the predictions of models that optimize foraging time. *Received 1 December 1986, accepted 16 July 1987.*

SINCE the concept of economic defendability was introduced to the study of territoriality (Brown 1964), numerous models, based on costs and benefits accrued to the territory holder, have been proposed to account for variations in the size of the area defended by territorial animals (Carpenter and MacMillen 1976, Dill 1978, Kodric-Brown and Brown 1978, MacLean and Seastedt 1979, Tullock 1979, Ebersole 1980, Hixon 1980, Wittenberger 1981, Schoener 1983). In animals that defend exclusive feeding areas, cost-benefit ratios are most often thought to be proximately influenced by food availability. This is supported by an inverse relationship between territory size and food abundance for a variety of vertebrate predators (e.g. Stenger 1958, Smith 1968, Holmes 1970, Slaney and Northcote 1974, Simon 1975, Dill et al. 1981, Davis 1982). Competitor pressure also may exert an effect on territory size (Yeaton and Cody 1974, Myers et al. 1979, Ewald et al. 1980, Norton et al. 1982), although the presence of territorial intruders need not be independent of food availability (Myers et al. 1979, Norton et al. 1982, Schoener 1983). Both food and intruders apparently influence territoriality by causing changes in the alloca-

tion of time and energy by the territory holder to various territorial activities. Territorial behavior then can be viewed as a consequence of the balance between the time (or energy) spent acquiring benefits (e.g. food) from the territory versus the time allocated to territorial defense. Hence, models that predict changes in territory size based on proximate constraints on energy acquisition are also capable of predicting concomitant changes in the allocation of feeding and defense times by the territory holder (e.g. Hixon 1980, Schoener 1983).

Schoener (1971) identified alternative strategies in the allocation of time and energy by foraging animals. Foragers that realize no reproductive gain by increasing foraging effort (i.e. have a fixed reproductive output) Schoener termed feeding-time minimizers. Animals whose fecundity is enhanced by energy gain were termed energy maximizers. These concepts have been integrated into models of territorial behavior (Dill 1978, Pyke 1979, Ebersole 1980, Hixon 1980, Schoener 1983). Predictions of territorial dynamics and time allocation for energy maximizers have often been contradictory (Schoener 1983). However, Hixon (1980)

and Schoener (1983) predicted that for time minimizers, territory size, feeding time, and defense time should decrease with increased food availability, increase with increased pressure from conspecific intruders against which the territory is defended (intruders that do not suppress food abundance), and increase with increasing pressure from heterospecific intruders that forage on the territory and hence reduce food availability. At present empirical tests for the specific predictions of the time-minimization models are lacking.

We studied the territorial behavior of the Willow Flycatcher (*Empidonax traillii*) to test the above predictions. Previous time and energy budget analyses of breeding Willow Flycatchers led Ettinger and King (1980) to classify this species as a feeding-time minimizer. Several aspects of the ecology of the Willow Flycatcher are consistent with assumptions of the model and render it a convenient species for testing the models (see Hixon 1980 and Schoener 1983 for discussion of assumptions). First, it occupies a relatively open and homogeneous habitat (King 1955, Walkinshaw 1966) such that prey items are presumably evenly distributed and behavioral observations facilitated. Second, like other *Empidonax* flycatchers, it confines its activities to a small feeding territory defended vigorously against conspecific intruders (Davis 1954, 1959; Davis et al. 1963). Finally, it feeds almost exclusively on invertebrate prey (Bent 1942) that are readily quantified in the field.

STUDY AREA AND METHODS

Most data were collected from Willow Flycatcher territories in the Badenoch Swamp, 14 km southeast of Guelph, Ontario (43°32′N, 80°13′W). The study area consisted primarily of dense thickets of 3–4 m high willow (*Salix* sp.), interspersed with grassy clearings and sparse secondary growth (<1.5 m height) of red-osier dogwood (*Cornus stolonifera*), hawthorn (*Crataegus* sp.), and trembling aspen (*Populus tremuloides*) saplings. White elm (*Ulmus americana*) and black ash (*Fraxinus nigra*) up to 25 m in height were scattered throughout the wetter areas of the swamp. Areas of standing water supported stands of dense cattail (*Typha* sp.). During the breeding seasons of 1984 and 1985, 9–11 pairs of Willow Flycatchers were present at the Badenoch site.

During 1984 additional observations were made at a site 5 km northeast of Guelph. This site ("Guelph Lake") had vegetation similar to Badenoch but contained only 3–4 breeding pairs of Willow Flycatchers. This site was abandoned by the flycatchers in the

following season, apparently because of agricultural development of the peripheral areas. Therefore, an additional site at Sayer's Mills, 19 km east of Guelph, was chosen for study in 1985. This was the driest of the three study areas, with standing water restricted to a small ephemeral creek on the western side of the site. Three pairs of Willow Flycatchers were present at Sayer's Mills in 1985.

An assumption of the model of optimal feeding territoriality is that territories are noncontiguous (Hixon 1980, Schoener 1983). We considered only territories where <50% of the boundary was shared with conspecifics and that bordered on suitable, unoccupied habitat (to permit territorial expansion). During late May (territory-establishment stage) in 1984 and 1985, 5 territories were selected for observation at Badenoch. In 1984, 2 additional territories were chosen at Guelph Lake and, in 1985, 2 at Sayer's Mills. Although 3 territorial males were color-banded early in the 1984 season, efforts to mark birds were soon abandoned when it became apparent that individual birds confined their activities to well-defined areas and could be distinguished readily from their neighbors. Each territory was visited randomly at least 4 times during each breeding season (May–August). Each visit was considered an independent repetition. Abandonment of territories by the flycatchers early in the season (twice in 1985) occasionally prevented repeated observations on a specific territory. In such cases additional noncontiguous territories were found as replacements; data from the new territories and the ones they replaced were treated separately. The sequence of observation of these territories followed the order previously determined for the abandoned territories.

Observations on all territories were made between 0700 and 1200 from a 2.5-m portable stepladder. Because weather factors probably influence the foraging behavior of insectivorous birds (Lederer 1972, Grubb 1979), as well as the distribution and availability of invertebrate prey (Digby 1958, Taylor 1963), data were collected only on rainless mornings with little or no wind (<15 km/h) and seasonal temperatures.

Territory size.—Territory size was determined by recording the position of singing perches, flight paths, and territorial disputes of both male and female Willow Flycatchers on 5-m grid maps of each study area constructed by ground mapping with compass and tape. The position of foraging bouts was also used to determine territory boundaries, although birds apparently never fed beyond the limits imposed by advertising perches. In September 1985 aerial photographs were taken of each study area from an approximate altitude of 1,000 m. The exact scale of each photograph was determined from ground-measured distances between prominent physiognomic features of the habitat. Field data were then superimposed on the photographs, and territory size was calculated as the minimum area enclosed by a poly-

gon connecting the outermost plotted points (Odum and Kuenzler 1955, Southwood 1971).

Intruder pressure.—Intruders that do not decrease food supplies on the flycatcher territory (INTR) were assessed by counting the number of territorial male flycatchers adjacent to the territory under observation. Such intruders were generally conspecifics, but also included the Alder Flycatcher (*E. alnorum*), a sibling species (Mayr 1964: 116) with which *E. traillii* is interspecifically territorial in areas of sympatry (Prescott 1987). Because territorial disputes between adjacent *Empidonax* flycatchers were infrequent, we considered a neighboring male to be a potential intruder if it used display perches less than 8 m outside the territory under observation.

The impact of intruders that decrease the food supply available to the territory holder was assessed by constructing an index of food overlap (COMP) that considered both the spatial and dietary overlap of heterospecific (nonexcluded) individuals on each flycatcher territory:

$$\text{COMP} = \sum \frac{(\% \text{ spatial overlap})\cdot(\% \text{ insectivory overlap})}{1 + |\text{difference in body mass}|},$$

where % spatial overlap was estimated for each intruding species by plotting its movements on the field maps (see above), and calculating the percentage of the observed flycatcher territory occupied. Percentage insectivory overlap with the Willow Flycatcher was obtained for each species from literature accounts of summer diets. Although Beal (1912) found Willow Flycatchers to be 96% insectivorous, a value of 100% was assumed here for ease of calculation. The denominator of the index attempts to correct for differences in prey-size overlap between coexisting species. Because differences in prey size selected by insectivorous birds are more closely related to differences in the bird's body mass than its bill size (Hespenheide 1971), we used the former measure. We added 1 to the denominator to prevent the calculated values from approaching infinity for potential competitors of similar body mass. Values of body mass for each heterospecific competitor were obtained from the literature.

Food availability.—Three trapping methods were employed to provide as unbiased an assessment as possible of the invertebrate food potentially available to Willow Flycatchers. One Malaise trap (Townes 1972) and one flight-intercept trap (Masner and Goulet 1981) were positioned at random (determined on field maps) along willow-grass interfaces within each territory for a period of 23 ± 1 h ("one day") beginning around noon of the day preceding the observation period. At the conclusion of each observation period, samples were collected from the traps and 50 sweeps, using a 40-cm-wide sweep net, were taken along 3–4 randomly chosen transects through the territory. The direction of each transect was chosen by spinning a

pointer from a central location within the territory. Samples obtained by each trapping method were cleaned of plant debris, combined into a single sample, and frozen for later analysis. Insects were sorted to order (adults and larvae separately) according to Borrer et al. (1976) and grouped into 2-mm size classes based on body length, excluding appendages. Each size class was oven dried at 100°C to constant mass (predetermined to be about 14 h), and immediately weighed (±0.0001 g) on a digital Sartorius® balance. After weighing all size classes were recombined, redried for 45–60 min, and reweighed. The combined mass was considered as an index of total insect abundance on each territory.

The relatively small Willow Flycatcher is unlikely to feed on all of the species and sizes of insects identified in the trap samples. We performed a dietary analysis of the Willow Flycatcher to assess the biomass of insects on each territory that was potentially available to the birds. Neck ligatures (Johnson et al. 1980) were placed on nestling flycatchers, and the size and taxonomic composition of food items delivered by the parents were recorded. Insects were collected on all territories where behavioral observations were made. The maximum length of preserved adults and larvae of each insect taxon found in all samples was assumed to be the maximum size also consumed by the parents. Taxa absent from the nestling samples were considered to be avoided by adult birds. Of course, adult birds may consume insects of a different size than those provided to the young. An analysis of 7 gut samples of adult flycatchers collected during the breeding season, however, suggested that adults generally consumed smaller prey items than those found in the nestling samples, and they were never known to take larger items (Prescott unpubl. data). Therefore, the use of nestling food samples to identify the largest insects of each order consumed seems justified. Following dietary analysis, the biomass of all size classes and types of insects found in the trap samples but lacking in the diet were subtracted from the total insect abundance. The resultant biomass was our index of food availability on each territory.

Time budgets.—Because male flycatchers establish and defend the breeding territory, time budgets were determined only for birds identified as males on the basis of behavior. Time spent in a specific activity was recorded by stopwatch for a minimum of 30 min (usually continuous) during each hour of the morning. The percentage of the time spent in each activity was calculated, based on the total time the male bird was in view during the observation period. Activities considered were: (1) Sitting (SIT), time spent perched away from the nest (see 7, below), including preening and nonterritorial vocalization (see 6). (2) Foraging (FOR), time spent in pursuit of insect prey. Pauses of <10 s between foraging bouts were included as feeding time. (3) Flying (FLY), all flights not associated with feeding or courtship displays. (4) Defense (DEF),

TABLE 2. Interspecific competitors and their frequency of occurrence on Willow Flycatcher territories. Values for body mass and % insectivory are incorporated into the competitive overlap index for each species, and ultimately in the calculation of COMP for a given territory (see text).

Species	% of territories	Mean % spatial overlap/territory (±SE)	Body mass (g)[a]	% insectivory[b]	Competitive overlap index[c]
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	1.7	0.17 ± 0.17	51.1	100	2.53X
Downy Woodpecker (*Picoides pubescens*)	6.7	0.50 ± 0.28	27.0	86	5.58X
Hairy Woodpecker (*P. villosus*)	6.7	0.50 ± 0.28	67.8	82	1.46X
Eastern Kingbird (*Tyrannus tyrannus*)	25.0	3.50 ± 1.65	39.5	82	2.94X
Eastern Phoebe (*Sayornis phoebe*)	1.7	0.08 ± 0.08	19.8	95	11.59X
Willow Flycatcher (*Empidonax traillii*)	—	—	12.6[d]	96[e]	—
Black-capped Chickadee (*Parus atricapillus*)	6.7	0.50 ± 0.28	10.8	91	32.50X
Veery (*Cartharus fuscescens*)	1.7	0.08 ± 0.08	31.2	63	3.21X
American Robin (*Turdus migratorius*)	16.7	3.67 ± 1.96	77.3	40	0.61X
Gray Catbird (*Dumetella carolinensis*)	73.3	29.17 ± 5.30	36.9	40	1.58X
Cedar Waxwing (*Bombycilla cedrorum*)	28.3	5.42 ± 2.34	32.5	20	0.96X
Golden-winged Warbler (*Vermivora chrysoptera*)	1.7	0.17 ± 0.17	8.8	100[f]	20.80X
Yellow Warbler (*Dendroica petechia*)	96.7	67.42 ± 6.24	9.5	100[f]	24.39X
Common Yellowthroat (*Geothlypis trichas*)	75.0	16.15 ± 2.49	10.1	100[f]	28.57X
Song Sparrow (*Melospiza melodia*)	60.0	21.00 ± 3.71	20.8	40	4.35X
Swamp Sparrow (*M. georgiana*)	91.7	45.67 ± 5.52	17.0	16	2.96X
Red-winged Blackbird (*Agelaius phoeniceus*)	70.0	19.50 ± 3.91	53.4	50	1.20X
Northern Oriole (*Icterus galbula*)	6.7	0.83 ± 0.48	33.7	80	3.62X
American Goldfinch (*Carduelis tristis*)	80.0	28.92 ± 2.86	13.0	4	2.86X

[a] From Dunning (1984) except where noted. Values represent weighted means of male and female if given separately.
[b] From Martin et al. (1951) except where noted. Values represent summer diets wherever possible.
[c] See text. X represents the percentage of spatial overlap of each competitor on a given flycatcher terrritory.
[d] Ettinger and King (1980). Mean mass of breeding male and female.
[e] Beal (1912).
[f] Estimated from accounts by Bent (1953).

One-tailed Pearson product moment correlations (Sokal and Rohlf 1981) were used to test for the predicted negative relationships of food availability (FOOD) with territory size (TSIZE), foraging time (FOR), and defense time (SINGDEF) and positive relationships of conspecific intruder pressure (INTR) and heterospecific competitor pressure (COMP) with TSIZE, FOR, and SINGDEF. Although simple bivariate correlations were employed in analyses involving FOOD, an increase in food availability could cause an increase in both COMP and INTR (Myers et al. 1979, Norton et al. 1982). Thus, for tests involving COMP and INTR, we used partial correlations to hold constant the effect of FOOD.

RESULTS

Fifteen different breeding territories were observed a total of 61 times during 1984 and 1985 (Table 1). Breeding activities occasionally were completed before 4 random visits could be made to each territory. Some other territories remained active later in the season because of renesting attempts and were visited up to 7 times. Body mass, degree of insectivory, and frequency of occurrence of each heterospecific competitor observed on Willow Flycatcher territories are provided in Table 2.

The Willow Flycatcher as a time minimizer.—Despite a fourfold difference in mean food availability among study territories (considering only territories visited at least 4 times; Table 1), 13 of 14 female flycatchers produced a first clutch of 4 eggs. For the one female that laid a 3-egg clutch (territory 85-2), we suspect that the laying was interrupted by observer disturbance. Three replacement (second) clutches contained 3 eggs each. In one polygynous mating (territory 85-2) two females successfully raised 6 young without a larger-than-average territory (Prescott 1986) or a higher food availability (one-tailed Mann-Whitney U-test, $n = 4, 15; U = 51$, $P > 0.05$) than on other territories during Stage 3. Evidently, increased food abundance did not contribute to increased reproductive output in this population of Willow Flycatchers. Male flycatchers spent 62.6 ± 3.2% of their available time sitting during the breeding season; only 4.9 ± 0.5% was allocated to foraging (Table 3). Thus, the foraging behavior of the Willow Fly-

TABLE 3. Sample sizes and means (±SE) of territorial characteristics and time budgets of male Willow Flycatchers for 3 stages and over all stages of breeding near Guelph, Ontario.[a]

Breeding stage[b]	n	TSIZE (m^2)	COMP[c]	INTR	FOOD[d] (g/day)	% of time spent in activity						
						NEST	COURT	SING	DEF	FLY	FOR	SIT
1	15	2,246 (218)	2,866.9 (193.5)	1.50 (0.31)	0.73 (0.15)	0.0 —	0.5 (0.2)	57.7 (6.3)	0.2 (0.1)	3.7 (0.6)	2.6 (0.4)	35.2 (5.6)
2	27	2,646 (183)	2,961.8 (137.1)	1.63 (0.23)	0.93 (0.08)	1.7 (1.4)	0.3 (0.1)	18.3 (4.5)	0.2 (0.0)	4.2 (0.4)	3.7 (0.5)	71.8 (4.2)
3	19	4,109 (214)	1,661.3 (123.2)	1.74 (0.17)	1.48 (0.07)	8.6 (0.9)	0.2 (0.1)	6.6 (3.9)	0.3 (0.1)	5.0 (0.4)	8.6 (1.0)	70.6 (3.4)
Overall	61	3,009 (153)	2,533.4 (113.7)	1.63 (0.13)	1.06 (0.07)	3.5 (0.8)	0.3 (0.1)	24.2 (3.8)	0.3 (0.0)	4.3 (0.3)	4.9 (0.5)	62.6 (3.2)

[a] NEST = time spent tending the nest or young, COURT = courtship time, SING = singing time, DEF = defense time, FLY = flying time, FOR = foraging time, SIT = sitting time (see text). Other acronyms are defined in Table 1.
[b] Stage 1 = territory establishment; Stage 2 = nest building, egg laying, and incubation; Stage 3 = nestling and fledgling periods.
[c] See text and Table 2.
[d] Dry mass, excluding orders and size classes of insects not consumed by Willow Flycatchers (see Table 4).

catchers we studied most closely conforms to the time-minimization strategy.

Diet anaylsis.—The maximum body lengths of each order of insect delivered to nestling Willow Flycatchers ($n = 333$), and therefore the maximum size assumed to be selected by adult birds, are presented in Table 4. Adult damselflies (Odonata) were not detected in the nestling diet but were captured frequently by adult birds, and on several occasions were fed to uncollared nestlings. As all damselflies found in the trap samples were of similar body length (24–30 mm), all were assumed to provide potential food for foraging flycatchers. Coleopteran larvae that were rare in the trap samples (Fig. 1) were primarily of the family Chrysomelidae, which, as a group, are known to exhibit chemical defenses against predation (Crowson 1981). We considered these beetle larvae to be "unavailable" to Willow Flycatchers. Adult coleopterans were rarely fed to nestlings (2.1% of nestling diet; Table 4) but constitute a major part of the diet of adult birds (Beal 1912, Prescott unpubl. data). The observed maximum length of 4 mm probably is an underestimate caused by the small sample size ($n = 7$). We used the 10-mm maximum beetle length found in stomachs of "Traill's" flycatcher (Hespenheide 1971) in subsequent calculations of insect availability. Molluscs and isopods were absent from the trap samples (Fig. 1) and were excluded from subsequent analyses.

Test of model.—Preliminary examination of variables included in correlation analyses resulted in the use of a $\log_{10}(x + 1)$ transformation of foraging time (hereafter, LFOR) to normalize

the distribution. Only 5 of the 36 calculated relationships were significant (one-tailed tests, $P < 0.05$; Table 5) as predicted by the time-minimization model. During Stage 1 LFOR was negatively correlated with FOOD ($P < 0.05$). After removing the effect of FOOD, TSIZE and COMP were positively correlated during Stage 2 ($P < 0.001$), as were SINGDEF and INTR during Stage 3 ($P < 0.05$). When all breeding stages were combined, SINGDEF correlated as predicted with both FOOD ($P < 0.05$) and COMP with the effect of FOOD removed ($P < 0.05$). The observed relationships showed no consistent pattern over stages of the breeding cycle. Generally, differences in food availability and con- and heterospecific competitors were not accompanied by predicted changes in territory size or time budgets.

DISCUSSION

The Willow Flycatcher appears to be a time minimizer (see also Ettinger and King 1980), but the data showed little support for the theoretical model proposed to predict changes in the allocation of time and space by such strategists. The lack of consistent relationships of territory size and time budgets with con- and heterospecific competitors and food availability suggests that the territorial behavior of the Willow Flycatcher is not mediated through differences in the allocation of time to various activities (see also Schartz and Zimmerman 1971). Further, the small amount of time spent feeding (4.9 ± 0.5% over all breeding stages) and the large proportion spent sitting (62.6 ± 3.2%) are
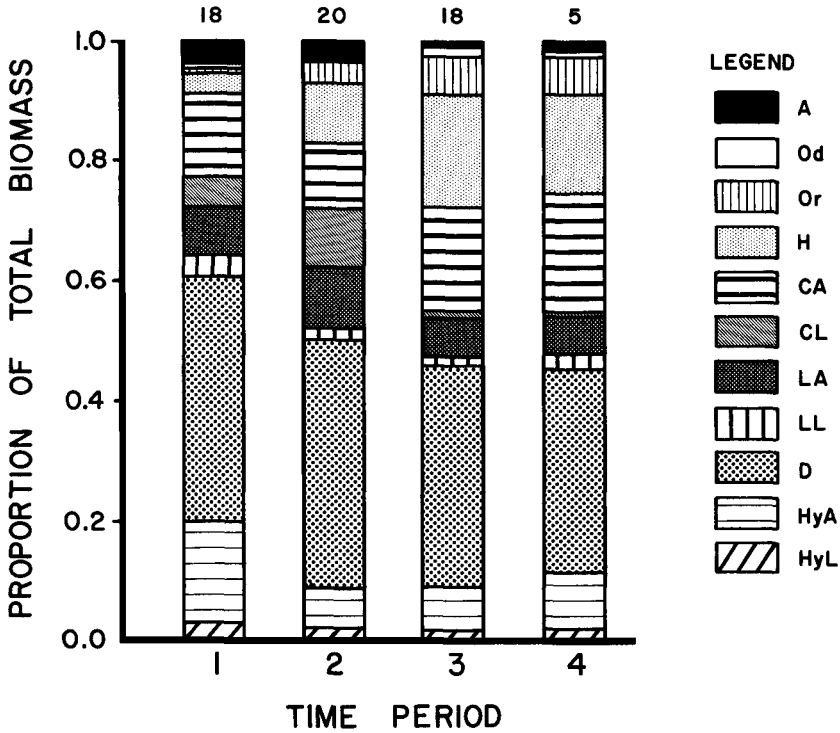
Fig. 1. Relative abundance of invertebrate taxa obtained from insect traps on Willow Flycatcher territories during 4 equal time periods (1 = 25 May to 12 June, 2 = 13–30 June, 3 = 1–18 July, 4 = 19 July to 4 August). Pairwise G-tests (Sokal and Rohlf 1981) showed no significant differences among the 3 study sites, nor between years ($P > 0.05$). Proportions of each taxon were calculated from pooled data. The numbers of territories from which means were derived are at the top of each vertical bar. A = Arachnida, Od = Odonata, Or = Orthoptera, H = Hemiptera, CA = Coleoptera adult, CL = Coleoptera larvae, LA = Lepidoptera adult, LL = Lepidoptera larvae, D = Diptera, HyA = Hymenoptera adult, HyL = Hymenoptera larvae.

strong evidence that constraints on feeding time did not impose an upper limit to the size of the territories occupied. Willow Flycatchers could have satisfied their foraging requirements on territories containing less food (i.e. smaller or less productive territories). The methods we used to assess food availability provided a measure of relative, rather than absolute, prey abundance between territories, and it was difficult to assess quantitatively whether territories contained more than sufficient food resources to support the flycatchers. Evidence is now accumulating (Beaver and Baldwin 1975, Franzblau and Collins 1980, Frakes and Johnson 1982, Blancher and Robertson 1984, Craig 1984, Franzreb 1984) that food is not in such short supply as to influence the foraging behavior or competitive interactions of territorial insectivorous birds. Wasserman (1983) demonstrated experimentally that a reduction in invertebrate

abundance of >30% was required before Rufous-sided Towhees (*Pipilo erythrophthalmus*) responded by increasing their territory size. Insectivorous birds, including Willow Flycatchers, therefore may occupy a larger territory than necessary (Armstrong 1965).

Defending a territory that is larger than minimal size might be advantageous to territorial animals if it does not require a large increase in defense investment. For the Willow Flycatcher there was no increase in defense time (SING-DEF) with increasing territory size, nor a decrease in either foraging or sitting time (one-tailed Pearson correlations, $P > 0.05$). The birds defended a larger than adequate territory while preserving a surplus of time available for foraging and other breeding activities. By maintaining a buffer of both time and space for feeding, foraging time need not be constrained by sudden changes in food availability or compet-

TABLE 4. Composition of the nestling diet and maximum length of each invertebrate taxon obtained from ligatured nestlings.

Invertebrate taxon	n	Maximum length (mm)
Mollusca	4	6
Arachnida	19	12
Isopoda	4	11
Orthoptera	15	17
Hemiptera[a]	56	9
Coleoptera adult	7	4
Lepidoptera adult	20	17
Lepidoptera larvae	10	28
Diptera adult	188	16
Hymenoptera adult	9	10
Hymenoptera larvae	1	22

[a] Includes Homoptera and Heteroptera.

itor pressure (Ettinger and King 1980, Herbers 1981). Insectivorous birds such as flycatchers may be especially susceptible to environmental variability, as the emergence and activity of their prey is weather dependent. It follows that territory size in insectivorous birds presumably evolved in response to ultimate rather than proximate levels of resource abundance (Orians 1971, Seastedt and MacLean 1979, Franzblau and Collins 1980; see also Myers et al. 1981). During years of average insect availability, food normally would not be limiting, and excess space and time would be available. This was probably the situation during the summers of 1984 and

1985 near Guelph. During years of low insect abundance or high competitor density, constraints on foraging time could be sufficient that the territorial behavior of male Willow Flycatchers better conforms to the predictions of the model. If the presence of competitors and food abundance do not determine the territory size or time budgets of Willow Flycatchers, then an alternative explanation is required to account for the observed variation in territory size. One explanation is that males adjust territory size in response to seasonal and individual differences in the energy requirements associated with different breeding activities. For example, the defended territory must be sufficiently large to provide the resources necessary to meet the energy expenditure of the parents and, when present, the growth and maintenance of the nestlings. The observation that territory size is related to interspecific difference in body size, and therefore metabolic requirement, among species of mammals (McNab 1963, Mace and Harvey 1983) and birds (Schoener 1968, Mace and Harvey 1983) is consistent with this idea.

To test this hypothesis we calculated three types of energy budgets to which territory size could potentially be adjusted or correlated. We hypothesized that male flycatchers might adjust the size of the defended area to the male's energy expenditure (MEE); to the male's energy requirement (MER), which includes the pro-

TABLE 5. Correlation coefficients, one-tailed significance tests, and predicted relationships of territorial responses (TSIZE, LFOR, and SINGDEF) with FOOD, INTR, and COMP for 3 stages, and over all breeding stages of the Willow Flycatcher.[a] Correlations involving FOOD represent simple bivariate correlations; those including INTR or COMP are partial correlations controlling for food availability. Sample sizes and definitions of abbreviations are given in Tables 1 and 3.

	Breeding stage	TSIZE	LFOR[b]	SINGDEF	Predicted relationship
FOOD	1	+0.2022	−0.5874*	+0.3339	
	2	−0.1500	+0.1131	−0.2433	Negative
	3	+0.1910	−0.1999	+0.3175	
	Overall	+0.3916	+0.2958	−0.2822*	
INTR[c]	1	+0.1105	−0.3746	−0.3475	
	2	+0.0735	−0.1759	+0.2593	Positive
	3	−0.6567	+0.0834	+0.4035*	
	Overall	+0.0068	+0.0322	−0.0288	
COMP[c]	1	+0.0721	−0.5650	−0.0759	
	2	+0.4751**	−0.1138	+0.3022	Positive
	3	+0.0604	−0.3046	−0.1657	
	Overall	−0.2110	−0.5622	+0.2786*	

[a] * = $P < 0.05$, ** = $P < 0.001$.
[b] $\log_{10}(\text{FOR} + 1)$.
[c] Partial correlation coefficients, removing the effect of food.

portion of energy to be supplied by the male
for nestling growth; or to the total energy re-
quirement of all the birds on the territory (TER).
The latter included MER, the energy expendi-
ture of the female, and the female's share of the
nestling expenditures. Calculations are provid-
ed in the Appendix, and rank correlations with
territory size in Table 6. During breeding Stages
1 and 2 there were no significant relationships
between either of the three energy budgets and
territory size ($P > 0.05$). MER and TER both
correlated positively with territory size during
Stage 3 ($P < 0.05$). When all breeding stages
were considered together, territory size corre-
lated positively with MEE ($P < 0.01$) and more
strongly with MER and TER ($P < 0.0001$). Ter-
ritory size in the Willow Flycatcher therefore
appears to be adjusted by the male in response
to the energy demands of all of the territory's
occupants, particularly when nestlings and
fledglings are present (Stage 3). Such a rela-
tionship might constitute evidence that terri-
tory size is adjusted in direct proportion to en-
ergy demand (i.e. only sufficient resources
defended) during the period of nestling growth.
If this were true, then feeding time would be
expected to show a positive relationship with
territory size during Stage 3, which was not the
case (Table 5). Territory size may be expanded
in response to energy requirements, but it prob-
ably is maintained at a size that still supplies
more than sufficient resources for the territorial
birds.

We believe that models based on optimal for-
aging time are not strictly applicable to Willow
Flycatchers or to other insectivorous passerines
that defend territories in the breeding season.
The model tested here was formulated origi-
nally for nonbreeding individuals. Hixon (1980)
argued that for feeding territories defended in
any season, factors that affect energy acquisition
should be the most important determinants of
territory size. Other defendable resources that
are unique to the breeding season (e.g. mates,
young, nest sites), however, impose conflicting
pressures on the birds that could influence ter-
ritory size, and feeding time need not be the
sole behavior optimized. Willow Flycatchers
apparently minimize the time spent in main-
tenance activities by adopting a "sit and wait"
foraging strategy. Birds can simultaneously en-
gage in vigilance, food searching and capture,
territorial advertisement, and resting (Ettinger
and King 1980). Feeding and defense need not

TABLE 6. Rank correlation coefficients of male en-
ergy expenditure (MEE), male energy requirement
(MER), and total energy requirement (TER) of the
territory with territory size for Willow Flycatchers
during the breeding season.[a] See Appendix for cal-
culation of energy budgets. Sample sizes are given
in Table 3.

Breeding stage	MEE	MER	TER
1	−0.0593	−0.0593	−0.2308
2	−0.1002	−0.1002	−0.0899
3	−0.0134	+0.4551*	+0.5294*
Overall	+0.3393**	+0.5210***	+0.4786***

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.0001$.

be mutually exclusive components of the time
budget, and theoretical optima for time invest-
ment in any one activity may be difficult to
predict. The extent to which the territorial be-
havior of other time-minimizing species con-
forms to the predictions of the model depends
on species ecology and the previously identi-
fied constraints on foraging behavior. Opti-
mality models provide an operational frame-
work for investigating the proximate
determinants of territorial behavior, and war-
rant further testing on a wide variety of species.

LITERATURE CITED

ARMSTRONG, J. T. 1965. Breeding home range in the
nighthawk and other birds; its evolutionary and
ecological significance. Ecology 46: 619–629.
BEAL, F. E. L. 1912. Food of our more important
flycatchers. U.S. Dept. Agric. Biol. Surv. Bull. 44.
BEAVER, D. L., & P. H. BALDWIN. 1975. Ecological
overlap and the problem of competition and sym-
patry in the Western and Hammond's flycatchers.
Condor 77: 1–13.

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows and their allies. U.S. Natl. Mus. Bull. 179.

———. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.

BLANCHER, P. J., & R. J. ROBERTSON. 1984. Resource use by sympatric kingbirds. Condor 86: 305–313.

BORRER, D. J., D. M. DELONG, & C. A. TRIPLEHORN. 1976. An introduction to the study of insects. New York, Holt, Rinehart & Winston.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160–169.

CARPENTER, F. L., & R. E. MACMILLEN. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194: 639–642.

CRAIG, R. J. 1984. Comparative foraging ecology of Louisiana and Northern waterthrushes. Wilson Bull. 96: 173–183.

CROWSON, R. A. 1981. The biology of the Coleoptera. New York, Academic Press.

DAVIS, D. E. 1954. The breeding biology of Hammond's Flycatcher. Auk 71: 164–171.

———. 1959. Observations on territorial behavior of Least Flycatchers. Wilson Bull. 71: 73–85.

DAVIS, J., G. F. FISLER, & B. S. DAVIS. 1963. The breeding biology of the Western Flycatcher. Condor 65: 337–382.

DAVIS, W. J. 1982. Territory size in *Megaceryle alcyon* along a stream habitat. Auk 99: 353–362.

DIGBY, P. S. B. 1958. Flight activity in the blowfly, *Calliphora erythrocephala*, in relation to wind speed, with special reference to adaptation. J. Exp. Biol. 35: 776–795.

DILL, L. M. 1978. An energy-based model of optimal feeding-territory size. Theor. Pop. Biol. 14: 396–429.

———, R. C. YDENBERG, & A. H. G. FRASER. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 59: 1801–1809.

DUNNING, J. B., JR. 1984. Body weights of 686 species of North American birds. West. Bird Banding Assoc. Monogr. No. 1.

EBERSOLE, J. P. 1980. Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucostictus*. Am. Nat. 115: 492–509.

ETTINGER, A. O., & J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. Auk 97: 533–546.

EWALD, P. W., G. L. HUNT JR., & M. WARNER. 1980. Territory size in Western Gulls: importance of intrusion pressure, defense investments, and vegetation structure. Ecology 61: 80–87.

FRAKES, R. A., & R. E. JOHNSON. 1982. Niche convergence in *Empidonax* flycatchers. Condor 84: 286–291.

FRANZBLAU, M. A., & J. P. COLLINS. 1980. Test of a hypothesis of territory regulation in an insectiv-

orous bird by experimentally increasing prey abundance. Oecologia 46: 164–170.

FRANZREB, K. E. 1984. Foraging habits of Ruby-crowned and Golden-crowned kinglets in an Arizona montane forest. Condor 86: 139–145.

GRUBB, T. C., JR. 1979. Factors controlling foraging strategies of insectivorous birds. Pp. 119–135 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll, Eds.). New York, Academic Press.

HERBERS, J. M. 1981. Time resources and laziness in animals. Oecologia 49: 252–262.

HESPENHEIDE, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113: 59–72.

HIXON, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115: 510–530.

HOLMES, R. T. 1970. Differences in population density, territoriality and food supply of Dunlin on arctic and subarctic tundra. Pp. 303–319 *in* Animal populations in relation to their food supply (A. Watson, Ed.). Oxford, Blackwell Scientific Publ.

JOHNSON, E. J., L. B. BEST, & P. A. HEAGY. 1980. Food sampling biases associated with the "ligature method." Condor 82: 186–192.

KING, J. R. 1955. Notes on the life history of Traill's Flycatcher (*Empidonax traillii*) in southeastern Washington. Auk 72: 148–173.

KODRIC-BROWN, A., & J. H. BROWN. 1978. Influence of economics, interspecific aggression, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. Ecology 59: 285–296.

LEDERER, R. J. 1972. Foraging behavior and niche overlap in seven species of North American flycatchers (Tyrannidae). Ph.D. dissertation, Urbana-Champaign, Univ. Illinois.

MACE, G. M., & P. H. HARVEY. 1983. Energetic constraints on home-range size. Am. Nat. 121: 120–132.

MACLEAN, S. F., & T. R. SEASTEDT. 1979. Avian territoriality: sufficient resources or interference competition? Am. Nat. 114: 308–312.

MARTIN, A. C., H. S. ZIM, & A. L. NELSON. 1951. American wildlife and plants. New York, Mc-Graw-Hill.

MASNER, L., & H. GOULET. 1981. A new model of flight interception trap for some hymenopterous insects. Entomol. News 92: 199–202.

MAYR, E. 1964. Systematics and the origin of species. New York, Dover.

McNAB, B. K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97: 133–140.

MUMFORD, R. E. 1964. The breeding biology of the Acadian Flycatcher. Univ. Michigan Mus. Zool. Misc. Publ. No. 125.

MYERS, J. P., P. G. CONNORS, & F. A. PITELKA. 1979.

Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 96: 551–561.

——, ——, & ——. 1981. Optimal territory size and the Sanderling: compromises in a variable environment. Pp. 135–158 *in* Foraging behavior: ecological, ethological and pyschological approaches (A. C. Kamil and T. D. Sargent, Eds.). New York, Garland Press.

NORTON, M. E., P. ARCESE, & P. W. EWALD. 1982. Effect of intrusion pressure on territory size in Black-chinned Hummingbirds (*Archilochus alexandri*). Auk 99: 761–764.

ODUM, E. P., & E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72: 128–137.

ORIANS, G. H. 1971. Ecological aspects of behavior. Pp. 513–546 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

PRESCOTT, D. R. C. 1986. Polygyny in the Willow Flycatcher. Condor 88: 385–386.

——. 1987. Territorial responses to song playback in allopatric and sympatric populations of the Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers. Wilson Bull. 99: in press.

PYKE, G. H. 1979. The economics of territory size and time budget in the Golden-winged Sunbird. Am. Nat. 114: 131–145.

SCHARTZ, R. L., & J. L. ZIMMERMAN. 1971. The time and energy budget of the male Dickcissel (*Spiza americana*). Condor 73: 65–76.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123–141.

——. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2: 369–404.

——. 1983. Simple models of optimal feeding-territory size: a reconciliation. Am. Nat. 121: 608–629.

SEASTEDT, T. R., & S. F. MacLEAN. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. Auk 96: 131–142.

SIMON, C. A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology 56: 993–998.

SLANEY, P. A., & T. G. NORTHCOTE. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. J. Fish. Res. Board Can. 31: 1201–1209.

SMITH, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. Ecol. Monogr. 38: 31–63.

SOKAL, R., & F. ROHLF. 1981. Biometry. San Francisco, Freeman.

SOUTHWOOD, T. R. E. 1971. Ecological methods, with special reference to the study of insect populations. London, Methuen & Co.

STEIN, R. C. 1958. The behavioral, ecological and morphological characteristics of two populations of the Alder Flycatcher, *Empidonax traillii* (Audubon). New York State Mus. Sci. Serv. Bull. No. 371.

STENGER, J. A. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75: 335–346.

TAYLOR, L. R. 1963. Analysis of the effect of temperature on insects in flight. J. Anim. Ecol. 32: 99–117.

TOWNES, H. 1972. A light weight Malaise trap. Entomol. News 83: 239–247.

TULLOCK, G. 1979. On the adaptive significance of territoriality: comment. Am. Nat. 113: 772–775.

WALKINSHAW, L. H. 1966. Summer biology of Traill's Flycatcher. Wilson Bull. 78: 31–46.

WALSBERG, G. E. 1983. Avian ecological energetics. Pp. 161–220 *in* Avian biology, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

——, & J. R. KING. 1978. The energetic consequences of incubation for two passerine species. Auk 95: 644–655.

WASSERMAN, F. E. 1980. Territorial behavior in a pair of White-throated Sparrows. Wilson Bull. 92: 74–87.

——. 1983. Territories of Rufous-sided Towhees contain more than minimal food resources. Wilson Bull. 95: 664–667.

WITTENBERGER, J. F. 1981. Animal social behavior. Boston, Duxbury Press.

WOLF, L. L. 1975. Energy intake and expenditures in a nectar-feeding sunbird. Ecology 56: 92–104.

YEATON, R. I., & M. L. CODY. 1974. Competitive release in island Song Sparrow populations. Theor. Pop. Biol. 5: 42–58.

APPENDIX. Calculation of energy budgets.

Male energy expenditure (MEE).—Energetic equivalents of activities included in time-budget analyses were used to calculate the energy expenditure of the male Willow Flycatcher. A basal metabolic rate (BMR) of 0.79 kJ/h (Ettinger and King 1980) was assumed. Sitting was assigned a value of 1.66 kJ/h (2.1 × BMR), singing a value of 1.83 kJ/h (1.1 × sitting), and flying a value of 7.13 kJ/h (Ettinger and King 1980). Foraging flights, which were generally more vigorous than forward flight, were assumed to consume 7.5 kJ/h; flights associated with defense and courtship were assigned an energetic equivalent of 8.0 kJ/h. The time spent at the nest tending young was considered more costly than perching and was estimated to require 3.0 kJ/h. Activity costs were summed over an 18-h period (Ettinger and King 1980). We assumed that the time allocated during the morning observation period was representative of activities over the entire day. Nighttime costs ("sleep") were estimated to require 1.36 kJ/h (18% less than sitting cost; Walsberg and King 1978) over 6 h.

Male energy requirement (MER).—The male requirement represents the energy expenditure of the male flycatcher (MEE, see above), and the proportion of the nestlings' requirements that the male must provide. We assumed that both parents feed the young equally, as is typical of *Empidonax* flycatchers (Bent 1942, Mumford 1964). The cost of nestling growth (E_n) was calculated from the average nestling requirement (Walsberg 1983) as:

$$\ln E_n = \ln 14.05 + 0.440 \ln M_b,$$

where M_b = adult body mass (12.6 g; Table 2). Of the estimated 42.84 kJ/day required per nestling, the male supplies half, or 21.42 kJ·nest-

ling^{-1}·day^{-1}. For fledglings, the maximum energy expenditure of nestling growth (Walsberg 1983) was employed:

$$\ln E_f = \ln 13.40 + 0.528 \ln M_b,$$

or 25.53 kJ·fledgling^{-1}·day^{-1} for each parent. The added cost of the requirement of the young is accrued only during breeding Stage 3; for Stages 1 and 2, MEE equals MER.

   Total energy requirement of the territory (TER).—TER includes the total energy requirement of the female plus the male MER (as above). Because time budgets for females were not recorded, we used the mean energy expenditure values of females for each stage of breeding calculated by Ettinger and King (1980: table 3). These are prenesting (breeding Stage 1), 65.2 kJ/day; incubation, 51.7 kJ/day; and for the nestling and fledgling periods (Stage 3), 53.1 kJ/day. For the nest-building and incubation stages, Ettinger and King's (1980: table 5) values for female expenditures (58.0 kJ/day) include an estimated cost of egg production (4.6 kJ/day), calculated based on a clutch size of 3 eggs. Female Willow Flycatchers near Guelph typically produce a 4-egg clutch, and we added 1.53 kJ/day (⅓ of 4.6 kJ/day) to the daily energy expenditure to account for the added energy cost. The female's share of the nestling and fledgling expenditures (21.42 and 25.53 kJ·young^{-1}·day^{-1}, respectively) were then added to all Stage 3 territories, and the total female expenditures added to those of the male (MER), to derive the value of TER for each territory.