# Fall Stopover Behavior of Willow Flycatchers Using a Riparian Corridor in Central California

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## ABSTRACT

Mist-netting of Willow Flycatchers (*Empidonax traillii*) was conducted daily in riparian habitat near the southern end of San Francisco Bay, California, during the fall migratory period (1986-1995) to determine the extent of use of this area as a migratory stopover site. A total of 340 individuals were captured (38 recaptures) during 91,962 net hours of operation. Capture/recapture methods were used to determine recapture rates (ten-year mean = 10.8%, range = 2.9% to 17.9%, SD = 4.7), the length of stopover (mean = 6 days, range 2 to 19 days, SD = 3.7, n = 35), gross mass changes (mean 0.7 g, range = -1.8 to 3.0 g, SD = 1.1, n = 35), and rates of change (mean = 0.1 g/day, range = -0.6 to 0.5 g/day, SD = 0.3, n = 35) of resting birds. Most of the individuals arriving on site had low fat reserves with 76% showing no visible fat deposits. The mean original mass of resting birds (11.1 g) was significantly lower than that of transients (11.4 g) which indicates that lighter (less fat) individuals were more likely to use the site for multiday refueling stops than heavier individuals. Both gross mass changes and rates of mass change were found to be positively related to length of stay. Flight range estimations indicated that the average resting bird could increase its potential flight range by 158 km.

## INTRODUCTION

In this paper I present capture/recapture mist-netting data that documents use of a riparian site by migrating Willow Flycatchers in fall. While a few studies have looked at feeding patterns (energy and time budgets) in this species, these studies have concentrated on the breeding grounds (e.g. Ettinger and King 1980, Frankes and Johnson 1982, and Prescott and Middleton 1988). Very little, however, is known about the migratory stopover patterns of Willow Flycatchers.

In California, races of Willow Flycatchers have been eliminated from most of their lower elevation breeding sites with most of the remaining breeding populations occurring in isolated mountain meadows of the Sierra Nevada, along the Kern, Santa Margarita, and San Luis Rey rivers, and downstream of the Trinity Dam (USDA Forest Service 1994). Fall migrants in the San Francisco Bay area are probably derived from populations that breed to the north of these troubled populations. Departure from the breeding sites does not occur until August (USDA Forest Service 1994).

## METHODS

These data were collected at the Coyote Creek Riparian Station, Alviso, California (37°26'N, 121°55'W). This research site is located along the lower stretch of Coyote Creek, approximately 9.2 km south of where the creek enters the southern end of San Francisco Bay. This site represents a remnant island of riparian habitat surrounded by extensive urban development and agriculture (for a detailed vegetation description of the site, see Otahal 1995). These data were collected during the fall migratory period (1 August to 29 October) for 1986 through 1995.

The *Empidonax* complex is notoriously difficult to identify to species, even in the hand. Therefore, extreme caution was used in identifying this species. Careful measurements, in addition to the standard ones (i.e., tail length, bill width, wing length) as well as plumage characteristics, were taken and compared to the species criteria described in Pyle et al. (1987). In most cases, species identification was confirmed by two or more banders. Also, all recaptures were identified to species with no reference to previous captures. Out of the 38 recaptures, there was no case in which species identifcation conflicted between original capture and recapture. Therefore, confidence is high that our species identification was reliable.

The birds were captured using standard mist-nets 2 m tall and 12 m long, with a mesh size of 32 or 36 mm. Three two-tiered, four-meter tall canopy nets were also used. The nets were established on permanent sites which were maintained throughout the season. The number of nets and the length of creek sampled varied from year to year (Table 1), but were held constant during any given year (with the exception of 1990 when additional nets were added later in the season).

The nets were operated in a staggered fashion with 12 to 45 nets open on any given day. Each individual net was opened at least twice, but not more than four times, during any seven-day period. The nets were opened just before sunrise and operated for approximately five hours. Nets were opened daily except in poor weather (i.e. rain, high winds, or flooding).

These nets were inspected at approximately 60-min intervals. Captured birds were taken to a central banding station, processed and released. All birds were banded with U. S. Fish and Wildlife Service bands. Wing length, mass (to the nearest 0.1 g), time of capture, location of capture, and molt characteristics were recorded for each bird. In order to get a general idea of fat loads, each individual was classed according to a four-point fat code (Hackman et al. 1984) with a code of "0" indicating no visible fat, "1" indicating fat lining the furcula, but concave, "2" indicating fat filling the furcula, but not mounded, and "3" furcular fat mounded and convex.

The data were subjected to four analyses. First, to establish the timing of migration on the site, I pooled the original capture records of Willow Flycatchers in five-day increments for each of the ten years of the study and plotted them graphically (Fig. 1).

**Table 1. Summary of netting effort and resulting captures of Willow Flycatchers during the fall (1 Aug through 30 Oct) migratory periods of 1986 through 1995 at the Coyote Creek Riparian Station, Alviso, CA.**

| Year | Number of Nets* | Net Hours** | Length of Creek Sampled (m) | First Captures | Captures /100 nh | Number Recaptured | Percent Recaptured |
|---|---|---|---|---|---|---|---|
| 1986 | 19.5 | 5706 | 760 | 40 | 0.7 | 3 | 7.5 |
| 1987 | 35.5 | 10577 | 805 | 34 | 0.3 | 1 | 2.9 |
| 1988 | 45.5 | 12159 | 1035 | 35 | 0.3 | 3 | 8.6 |
| 1989 | 49.0 | 12543 | 1165 | 24 | 0.3 | 1 | 4.2 |
| 1990*** | 57.0 | 8345 | 1165 | 30 | 0.4 | 4 | 13.3 |
| | 63.5 | | 1959 | | | | |
| 1991 | 58.0 | 7487 | 1959 | 19 | 0.3 | 3 | 15.8 |
| 1992 | 62.5 | 9210 | 1959 | 52 | 0.6 | 7 | 13.5 |
| 1993 | 56.5 | 9221 | 1165 | 23 | 0.2 | 3 | 13.0 |
| 1994 | 51.5 | 9449 | 1165 | 56 | 0.6 | 10 | 17.9 |
| 1995 | 67.5 | 7265 | 2236 | 27 | 0.4 | 3 | 11.1 |

* One net = 12m x 2m
** One net hour = one 12m x 2m net operated for one hour.
*** First set is for August; second is for September to October.

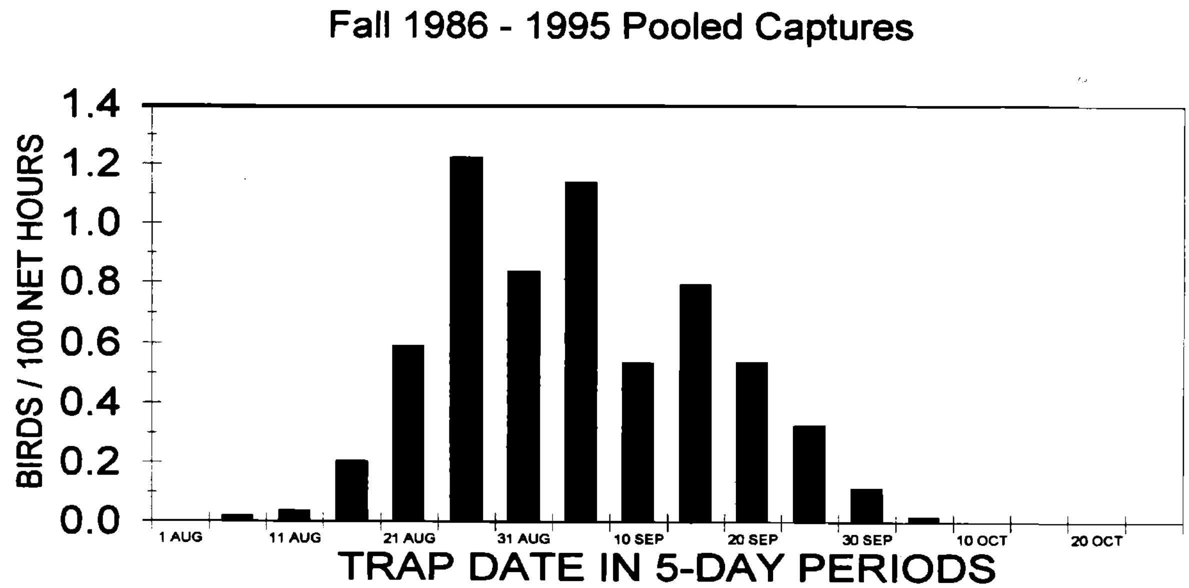


**Fig. 1**. Rates of new captures of Willow Flycatchers during fall migration (1985-1995 pooled) at the Coyote Creek Riparian Station, Alviso, CA (n=383).

Next, I determined the percentage of resting birds (those recaptured at least once). Individuals captured only once and not recaptured on a later day (transients) were assumed to have left the site the evening of capture (Cherry 1982, Loria and Moore 1990). A conservative estimate of the percentage of resting birds was determined by dividing the number of birds recaptured at least once by the total number of original captures. Birds recaptured multiple times within a season were considered a single recapture. In cases of multiple recaptures, data were used from the final recapture only.

I determined minimum stopover length for each bird by counting the number of days between the original capture and the final recapture and adding one (Bairlein 1985, Biebach et al. 1986, Lavee et al. 1991). Thus, a bird which was not recaptured would have a stopover of one day while a bird which was recaptured the day after banding would have a stopover of two days and so on. This is a highly conservative estimate of stopover length since it is unlikely that all individuals are both captured on the first day they arrive on site and on the last day they use the site (Cherry 1982, Moore and Kerlinger 1987, Loria and Moore 1990, Kaiser 1995).

The fourth analysis consisted of determining the mass change of resting birds and the rate of this change. I calculated the mass change by subtracting the mass upon initial capture from the mass recorded during final recapture. Some authors have shown that there are daily cycles of mass change in migratory birds, and if comparisons of mass change are made from one capture to the next, the weights must be taken at the same time of day (Rappole and Warner 1976), or corrected to the same time by using an established rate of mass gain during the daylight hours (Cherry 1982, Moore and Kerlinger 1987, Loria and Moore 1990). Almost all (98.5%) of the birds in this study were captured within a six-hour period (between 06:00 and 12:00), and no significant changes in mass were detected over this period of time (least squares linear regression, $P$ = 0.33, $R^2 < 0.01$, n = 328, 12 cases omitted due to missing mass values, masses log transformed to improve normality of sampling distribution). Therefore, the raw masses were used without correcting for time of day. The mass of birds captured more than once in a day was determined by taking the average for that day.

I then calculated the rate of mass change by dividing the change in mass by the length of stopover minus one. Since the birds were recaptured during the morning hours, I subtracted one day from the stopover period before division since these birds had not had the last day of stopover to put on mass (fat). This gives a more accurate estimate of the rate of change than if the mass change was simply divided by the length of stay (Cherry 1982).

Finally, I determined the increase in the theoretical flight range as a result of gains in fat. Changes in mass may reflect changes in flight musculature, water, and material in the digestive tract, but essentially all the mass gain during stopover is due to accumulation of fat (Connell et al. 1960, Nisbet et al. 1963, Rogers and Odum 1964, Rogers and Odum 1966, Hicks 1967). Therefore, mass changes observed here were considered to be changes in fat content. Theoretical flight ranges were estimated by first converting the increase in mass (fat) into energy equivalents by assuming a choleric density of 39.8 kJ/g of change (Kaiser 1992). After calculating average total body mass measurements for resting birds on final recapture, I calculated the general flight metabolism using a formula which estimates energy expenditure during migratory flights (Kaiser 1992): flight metabolism = 0.36 kJ * total body mass * flight time in hours.

By rearrangement of this flight metabolism formula, the potential flight time provided by a given amount of energy can be derived: flight time in hours = energy available / (0.36 x total body mass).

I then converted this flight time to flight distance by assuming that birds of this size fly at a rate of 23 km/hr (Pennycuick 1989). I multiplied the estimated flight time by the assumed flight speed to convert it to potential flight range increase.

I then subjected the length of stay, mass change and rate of change data to analysis using least squares linear regressions to see how these parameters changed with length of stay. All analyses were conducted using the Number Cruncher Statistical Systems for Windows, version 6.0.21 (Hintze 1996).

## RESULTS

***General Capture Statistics*** - Fall passage began around 5 August and continued through late September and early October, with a general peak near the beginning of September (Fig. 1). Annual capture rates ranged from 0.2 to 0.7 captures per 100 net hours with a ten-year mean of 0.4 (Table 1). Recapture rates varied from 2.9% to 17.9% (SD = 4.7) with a ten-year mean of 10.8%. Seventy-six percent of first captures showed no visible fat deposits (class code "0") and the others showed only light deposits (19% had class "1" fat deposits, 5% had class "2", and no individual had class "3"). The mean mass of resting birds upon original capture was 11.1 g (range 8.5 to 13.4 g, SD = 1.1, n = 35, three resting birds omitted due to missing masses), whereas the mean mass of transient birds upon original capture was 11.4 g (range 9.5-14.3 g, SD = 1.0, n = 291, eleven birds omitted due to missing masses). This difference was found to be statistically significant ($P = 0.03$, Mann-Whitney $U$ test). When original capture masses were plotted against time of capture, only a slight, statistically insignificant, increase in body mass was detected for both transients (least squares linear regression, $P = 0.39$, $R^2 < 0.01$, n = 291) and resting birds (least squares linear regression, $P = 0.33$, $R^2 = 0.03$, n = 35, masses log transformed to improve normality of sampling distribution in both cases) indicating only slight variations in mass due to capture time of day (for the morning hours 06:00 to 12:00).

***Length of Stay and Mass Change*** - The mean length of stopover of resting birds was six days (range 2 - 19 days, SD = 3.7, n = 35, Fig. 2). The mean mass change of resting birds was 0.7 g and ranged from -1.8 to 3.0 g (SD = 1.1, n = 35, Fig. 3). A $t$-test showed that this change was significantly ($P < 0.01$) greater than zero. There was a significant ($P < 0.01$, $R^2 = 0.55$, n = 35) positive linear relationship found between length of stay and the mass change of individuals (Fig. 4) given by: Mass Change = (-0.6) + (0.2) Length of Stay.

***Rates of Mass Change*** - Mass change rates ranged from -0.6 to 0.5 g/day (mean = 0.1, SD = 0.3, n = 35). A statistically significant log linear relationship ($P < 0.01$, $R^2 = 0.49$, n = 35) was found between mass change and length of stay (Fig. 5). The mass change rate was log transformed to improve the normality of the sampling distribution and a constant (1) was added to the rate to prevent zero and negative values which can not be log transformed. The equation for this line is given by:log (Mass Change Rate + 1) = -0.07 + 0.05 (Length of Stay).

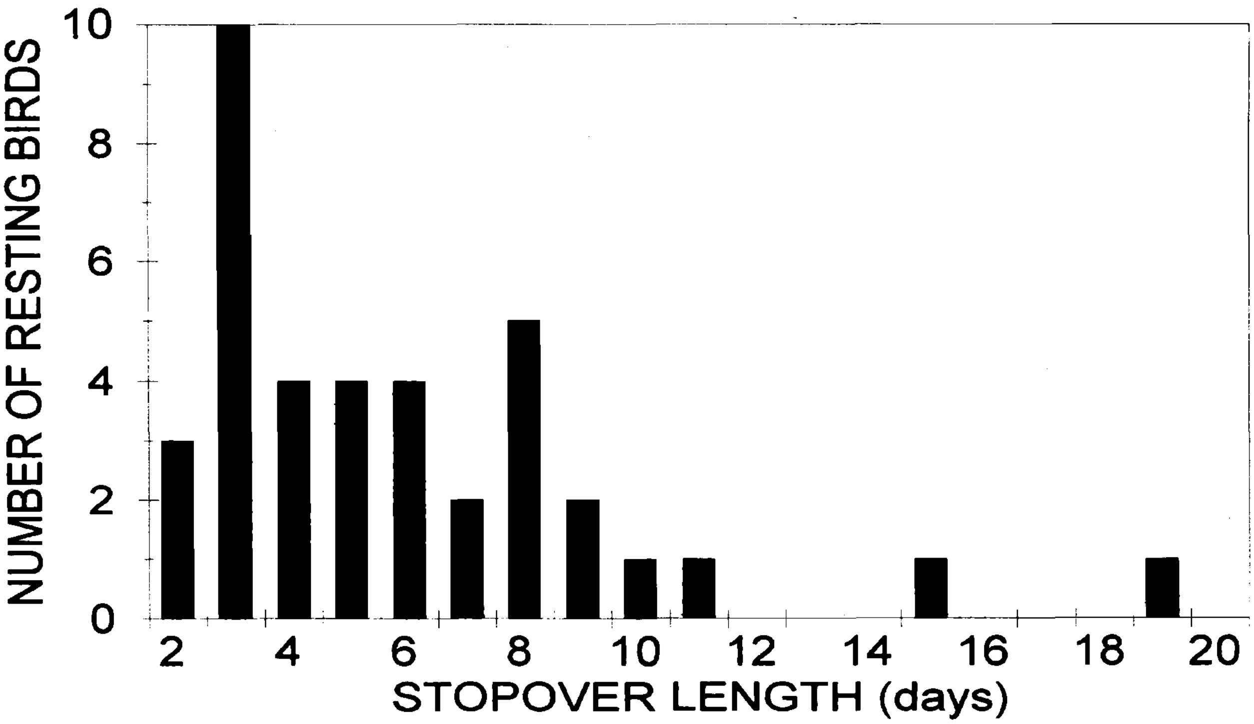


**Fig. 2**. Length of stay distribution for resting Willow Flycatchers during fall migration (1986-1995 pooled) at the Coyote Creek Riparian Station, Alviso, California.

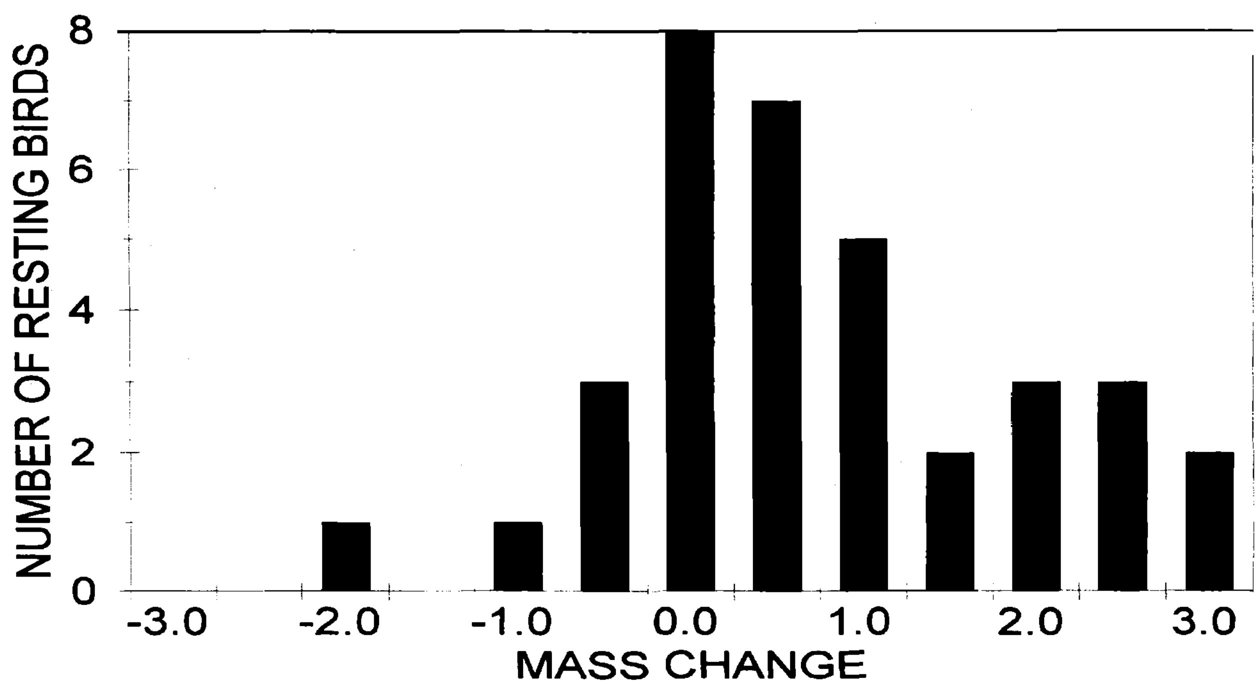


**Fig. 3**. Mass change distribution for resting Willow Flycatchers during fall migration (1986-1995 pooled) at the Coyote Creek Riparian Station, Alviso, California. Three values omitted due to missing values (n=35).

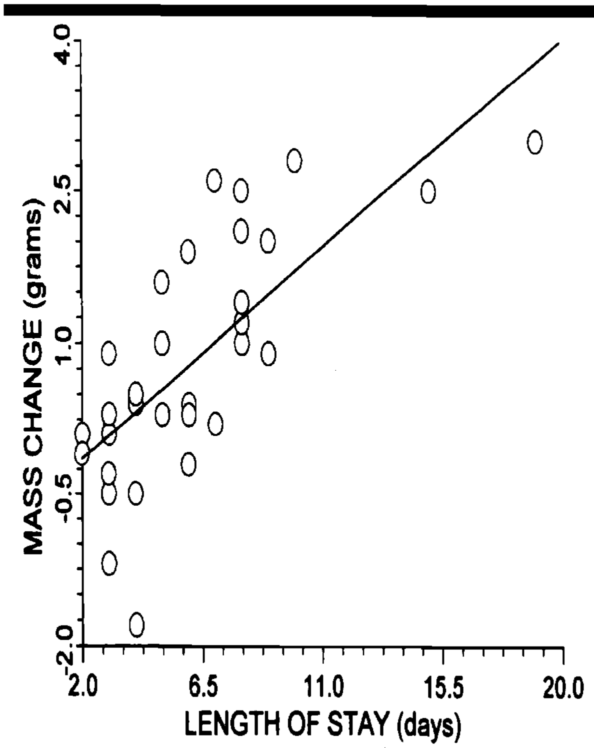


**Fig. 4.** Mass change of resting Willow Flycatchers as it relates to length of stay during fall migration (1986-1995 pooled) at the Coyote Creek Riparian Station, Alviso, CA. Three values not plotted due to missing values (n=35, some values overlap making n appear as 30).

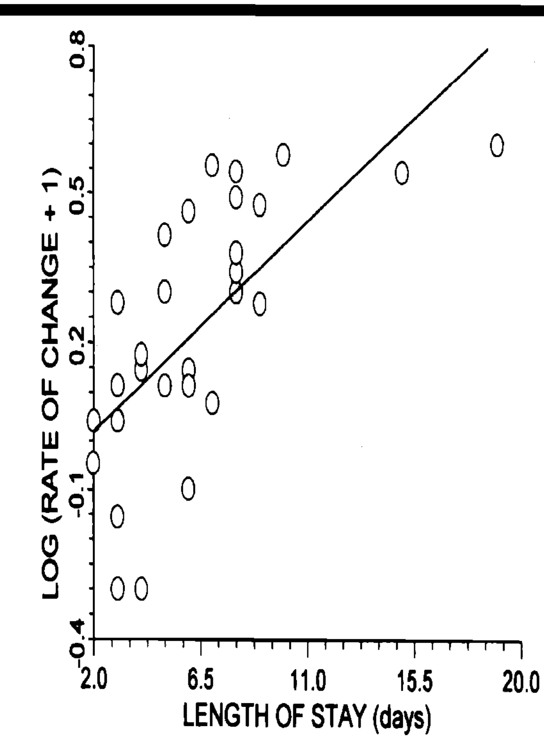


**Fig. 5.** Rate of mass change in Willow Flycatchers as it relates to length of stay during fall migration (1986-1995 pooled) at the Coyote Creek Riparian Station, Alviso, California. Three values not plotted due to missing values (n=35, some values overlap making n appear as 30).

***Change in Flight Range*** - The average mass gain of 0.7 g in resting birds would result in an average energy gain of 27.9 kJ. The mean mass of resting birds upon final capture was 11.8 g (range 8.4 - 15.2 g, SD = 1.3, n = 35) which would give an average flight metabolism of 4.2 kJ / hr of flight. Thus, resting birds gain 6.6 hours of potential flight time on average. Assuming a flight speed of 23 km / hr, average increase in flight range is 158 km.

## DISCUSSION

The relatively small number of recaptured birds and the rather small mass gains could be interpreted as indicating that only a small minority of the birds are finding this site useful, but this view changes when other factors are considered. First, these recapture data should be viewed as very conservative estimates. The capture/recapture methodology itself leads to an under estimation of length of stay, mass change and rate of change. It is unlikely that an individual is captured on the first day it arrives on site and on the last day it uses the site (Cherry 1982, Moore and Kerlinger 1987, Loria and Moore 1990), so the length of stay is under estimated. Analysis of capture/recapture data using Jolly-Seber models for open populations revealed that, in small bird species, the estimated duration of stay is, on average, at least twice the observed (minimum) resting time (Kaiser 1995). Given that mass change and rate of fat deposition in Willow Flycatchers seem to be related to stopover length (Figures 4 and 5), both of these variables would be underestimated using this methodology. Given the conservative nature of these estimates, the results I present here should be considered minimum values.

Also, individuals which stay for one day may still be using the site as a fueling stop. For example, Winker et al. (1992a) have suggested that some Swainson's Thrushes (*Catharus ustulatus*) may exhibit a "feed-by day, fly-by night" strategy, whereby sufficient fat reserves are accumulated in a single day to allow a full (or near-full) night's flight. The results presented here indicate that there is no significant increase in mass of transient individuals over the first six hours in the morning which would tend not to support this hypothesis. However, if these same analyses were carried out to include the entire day, instead of just the morning hours, these increases could become significant.

These low recapture numbers and low mass gains could be an indication that this is a poor site for mass (fat) deposition, or possibly that individuals are staying only long enough to gain enough fat reserves to get to the next stopover site. This second hypothesis is supported by the fact that the resting birds in this study, on average, gained only enough fuel (fat) for 6.6 hours of flight (or about one night of flight time) before leaving the area.

It should also be noted that the mean original mass of resting birds (11.1 g) was significantly lower than that of transients (11.4 g) which indicates that lighter (less fat) individuals were more likely to use the site for multi-day refueling stops than heavier (more fat) individuals. The potential importance of this site is also reflected by the large number (76%) of individuals with no visible fat deposits upon arrival.

The rate of mass change shows a pattern of increase with length of stay (Fig. 5). The logarithmic nature of this relationship, however, indicates that this effect is greatest with short resting birds and becomes reduced with longer staying birds. The rate starts off negative, followed by an initial rapid increase in mass deposition rates which then tends to level off. There are several possible explanations for this logarithmical pattern. Handling of the birds could cause mass losses which then take time to recover. It has been suggested that the stress of handling (being captured in nets and being held for a period of time before processing) and the disruption of feeding schedules associated with capture may induce initial mass loss (Rogers and Odum 1966, Winker et al. 1992b, Refsnider 1993). A second possible cause of this pattern could be the initial unfamiliarity of the site to new arrivals which results in initial losses in mass until the individual becomes familiar with the food resources available. Also, it has been suggested (Biebach 1985, Terrill 1990a, Terrill 1990b, Moore et al. 1995) that individuals that are unable to obtain food resources sufficient enough to gain fat have a tendency to leave the next night. Thus, the individuals losing mass would more likely leave after a short period of time.

Some authors have noted changes in mass of birds associated with changes in body structure such as body molt (Winker et al. 1992a, Baggott 1975, Kaiser 1992) and ossification of bones in juvenile birds (Bezzel and Prinzinger 1990). Willow Flycatchers, like most other *Empidonax* flycatchers, undertake their annual molt on the wintering grounds following autumnal migration (Ettinger and King 1980) and none of the birds in this study exhibited molt. While the majority (72%) of the resting individuals had incompletely ossified skulls, the relatively short stopover time probably reduced the mass change effect of bone pneumatization.

Data on related species can help place these findings into perspective. Using similar capture/recapture methods, Winker et al. (1992b) reported that resting Least Flycatchers (*Empidonax minimus*) had a mean fall recapture rate of 4%, a mean stopover of four days, and a mean mass gain of 0.03 g/day at their wooded suburban-residential site in Washington County, Minnesota. Morris et al. (1996) reported that resting "Traill's" Flycatchers (*Empidonax alorum* and *E. traillii*) had a mean recapture rate of 9%, a mean fall stopover period of four days, and a mean mass gain of 0.4 g/day at their Appledore Island, Maine, study site. Winker et al. (1992b) and Morris et al. (1996) both used a different method of determining length of stay, subtracting the last recapture day from the initial capture day without adding one; therefore, one day was added to their reported stopover periods in order to make the periods comparable to those reported from this study. In combination, these results indicate that there is much variability in stopover patterns due to species and habitat characteristics.

Similar studies such as these need to be conducted in other riparian areas as well as other habitat types in order to determine the relative importance of this site to the migration of Willow Flycatchers. It would be important to compare these results with other sites to help determine if this species uses the "feed-by day, fly-by night" strategy (indicating the need for preserving many small stopover habitat sites for successful migration) or, alternatively, that these results reflect a habitat "sink" where birds can not accumulate large fat reserves.

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## LITERATURE CITED

Baggott, G. K. 1975. Molt, flight muscle "hypertrophy" and pre-migratory lipid deposition of the juvenile Willow Warbler, *Phylloscopus trochilus. J. Zool.*, Lond. 175:299-314.

Bairlein, F. 1985. Body weights and fat deposition of Palaeartic passerine migrants in the central Sahara. *Oecologia* 66:141-146.

Bezzel, E. and R. Prinzinger. 1990. Ornithologie. Stuttgart. p. 552.

Biebach, H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia* 41:695-697.

Biebach, H., W. Friedrich, and G. Heine. 1986. Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69:370-379.

Cherry, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. *Auk* 99:725-732.

Connell, C. E., E. P. Odum and H. Kale. 1960. Fat-free masses of birds. Auk 77:1-9.

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

Frankes, R. A. and R. E. Johnson. 1982. Niche convergence in *Empidonax* flycatchers. *Condor* 84:286-291.

Hackman, D. C., M. Garland, P. Minke, and B. Schaffer. 1984. Handling and examination of live birds, p. 32-37 *in* Banders information resource data manual (T. Mutchler, ed.),.Eastern Bird Banding Association, Hellertown, PA.

Hicks, David L. 1967. Adipose tissue composition and cell size in fall migratory thrushes (*Turdidae*). *Condor* 69:387-399.

Hintze, J. L. 1996. Number Cruncher Statistical Systems. Kaysville, Utah.

Kaiser, A. 1992. Fat deposition and theoretical flight range of small autumn migrants in southern Germany. *Bird Study* 39:96-110.

Kaiser, A. 1995. Estimating turnover, movements and capture parameters of resting passerines in standardized capture-recapture studies. *J. Appl. Statistics* 22:1039-1047

Lavee, D., U. N. Safriel, and I. Meilijson. 1991. For how long do trans-Saharan migrants stop over at an oasis? *Ornis Scand.* 22:33-44.

Loria, D. E. and F. R. Moore. 1990. Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus. Behav. Ecol.* 1:24-35.

Moore, F. R. and P. Kerlinger. 1987. Stopover and fat deposition by North American wood warblers (*Parulinae*) following spring migration over the Gulf of Mexico. *Oecologia* 74:47-54.

Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation, p. 121-144 *in* Ecology and management of Neotropical migratory birds (T. E. Martin and D. M.Finch, eds.). Oxford Univ. Press, New York.

Morris, S. R., D. W. Holmes, and M. E. Richmond. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor* 98:395-409.

Nisbet, I. C. T., W. H. Drury, Jr., and J. Baird. 1963. Mass loss during migration. *Bird-Banding* 34:107-159.

Otahal, C. D. 1995. Sexual differences in Wilson's Warbler migration. *J. Field Ornithol.* 66:60-69.

Pennycuick, C. J. 1989. Bird flight performance. Oxford Univ. Press, New York.

Prescott, D. R. C. and A. L. A. Middleton. 1988. Feeding-time minimization and the territorial behavior of the Willow Flycatcher (*Empidonax traillii*). *Auk* 105:17-28.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

Rappole, J. H. and W. Warner. 1976. Relationship between behavior, physiology and weather in avian transients at a migration stopover site. *Oecologia* 26:193-212.

Refsnider, J. M. 1993. Weight loss by birds when held for banding. *N. Am. Bird Bander* 18:90-97.
Rogers, D. T., Jr., and E. P. Odum. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. *Auk* 81:505-513.
Rogers, D. T., Jr., and E. P. Odum. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. *Wilson Bull.* 78:415-433.
Terrill, S. B. 1990a. Ecophysiological aspects of movements by migrants in the wintering quarters, p. 130-143. *in* Bird migration (E. Gwinner, ed.), Springer-Verlag, Berlin.
Terrill, S. B. 1990b. Food availability, migratory behavior, and population dynamics of terrestrial birds during the nonproductive season. *Studies in Avian Biology* 13:438-443.
USDA Forest Service. 1994. Neotropical migratory bird reference book, Vol. 1. Pacific Southwest Reg.
Winker, K., D. W. Warner and A. R. Weisbrod. 1992a. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site, p. 384-402 *in* Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, eds.), Smithsonian Institution Press, Washington, DC.
Winker, K., D. W. Warner and A. R. Weisbrod. 1992b. Daily mass gains among woodland migrants at an inland stopover site. *Auk* 109:853-862.