

WINTER FORAGING BEHAVIOR BY EASTERN PHOEBES (*Sayornis phoebe*) IN
CENTRAL TEXAS

THESIS

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By

Jeffrey R. Troy, B.S.

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Jeffrey R. Troy, B.S.

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TABLE OF CONTENTS

| | Page |
|--|------|
| ACKNOWLEDGEMENTS..... | iv |
| LIST OF FIGURES..... | vii |
| ABSTRACT..... | viii |
| CHAPTER | |
| I. THE EFFECTS OF WEATHER AND HABITAT CONDITIONS ON FORAGING BEHAVIOR IN WINTERING EASTERN PHOEBES (<i>Sayornis phoebe</i>) | 1 |
| Introduction | 1 |
| Materials and Methods | 3 |
| Analysis. | 5 |
| Results | 6 |
| Discussion | 11 |
| II. PERCH RETURN FREQUENCY IN WINTERING EASTERN PHOEBES (<i>Sayornis phoebe</i>) | 16 |
| Introduction | 16 |
| Materials and Methods | 17 |
| Analysis | 19 |
| Results | 19 |
| Discussion | 20 |
| III. AVERAGE SALLY DISTANCE VERSUS AVERAGE GIVE-UP DISTANCES IN WINTERING EASTERN PHOEBES (<i>Sayornis phoebe</i>)..... | 23 |

| | |
|--|----|
| Introduction | 23 |
| Materials and Methods | 23 |
| Analysis | 24 |
| Results | 25 |
| Discussion | 25 |
| IV. SWARM FORAGING IN EASTERN PHOEBES (<i>Sayornis phoebe</i>)..... | 26 |
| V. POTENTIAL WINTER TERRITORIALITY IN EASTERN PHOEBES (<i>Sayornis phoebe</i>) | 28 |
| APPENDICES..... | 30 |
| LITERATURE CITED..... | 39 |

LIST OF FIGURES

| | Page |
|-----------|---|
| Figure 1. | Foraging effort (horizontal distance traveled per foraging movement) as a function of ambient temperature in wintering Eastern Phoebes > 50 m from permanent or seasonal water sources in Central Texas in 2004-20058 |
| Figure 2. | Foraging rate (foraging movements per minute) as a function of calendar date (beginning with November 12) in wintering Eastern Phoebes in Central Texas in 2004-20059 |
| Figure 3. | Percentage of foraging movements that were aerial hawks as a function of ambient temperature in wintering Eastern Phoebes in Central Texas in 2004-200510 |
| Figure 4. | Perch return frequency as a function of perch availability in wintering Eastern Phoebes in Central Texas from November 2004 through February 200520 |

ABSTRACT

WINTER FORAGING BEHAVIOR BY EASTERN PHOEBES (*Sayornis phoebe*) IN
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By

Jeffrey R. Troy, B.S.

Texas State University – San Marcos

December 2005

SUPERVISING PROFESSOR: JOHN T. BACCUS

I investigated potential effects of weather and habitat conditions on foraging effort, foraging rate, aerial hawking percentage, height of sally initiation and sally distance in Eastern Phoebes during the winter of 2004-2005. I also examined perch return frequency as a function of vegetative (perch) availability and sally distance, and tested the hypothesis that average “give-up” distances were > 2 times that of average sally distances. I found effort per foraging movement decreased with increasing ambient temperature in birds that foraged > 50 m from water sources, but not in birds that foraged ≤ 25 m from water. Foraging rate increased with progression of calendar date. Aerial hawking percentage increased as ambient temperature increased. Average height of sally initiation was not significantly affected by weather or habitat conditions. Average sally distance did not vary with ambient temperature or height of sally initiation, but did tend to increase in increasingly open habitats. Perch return frequency tended to decrease with

increased vegetative availability, but was unaffected by average sally distance. These results suggest that temperature and habitat conditions affected some foraging behaviors in Eastern Phoebe. Average “give-up” distances were greater than twice that of average sally distances, presumably giving birds new fields of view from new perches. Other observed behaviors of interest include 5 individuals that foraged through aerial insect swarms and appeared to capture more than 1 prey item during single aerial foraging events, as well as aggressive behaviors that could be viewed as indirect evidence of winter territoriality.

CHAPTER 1

THE EFFECTS OF WEATHER AND HABITAT CONDITIONS ON FORAGING BEHAVIOR IN WINTERING EASTERN PHOEBES (*Sayornis phoebe*)

Introduction

Ecological literature suggests short-term weather variations affect foraging behaviors in flycatching birds, including the Tyrannidae (Leck 1971, Verbeek 1975a and 1975b, Foreman 1978, Murphy 1987, Teather 1992), Muscicapidae (Davies 1977), and Turdidae (Pinkowski 1977, Moreno 1984). Few studies examined possible effects of habitat variations on these behaviors, and none have investigated Eastern Phoebe (*Sayornis phoebe*) foraging behavior as a function of weather or habitat during the non-breeding season.

The Eastern Phoebe is a common and widespread species of Tyrant Flycatcher (Tyrannidae), which winters throughout the southeastern United States and reaches peak concentrations in eastern and central Texas and northern Florida (Weeks 1994). This species inhabits both woodlands with streams and rocky ravines, and open areas (Teres 1980). Its diet consists largely of flying insects, which are mainly pursued by flycatching; however, prey items are also gleaned from the ground, leaves and other substrates (Weeks 1994).

Some predators expend energy actively searching for and capturing prey (Schoener 1969). The purpose of this energy expenditure (foraging effort) by birds during the non-breeding season is self-maintenance. Studies of the Common Ringed Plover (*Charadrius hiaticula*) (Pienkowski et al. 1984), Piping Plover (*Charadrius melodus*) (Johnson and Baldassarre 1988), Canvasback (*Aythya valisineria*) (Hohman and Rave 1991), male American Redstart (*Setophaga ruticilla*) (Lovette and Holmes 1995), and Black Phoebe (*Sayornis nigricans*) (Verbeek 1975b) attributed differences in winter foraging effort to the effects of season, weather, and habitat on prey availability.

Temperature, wind, and cloud cover are factors that affected prey-catching methods (Davies 1977, Pinkowski 1977, Murphy 1987, Teather 1992), perch height (Pinkowski 1977, Teather 1992), and sally distance (Murphy 1987, Teather 1992) in flycatching species, likely due to the effects of ambient temperature (Taylor 1963, Kingsolver 1983) and short-term meteorological variations (i.e., cloud cover) on thermoregulation in flying insects (Kingsolver 1983). Evidence also exists suggesting sally distance is positively correlated with perch height in some flycatching birds (Leck 1971, Verbeek 1975, Moreno 1984, Murphy 1987, Teather 1992).

While effects of weather conditions on foraging behavior in Eastern Phoebes seems possible given the above results, habitat variations could potentially affect these same behaviors. For example, density and spread of vegetation within the local environment could affect the foraging methods used in prey capture; birds in more open habitats may forage more by aerial hawking versus gleaning from leaves in more densely vegetated environments. Sally distances might increase as density and spread of vegetation decreases and habitats become more open.

To compensate for the impact of weather and habitat conditions on prey activity and availability, Eastern Phoebe may vary expenditure of foraging effort, use different foraging techniques (aerial hawking or gleaning), and adjust perch height and sally distance in pursuit of prey during the non-breeding season.

My objectives in this study were to investigate potential variation in foraging effort (horizontal distance traveled per foraging movement [attempted prey capture]), foraging rate (foraging movements per minute), aerial hawking percentage, height of sally initiation and sally distance (distance from perch to prey) in wintering Eastern Phoebe as a function of differing weather and habitat conditions.

Materials and Methods

I observed foraging Eastern Phoebe in state, county, and city parks in Bastrop, Colorado, Hays, Travis and Williamson counties of Texas from November 2004 through February 2005. I collected data during winter months because of the high seasonal abundance of Eastern Phoebe, and the assumption that birds were concentrating only on foraging and other self-maintenance behaviors.

I observed birds using 10x42 binoculars. Observations began 1 minute after a bird was located or when the bird made a foraging movement. I monitored time periods using a stopwatch. Each attempt at prey capture was considered a foraging movement (Murphy 1987) due to the difficulty of determining the success of an attempted prey capture. I recorded the type of foraging movement, based on Fitzpatrick's (1980) classification of Tyrannid prey capture methods, for each attempted prey capture and size of captured prey. I placed prey items into 2 size classes: "large" (estimated size \geq beak length of the bird) and "small" (estimated size $<$ beak length). Estimated horizontal

distances traveled by each bird (m), including sally distance (distance from perch to prey), distance from prey to new perch, distance from unsuccessful perch to new perch, and estimated perch height (m) were recorded during an observation period. I visually estimated short distances and perch heights as follows: 0.15 m, 0.3 m, 0.5 m, 1 m, 1.5 m, 2 m, 3 m, 4 m, etc. I used a Nikon Laser 400 range finder (Nikon Inc., USA) to estimate longer distances and greater heights. Observations ended when the bird flew out of sight or had an intra- or interspecific interaction. I ended an observational period after collecting at least 4 minutes of observational time or if the bird looked directly at me (suggesting an awareness of my presence). Eastern Phoebe are active birds and do not usually remain perched and in constant view for an extended time; hence, some observational periods were broken into multiple segments in order to achieve 4 minutes. Most such observational periods were only segmented once; however some were segmented 2 times. I only used individuals with 4-20 observational minutes in analyses.

After collection of foraging data, measurements of ambient temperature and visible light were taken with a LCD Digital Thermometer and LI-COR light meter (LI-COR Biosciences, Lincoln, NE), respectively. Light intensities were grouped in increments of 50 lux due to variability in light meter readings in the field.

I characterized the type of local microhabitat into 1 of 5 ascending numerical categories of importance based on vegetative density and availability in a 360° horizontal radius from the foraging location. Open habitats with sparse vegetation for perching received a “1”. Edge habitats, in which a bird foraged on the edge of 2 very different habitat types (i.e., either where forest habitat met with a water source or open habitat), received a “2”. Park habitats with scattered trees and no understory and midstory

vegetation received a “3”. Scattered trees with sparse understory and midstory vegetation received a “4”. Forest habitats with thick understory and midstory vegetation received a “5”. I placed the distance from the foraging location of the bird to the nearest permanent or seasonal water source into 3 categories (0-25 m, 26-50 m, > 50 m). I estimated wind speed into 2 categories using a variation of the Beaufort scale: (0-8 kmph) and (9-25 kmph). I obtained a GPS-coordinate for the location of each foraging bird using a Garmin GPS V Personal Navigator (Garmin International, Inc., Olathe, Kansas). All information was recorded using a hand-held tape recorder and transcribed at a later time. While collecting these data, I wore dark-colored clothing to be less conspicuous to foraging birds. I did not collect data during rain or any other precipitation events due to the potential difficulty in locating phoebes and observing their behavior under such conditions.

Analysis

Winter Foraging Effort, Foraging Rate, and Aerial Hawking Percentage

I investigated the effects of 5 weather and microhabitat variables and calendar date on: 1) winter foraging effort (horizontal distance traveled per foraging movement), 2) foraging movement rate (foraging movements per minute), and 3) foraging diversity (percent of aerial hawking foraging movements) in Eastern Phoebes using a series of simple regression analyses to test for significant correlations between each predictor and each of the response variables. The weather and microhabitat predictors for these analyses included: 1) calendar date, 2) ambient temperature, 3) light intensity, 4) microhabitat type, 5) distance to the nearest permanent or seasonal water source, and 6) wind speed. I then investigated all possible combinations of the significant predictors

and their 1°, 2°, and 3° interaction terms using a model selection procedure based on AIC_c values (corrected for small sample size) (Sugiura 1978), Akaike weights, and number of parameters in models. Only birds ≥ 2 foraging movements and at least 4 minutes of observational time were used in the analyses of foraging effort and foraging rate. Birds with ≥ 4 foraging movements and at least 4 minutes of observational time were used in the aerial hawking percentage analysis. Analyses were performed in S-PLUS Version 7.0 (Insightful, Seattle, WA).

Height of Sally Initiation and Sally Distance

I investigated the effects of 3 predictors on: average sally height (height of perch from which sallying was initiated) and average sally distance (distance from perch to prey item) using a series of simple regression analyses. The 3 predictors included: estimated wind speed, ambient temperature, and microhabitat type. I also used a simple regression analysis to test for the effect of average sally height on average sally distance. Only birds with ≥ 2 foraging movements were used in these analyses. Analyses were performed in S-PLUS Version 7.0.

Results

General Foraging Behavior

I observed 518 foraging movements made by 65 Eastern Phoebe from November 2004 through February 2005. Eastern Phoebes foraged primarily by aerial hawking; 54.1% of insectivorous foraging movements were aerial hawks, 29.5% sally gleans, and 15.6% perch-to-ground sallies. Other infrequently observed foraging behaviors included 4 prey items gleaned from water surface by 3 individuals, and 5 small fruits eaten by 1

bird while continuously perching on a weed stalk. In addition, 13 foraging movements were classified as unknown, all of which were likely insectivorous. Large prey items (insects \geq beak length of the bird) constituted only 2.3% of all insectivorous foraging movements.

Winter Foraging Effort

Eastern Phoebe traveled an average horizontal distance of 8.30 m (SE = 0.787, $n = 55$) per foraging movement. Habitat type, wind speed, and light intensity showed no initial correlations with horizontal distance traveled per foraging movement ($P > 0.05$). Using the model selection procedure ($AIC_c = 185.4433$, Akaike weight = 0.163403) (see Appendix 2), I chose the regression containing ambient temperature, distance to the nearest seasonal or permanent water source, and the interaction between these 2 variables as the best model for explaining variation in horizontal distance traveled per foraging movement (foraging effort) ($F_{3,51} = 6.021$, $P = 0.001363$, $r^2 = 0.262$). I investigated the interaction using only birds in category 1 (0-25 m from water) and category 3 (birds > 50 m from water) since I only observed 2 birds in category 2 (26-50 m from water). Simple regression analyses suggested that distance traveled per prey item did not vary significantly with ambient temperature in Eastern Phoebe observed ≤ 25 m from water sources ($P = 0.2216$), but did vary inversely with temperature in Eastern Phoebe observed > 50 m from water sources ($F_{1,27} = 8.915$, $P = 0.0059$, $r^2 = 0.248$) (Fig.1).

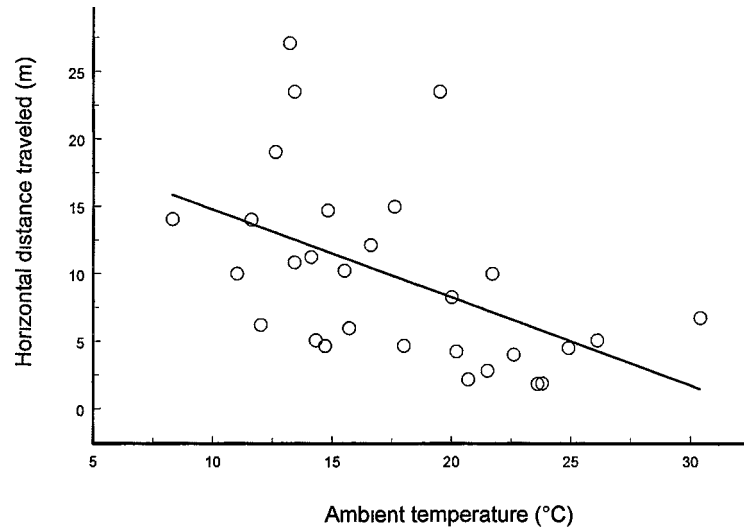


Figure 1. Foraging effort (horizontal distance traveled per foraging movement) as a function of ambient temperature in wintering Eastern Phoebes > 50 m from permanent or seasonal water sources in Central Texas in 2004-2005.

Foraging Rate

On average Eastern Phoebes made 1.28 foraging movements per minute (SE = 0.165, $n = 55$). Light intensity, ambient temperature, and distance to the nearest permanent or seasonal water source showed no initial correlations with foraging movements per minute ($P > 0.05$). Using the model selection procedure ($AIC_c = 21.82334$, Akaike weight = 0.158651) (see Appendix 3), I chose the model containing only calendar date as the best variable explaining variation in foraging rate. Foraging rate varied directly with calendar date ($F_{1,54} = 8.316$, $P = 0.0056$, $r^2 = 0.133$) (Fig.2). I removed 5 individuals observed foraging into insect swarms and taking multiple prey during repeated aerial foraging events and re-examined this regression model. Rate of

prey capture again varied directly with calendar date ($F_{1,49} = 6.406$, $P = 0.0146$, $r^2 = 0.116$).

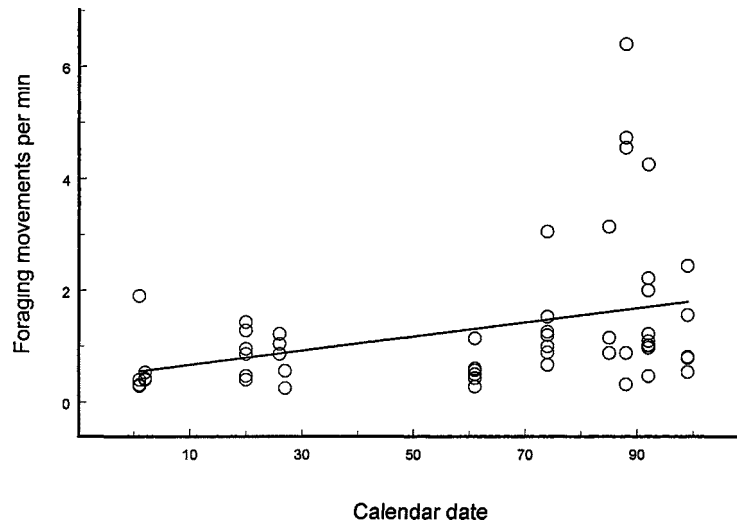


Figure 2. Foraging rate (foraging movements per minute) as a function of calendar date (beginning with November 12) in wintering Eastern Phoebes in Central Texas in 2004-2005.

Aerial Hawking Percentage

Eastern Phoebes foraged by aerial hawking an average of 47.5% of the time (SE = 6.647, $n = 51$). Light intensity, calendar date, wind speed, and habitat type showed no significant correlations with percentage of foraging movements that were aerial hawks. Using the model selection procedure ($AIC_c = 350.8971$, Akaike weight = 0.387344) (see Appendix 4), I chose the model containing only ambient temperature as the best variable

explaining variation in aerial hawking percentage. Aerial hawking percentage varied directly with ambient temperature ($F_{1,49} = 10.04$, $P = 0.0026$, $r^2 = 0.170$) (Fig.3).

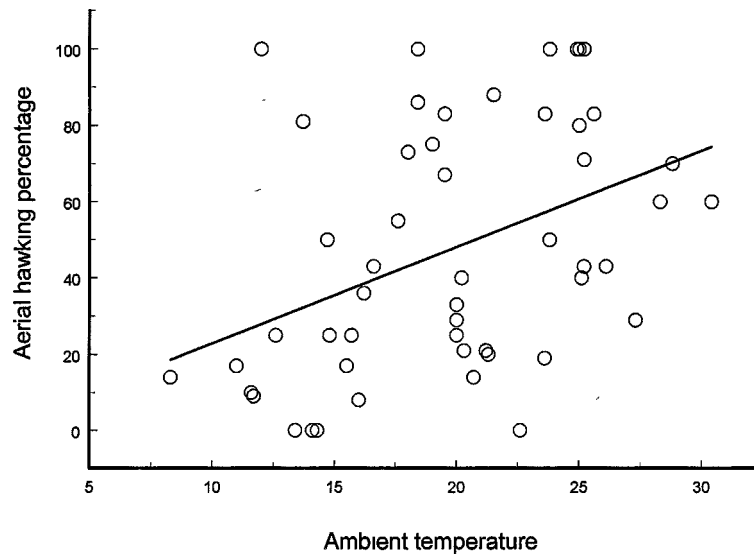


Figure 3. Percentage of foraging movements that were aerial hawks as a function of ambient temperature in wintering Eastern Phoebe in Central Texas in 2004-2005.

Height of Sally Initiation and Sally Distance

The average height of sally initiation for Eastern Phoebe was 3.65 m (SE = 0.481, $n = 53$). Average height of sally initiation did not vary with wind speed, ambient temperature, or vegetative availability ($P > 0.05$). The average sally distance for Eastern Phoebe was 2.01 m (SE = 0.180, $n = 53$). Average sally distance did not vary with wind speed, ambient temperature, or average sally height ($P > 0.05$), but did vary inversely with vegetative availability ($r = -0.321$, $P = 0.0193$).

Discussion

Winter Foraging Effort

Ambient temperature affected foraging effort in wintering Eastern Phoebes that foraged > 50 m from permanent and seasonal water sources. At lower temperatures, these birds tended to travel greater horizontal distances per foraging movement than birds feeding at higher temperatures, presumably due to reduced overall insect activity during colder conditions (Taylor 1963, Kingsolver 1983). Black Phoebes traveled greater distances per day during winter because of lower food abundance compared to other seasons (Verbeek 1975b). Similarly, Pienkowski et al. (1984) found Common Ringed Plovers spent more time foraging on colder days, and Piping Plovers spent less time foraging on warmer substrates (Johnson and Baldassarre 1988). These results suggest birds expend more foraging effort at colder temperatures, presumably because of suppressed prey activity and availability under colder conditions.

Some unaccounted variation in my analysis of winter foraging effort may stem from unmeasured variables, including recent rainfall and spatial distribution of prey patches within the local environment. Insect abundance positively correlated with increased precipitation during the preceding 2-week (Dunham 1978) and 3-week time intervals (Tanaka and Tanaka 1982) in Texas and Grenada, respectively; therefore, increased local precipitation could have affected foraging effort in Eastern Phoebes by affecting overall insect abundance. Measurement of such a variable may prove difficult with the methods of data collection used in this study. The distribution of local prey patches could have also affected temporary foraging effort. Birds found temporally and spatially between patches of abundant prey may have expended more foraging effort

temporarily in search of insects until a new prey patch was located. It is possible that I gathered data on some individuals between prey patches. These birds could have expended more effort per foraging movement during the observation than birds observed nearer prey patches.

Aerial Hawking Percentage

Ambient temperature was positively correlated with aerial hawking percentage for Eastern Phoebes, and was therefore inversely correlated with gleaning percentage (sally gleaning % + perch-to-ground sallying %). This suggests that at warmer temperatures Eastern Phoebes attempted to capture a greater percentage of prey out of the air, and at colder temperatures birds attempted prey capture from the ground and other substrates, presumably due to the effect of air temperature on flying insect activity (Kingsolver 1983). These findings are similar to those for Eastern Bluebirds (Pinkowski 1977) and Eastern Kingbirds (Murphy 1987).

Aerial hawking percentage varied inversely with cloud coverage in Eastern Kingbirds (Murphy 1987). In my study, visible light did not affect aerial hawking percentage. Coverage of clouds may still have affected this percentage; however, such information was unavailable for analysis. Factors such as canopy coverage in habitats with greater vegetative coverage potentially masked the effect of cloud cover with respects to light meter readings. This result suggests that very local light intensity may not have a pronounced effect on flying insect abundance and that cloud coverage may be a better alternative for determining the possible effect of light on flycatcher foraging behavior.

Habitat conditions may have accounted for additional variation in aerial hawking percentage, despite its lack of relationship with overall habitat type in this study. It seems likely that Eastern Phoebes would be more likely to take aerial prey in more open habitats; correspondingly, in more thickly-vegetated habitats birds might be more likely to glean prey from leaves, either because of the closer proximity of insects on leaves compared to insects flying in the distance or because of vegetation obscuring flying insects from view. It also seems plausible that in more open habitats (park-like), with scattered trees and bare ground or short grass, birds might take more prey from the ground or from the air, rather than from leaves because of the lack of taller grass and foliage density compared to other habitat types. In light of these possibilities and the results from this study, perhaps categorizing habitats into basic landscape categories is insufficient for an analysis of the impact of habitat on foraging behavior. Complex relationships may exist between multiple habitat variables and foraging behaviors in flycatching species, requiring more detailed habitat measurements in future studies. For example, rather than combining habitats into a few types, perhaps researchers should measure many variables, possibly including: percent coverage of bare ground/short grass (< 0.1 m in height)/leaf litter, coverage of tall grass (0.5-1 m in height), overall vegetative density and height, and canopy coverage.

As with winter foraging effort, recent rainfall and spatial distribution of prey patches in the local environment could have affected foraging diversity by affecting aerial hawking percentage in Eastern Phoebes. More abundant aerial prey resulting from recent rainfall could have been positively correlated with aerial hawking percentage in Eastern Phoebes. Also, Eastern Phoebes found between patches of abundant aerial prey may

have temporarily resorted to gleaning and perch-to-ground sallying until another aerial prey patch was located.

Height of Sally Initiation and Sally Distance

In my study, I analyzed average height of sally initiation instead of average perch height, which has been more commonly used in flycatcher foraging studies. I chose this variable because height from which sallies are initiated and sally distance should show at least an equally strong correlation as perch height and sally distance, if not a slightly stronger one. Average height of sally initiation was not affected by ambient temperature, wind speed, or vegetative density and availability. These results differ from those in other flycatching birds, in which perch height was found to vary directly with ambient temperature (Pinkowski 1977, Murphy 1987) and inversely with wind speed (Murphy 1987, Teather 1992).

Average sally distance was not affected by wind speed, ambient temperature, or average height of sally initiation in this study. These results, again, differ from those of other flycatcher studies, in which average sally distance was positively correlated with ambient temperature (Murphy 1987, Teather 1992) and perch height (Leck 1971, Verbeek 1975a, Moreno 1984, Murphy 1987, Teather 1992), and negatively correlated with wind speed (Teather 1992). Average sally distance was, however, inversely correlated with vegetative availability, suggesting Eastern Phoebes flew greater distances from perch to prey item in more open habitats. These longer distances are likely the result of larger fields of view in open habitats.

A possible explanation for these differing results, when compared to other studies, may lie in the results of a study of flycatcher foraging tactics in southwestern Virginia

(Via 1979). In this study, Eastern Phoebes foraged from the greatest diversity of substrates compared to 7 other coexisting flycatcher species, initiating the majority of foraging movements from the lower-outer portions of trees, man-made structures, annual herbs, and from the ground. This suggests foraging was concentrated to areas within a few meters of the ground. In light of this information, perhaps foraging behavior related to perch height and sally distance in Eastern Phoebes are not so much affected by weather conditions as in other flycatching species that are not so closely tied to foraging from lower heights.

CHAPTER 2

PERCH RETURN FREQUENCY IN WINTERING EASTERN PHOEBES (*Sayornis phoebe*)

Introduction

Few studies have investigated the frequency of perch return in flycatching birds after a foraging movement. Leck (1971) and Murphy (1987) found sally distance appeared to influence the probability of perch return in Eastern Kingbirds (*Tyrannus tyrannus*). Davies (1977) found Spotted Flycatchers (*Muscicapa striata*) were more likely to return to a perch when a prey item was captured quickly. The likelihood of return to the same perch almost doubled if birds captured their first prey item within 5 seconds of their arrival than if they waited 30 or more seconds; the same being true for subsequent prey captures from the same perch. Lastly, Moreno (1984) found perch return rates for Wheatears (*Oenanthe oenanthe*) depended on the search times preceding sallying, but Stonechats (*Saxicola torquata*) did not rely on preceding search times, which could be viewed as possible evidence that some other mechanism might be influencing this behavior. In addition to the results of these studies, Leck (1971) and Verbeek (1975) suggested that the availability of “suitable” perches (i.e., those preferably used by a species) might be a significant variable affecting the choice of perch return; however, this hypothesis remains untested.

The results of these studies present evidence for the influence of 2 different factors on the choice of perch return in some flycatching species with Leck (1971) and Verbeek (1975) suggesting the potential influence of an additional factor, perch availability. The possibility exists that these factors are specific to different groups or species that fill this foraging niche. Alternatively, a combination of factors may actually influence this behavior in some species. My objective in this study was to examine the potential effects of availability of perches and sally distance on perch return frequency in wintering Eastern Phoebes.

Materials and Methods

I observed foraging Eastern Phoebes in state, county, and city parks in Bastrop, Colorado, Hays, Travis and Williamson counties of Texas from November 2004 through February 2005. I collected data during winter months because of the high seasonal abundance of Eastern Phoebes, and the assumption that birds were concentrating only on foraging and other self-maintenance behaviors.

I observed birds using 10x42 binoculars. Observations began 1 minute after a bird was located or when the bird made a foraging movement. I monitored time periods using a stopwatch. Each attempt at prey capture was considered a foraging movement (Murphy 1987) due to the difficulty of determining the success of an attempted prey capture. Estimated horizontal distances traveled by each bird (m), including sally distance (distance from perch to prey), distance from prey to new perch, distance from unsuccessful perch to new perch, and estimated perch height (m) were recorded during an observation period. I visually estimated short distances as follows: 0.15 m, 0.3 m, 0.5 m, 1 m, 1.5 m, 2 m, 3 m, 4 m, etc. I used a Nikon Laser 400 range finder (Nikon Inc., USA)

to estimate longer distances. Observations ended when the bird flew out of sight or had an intra- or interspecific interaction. I ended an observational period after collecting at least 4 minutes of observational time or if the bird looked directly at me (suggesting an awareness of my presence). Eastern Phoebe are active birds and do not usually remain perched and in constant view for an extended time; hence, some observational periods were broken into multiple segments in order to achieve 4 minutes. Most such observational periods were only segmented once; however some were segmented 2 times. I only used individuals with 4-20 observational minutes in analyses.

I characterized the type of local microhabitat into 1 of 5 ascending numerical categories of importance based on vegetative density and availability (corresponding to density and availability of perches) in a 360° horizontal radius from the foraging location. Open habitats with sparse vegetation for perching received a “1”. Edge habitats, in which a bird foraged on the edge of 2 very different habitat types (i.e., either where forest habitat met with a water source or open habitat), received a “2”. Park habitats with scattered trees and no understory and midstory vegetation received a “3”. Scattered trees with sparse understory and midstory vegetation received a “4”. Forest habitats with thick understory and midstory vegetation received a “5”. I obtained a GPS-coordinate for each foraging bird using a Garmin GPS V Personal Navigator (Garmin International, Inc., Olathe, Kansas). All information was recorded using a hand-held tape recorder and transcribed at a later time. While collecting these data, I wore dark-colored clothing to be less conspicuous to foraging birds. I did not collect data during rain or any other precipitation events due to the potential difficulty in locating phoebes and observing their behavior under such conditions.

Analysis

I examined the effects of 2 predictor variables on perch return frequency (frequency of perch return after the occurrence of a foraging movement during an observational period) in wintering Eastern Phoebes in Central Texas using simple regression analyses to test for significant correlations. The 2 predictors were perch availability (based on vegetative availability within the vicinity of the bird) and average sally distance (the distance from perch to prey item). Only birds with ≥ 2 foraging movements were used in this analysis. I also used paired t-tests to examine potential differences in average sally distances preceding “return” and “new” perches, as well as average distances from prey item to perch for “return” and “new” perches. Only birds with ≥ 2 “return” and “new” perch flights were used in these analyses. These analyses were performed using S-PLUS Version 7.0 (Insightful, Seattle, WA).

Results

Eastern Phoebes showed an average perch return frequency of 0.09 (SE = 0.015, $n = 54$) per foraging movement with an average sally distance of 1.98 m (SE = 0.175, $n = 54$). Perch return frequency varied independently of average sally distance ($P = 0.876$), but did vary inversely with perch availability ($F_{1,52} = 7.073$, $P = 0.0103$, $r^2 = 0.120$) (Fig. 4). After removing a potential outlier from the analysis, I re-examined the regression model and found a slight increase in additional variation explained by perch availability ($F_{1,51} = 10.32$, $P = 0.0022$, $r^2 = 0.168$). Average sally distances preceding “return” and “new” perches did not differ ($t = 0.5883$, $df = 7$, $P = 0.5748$). Similarly, average distances from prey item to perch for “return” versus “new” perches were not significantly different ($t = 1.7292$, $df = 7$, $P = 0.1274$).

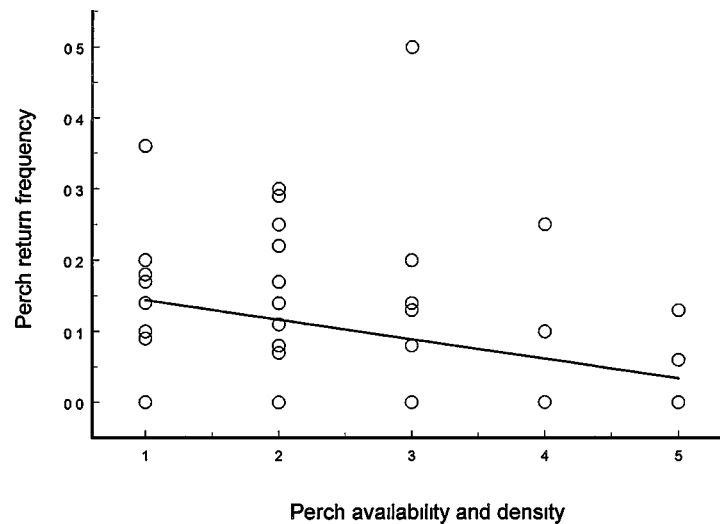


Figure 4. Perch return frequency as a function of perch availability in wintering Eastern Phoebe in Central Texas from November 2004 through February 2005.

Discussion

Perch availability was a significant factor explaining variation in perch return frequency in wintering Eastern Phoebe. The negative correlation between availability of perches and frequency of perch return after a foraging movement suggests that Eastern Phoebe were more likely to return to perches in open habitats containing a lower availability of suitable perches than in more densely-vegetated habitats containing a greater availability of vegetation (and perches) in a 360° radius from the location of the bird. My results provide evidence for the suggestions of Leck (1971) and Verbeek (1975a) that availability of “suitable” perches might be a factor affecting perch return in flycatching birds. Available perch density is likely to affect the outcome of this behavior; however, the availability of perches in a 360° radius from the bird may have greater

effect. For example, the density of perches might be higher in edge habitats, where dense forest interfaces open habitat, than in park habitats; however, these perches exist only on one side of edge habitats. In park habitats, the overall density of perches could be less than in edge habitats; however, greater availability and accessibility of perches exist in any given direction from the bird. Depending on the direction of a bird's foraging flight, a suitable perch may be sighted in the direction of its flight path, and the bird may continue to fly to the newly sighted perch instead of returning to the previous one.

Average sally distance affected perch return in Eastern Kingbirds (Leck 1971; Murphy 1987); however, sally distance did not affect perch return frequency in Eastern Phoebe. Average sally distances and average distances from prey item to perch between "return" and "new" perches were similar in the Eastern Phoebe. Although sample sizes were small ($n = 8$), my data suggest that distances flown did not affect return to the previous perch in Eastern Phoebe.

Davies (1977) and Moreno (1984) found perch return was dependent upon search times preceding sallying in Spotted Flycatchers and Wheatears, respectively. I did not record search times preceding sallying. Although 12% of the variation in perch return frequency can be attributed to availability of perches (about 17% with a potential outlier removed), it is possible that time preceding sallying could have accounted for much additional variation. Perhaps time preceding sallying plays a role in the overall outcome of this decision in many flycatching species, but when presented with the problem of low alternate perch availability (as in more open habitats), birds may be more likely to return to the same perch simply because of the lack of other perches within a reasonable distance. The possibility also exists that perch availability could have been a greater

influence in this study. I considered perches as “returned” when a bird landed within a few estimated centimeters from its previous perch location (Via 1979) after a foraging movement. However, it is possible that some Eastern Phoebes flew to “new” perches only a short distance from their previous ones. To an Eastern Phoebe using a potential prey patch, a new perch within a short distance from its previous one may be considered as the same due to its close proximity to the prey (i.e., Eastern Phoebes, as well as other flycatching species, may return to an area near their original perch location because birds may focus on the area and not the exact location). This factor, as well as time preceding sallying, should be taken into consideration in future studies of perch return in flycatching species.

CHAPTER 3

AVERAGE SALLY DISTANCE VERSUS AVERAGE GIVE-UP DISTANCE IN WINTERING EASTERN PHOEBES (*Sayornis phoebe*)

Introduction

Pinkowski (1977) found evidence suggesting that Eastern Bluebirds (*Sialia sialis*) moved from unsuccessful perches (those from which no prey were captured) to new perches, a “give-up distance” slightly more than twice the average sally distance, giving them a new perceptual field while minimizing the energy expended in flight to the new perch. Fitzpatrick (1981) found similar evidence for lengths of these “give-up distances” in many South American species of Tyrant Flycatchers. My objective in this study was to gather evidence that average give-up distances are greater than twice that of average sally distances in wintering Eastern Phoebes.

Materials and Methods

I observed foraging Eastern Phoebes in state, county, and city parks in Bastrop, Colorado, Hays, Travis and Williamson counties of Texas from November 2004 through February 2005. I collected data during winter months because of the high seasonal abundance of Eastern Phoebes, and the assumption that birds were concentrating only on foraging and other self-maintenance behaviors.

I observed birds using 10x42 binoculars. Observations began 1 minute after a bird was located or when the bird made a foraging movement. I monitored time periods

using a stopwatch. Each attempt at prey capture was considered a foraging movement (Murphy 1987) due to the difficulty of determining the success of an attempted prey capture. Estimated horizontal distances traveled by each bird (m), including sally distance (distance from perch to prey), distance from prey to new perch, distance from unsuccessful perch to new perch, and estimated perch height (m) were recorded during an observation period. I visually estimated short distances as follows: 0.15 m, 0.3 m, 0.5 m, 1 m, 1.5 m, 2 m, 3 m, 4 m, etc. I used a Nikon Laser 400 range finder (Nikon Inc., USA) to estimate longer distances. Observations ended when the bird flew out of sight or had an intra- or interspecific interaction. I ended an observational period after collecting at least 4 minutes of observational time or if the bird looked directly at me (suggesting an awareness of my presence). Eastern Phoebe are active birds and do not usually remain perched and in constant view for an extended time; hence, some observational periods were broken into multiple segments in order to achieve 4 minutes. Most such observational periods were only segmented once; however some were segmented 2 times. I only used individuals with 4-20 observational minutes in analyses.

I obtained a GPS-coordinate for each foraging bird using a Garmin GPS V Personal Navigator (Garmin International, Inc., Olathe, Kansas). All information was recorded using a hand-held tape recorder and transcribed at a later time. While collecting these data, I wore dark-colored clothing to be less conspicuous to foraging birds. I did not collect data during rain or any other precipitation events due to the potential difficulty in locating phoebes and observing their behavior under such conditions.

Analysis

I divided the average give-up distance by the average sally distance for each

Eastern Phoebe. I then performed a one-sample t-test with the one-tailed alternative to determine whether values derived by dividing the average give-up distance by the average sally distance were > 2 . Only birds with ≥ 2 foraging movements and ≥ 2 flights from unsuccessful perches were used in this analysis. This analysis was performed using S-PLUS Version 7.0 (Insightful, Seattle, WA).

Results

Eastern Phoebes flew an average sally distance of 1.79 m (SE = 0.223, $n = 37$) and an average give-up distance of 4.48 m (SE = 0.471, $n = 37$). The average give-up distances were greater than twice the average sally distance in wintering Eastern Phoebes ($t = 3.2782$, $df = 36$, $P = 0.0012$).

Discussion

Average give-up distances in wintering Eastern Phoebes were greater than twice the average sally distance. Similar to Eastern Bluebirds (Pinkowski 1977) and species of South American Tyrant Flycatchers (Fitzpatrick 1981), Eastern Phoebes traveled from unsuccessful perches a distance greater than twice the average sally distance, presumably giving each bird a new field of view that did not overlap with its previous one. These give-up distances are thought to minimize energy spent in flight to a new perches as well as providing birds with entirely new fields of view (Pinkowski 1977) and potentially a patch of prey with a higher prey density. This method of prey searching is likely a very efficient way for flycatchers to make use of available foraging habitat.

CHAPTER 4

SWARM FORAGING IN EASTERN PHOEBES (*Sayornis phoebe*)

In February 2005, I observed 5 Eastern Phoebes actively foraging into flying insect swarms over flowing streams and in grassland habitats. While foraging through swarms, birds made a series of back-and-forth flights, in fairly rapid succession, appearing to take more than 1 prey item during each aerial foraging event. The Torrent Tyrannulet (*Serpophaga cinerea*) exhibited similar behavior alongside flowing water, but the Black Phoebe (*Sayornis nigricans*), a congener of the Eastern Phoebe, did not forage in a similar manner (Smith 1971).

This behavior may be a case of opportunistic foraging upon abundant prey. Instead of perching after each prey capture, the bird may take advantage of additional prey items located near an available perch. In doing so, the bird may conserve energy expended in foraging. The Eastern Phoebes observed may have taken advantage of swarming insects for no other reason than energetic gain for self-maintenance; however, these birds may have taken advantage of an extra energy source in preparation of migration and breeding that would begin in only a few weeks. An alternate explanation is that swarming insects may not be as energetically beneficial to Eastern Phoebes as larger prey items; therefore, an individual would have to catch more prey to fulfill its energetic requirements. The close proximity of the smaller prey items to the bird and to each other may make such a foraging event worthwhile with respects to energetics. The

possibility exists that not all jerking motions were attempts to capture prey. It was difficult to determine whether each observed jerking motion resulted in the capture of prey, or whether some motions were actually repositioning movements to better view the swarm and attempt to capture other prey. A video camera may be required to more accurately assess this situation and answer this question.

CHAPTER 5

POTENTIAL WINTER TERRITORIALITY IN EASTERN PHOEBES (*Sayornis phoebe*)

As with Black Phoebes (*Sayornis nigricans*) (Verbeek 1975b), it is possible that Eastern Phoebes actively defend winter territories. Though I found no direct evidence for defense of winter territories (i.e., monitoring of marked individuals) in this species, indirect evidence was found. Eastern Phoebes were solitary during winter and highly intolerant of conspecifics. During field observations, I observed multiple intraspecific interactions. These interactions often involved “aggravated” vocalizations (strongly accentuated *chip* notes and occasional rapid *fee-bee-bee-bee* calls) (Bent 1942) and chasing. Aggravated calling seemed to predict that other Eastern Phoebes were in the vicinity of vocalizing phoebes (i.e., when an Eastern Phoebe vocalized in this manner, another Eastern Phoebe was either vocalizing in a similar manner or had been sighted). On 2 occasions, a small number of Eastern Phoebes (< 5) occurred in close proximity (within an estimated 50-75 m radius) of one another aggressively calling and occasionally chasing. The aggressive activity was so intense that I could not collect foraging data from these birds for an extended period of time. These loose aggregations occurred near water sources with surrounding trees, under- and midstory vegetation. Perhaps this type of habitat is preferable to this species during winter, as such aggregations were not observed in other habitats.

Eastern Phoebes, along with some other Tyrant Flycatchers, exhibit the behavior of tail pumping or wagging. There is evidence suggesting that the motion of pumping might be species specific, though its function remains unknown (Sibley 2001). I observed exaggerated tail pumping in 2 Eastern Phoebes near a loose aggregation of individuals. This observation occurred about 16 km east of Austin, Texas in December 2004. These two birds, perched within 1 m of each other, made aggravated vocalizations that appeared directed at one another. Both birds pumped their tails in a slightly exaggerated manner while calling. In light of this observation, perhaps tail pumping is a subtle visual cue of territory used in conjunction with various vocalizations.

APPENDICES

Appendix 1. Foraging data for wintering Eastern Phoebes in Central Texas gathered from November 2004 through February 2005.

Appendix 1. Section 1.

| Temperature (Celsius) | Date | Light | Habitat | Water | Wind | avg sally height | avg sally dist |
|--------------------------|--------|-------|---------|-------|------|---------------------|-------------------|
| 13.4 | 12-Nov | 50 | 5 | 3 | 1 | 10 | 1 |
| 13.4 | 12-Nov | 50 | 4 | 3 | 1 | 9.2 | 0.9 |
| 12 | 12-Nov | 100 | 4 | 3 | 2 | 0.89 | 1.1 |
| 11.7 | 12-Nov | 50 | 4 | 1 | 2 | 10 | 1.5 |
| 13.2 | 13-Nov | 50 | 4 | 3 | NA | 1.5 | NA |
| 14.1 | 13-Nov | 50 | 4 | 3 | NA | 3.33 | 3 |
| 14.8 | 13-Nov | 50 | 4 | 3 | 2 | 5.63 | 0.81 |
| 12.6 | 13-Nov | 100 | 4 | 3 | NA | 2 | 1 |
| 17.8 | 25-Nov | 550 | 2 | 1 | 2 | 2.13 | 0.875 |
| 11.6 | 1-Dec | 50 | 2 | 3 | 1 | 2.6 | 1.77 |
| 19 | 1-Dec | 450 | 5 | 1 | 1 | 2.5 | 0.5 |
| 20.3 | 1-Dec | 100 | 1 | 1 | 1 | 2.69 | 0.97 |
| 19.5 | 1-Dec | 100 | 1 | 1 | 1 | 1.31 | 3.33 |
| 20.2 | 1-Dec | 200 | 2 | 1 | 2 | 4.5 | NA |
| 18 | 1-Dec | 150 | 5 | 3 | 1 | 0.7 | 0.88 |
| 16.2 | 1-Dec | 100 | 1 | 1 | NA | 4.2 | 0.68 |
| 20.7 | 7-Dec | 50 | 5 | 3 | 1 | 2.36 | 0.71 |
| 20 | 7-Dec | 150 | 2 | 1 | 2 | 3.4 | 1.97 |
| 25.6 | 7-Dec | 600 | 2 | 1 | 2 | 6.08 | 2.29 |
| 20 | 8-Dec | 100 | 4 | 3 | 1 | 1.08 | 0.75 |
| 20 | 8-Dec | 150 | 2 | 1 | 1 | 11.67 | 1.75 |
| 19.5 | 11-Jan | 100 | 2 | 3 | 2 | 7.83 | 2.08 |
| 21.5 | 11-Jan | 100 | 5 | 1 | 1 | 1.56 | 0.52 |
| 21.7 | 11-Jan | 150 | 4 | 3 | 2 | 2 | 1.33 |
| 22.6 | 11-Jan | 200 | 1 | 3 | 2 | 1.5 | 2.1 |
| 25.1 | 11-Jan | 100 | 5 | 3 | 1 | 1 | 1.38 |
| 26.1 | 11-Jan | 50 | 5 | 3 | 1 | 0.92 | 1.83 |
| 28.3 | 11-Jan | 50 | 5 | 1 | 1 | 8 | 1.2 |
| 8.3 | 3-Feb | 50 | 3 | 3 | 2 | 4 | 1.72 |

| Temperature (Celsius) | Date | Light | Habitat | Water | Wind | avg sally height | avg sally dist |
|--------------------------|--------|-------|---------|-------|------|---------------------|-------------------|
| 11 | 3-Feb | 200 | 3 | 3 | 2 | 1 33 | 1 33 |
| 15 5 | 3-Feb | 250 | 3 | 3 | 1 | 1 7 | 2 59 |
| 11 7 | 3-Feb | 300 | 1 | 1 | 1 | 0 68 | 0 89 |
| 17 6 | 3-Feb | 400 | 1 | 3 | 1 | 1 61 | 5 39 |
| 16 | 3-Feb | 350 | 3 | 2 | 2 | 2 35 | 1.63 |
| 14 3 | 3-Feb | 350 | 1 | 3 | 2 | 1 43 | 2 21 |
| 13 7 | 14-Feb | 50 | 2 | 1 | 1 | 0 52 | 0 65 |
| 21 2 | 14-Feb | 200 | 2 | 1 | 1 | 0 56 | 0 7 |
| 30 4 | 14-Feb | 700 | 2 | 3 | 1 | 0 8 | 2 33 |
| 25 | 17-Feb | 700 | 2 | 1 | 1 | 1 35 | 1 25 |
| 25 | 17-Feb | 700 | 2 | 1 | 1 | 0 8 | 1 83 |
| 21.3 | 17-Feb | 300 | 3 | 2 | 1 | 2 8 | 6 2 |
| 18 4 | 17-Feb | 150 | 2 | 1 | 2 | 1 33 | 4 83 |
| 18 4 | 17-Feb | 150 | 4 | 1 | 2 | 1 63 | NA |
| 21 5 | 21-Feb | 100 | 1 | 3 | 2 | NA | NA |
| 23 8 | 21-Feb | 150 | 1 | 3 | 2 | 3 | 1 33 |
| 24 9 | 21-Feb | 150 | 1 | 3 | 2 | 8 | 2 11 |
| 25 2 | 21-Feb | 250 | 1 | 1 | 2 | 1 21 | 2 62 |
| 25 2 | 21-Feb | 250 | 3 | 1 | 2 | 1 93 | 4 14 |
| 25 6 | 21-Feb | 250 | 1 | 3 | 2 | NA | NA |
| 25 1 | 21-Feb | 300 | 1 | 3 | 2 | 1 | 2 62 |
| 28 8 | 21-Feb | 300 | 2 | 1 | 1 | 6 54 | 3 88 |
| 23 8 | 21-Feb | 200 | 2 | 1 | 1 | 1 08 | 2 75 |
| 27 8 | 21-Feb | 300 | 2 | 1 | 1 | NA | NA |
| 27 3 | 21-Feb | 150 | 2 | 1 | 1 | 0 64 | 2 05 |
| 25 2 | 21-Feb | 100 | 3 | 1 | 1 | 11 67 | 3 67 |
| 14 7 | 28-Feb | 200 | 5 | 3 | 1 | 11 1 | 0 95 |
| 16 6 | 28-Feb | 550 | 3 | 3 | 1 | 3 71 | 3 86 |
| 15 7 | 28-Feb | 600 | 3 | 3 | 1 | 3 75 | 3 44 |
| 23 6 | 28-Feb | 250 | 5 | 3 | 1 | 10 75 | 1 06 |
| 20 2 | 28-Feb | 400 | 3 | 3 | 1 | 2 44 | NA |
| 23 6 | 28-Feb | 400 | 2 | 1 | 1 | 10 17 | 2 5 |

Appendix 1. Section 2.

| Avg giveup dist | Large prey | Prey/minute | Meters per foraging movement | Perch return frequency | Site | Aerial hawking % |
|-----------------------|---------------|-------------|---------------------------------------|------------------------------|------|------------------------|
| 3 43 | 0 | 0 29 | 10 59 | 0 | 1 | 0 |
| 4 59 | 2 | 0 31 | 23 5 | 0 | 1 | 0 |
| 8 25 | 0 | 1 9 | 6 2 | 0 1 | 1 | 100 |
| Na | 0 | 0 4 | 3 | 0 | 1 | 100 |
| 4 56 | 0 | 0 4 | 27 09 | 0 | 1 | 0 |
| 3 33 | 0 | 0 42 | 11 25 | 0 | 1 | 0 |
| 4 04 | 0 | 0 42 | 14 71 | 0 | 1 | 25 |
| 4 31 | 0 | 0 53 | 14 67 | 0 | 1 | 25 |
| 7 75 | 1 | NA | 9 5 | 0 25 | NA | NA |
| 9 89 | 0 | 1 43 | 14 09 | 0 3 | 2 | 10 |
| NA | 0 | 0 47 | 2 38 | 0 | 2 | 75 |
| 4 88 | 2 | 0 95 | 11 03 | 0 14 | 2 | 21 |
| NA | 0 | 1 43 | 6 5 | 0 17 | 2 | 83 |
| 1 5 | 0 | 0 4 | 7 25 | 0 | 2 | 0 |
| 2 24 | 1 | 1 28 | 4 67 | 0 | 2 | 73 |
| 7 23 | 0 | 0 86 | 6 14 | 0 36 | 2 | 36 |
| 1 5 | 0 | 1 04 | 2 17 | 0 | 2 | 14 |
| 4 89 | 1 | 1 22 | 8 6 | 0 | 2 | 29 |
| 4 79 | 0 | 0 86 | 8 65 | 0 | 2 | 83 |
| 1 62 | 1 | 0 25 | 8 26 | 0 25 | 3 | 25 |
| NA | 0 | 0 56 | 4 08 | 0 | 3 | 33 |
| 6 19 | 0 | 0 57 | 23 5 | 0 17 | 4 | 67 |
| 1 15 | 0 | 0 48 | NA | 0 13 | 4 | NA |
| 4 5 | 0 | 0 6 | 10 | 0 | 4 | 67 |
| NA | 0 | 0 5 | 4 | 0 | 4 | 0 |
| 6 67 | 0 | 1 14 | 6 74 | 0 | 4 | 40 |
| 1 5 | 0 | 1 4 | 5 07 | 0 | 4 | 43 |
| 1 | 1 | 0 28 | 2 9 | 0 | 4 | 60 |
| 3 42 | 0 | 0 67 | 14.05 | 0 14 | 4 | 14 |
| 7 5 | 0 | 1 | 10 | 0 5 | 4 | 17 |
| NA | 0 | 3 05 | 10 22 | 0 13 | 4 | 17 |
| 4 31 | 0 | 0 89 | 7 77 | 0 | 4 | 9 |
| 6 | 0 | 1 53 | 15 | 0 09 | 4 | 55 |

| Avg giveup dist. | Large prey | Prey/minute | Meters per foraging movement | Perch return frequency | Site | Aerial hawking % |
|------------------------|---------------|-------------|---------------------------------------|------------------------------|------|------------------------|
| 3.71 | 0 | 1.2 | 4.82 | 0.08 | 4 | 8 |
| NA | 0 | 1.26 | 5.07 | 0 | 4 | 0 |
| 1.36 | 0 | 3.14 | 1.88 | 0.08 | 5 | 81 |
| 0.81 | 0 | 1.15 | 2.12 | 0.29 | 5 | 21 |
| 4 | 0 | 0.88 | 6.73 | 0 | 5 | 60 |
| NA | 0 | 6.4 | 2.16 | 0.14 | 6 | 100 |
| NA | 0 | 3.3 | 4.36 | 0.11 | 6 | 80 |
| 14.5 | 1 | 0.32 | 13.7 | 0.2 | 6 | 20 |
| 1.33 | 0 | 4.73 | 6.23 | 0.22 | 6 | 86 |
| 4.25 | 1 | 0.88 | 9.25 | 0 | 6 | 100 |
| NA | 0 | 0.47 | 1.88 | 0.2 | 7 | 88 |
| NA | 0 | 4.25 | 1.88 | 0.2 | 7 | 100 |
| NA | 0 | 2 | 4.5 | 0.18 | 7 | 100 |
| 4.33 | 1 | 1.09 | 8.17 | 0 | 7 | 43 |
| NA | 0 | 1.01 | 7.14 | 0.14 | 7 | 71 |
| NA | 0 | NA | NA | NA | 7 | NA |
| 2 | 0 | 1.34 | 4.9 | 0.1 | 7 | NA |
| NA | 0 | 2.22 | 9.43 | 0.07 | 8 | 70 |
| NA | 0 | 1.22 | 6.25 | 0.17 | 8 | 50 |
| 6.27 | 0 | NA | 34.35 | NA | 8 | NA |
| NA | 0 | 0.97 | 3.62 | 0.14 | 8 | 29 |
| NA | 1 | 1.02 | 7.17 | 0 | 8 | 100 |
| 3.71 | 0 | 2.44 | 4.65 | 0 | 9 | 50 |
| 3.65 | 0 | 0.54 | 12.14 | 0 | 9 | 43 |
| NA | 0 | 0.81 | 5.96 | 0 | 9 | 25 |
| 3.43 | 0 | 0.79 | 4.71 | 0.06 | 9 | 19 |
| NA | 0 | 1.56 | 4.23 | 0 | 10 | 40 |
| 8 | 0 | 0.8 | 9.72 | 0.17 | 11 | 83 |

Appendix 1: Section 3. Sites of data collection.

| Site | GPS-coordinate | UTM |
|---------------------------------|----------------|------------|
| 1. Roy G. Guerrero Park | 14R0625386 | UTM3346465 |
| 2. Hornsby Bend | 14R0629626 | UTM3344454 |
| 3. Brackenridge Field Lab | 14R0617566 | UTM3350739 |
| 4. Granger Lake | 14R0656905 | UTM3394763 |
| 5. McKinney Falls State Park | 14R0622347 | UTM3339659 |
| 6. 5 Mile Dam | 14R0606479 | UTM3312413 |
| 7. Attwater Prairie Chicken NWR | 14R0765168 | UTM3284794 |
| 8. Eagle Lake | 14R0758038 | UTM3272626 |
| 9. Buescher State Park | 14R0677174 | UTM3325593 |
| 10. Bastrop State Park | 14R0665535 | UTM3332090 |
| 11. Lake Bastrop | 14R0665167 | UTM3335589 |

Appendix 2. AIC_c values and weights for winter foraging effort models.

| Model | AIC _c | Weight |
|--------------------|------------------|----------|
| Temp | 191.2129 | 0.009129 |
| Water | 192.5855 | 0.004596 |
| Date | 191.2213 | 0.00909 |
| T+W | 191.527 | 0.007802 |
| T+D | 191.1141 | 0.009591 |
| W+D | 189.7116 | 0.019338 |
| T+W+TW | 185.4433 | 0.163403 |
| T+D+TD | 190.3554 | 0.014016 |
| W+D+WD | 186.0951 | 0.117957 |
| T+W+D | 191.1606 | 0.009371 |
| T+W+D+TW | 184.9697 | 0.207062 |
| T+W+D +WD | 187.5274 | 0.057637 |
| T+W+D +TD | 190.9598 | 0.01036 |
| T+W+D +TW+TD | 185.9692 | 0.125621 |
| T+W+D +TD+WD | 189.9606 | 0.017074 |
| T+W+D +TW+WD | 185.566 | 0.15368 |
| T+W+D+TD+TW+DW | 187.828 | 0.049594 |
| T+W+D+TD+TW+DW+TWD | 190.2629 | 0.014679 |

Appendix 3. AIC_c values and weights for foraging rate models.

| Model | AIC _c | Weight |
|--------------------|------------------|----------|
| Date | 21.82334 | 0.158651 |
| Habitat | 25.66329 | 0.023260 |
| Light | 22.95398 | 0.090142 |
| D+H | 22.61625 | 0.106724 |
| D+L | 21.78595 | 0.161645 |
| H+L | 23.49255 | 0.068862 |
| D+H+DH | 24.05160 | 0.052069 |
| D+L+DL | 23.88451 | 0.056606 |
| H+L+HL | 25.74823 | 0.022293 |
| D+H+L | 23.24241 | 0.078036 |
| D+H+L+DH | 24.53471 | 0.040896 |
| D+H+L+DL | 24.95328 | 0.033173 |
| D+H+L+HL | 24.46212 | 0.042407 |
| D+H+L+DH+DL | 26.81154 | 0.013100 |
| D+H+L+DH+HL | 26.68982 | 0.013922 |
| D+H+L+DL+HL | 26.12018 | 0.018510 |
| D+H+L+DH+DL+HL | 28.78983 | 0.004872 |
| D+H+L+DH+DL+HL+DHL | 26.56295 | 0.014834 |

Appendix 4. AIC_c values and weights for aerial hawking percentage models.

| Model | AIC _c | Weight |
|-------------|------------------|----------|
| Temperature | 350.8971 | 0.387344 |
| Water | 354.4497 | 0.065563 |
| T+W | 350.7410 | 0.418787 |
| T+W+TW | 353.1069 | 0.128305 |

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VITA

Jeffrey R. Troy was born in Temple, Texas on January 23, 1981, the son of Phillip T. Troy and Cynthia Ross Troy. After completing his work at Temple High School, Temple, Texas, in 1999, he entered the University of Texas at Austin. He received a Bachelor of Science in Zoology from the University of Texas in May 2003. In August 2003, he entered the Graduate College of Texas State University-San Marcos.

Permanent address: 4009 Ermine Trail
Temple, Texas 76504

This thesis was typed by Jeffrey R. Troy.