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BREEDING TERRITORY SETTLEMENT PATTERNS AND MATE CHOICE IN A MONOCHROMATIC TYRANNID FLYCATCHER

Matthias Leu

A dissertation submitted in partial fulfillment of the
requirements for the degree of

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Abstract

Breeding territory settlement patterns and mate choice in a monochromatic Tyrannid flycatcher

Matthias Leu

Chairperson of Supervisory Committee:
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What factors influence a male's ability to acquire a high-quality territory and what cues do females use to select a mate in the monochromatic Pacific-slope flycatcher (*Empidonax difficilis*)? I addressed this question by showing that territory settlement patterns occur "preemptively" on the breeding grounds along a habitat-quality gradient defined by red alder (*Alnus ruba*) and preferred nesting substrate (adventitious nest substrate) densities. Early arriving adult males excluded later arriving males, including yearling males, from gaining access to high-quality habitat. Acquisition of high-quality territories was influenced by arrival time, which in turn was influenced by body condition and fat scores. Once on the breeding grounds, males in high-quality habitat were not repeatedly challenged by males arriving later on the breeding grounds because there was no difference among habitat quality types with regard to territorial defense song rate, testosterone and corticosterone plasma concentrations, and response time to simulated territorial intrusions. Upon arrival, females differentiated among habitat quality types by selecting habitat according to presence of red alder and/or male body condition. Song behavior, testosterone plasma level, and response time to territorial intrusions did not correlate with pairing date. To discern whether territory quality is important in female territory settlement patterns, I removed the preferred nest substrate in treatment plots, thereby altering territory quality. This experiment showed that the availability of preferred nest substrate seemed not to play a role in female settlement patterns in high-quality habitat instead females seem to select territory quality according to a hierarchical process. Upon arrival, females selected habitat at the macro scale (i.e., presence of red alder) but as they geared up for breeding, the habitat selection process was fine-tuned. If a territory lacked preferred nest substrate, females abandoned their mates more frequently in treatments than controls. Abandonment of males occurred when females started to build nests because the lag between pairing and abandoning of mate was not different from the lag between pairing and initiation of first clutches in successful pairs breeding in treatments and controls. This suggests that female territory settlement patterns in Pacific-slope flycatchers may be adjusted throughout the pairing phase.

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DEDICATION

I would like to dedicate this dissertation to Cheryl Leu. my partner and my friend who has helped me to see life in a different way.

CHAPTER I: INTRODUCTION

Most animals are territorial during their reproductive cycle. As a result, territorial behavior leads to non-random distributions of animals in habitats occupied during breeding (e.g., Krebs 1971, Orians and Wittenberger 1991). Theory predicts that the distribution of individuals on breeding territories follows either an "ideal-free" or a "despotic" distribution (Fretwell and Lucas 1970). According to the "ideal free" distribution model individuals have an equal chance of establishing a breeding territory and equal breeding success in all available habitat types. In contrast, the "despotic" distribution model predicts that fit individuals will exclude less fit individuals from habitat in which reproductive success is highest. Thus, competition for breeding territories in high-quality habitat is intense, and individuals that ultimately gain access to breeding territories in high-quality habitats should be superior in competitive ability (Milinski and Parker 1991).

In most migratory songbirds, males are the first to arrive on the breeding grounds (e.g., Holmes et al. 1996, Petit and Petit 1996). What characteristics allow males to secure high-quality breeding territories? Furthermore, what male characteristics are important in female mate choice? An individual's ability to obtain access to a limited resource, such as a high-quality breeding territory, may depend both on its physical constitution and behavioral strategy (Milinski and Parker 1991). In turn, it is well established that hormones "orchestrate and maintain" behavior (Balthazart 1983, Harding 1983, Wingfield et al. 1990a, Wingfield et al. 1994, Wingfield et al. 1999a) and that hormone levels can be altered by parasites (for review see Hillgarth and Wingfield 1997b).

In this study, I explore the settlement patterns of a Neotropical migrant on the breeding grounds and investigated what physiological and behavioral characteristics influence male territory acquisition and female mate choice. The Pacific-slope flycatcher (*Empidonax difficilis*), a socially monogamous monochromatic Tyrannid flycatcher, is an excellent species to test theories of habitat settlement patterns in passerines. This species occupies a variety of habitat types, situated directly adjacent to each other, that differ in the amount of red alder (*Alnus ruba*). Furthermore, this species seems to prefer a nesting substrate (clump of adventitious branches) found close to the ground, thus facilitating measurement of reproductive success. I used correlative and experimental approaches to investigate the following questions: (1) does red alder density influences habitat settlement patterns, (2) does the interaction of physiology, behavior, ectoparasites and sex hormones affect a male's ability to acquire a high-quality territory, (3) do females select males according to territory quality? This study will lead to an increased understanding of the mechanisms in "despotic" arrangements and how mate choice operates in monochromatic passerines.

In chapter II, I investigate how Pacific-slope flycatchers settle on the breeding grounds. Particularly, I test whether this species follows either an "ideal-free" or a "despotic" distribution on the breeding grounds (Fretwell and Lucas 1970). To test habitat settlement patterns in this species, I selected three habitat types *a priori* according to a red alder abundance and shrub density gradient. If Pacific-slope flycatchers follow a despotic distribution on the breeding ground then reproductive success should differ among habitat types.

In chapter III, I verify the critical assumption of competitive exclusion under the "despotic" distribution model (Fretwell and Lucas 1970), which predicts that individuals differ in competitive ability. The competitive ability of an individual may depend on its relative physical condition and its behavioral strategy (Milinski and Parker 1991). To investigate this, I measured song rate, responses to territorial challenges, testosterone plasma levels, physiological measures and ectoparasite loads.

In chapter IV, I explore what factors influence female mate choice in this monochromatic flycatcher species. Is it territory quality? I used both a correlational and experimental approach to investigate this question. In the correlative study, I captured males to assess body condition, and exposed males to territorial intrusions. I also measured whether song rate influences female mate choice. In the experimental study, I removed the preferred nesting substrate to test whether females use this as a cue of territory quality.

CHAPTER II: BREEDING TERRITORY SETTLEMENT PATTERNS OF PACIFIC-SLOPE FLYCATCHERS (*EMPIDONAX DIFFICILIS*): INFLUENCES OF HABITAT AND CLIMATIC FACTORS

INTRODUCTION

Most animals are territorial during their reproductive cycle. As a result, territorial behavior leads to non-random distributions of animals in habitats occupied during breeding (e.g., Krebs 1971). An important question is what proximate factors influence the distribution of animals in habitat and how this affects population regulation (for review see Gordon 1997, Newton 1998)? Furthermore, with the recent increase in habitat destruction and conversion from contiguous to fragmented habitat, identifying sink and source habitats is pivotal in species conservation (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996). A traditional approach in defining habitat quality was to equate wildlife density estimates with habitat quality. However, many authors have correctly argued that density alone cannot be used as an indicator of habitat quality because habitat types containing high numbers of territorial but non-breeding individuals would erroneously be defined as source habitats (e.g., van Horne 1983, Vickery et al. 1992a). To circumvent this problem, fitness-related measures need to be incorporated into habitat quality studies. One avenue to define habitat quality is to employ the Fretwell-Lucas model (Fretwell and Lucas 1970).

The Fretwell-Lucas model predicts that the distribution of individuals on breeding territories follows either an "ideal-free" or a "despotic" distribution (Fretwell and Lucas 1970). According to the "ideal free" distribution model, individuals have an equal chance of establishing a breeding territory and equal reproductive success in all available habitat types (Brown 1969, Fretwell and Lucas 1970). This distribution has been mainly tested with regard to the distributions of fish foraging in patchy habitats (for discussion see Milinski and Parker 1991, Tregenza 1994, Tyler and Gilliam 1995, Wahlström and Kjellander 1995, Tregenza et al. 1996, but see Doncaster 2000). In contrast, the "despotic" distribution model predicts that breeding success differs among habitat types and that fit individuals will exclude less fit individuals from habitat in which reproductive success is highest (Fretwell and Lucas 1970). Support for this distribution model (for review see Holmes et al. 1996, Petit and Petit 1996) has been found in shorebirds (Ens et al. 1995), forest-dwelling cup nesters (Andrén 1990, Holmes et al. 1996); and (3) forest dwelling cavity nesters (nest box studies Krebs 1971, van Balen and Potting 1990, Petit and Petit 1996).

Despite existing evidence for the Fretwell-Lucas model, this model has been rarely tested with regard to open cup nesting migratory passerine species (but see Holmes et al. 1996). Furthermore, although habitat selection has been studied rigorously (for reviews see Hildén 1965, Cody 1985, Martin 1988, Morrison et al. 1998), evidence for this phenomenon still remains elusive. One reason is that very few studies investigate a suite of proximate factors (e.g., floristic composition and structure, nest-site availability, predation rates, and food availability) that influence habitat selection (but see Petit and Petit 1996).

In this paper, I test whether an open cup nesting flycatcher species follows either an "ideal free" or "despotic" distribution on the breeding grounds. I chose the Pacific-slope flycatcher (*Empidonax difficilis*), a common non-oscine passerine of western North American forests, as my model species for the following reasons. First, this species is ubiquitous in low elevation forests of the Pacific-Northwest (Manuwal and Huff 1987). Second, Pacific-slope flycatchers occupy several habitat types where red alder (*Alnus ruba*), associated with berry producing shrubs, seems to be an important habitat component (McComb 1994, Pearson and Manuwal 2001). Red alders produce adventitious branch clumps (i.e., branches growing from the bark) that seem to be preferred by Pacific-slope flycatchers as nest substrate (Pearson and Leu unpl. data). Therefore, I investigated habitat settlement patterns along two habitat gradients: red alder-shrub (high to low) and adventitious nest substrate (high to low) in deciduous (high), mixed (medium) and coniferous habitat (low). This step is important because identifying habitat types *a priori* to measuring fitness parameters circumvents circularity of fitness defining habitat suitability (Rodenhouse et al. 1997). Third, nests of this species are built at low heights, facilitating measurements of fitness parameters (Davis et al. 1963, Sakai 1988).

Both the "ideal free" or "despotic" distribution models make predictions that either do or do not differentiate between the two models (for review see Petit and Petit 1996). For example, both models predict that male density and arrival time (both sexes) should differ among habitat types with higher densities and earlier arrival time in the optimal habitat. In contrast, unlike the "ideal free", the "despotic" distribution model predicts that breeding success should be higher in optimal compared to sub-optimal habitat. In order to differentiate between the two models, habitat-specific fitness needs to be determined. Therefore, I measured indirect fitness variables, including age class distributions, female arrival time and pairing success (Slagsvold 1986, Potti and Montalvo 1991, Holmes et al. 1996, Petit and Petit 1996) and direct fitness variables, including number of breeding attempts and reproductive success, in the three *a priori* defined habitat types. If fitness differs among the three habitat types, suggesting a "despotic" distribution, then I predict that (1) adult males should occupy optimal habitat, (2) males in optimal habitat should have a higher pairing success, and (3) clutch size, number of breeding attempts, and reproductive success should be higher in optimal habitat. Furthermore, because the aforementioned variables co-vary with climatic factors (e.g., Brown and Bomberger-Brown 1996, Newton 1998), I investigated whether rainfall and air temperature influence settlement patterns. Lastly, because past breeding success (e.g., Blancher and Robertson 1985, Lanyon and Thompson 1986) and food availability (for review see Martin 1987, Whitaker et al. 2000) also influence settlement patterns in passerines, I collected data with regard to site fidelity and foraging activity budgets.

METHODS

Study site — All data were collected in the Capitol Forest (Washington Department of Natural Resources; 46° 55' N, 121° 10' W) Southwest of Olympia, Washington during four breeding seasons (1997-2000). The Capitol Forest is in the western hemlock zone (Franklin and Dyrness 1988). Depending on aspect and moisture gradient, the overstory consists mainly of Douglas-fir (*Pseudotsuga menziesii*) and red alder, interspersed with western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). The shrub layer, interspersed with late successional conifers (e.g., western hemlock and western red cedar), consists of various *Vaccinium* species, salmonberry (*Rubus spectabilis*), devilsclub (*Oplopanax horridum*), cascara (*Rhamnus purshiana*), and vine maple (*Acer circinatum*). The topography is defined by hills, running East-West, with steep flanks that are bifurcated by riparian corridors. These riparian corridors consist mainly of red alder, interspersed with western hemlock, and western red cedar in the flood plain and are surrounded by coniferous habitat along the step flanks.

Research sites and habitat plots — Between 1997 and 1999, I established a total of 11 research sites (mean nearest neighbor distance among research sites was 1.47 ± SE of 0.15km). Each research site consisted of habitat plots, where deciduous (high alder abundance), mixed (medium alder abundance) coniferous habitat plots (low alder abundance) were directly adjacent to each other. Five research sites contained all three habitat types, four contained only mixed and coniferous habitat, one contained deciduous and coniferous habitat, and one contained deciduous and mixed habitat ($n_{\text{deciduous}} = 7$, $n_{\text{mixed}} = 9$, $n_{\text{coniferous}} = 7$). Because of logging operations, not all research sites were visited each year. Out of the 11 research sites, eight were visited between 1997 and 1999, one was visited in 1997 and 1998, and two were visited only in 1998 and 1999.

Habitat verification — Habitat characteristics were measured according to modified procedures described by James and Shugart (1970) and Noon (1981). Using a circle of 11.28m radius (0.25 acre) centered on nests, I measured density (number/plot) of coniferous trees, red alders (separated into trees with adventitious branches versus those with none) and deciduous trees greater than 4m tall. I measured shrub (< 4m tall) cover (%) by using a density board (1m wide and 3m tall) in each of the cardinal directions using the methods described by Wight (1938), DeVos and Mosby (1969), and Noon (1981), and by counting the number of shrub stems in each circle. Using the 1997 data, I found shrub density correlated significantly with the density board estimates ($r = 0.73$, $n = 16$, $p = 0.001$). As a result, I measured shrub-cover using the density board only in subsequent years.

Using habitat plot averages [nests were found on 18 of the 26 plots; deciduous habitat = 6 (85.7%), mixed habitat = 7 (77.8%), and coniferous habitat = 5 (50.0%)], percent of red alder differed significantly among habitat types ($F_{2,15} = 26.30$, $p < 0.0005$; Fig. 1). Red alder was significantly higher in deciduous compared to mixed habitat ($p = 0.006$), and was higher in mixed compared to coniferous habitat ($p = 0.003$; Fig. 1). Furthermore, number of red alders with adventitious branches correlated significantly with the total number of red alders measured per habitat plot ($r = 0.75$, $n = 69$, $p < 0.0005$). Shrub cover also differed significantly among habitat types ($F_{2,15} = 4.72$, $p = 0.026$; Fig. 1). Post-hoc analysis revealed that shrub density did not differ between deciduous and mixed habitat ($p = 0.35$), as well as

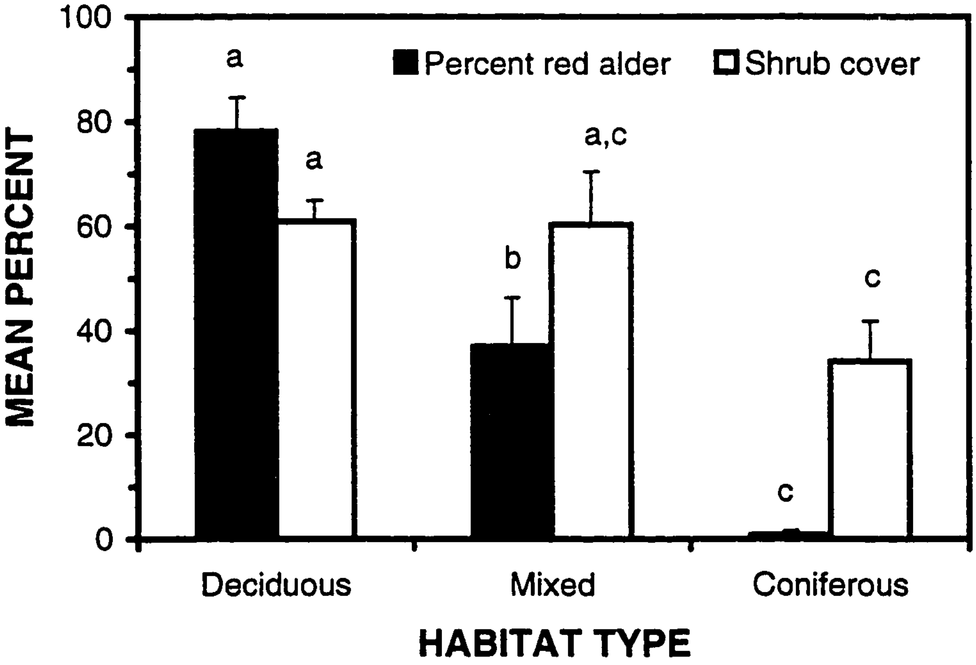

Figure 1: Mean (± SE) percent red alder and shrub cover in deciduous (n = 6), mixed (n = 7), and coniferous habitat (n = 5). Means not sharing letter are significantly different ($p \leq 0.05$).

between mixed and coniferous habitat (p = 0.20), but differed between deciduous and coniferous habitat (p = 0.02, Fig. 1).

Weather patterns — The Washington Department of Natural Resources operates a weather station situated within < 5km of each research sites. From 1997 to 1999, data were collected with regard to daily high, average, and low air temperatures as well as daily rainfall.

Male density and territory turnover rates — I measured density of males in 11 predetermined habitat plots during 1998 and 1999 ($n_{deciduous} = 3$, $n_{mixed} = 5$, $n_{coniferous} = 3$). The average plot size for deciduous habitat was smaller (3.4 ha ± 0.18), compared to mixed (6.5 ha ± 0.64) and coniferous habitat (6.3 ha ± 1.24) because the deciduous habitat type is found only along narrow riparian corridors. I delineated territories by using the spot mapping method summarized by Ralph (1993). For each habitat plot, a map was created and the locations of singing males were mapped. Territories that only partially overlapped with the study area were counted as half territories.

To measure territory occupancy among years, I created maps of each habitat plot (n = 27) and plotted singing males. Unlike the density plots, the territory turnover plots were not confined to a specific area but defined by habitat ecotones. Territories that overlapped habitat types were not used for analyses. To my surprise, territory size and location differed little among years in all habitats. Furthermore, once males settled on their territory, nearly all stayed on their territory until the breeding season commenced. I only found three males (1 in mixed and 2 in coniferous habitat) that arrived on the breeding grounds and approximately two weeks later abandoned their territory. Over the three years of study, I visited habitat plots every second to fourth day, depending on weather conditions, to check occupancy status.

Male capture and site fidelity — I captured males with mist nets using a song play back and a mount of a flycatcher specimen. Upon capture, each male was banded with a USFWS aluminum band. I refrained from using color bands for two reasons: (1) color bands could not be seen on Pacific-slope flycatchers because feathers on the belly covered the bands and (2) light conditions in the forest environment rendered color identification impossible in most observations. From 1998 through 2000, I attempted to capture territorial males to assess site fidelity. I captured males on 93 territories and was able to check site fidelity in 30 (32.2 %) territories. This low recapture-attempt rate was due to logging operations (i.e., no access to sites or site had been logged) and to the low capture success. Permits to capture flycatchers have been issued by the University of Washington's Animal Care Committee (ACC # 2857-06), the U.S. Fish and Wildlife Service (Permit # 20337), and the Washington Department of Fish and Wildlife (Permit # WN-0085).

Age class identification — Following Johnson (1974), age classes (adults versus yearlings) were distinguished by a combination of plumage characteristics and skull ossification. At the population level, yearling males undergo an incomplete first prebasic molt, replacing some to all primaries, secondaries, greater primary coverts, and body plumage. The tail feathers are not replaced in this molt. Pacific-slope flycatchers also undergo a limited prealternate molt, replacing some feathers on the throat, breast and dorsum. Thus, yearling males can be distinguished from adult males according to the following characteristics: (1) shape of rectrices; (2) differences in plumage wear of rectrices; (3) texture of body plumage (yearling plumage is more lax and less intensive in pigmentation); (4) patchiness of plumage (yearlings can have up to three generations of feathers); and (5) coloration of greater primary covert edges (edges are narrower in yearling birds, Johnson 1974). In Tyrannid flycatchers, unlike other passerines, skull ossification is not as rapid and is not completed within the first half year of life (see discussion in Johnson 1974). Because the skin on the head is transparent in Tyrannid flycatchers, ossification can be used as an independent characteristic for aging

Pacific-slope flycatchers (Johnson 1974). Overall, I was able to determine the age class in 88.9% (n = 126) of captured males.

Arrival and pairing dates — Habitat plots were sampled each year at the beginning of April, well before males arrived (earliest male arrival April 23), to collect data on arrival and pairing dates. Depending on weather conditions, I visited each habitat plot about every second to fourth day. I used mid points between visits to estimate arrival and pairing date. I decided that males were paired when females were present on the territory (males change from mainly singing mate attracting to singing mainly territorial defense songs, Johnson 1980, Ainsley 1992).

Nest searches and nest height — Following Martin and Greupel (1993) territories were searched systematically to find nests. Nests were checked (i.e., presence of female) from a distance every 3-5 days to gather breeding stage specific nest survival data. Females were flushed off the nest only to determine clutch size and hatching success.

Upon fledging of nestlings, nest height was measured with a measuring tape, and for tall nests with a clinometer and a measuring tape. Combining habitats, nest height did not differ ($F_{2,65} = 1.31$, $p = 0.28$) between first ($\bar{x} = 3.28$ m ± 0.64, n = 28), replacement of first ($\bar{x} = 7.73 \pm 4.06$, n = 3), and second clutches (i.e., second breeding attempt after first nest fledged: $\bar{x} = 4.96$ m ± 1.42, n = 8), nor did it differ at the habitat scale (deciduous habitat: $F_{2,36} = 2.25$, $p = 0.12$; mixed habitat: $F_{2,36} = 0.95$, $p = 0.41$). Therefore, I combined nest height of all nests for analysis. In coniferous habitat I did not find replacement or second clutches.

Clutch initiation date — I visited each territory every third to fourth day (in some cases the interval between visits was larger because of bad weather) to find nests, to assess clutch initiation dates, number of broods, and to collect breeding behavioral data. I used the date when the first egg was laid as the clutch initiation date. In cases where nests were found with nestlings or territories with fledglings, I back-calculated clutch initiation date by using four days for clutch completion (mean clutch size 3.8 = ± 0.06, n = 36), an average incubation period of 15 days and an average nestling period of 16 days (Davis et al. 1963).

Breeding success — I measured breeding success in two ways. First, I calculated the percent of failed nests. Second I used Mayfield daily nest mortality rates to estimate nesting success (Mayfield 1961, Mayfield 1975). To calculate daily mortality rates, I did not incorporate hatching probabilities because hatching success was 96.7 % (n_{eggs} = 123; discussed below). I used the midpoint between visits to determine failure and fledgling date. For analysis, I used the methods of Johnson (1979) for testing differences in daily mortality rates among habitat types. I was able to discern the fate of 94.5% (n = 74) of the nests and only four nests had to be omitted from the analysis (Manolis et al. 2000). Because > 20 nests per variable are needed to get unbiased daily nest survival probabilities (Hensler and Nichols 1981, Martin et al. 2000), I was able to compare daily nest survival probabilities only between deciduous and mixed habitat.

Second, because nests of Pacific-slope flycatchers are hard to find, I assigned a breeding index (following Vickery et al. 1992b) to each territory as follows: 1 = male present > four weeks, 2 = paired, 3 = nesting behavior (e.g., female warning, female carrying nesting material), 4 = adult carrying food (in most cases I found the nest observing this behavior), 5 = fledglings present, 6 = male and female observed >3 weeks after fledging of young, 7 = same as 3 but second brood, 8 = same as 4 but second brood , 9 = same as 5 but second brood.

Foraging behavior — Using the focal approach (for review see Morrison et al. 1998), I collected foraging behavior data on each nest during the late nestling period (>7 days after hatching), at the time when females were no longer brooding nestlings. I observed each pair feeding nestlings during two 30 minute periods, one between 10:00-12:00 and the other between 13:00-15:00 in order to control for possible differences in morning and afternoon foraging patterns. I began each observation period immediately after the first feeding had taken place, in an attempt to reduce bias due to unequal disturbance caused by the observers. I measured horizontal foraging distances with a tape from the nest to each center of foraging activity (≈ 8-15 foraging activity centers per nest). To minimize impact, I took these measurements after the young had fledged or after the nest had been depredated. Because not all prey captures were directly observable, I standardized the measurements by taking the distance to the estimated center of foraging activity, rather than to the exact spot at which foraging occurred (e.g. to the trunk of a tree in which canopy foraging had taken place). To standardize for time of year, I chose nests that were initiated at similar dates with regard to habitat type ($t = -1.16$, $df = 12$, $p = 0.27$), breeding success ($t = 1.06$, $df = 12$, $p = 0.31$), and nest substrate type ($t = -1.07$, $df = 12$, $p = 0.33$).

Statistical analyses — I analyzed the data at two levels. First, at the habitat level, I analyzed the data by combining years. This analysis determines long-term differences and similarities among habitat types (a necessity for studies determining differences in fitness among habitats). Because of possible site fidelity and to avoid pseudoreplication (Hurlbert 1984), I used the mean arrival, pairing and clutch initiation dates (all years combined) for each habitat plot. I standardized the data between years and among habitat plots by subtracting the yearly mean from each respective arrival, pairing and clutch initiation date. Second, at the year level, I analyzed the data with regard to between year and habitat type differences to investigate whether environmental factors (e.g., temperature and rain) influence the breeding phenology of Pacific-slope flycatchers. For this analysis, I used the Julian arrival, pairing, and clutch initiation dates.

I tested each variable for normality and used appropriate transformations for skewed data. In cases where transformation did not improve normality, I used non-parametric statistics (Zar 1984). To test differences among habitats, I used ANOVA with Tukey post-hoc analyses for normal data and the Kruskal-Wallis test and post-hoc analyses described by Zar (1984) for non-normal data. To test differences between years and habitat, I used a two-way ANOVA with habitat and year as factors. I was unable to use repeated measures of ANOVA because not all habitat plots were visited each year. In cases where the interaction term was significant, I used a one-way ANOVA to test for year effects within habitat types. To test frequency distributions among habitats, I used G-tests (Log-likelihood ratio test, Zar 1984). All statistical analyses were done using SYSTAT 7.0 (SYSTAT 1997). All p-values reported throughout this paper are two-tailed tests. For all analysis I used $p \leq 0.05$ as the level of statistical significance. Results of tests reporting means are indicated as means ± SE.

RESULTS

Weather patterns — Mean weekly air temperatures (April 1 - July 31, Fig. 2) were similar between 1997 ($\bar{x}$ = 13.0 ± 0.3 ^{0}C) and 1998 ($\bar{x}$ = 13.4 ± 0.4 ^{0}C) but were lower in 1999 ($\bar{x}$ = 11.8 ± 0.4 ^{0}C), whereas mean weekly maximum air temperatures did not differ among years (1997: $\bar{x}$ = 20.1 ± 0.5 ^{0}C; 1998: $\bar{x}$ = 20.1 ± 0.6 ^{0}C; 1999: $\bar{x}$ = 19.2 ± 0.6 ^{0}C, Fig. 2). In contrast, mean weekly minimum air temperatures (Fig. 2) were lower in 1999 ($\bar{x}$ = 4.3 ± 0.4 ^{0}C) compared to 1997 ($\bar{x}$ = 5.9 ± 0.3 ^{0}C) and 1998 ($\bar{x}$ = 6.6 ± 0.4 ^{0}C). Particularly, mean minimum temperatures were lower from the end of April through the middle of May (Fig. 2). The average daily rainfall was higher in 1997 ($\bar{x}$ = 39.6 ± 8.0mm) compared to 1998 ($\bar{x}$ = 15.1 ± 3.4mm; $p = 0.032$) and 1999 ($\bar{x}$ = 21.8 ± 3.7mm; $p = 0.90$), but similar in 1998 and

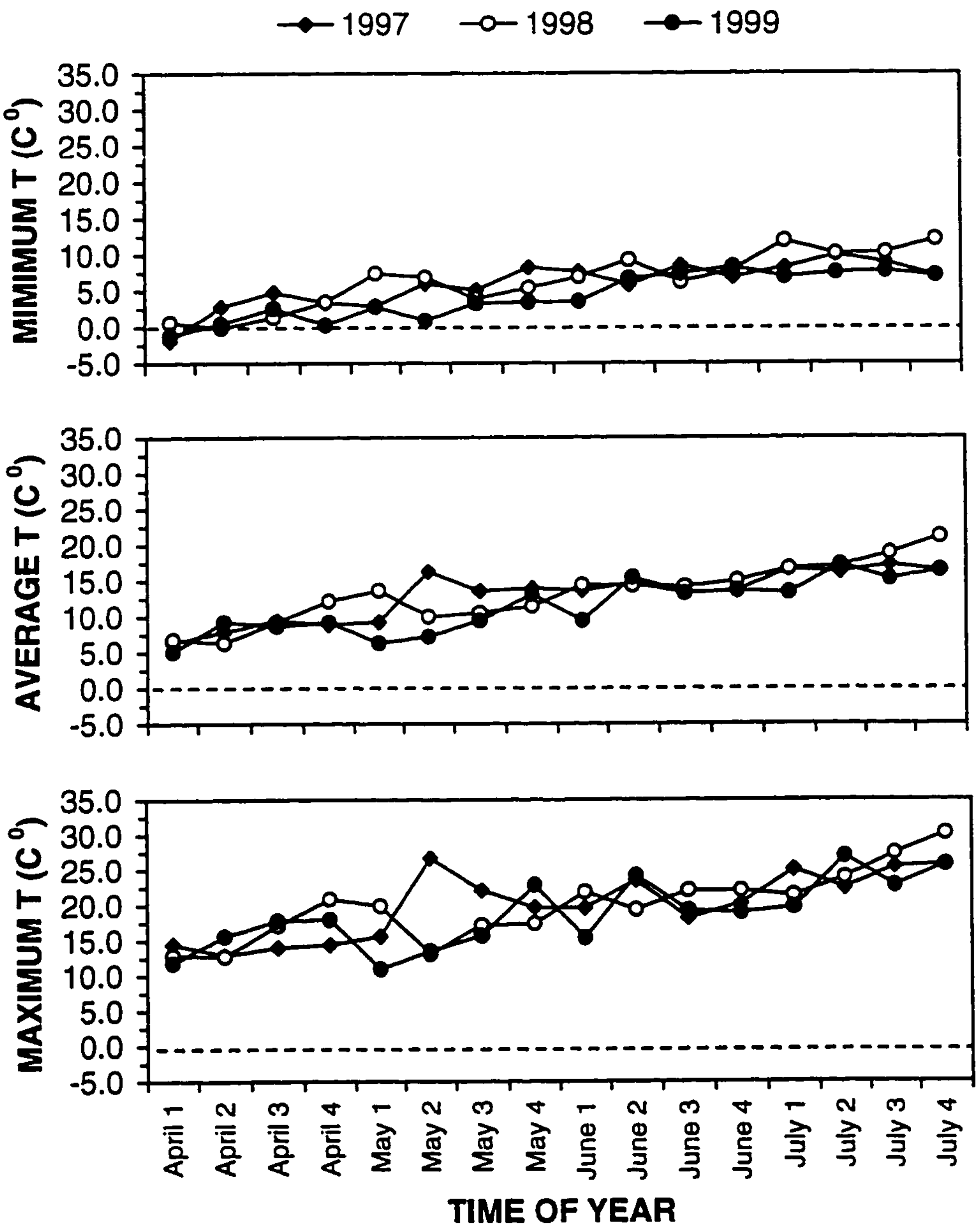

Figure 2: Mean (SE not shown for clarity) weekly minimum, average, and maximum air temperatures in Capitol Forest from 1997 – 1999.

1999. Although 1998 had the lowest daily rainfall, there were more days with rain (64.8 %) compared to 1997 (46.7 %) and 1999 (48.4 %), but were similar in 1997 and1999.

Male densities — Male densities differed among years ($F_{1,16}$ = 13.09, $p < 0.002$; Fig. 3) and habitat ($F_{2,16}$ = 72.09, $p < 0.0005$; Fig. 3) and there was a nearly almost significant interaction between habitat and year ($F_{2,16}$ = 3.06, p = 0.08). Male density was higher in deciduous habitat compared to mixed (p = 0.001) and coniferous habitat ($p < 0.0005$). In mixed habitat, there was a trend that densities of males were higher compared to coniferous habitat (p = 0.06). Densities of males did not differ between 1998 and 1999 in deciduous habitat (Paired t-test = 1.00, df =2, p = 0.42), but were lower in 1999 compared to 1998 in mixed (Paired t-test = 5.08, df =2, p = 0.007) and coniferous habitat (Paired t-test = 5.28, df =2, p = 0.03).

Territory occupancy — Territory occupancy probabilities measured over three years differed significantly among habitat types (G-test = 42.46, df = 2, $p < 0.0005$; Table 1). Occupancy probability was higher in deciduous habitat compared to mixed habitat (G-test = 6.11, df = 2, p = 0.047), and was higher in mixed compared to coniferous habitat (G-test = 21.50, df = 2, $p < 0.0005$).

Site fidelity and movement among habitats — Only 23.3% of 30 territories were re-occupied by the same male. No male was recaptured twice. Overall, sited fidelity differed among habitats (G-test = 8.73, df = 2, p = 0.001; Table 1). Recapture rate was higher in deciduous habitat compared to mixed habitat (G-test = 4.07, df = 1, p = 0.04). I never recaptured a male in coniferous habitat. The recapture rates did not differ between mixed and coniferous habitat (G-test = 1.22, df = 1, p = 0.27).

I was able to document a movement between habitat types by one male. This male, occupying coniferous habitat, was banded as a yearling male in 1997 and was subsequently recaptured in 1998 occupying mixed habitat (distance between captures locations = 2.5 km).

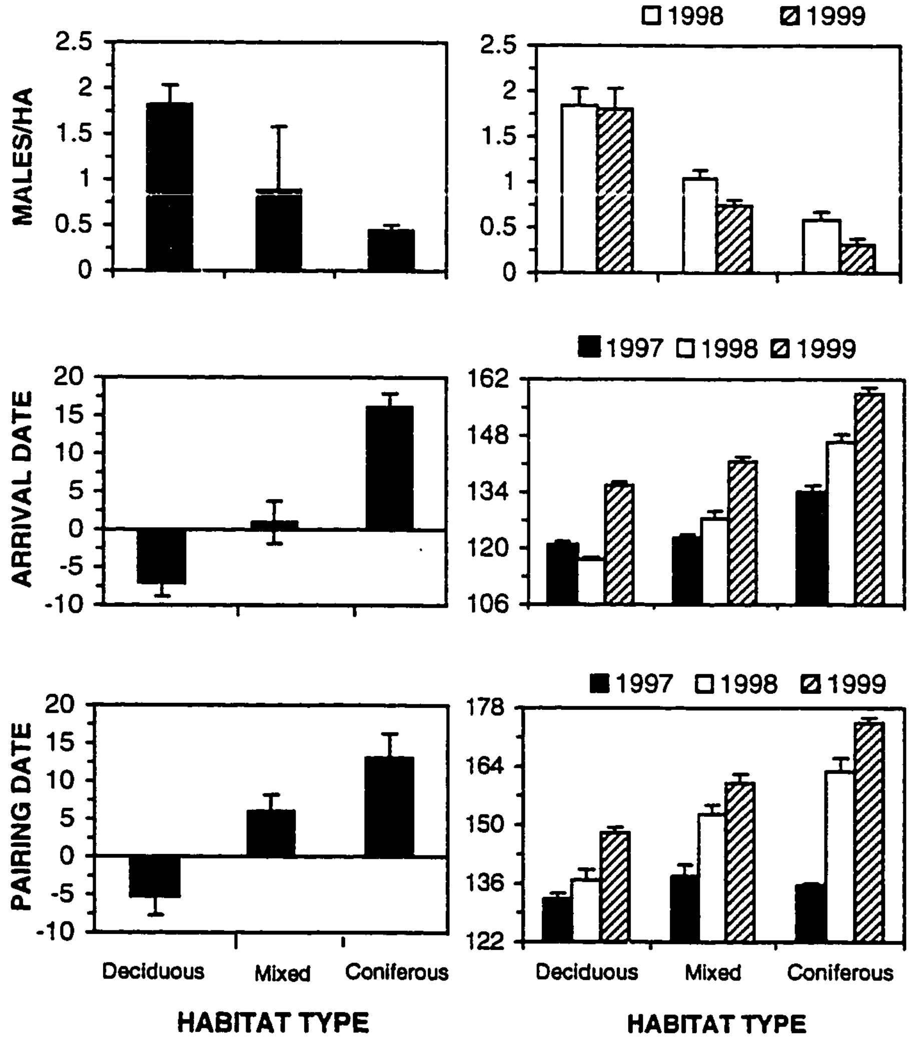

Figure 3: Habitat (left panel) and yearly (right panel) values for male density, arrival date [habitat: standardized dates = date –yearly mean; year: Julian date (106 = April 15; 162 = June 10)], and pairing date [habitat: standardized dates = date –yearly mean; year: Julian date (122 = May 1; 176 = July 24)]. Shown are means (± SE).

Table 1: Population, breeding, and nesting parameters according to habitat types.

	Habitat			
	Deciduous	Mixed	Coniferous	p-values [c]
Territory occupancy [a]	90.9 (22)	63.9 (36)	18.4 (38)	***
Site fidelity [a]	50.0 (12)	10.0 (10)	0.0 (8)	**
Adult males [a]	94.2 (34)	92.2 (51)	15.0 (20)	***
Lag arrival and pairing:				
1997 [b]	12.7 ± 1.9 (15)	13.1 ± 2.2 (8)	5.5 ± 0.5 (2)	not avail.
1998 [b]	18.6 ± 2.5 (25)	29.0 ± 2.3 (35)	20.3 ± 3.6 (11)	**
1999 [b]	13.1 ± 1.5 (40)	20.9 ± 1.8 (32)	22.1 ± 1.7 (8)	***
Pairing success:				
1997 [a]	100.0 (12)	85.7 (14)	13.3 (15)	***
1998 [a]	100.0 (25)	80.0 (50)	38.1 (42)	***
1999 [a]	100.0 (32)	84.2 (38)	44.0 (25)	***
Adventitious substrate nests [a]	76.5 (51)	34.8 (23)	0.0 (9)	***
Nest height [b]	3.73 ± 0.57 (51)	6.40 ± 1.40 (23)	8.26 ± 3.33 (9)	ns
First clutch initiation date:				
1997 (May 1 = 122) [b]	144 ± 3 (5)	162 ± 6 (3)	178 (1)	*
1998 (May 1 = 122) [b]	142 ± 4 (7)	159 ± 3 (11)	181 ± 6 (2)	**
1999 (May 1 = 122) [b]	160 ± 1 (22)	168 ± 2 (9)	198 ± 6 (4)	***
Second breeding attempts [a]	28.2 (85)	2.8 (107)	0.0 (84)	***

[a] % (n)

[b] $\bar{x}$ ± SE (n)

[c] ns = not significant, na= not available (sample size to small), * p < 0.05, ** p < 0.01, and *** p < 0.005.

Age class distribution — Male age class distribution differed significantly among habitats (G-test = 50.23, df = 2, $p < 0.0005$; Table 1). A higher percentage of adult males were in deciduous (G-test = 37.93, df = 1, $p < 0.0005$) and mixed habitat (G-test = 41.28, df = 1, $p < 0.0005$) compared to coniferous habitat; but did not differ between deciduous and mixed habitat (G-test = 0.12, df = 1, p = 0.73). Age class distribution among habitats did not differ among years (1997: 70.0 %, n = 30; 1998: 85.7 %, n = 42; 1999: 80.0 %, n = 35; G-test = 2.60, df = 2, p = 0.27).

Arrival dates — Standardized dates differed significantly among habitat types ($F_{2,23} = 28.38$, $p < 0.0005$; Fig. 3). Males arrived earlier in deciduous compared to coniferous habitat ($p < 0.0005$), there was a trend for males to arrive earlier in deciduous compared to mixed habitat (p = 0.056) and males occupying mixed habitat arrived earlier compared to males in coniferous habitat ($p < 0.0005$). Arrival time also differed between age classes (t-test = -18.75, df = 84, $p < 0.0005$); adult males ($\bar{x} = -6.7 \pm 0.9$; n = 73) arrived earlier compared to yearling males 2.9, n = 13).

Arrival dates differed significantly among years ($F_{2,273} = 100.70$, $p < 0.0005$; Fig. 3) and habitat ($F_{2,273} = 92.89$, $p < 0.0005$), and there was a significant interaction between habitat and year ($F_{4,273} = 4.00$, p = 0.004). At the habitat scale, arrival dates differed with regard to year in all habitats (deciduous: $F_{2,95} = 146.40$, $p < 0.0005$, mixed: $F_{2,108} = 28.86$, $p < 0.0005$, coniferous: $F_{2,70} = 19.17$, $p < 0.0005$). Males in deciduous habitat arrived later in 1999 compared to 1997 ($p < 0.0005$) and 1998 ($p < 0.0005$), but arrived earlier in 1998 compared to 1997(p = 0.03). In mixed habitat there was no difference in male arrival date between 1997 and 1998 (p = 0.24), but males arrived significantly later in 1999 compared to 1997 (p <

0.0005) and 1998 ($p < 0.0005$). Lastly, males arrived in coniferous habitat progressively later each year (1997 – 1998: $p = 0.005$; 1998 – 1999: $p < 0.0005$).

Pairing dates — Standardized pairing dates differed significantly among habitat types ($F_{2,22}$ = 10.81, $p = 0.001$; Fig. 3). Males paired earlier in deciduous compared to mixed habitat (p = 0.02) and coniferous habitat ($p < 0.0005$) whereas males occupying mixed habitat did not pair earlier than males in coniferous habitat ($p = 0.16$). Adult males ($\bar{x}$ = - 2.1 ± 1.6, n = 61) paired earlier compared to yearling males ($\bar{x}$ = 12.4 ± 0.4.7, n = 7;t-test = - 14.58, df = 66, p = 0.004).

Pairing dates differed significantly among years ($F_{2,180}$ = 33.81, $p < 0.0005$; Fig. 3) and habitat ($F_{2,180}$ = 24.86, $p < 0.0005$; Fig. 3), and there was an almost significant interaction between habitat and year ($F_{4,180}$ = 2.35, $p = 0.06$). Pairing dates differed with regard to year in all habitats (deciduous: $F_{2,81}$ = 19.87, $p < 0.0005$, mixed: $F_{2,79}$ = 11.72, $p < 0.0005$, coniferous: $F_{2,20}$ = 20.99, $p < 0.0005$; Fig. 3). Males in deciduous habitat paired later in 1999 compared to 1997 ($p < 0.0005$) and 1998 ($p < 0.0005$), but paired at similar dates in 1997 and 1998 (p = 0.32). In mixed and coniferous habitat, males paired progressively later [mixed: 1997 – 1998: $p = 0.004$; 1998 – 1999: $p = 0.046$; deciduous: 1997 – 1998: $p = 0.001$; 1998 – 1999: p = 0.009).

Lag arrival-pairing — Time spent unpaired by males differed significantly among habitats ($F_{2,173}$ = 16.39, $p < 0.0005$). Males in deciduous habitat ($\bar{x}$ = 14.7 ± 1.2, n = 70) spent the shortest time unpaired compared to mixed ($\bar{x}$ = 23.9 ± 1.5, n = 75; $p < 0.0005$) and coniferous habitat ($\bar{x}$ = 19.6 ± 2.2, n = 21; $p = 0.045$). In contrast, males spent equal periods unpaired in mixed and coniferous habitat ($p = 0.38$).

Time between male arrival and pairing differed among years ($F_{2,167} = 7.83$, $p = 0.001$; Table 1) and habitat ($F_{2,167} = 7.68$, $p = 0.001$; Table 1), and there was an almost significant interaction between habitat and year ($F_{4,167} = 2.18$, $p = 0.074$). Time between arrival and pairing differed with regard to year in mixed ($F_{2,72} = 9.72$, $p < 0.0005$) and coniferous habitat ($F_{2,70} = 6.18$, $p = 0.009$); but not in deciduous habitat ($F_{2,77} = 1.31$, $p = 0.27$; Table 1). In mixed habitat, time between arrival and pairing was longer in 1998 compared to 1997 ($p < 0.0005$) and 1999 ($p = 0.018$), and approached significance between 1997 and 1999 ($p = 0.06$). In coniferous habitat, the time elapse between arrival and pairing was shorter in 1997 compared to 1998 ($p = 0.02$) and 1999 ($p = 0.007$), but there was no difference between 1998 and 1999 ($p = 0.56$).

Pairing success — Pairing success differed significantly among habitats (G-test = 98.7, df = 2, $p < 0.0005$; Table 1); every male occupying deciduous habitat paired. In contrast, fewer males paired in mixed habitat (G-test = 20.02, df = 1, $p < 0.0005$), and compared to mixed habitat, even fewer males paired in coniferous habitat (G-test = 89.17, df = 1, $p < 0.0005$; Table 1). Pairing success was higher in adult (91.5%, $n = 71$) compared to yearling males (45.0%, $n = 20$; G-test = 18.99, df = 1, $p < 0.0005$). However, pairing success did not differ among years in each habitat type (deciduous: G-test = 0.0, df = 2, $p = 1.0$; mixed: G-test = 0.39, df = 2, $p = 0.82$; and coniferous: G-test = 4.65, df = 2, $p = 0.098$; Table 1).

Nest substrate and height selection — Pacific-slope flycatchers nested in different nest substrate in each habitat type (G-test = 24.40, df = 2, $p < 0.0005$; Table 1). In deciduous habitat, more nests were built in adventitious substrate compared to mixed habitat (G-test = 11.74, df = 1, $p = 0.001$; Table 1) and more nests were built in adventitious substrate in mixed compared to coniferous habitat (G-test = 6.27, df = 1, $p = 0.012$). Within habitat types, more nests 76.2% ($n = 42$) were built in adventitious nest substrate in deciduous habitat (G-test =

6.29, df = 1, $p = 0.012$; Table 2) but not in mixed habitat (34.8%, n = 23, G-test = 1.10, df = 1, $p = 0.30$; Table 1). In coniferous habitat, all nests were built in crotch nest substrate. Percent adventitious nests correlated significantly with the relative abundance of red alder ($r = 0.67$, $p = 0.002$, n = 18).

There is a strong trend suggesting that nest height differed among habitats ($F_{2,80} = 2.97$, $p = 0.057$; Table 1). Nests built in adventitious substrate ($\bar{x} = 2.18 \pm 0.24$, n = 47) were significantly lower compared to nests built in crotch substrate ($\bar{x} = 8.58 \pm 1.23$, n = 36; $t = -6.42$, df = 81, $p < 0.0005$). Overall, nest height correlated with shrub density ($r = -0.23$, $p = 0.04$, n = 81), indicating that nests are built at low heights when sufficient cover is available.

Clutch initiation — Standardized clutch initiation dates of first clutches differed significantly among habitat types ($F_{2,61} = 51.16$, $p < 0.0005$). First clutches were initiated earlier in deciduous habitat compared (standardized date: $\bar{x} = -8.0 \pm 1.3$, n = 33) to mixed (standardized date: $\bar{x} = 3. \pm 1.9$, n = 23; $p < 0.0005$) and coniferous habitat (standardized date: $\bar{x} = 26.7 \pm 4.0$, n = 7; $p < 0.0005$), and earlier in mixed compared to coniferous habitat ($p < 0.0005$). With regard to nest substrate, first clutches were initiated earlier in adventitious (standardized date: $\bar{x} = -5.1 \pm 2.1$, n = 25) compared to crotch nests (standardized date: $\bar{x} = 7.8 \pm 3.9$, n = 20) ($t = -3.07$, df = 43, $p = 0.004$). However, there was no difference in clutch initiation date with regard to nest substrate in both deciduous ($t = -4.31$, df = 21, $p = 0.51$) and mixed habitat ($t = 5.73$, df = 13, $p = 0.28$).

Clutch initiation dates of first clutches differed among years ($F_{2,55} = 18.63$, $p < 0.0005$), and habitat ($F_{2,55} = 37.93$, $p < 0.0005$), but the interaction between habitat and year was not significant ($F_{4,55} = 1.89$, $p = 0.13$; Table 1). First clutches were initiated earlier in

Table 2: Number and fate of nests with regard to nest substrate (A = adventitious, C = crotch) and habitat type.

	Deciduous		Mixed		Coniferous	
	A	C	A	C	A	C
Egg laying:						
Abandoned	1	0	0	0	0	0
Depredated	0	0	0	0	0	0
Incubation:						
Abandoned	0	0	0	1	0	0
Depredated	1	2	1	2	0	0
Nestling:						
Abandoned	0	0	0	0		
Depredated	5	1	3	4	0	4
Fledged	24	7	4	7	0	3
Unknown stage:						
Abandoned	0	0	0	0	0	2
Depredated	1	0	0	1	0	0
TOTAL	32	10	8	15	0	9

1997 ($p = 0.023$) and 1998 ($p = 0.01$) compared to 1999, but did not differ between 1997 and 1998 ($p = 0.91$).

Interestingly, lag between pairing and clutch initiation did not differ among habitat types (deciduous: $\bar{x} = 14.1 \pm 0.9$, $n = 28$; mixed: $\bar{x} = 17.2 \pm 2.1$, $n = 18$; coniferous: $\bar{x} = 21.8 \pm 5.6$, $n = 4$; $F_{2,47} = 1.05$, $p = 0.34$), nor among years (1997: $\bar{x} = 17.4 \pm 6.5$ days, $n = 5$; 1998: $\bar{x} = 18.2 \pm 1.8$ days, $n = 13$; 1999: $\bar{x} = 14.7 \pm 1.0$ days, $n = 32$; $F_{2,40} = 1.70$, $p = 0.20$) and habitat ($F_{1,40} = 1.46$, $p = 0.24$; interaction: $F_{2,40} = 1.33$, $p = 0.28$).

Replacements of first clutches as well as second clutches were initiated on average around July 2 (replacement of first clutches: Julian date $\bar{x} = 184 \pm 5$, second clutches: Julian date $\bar{x} = 184 \pm 3$).

Clutch size, hatching success, brood size, and number of clutches — First clutches were significantly larger ($\bar{x} = 3.9 \pm 0.05$, $n = 25$) compared to replacement and second clutches ($\bar{x} = 3.5 \pm 0.2$, $n = 6$; Mann-Whitney $U = 106.5$, $p = 0.01$). Clutch size of first nests did not differ between deciduous ($\bar{x} = 3.9 \pm 0.06$, $n = 15$) and mixed habitat ($\bar{x} = 4.0 \pm 0.0$, $n = 9$; Mann-Whitney $U = 63.0$, $p = 0.60$). Because of small sample size ($n = 1$), I could not compare clutch size found in coniferous habitat with the other habitat types. Using deciduous and mixed habitat, clutch size did not differ among years (1997: 4.0 ± 0.0, $n = 5$; 1998: 4.0 ± 0.0, $n = 7$; 1999: 3.9 ± 0.3, $n = 12$; Kruskal-Wallis = 1.00, $p = 0.607$). Overall, hatching success was 96.7 % ($n_{eggs} = 123$), 96.5 % for first clutches ($n_{eggs} = 86$), and 94.4 % for replacement and second clutches ($n_{eggs} = 18$).

Brood size of first clutches differed significantly among habitat types (Kruskal-Wallis = 12.53, $p = 0.002$) where it was the same between deciduous ($\bar{x} = 3.9 \pm 0.09$, $n = 15$) and mixed habitat ($\bar{x}$ = 3.9 ± 1.1, n = 10), but was lower in coniferous habitat ($\bar{x}$ = 2.4 ± 0.5, n = 5). Combining deciduous and mixed habitat, brood size did not differ among years (1997: 3.7 ± 0.2, n = 6; 1998: 4.0 ± 0.0, n = 5; 1999: 3.9 ± 0.3, n = 14; Kruskal-Wallis = 3.44, p = 0.18).

Number of second breeding attempts differed among habitats (G-test = 48.26, df = 2, $p < 0.0005$; Table 1). In deciduous habitat, more pairs attempted second breeding compared to pairs in mixed habitat (G-test = 27.40, df = 1, $p < 0.0005$), and showed a trend between mixed and coniferous habitat (G-test = 3.52, df = 1, p = 0.061). Using deciduous habitat only, number of second breeding attempts differed between years (G-test = 12.08, df = 2, p = 0.002). Fewer second clutches were initiated during 1999 (9.1%, n = 33) compared to 1998 (33.3%, n = 27; G-test = 5.57, df = 1, p = 0.02), but did not differ between 1997 (48.0%, n = 25) and 1998 (G-test = 1.16, df = 1, p = 0.28).

Breeding success — I collected breeding success data on 74 nests (Table 2). Of these nests, 5.4% (n = 4) were abandoned during incubation, but no nests were abandoned during the nestling period. Overall, 33.8% (n = 25) of the nests were lost to predation, where 68.0% (n = 25) of the nests were preyed upon during the nestling phase. No nests were lost due to weather. With regard to nest substrate, 2.5% (n =40) of all adventitious nests were abandoned compared to 8.8% (n = 34) of crotch nests (Table 2).

Mayfield daily mortality rates were lower in deciduous habitat (number of failed nests = 12, nest hours = 647) compared to mixed habitat (number of failed nests = 11, nest hours = 281; z-test = 1.62, p = 0.05; Fig. 4). Sample sizes were too small in coniferous habitat (number of failed nests = 4, nest hours = 97) and were not included in the analysis. The percent of failed nests, depredated and abandoned nests combined, differed among habitats (G-test = 7.50, df = 2, p = 0.02; Fig. 4). Nest failure was lower in deciduous habitat compared to mixed (G-test = 4.32, df = 1, p = 0.04) but did not differ between mixed and coniferous

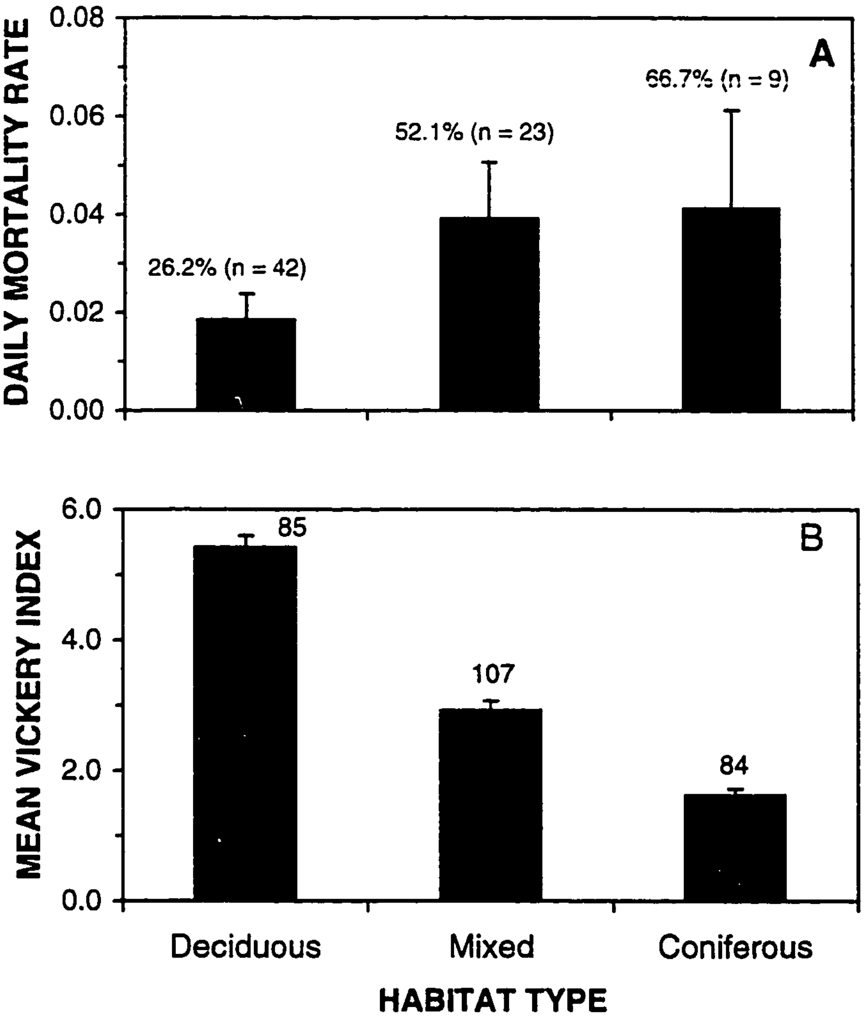

Figure 4: Mean (± SE) daily mortality rates (A), percent failed nests (A), and breeding indices (B) for Pacific-slope flycatchers according to habitat type. For mean daily mortality rates, error bars are maximum-likelihood estimators (following Johnson 1979). For definitions of breeding indices see methods and Vickery et al. (1992).

habitat (G-test = 0.56, df = 1, $p = 0.45$). Therefore, both analyses revealed that breeding success is highest in deciduous compared to mixed habitat. With regard to nesting substrate, daily mortality rates were lower in nests built in adventitious substrate (0.017 ± 0.0051; number of failed nests = 11, nest hours = 641) compared to nests built in crotch substrate (0.042 ± 0.01; number of failed nests = 16, nest hours = 384; $z = 2.14$, $p = 0.02$). A similar trend was found when using percent of successful nests; nests built in adventitious substrate were more successful compared to crotch nests (G-test = 3.81, df = 1, $p = 0.05$; Table 2). However, within habitat types, there was no difference in breeding success, using percent successful nests, in deciduous (G-test = 0.22, df = 1, $p = 0.64$) and mixed habitat (G-test = 0.00, df = 1, $p = 1.0$). Breeding success did not differ among years using percent of successful nest (1997: 66.7%, $n = 21$; 1998: 53.6%, $n = 28$; 1999: 64.0%, $n = 25$; G-test = 1.02, df = 2, $p = 0.60$), nor using Mayfield daily mortality rates (1997: 0.027 ± 0.011; 1998: 0.0033 ± 0.010; 1999: 0.0021 ± 0.07; 1997 and 1998: $z = 0.41$, $p = 0.34$; 1998 and 1999: $z = 1.01$, $p = 0.16$).

Breeding indices differed significantly among habitats (Kruskal-Wallis = 143.42, $p < 0.0005$, Fig. 4). Breeding indices were higher in deciduous compared to mixed habitat ($p < 0.0005$) and were higher in mixed compared to coniferous habitat ($p < 0.0005$). Overall, breeding indices corroborate Mayfield daily mortality rates, in that breeding success is higher in deciduous habitat compared to mixed habitat and coniferous habitat. Breeding indices differed among years (1997: $\bar{x} = 4.1 \pm 0.4$, $n = 58$; 1998: $\bar{x} = 3.0 \pm 0.2$, $n = 122$; 1999: $\bar{x} = 3.2 \pm 0.2$, $n = 105$; Kruskal-Wallis = 7.71, $p = 0.02$). Breeding indices were significantly higher in 1997 compared to 1998 ($p < 0.0005$) and 1999 ($p < 0.0005$), but did not differ between 1998 and 1999 ($p = 0.9$). At the habitat level, breeding indices did not differ among years in mixed (Kruskal-Wallis = 0.88, $p = 0.88$) and coniferous habitat (Kruskal-Wallis =

2.61, p = 0.27). In contrast, they differed among years in deciduous habitat (Kruskal-Wallis = 7.71, p = 0.028). Breeding indices did not differ between 1997 ($\bar{x}$ = 6.2 ± 0.4, n = 25) and 1998 ($\bar{x}$ = 5.5 ± 0.4, n = 27; p = 0.37), but were higher in1997 compared to 1999 ($\bar{x}$ = 4.7 ± 0.2, n = 33; p = 0.006), but did not differ between 1998 and 1999 (p = 0.19).

Foraging behavior — Number of foraging bouts per hour did not differ between deciduous and mixed habitat (t = - 1.24, df = 10, p = 0.24; Table 3) nor did the average distance to foraging centers (t = - 0.96, df = 11, p = 0.36; Table 3). With regard to nesting success, there was no difference between depredated and successful nests for number of foraging bouts per hour (t = 0.46, df = 10, p = 0.65; Table 3), but there was a trend that the average distance to foraging centers was longer in depredated compared to successful nests (t = 1.92, df = 11, p = 0.08; Table 3). Lastly, with regard to nest substrate, the number of foraging bouts per hour did not differ between adventitious and crotch nests (t = - 0.63, df = 10, p = 0.54; Table 3), but the average distance to foraging centers was larger in crotch compared to adventitious nests (t = - 2.41, df = 11, p = 0.04; Table 3).

DISCUSSION

Settlement patterns and habitat

On the breeding grounds in western Washington, Pacific-slope flycatchers clearly settle first in deciduous habitat dominated by red alder. In deciduous habitat, male density was highest, territories were occupied every year, site fidelity was highest, and males arrived earliest (Table 4). Furthermore, in deciduous habitat, males paired earliest, lag between arrival date and pairing date was shortest, and breeding success and number of second breeding attempts was highest (Table 4). This clearly points to a habitat quality gradient: deciduous (high quality) > mixed (medium quality)> coniferous (low quality). In high-quality habitat, other studies

Table 3: Mean (± SE) number of feeding bouts (deciduous habitat n = 5, mixed habitat n = 7) and distance (m) to foraging centers (deciduous habitat n = 6, mixed habitat n = 7).

	Number of feeding bouts ($\bar{x}$ ± SE)	p-value[a)]	Distance to foraging centers ($\bar{x}$ ± SE)	p-value[a)]
Habitat type:				
Deciduous	15.0 ± 2.4	ns	7.7 ± 2.7	ns
Mixed	20.1 ± 3.0		11.1 ± 2.4	
Nesting success:				
Depredated	19.0 ± 3.5	ns	12.9 ± 2.2	ns
Successful	17.0 ± 1.0		6.7 ± 2.3	
Nest substrate:				
Adventitious	16.4 ± 1.4	ns	4.9 ± 0.8	*
Crotch	19.1 ± 2.9		12.4 ± 2.4	

[a)] ns = not significant, * <0.05

Table 4: Habitat influences on breeding phenology [>> = different ($p < 0.05$), > = trend ($p < 0.1$), = same ($p > 0.10$), na = not available].

Variable	Deciduous		Mixed		Coniferous
Male Density		>>		>	
Territory occupancy		>>		>>	
Site fidelity		>>		=	
Percent adult males		=		>>	
Arrival date		<		<<	
Pairing date		<<		=	
Lag pairing		<<		=	
Pairing success		>>		>>	
Lag clutch initiation		=		=	
Clutch initiation		<<		<<	
Clutch size		=		na	
Brood size		=		>>	
Second breeding attempt		>>		>	
Breeding success		>>		>>	

found that (1) male densities were higher (Krebs 1971, van Balen and Potting 1990, Holmes et al. 1996, Petit and Petit 1996, Silverin 1998), (2) males arrived and paired earlier (Lanyon and Thompson 1986, Rendell and Robertson 1990, Petit and Petit 1996, Hasselquist 1998, Pearson and Manuwal 2000), (3) site fidelity was higher (Blancher and Robertson 1985, Lanyon and Thompson 1986, Slagsvold and Lifjeld 1990, Cuadrado and Hasselquist 1994, Holmes et al. 1996), and (4) pairing success was higher (Lundberg and Alatalo 1992, Holmes et al. 1996, Petit and Petit 1996). Similarly, differences in reproductive success have been documented with regard to (1) habitat fragmentation size (Møller 1991a); (2) moisture gradient (Petit and Petit 1996); (3) shrub-density gradient (Holmes et al. 1996), (4) habitat type (Silverin 1998), and (5) environmental gradient (Sanz 1995).

Females also settled along a red alder abundance gradient; males occupying deciduous habitat paired significantly earlier compared to the other habitat types (Table 4). The variation in female arrival dates suggests that (1) females search among habitat types for high-quality territories (e.g., Alatalo et al. 1986, Slagsvold 1986) or males (e.g. Møller 1988, Kempenaers et al. 1992, Buchanan and Catchpole 1997), and/ or (2) females in fit condition may arrive earlier and therefore settle in the optimal habitat first. In support of this, Johnson (1973) found variation in terms of arrival time along the spring-migratory route in female Pacific-slope flycatchers within and between age classes.

Adult males seem to exclude yearling males from gaining access to high-quality deciduous habitat (Table 4). There were higher numbers of adult males in deciduous and mixed habitat, whereas yearling males were mainly found in coniferous habitat. Age class segregation between habitat types has been also documented for cavity nesting passerines (e.g., Krebs 1971, Alatalo et al. 1984, Petit and Petit 1996), and for open cup nesting species (Holmes et al. 1996, Hasselquist 1998). For example, when breeding pairs of great tits (*Parus* *major*) were removed, replacement individuals were mainly yearling individuals (Krebs 1971). There was also a difference in arriving time between age classes; yearling males arrived later. There is strong evidence that adults arrive earlier on the breeding grounds in many migratory passerines (e.g., Slagsvold 1986, Potti and Montalvo 1991, Holmes et al. 1996, Petit and Petit 1996). Age class related differences in arrival time along the spring-migratory route in Pacific-slope flycatchers have been documented by Johnson (1973). Adult males also paired more frequently compared to yearling males. This age effect on pairing success has also been shown in other songbirds (Morton et al. 1990, Holmes et al. 1996, Petit and Petit 1996, Pearson and Manuwal 2000).

My data suggest that in Pacific-slope flycatchers, clutch and brood size did not differ between high-quality deciduous and medium-quality mixed habitat but that brood size was lower in coniferous habitat (Table 4). Difference in clutch size in relation to habitat quality have been reported in some song bird studies (e.g., Sanz 1995) but not in others (Møller 1991a, Holmes et al. 1996, Petit and Petit 1996). Because modal clutch size is four in first clutches, Pacific-slope flycatchers can only increase productivity by increasing the number of breeding attempts per breeding season. The number of pairs attempting a second brood was higher in deciduous compared to the other two habitat types (Table 4). The number of broods per breeding season could be influenced by food availability. Although, the number of feeding bouts to the nest did not differ between deciduous and mixed habitat (indicating similar prey abundance), mixed habitat, lacking permanent water resources, may dry up faster during the non-rainy period normally prevailing during the latter part of the summer in the Pacific Northwest. In deciduous habitat, however, insect populations may be stable or even increase throughout the breeding season because of the presence of water.

Why is deciduous habitat high-quality habitat? Deciduous habitat has the highest densities of red alders and therefore highest density of adventitious nest substrate (number of red alder correlate with number of adventitious nest substrate). Adventitious nest substrate is an important habitat feature for Pacific-slope flycatchers for two reasons. First, in deciduous habitat, where both crotch and adventitious nest substrate are available, more nests were built in adventitious nest substrate. Second, combining habitats, nests built in adventitious substrate were initiated earlier which increases the chance for a second breeding attempt. However, within habitat types, there was no difference in clutch initiation of first clutches between nest substrates. Because adventitious nests were built at significantly lower heights compared to crotch nests, micro-climatic factors may influence nest height selection and consequently first clutch initiation dates both among and within habitat types. Presumably, air temperatures and wind speed fluctuate less near the ground compared to mid canopy level or in the crown and this may reduce incubation costs (Marzluff 1988). The importance of micro-climatic factors on nest site selection has been shown in pinyon jays (*Gymnorhinus cyanocephalus*) where nests are built at low heights in trees (for cover) and away from the trunk to reduce incubation costs during cold spring days (Marzluff 1988). Similarly, loggerhead shrikes (*Lanius ludovicianus*) built nests closer to the ground during the early part of the breeding season but built nests higher later in the breeding season because of increasing ground temperatures during hot summer days (Leu 1995, Woods and Cade 1996). However, nest-height selection may also be influenced by shrub density and therefore cover. I found a significant negative correlation between nest height and shrub density, indicating that nests are built at lower height when cover is available. Cover in the vicinity of the nest seems to be an important habitat characteristic because adult activity patterns around the nests are concealed and therefore predation rates on nests as well as adults may be lower (Martin and Roper 1988, Martin 1992, Kelly 1993). Third, nests built in adventitious nest substrate were more successful compared to nests built in crotch substrate. This difference could be explained by nest predator behavior. Although both adventitious and crotch nest substrate are readily available, adventitious nest substrate occurs at higher densities because of its patchy distribution (Leu unpl. data). Therefore, greater nest site densities translate into a greater number of potential nests that a predator needs to investigate, thereby decreasing the probability that a particular nest is discovered (Martin and Roper 1988). Alternatively, higher predation rates on crotch nests may be explained by adult feeding activities around the nests. Pairs feeding nestlings in crotch nests foraged significantly further from the nest compared to adults feeding nestlings in nest built in adventitious substrate. There was a trend for predation rates to be higher for nests in which adults flew further from the nest to feed. Increased activity patterns (i.e., larger distance covered during feeding bouts) around the nest apparently attracted more predators. Also, these individuals spent more time in unconcealed habitat thereby possibly luring potential predators, especially Steller's jay (*Cyanocitta stelleri*), gray jay (*Perisoreus canadensis*), and Douglas squirrels (*Tamiasciurus douglasii*), to nests (Kelly 1993). Alternatively, suitable insect prey may be more patchily distributed in mixed habitat, which would increase foraging distance. Therefore pairs that have to forage further away from the nest cannot respond as quickly to deter potential nest predators. For example, Schmidt (1999) predicted that nest predation should increase when prey availability decreases because there is a trade-off between foraging and nest vigilance. Lastly, I did not find differences in predation rates on nest substrate type within a habitat type, indicating that maybe predator densities and species differ among habitat types. Anecdotal evidence suggests that Douglas squirrels are less common in deciduous habitat.

Settlement patterns and climatic factors

Whereas maximum air temperatures were the same among years, mean rainfall was highest in 1997 and mean minimum air temperature was lowest in 1999. In 1999, minimum air temperatures were lowest during the end of April through the middle of May, the period when both male and female Pacific-slope flycatchers arrive on the breeding grounds in Washington. During 1999 but not during 1998, male densities decreased in mixed and coniferous habitat. In 1999, fewer males returned to the breeding grounds resulting in fewer territories occupied in mixed and coniferous habitat. However, all territories were occupied in deciduous habitat (Table 5). This supports the notion that deciduous habitat is of high quality for Pacific-slope flycatchers. Whether the decrease in population size is a result of increased mortality during migration or because more individuals settle further south needs further investigation. Furthermore, during 1999 but not during 1997 and 1998, both males and females arrived later in all habitats, and first clutches were initiated later in all habitat types which resulted in fewer pairs initiating second breeding attempts in deciduous habitat (Table 5). This suggests that minimum air temperature, rather than rainfall, influences breeding phenology in Pacific-slope flycatchers. Similarly, DeSante and Greupel (1987) found that rainfall had no influence on productivity (i.e., number of hatching year birds) of aerial foraging species breeding in coastal California. Arrival time on colonies was later during a year of cold temperatures in cliff swallows (*Petrochelidon pyrrhonota*; Brown and Bromberger-Brown 2000).

In great tits, clutch initiation dates were greatly influenced by caterpillar hatching dates which in turn were influenced by temperature (Van Noordwijk et al. 1995). Similarly, clutch initiation dates were influenced by low temperatures and increased rainfall in North American chickadee species (for review see Smith 1991) and white-crowned sparrows (*Zonotrichia leucophrys pugetensis*; Wingfield et al. 1983, Wingfield 1984b). In the case of

Table 5: Climatic (cold vs. warm years) influences on breeding phenology [↓ = different ($p < 0.05$), same ($p > 0.05$), na = not available].

Variable	Deciduous	Mixed	Coniferous
Male Density	same	↓	↓
Percent adult males	same	same	same
Arrival date	↓	↓	↓
Pairing date	↓	↓	↓
Lag pairing	same	same	same
Pairing success	same	same	same
Lag clutch initiation	same	same	same
Clutch initiation	↓	↓	↓
Clutch size	same	same	na
Brood size	same	same	na
Second breeding attempt	↓	same	same
Breeding success	same	same	same

the Pacific-slope flycatcher, low temperature along the migratory route and on the breeding grounds could delay arrival and timing of breeding because bud flush in red alder is influenced by low temperature (Ager et al. 1993) which very likely influences insect availability.

Time elapsed between pairing and first clutch initiation date was the same across all years and did not differ among habitats (Table 4 and 5). This suggests that when females arrive on the breeding grounds, regardless of weather conditions, they need a period of about 16 days to gear up for breeding. Furthermore, clutch size and breeding success did not differ significantly among years. In contrast, breeding indices (a measure of overall reproductive output) differed among years only in deciduous habitat because in 1999 very few second breeding attempts occurred.

How does the distribution of Pacific-slope flycatchers on the breeding grounds follow theoretical models?

Because fitness related measures, such as pairing success, reproductive success, and number of breeding attempts differed among habitat types (Table 5), the Pacific-slope flycatcher clearly follows a "despotic" distribution on the breeding grounds. The "despotic distribution" model seems to be the prevalent model in songbirds compared to the "ideal free" distribution (see introduction). The "despotic" distribution assumes that later arriving individuals are excluded from gaining access to optimal habitat (for review see Bernstein et al. 1991). Therefore, there should be intense competition for breeding territories in optimal habitat. While this study did not address this question directly, the data suggest that yearling males occupy low-quality habitat more frequently than adult males. To elucidate this age class distribution further, there are four spin-off models of the "despotic" distribution model proposed by Ens (1995). (1) the "low benefit-low cost hypothesis" suggests that by settling in sub-optimal habitat, associated cost of settling in high quality habitat are reduced (e.g., reduced mortality); (2) the "inferior phenotype hypothesis" suggests that individuals inferior in body condition occupy sub-optimal habitat; (3) the "breeding skill hypothesis" suggests that it is advantageous for younger individuals to settle in sub-optimal habitat first where breeding skills, such as acquiring local knowledge of territory quality, can be fine tuned; and (4) the "queue hypothesis" suggests that floaters have to develop hierarchical relationships to gain access to optimal habitat. In the case of the Pacific-slope flycatcher, the "breeding skill hypothesis" seems to apply with regard to the observed age class distributions because yearling males settled in low-quality habitat directly adjacent to high-quality habitat. This may allow yearling males to gain knowledge about site specific habitat quality during their first year on the breeding grounds (see also Slagsvold and Lifjeld 1990).

Although not directly tested, long-term studies and data on demographic rates are a necessity for an appropriate design (for review see Dias 1996), the results of this study suggest a sink and source dynamic among habitats (Pulliam 1988, Pulliam and Danielson 1991). The data indicate that deciduous habitat acts as a source habitat (i.e., demographic surplus) because reproductive output was highest, both in terms of breeding success and breeding attempts (Table 4). Furthermore, during 1999 when fewer males arrived on the breeding grounds, territories in deciduous habitat were all occupied compared to the reduction in occupied territories in both mixed and coniferous habitat (Table 4). In contrast, coniferous habitat is a sink habitat (i.e., demographic deficit) because only few males paired, reproductive output was lowest (smaller brood sizes), nest predation rates were highest, and populations decreased during 1999 when fewer males arrived on the breeding grounds (Table 4). Clearly, populations occupying coniferous habitat are only viable with immigration from deciduous habitat. However, mixed habitat could act as a source habitat during climatically favorable years and as a sink habitat during years with adverse weather patterns. Clearly, whether these habitat types act as sources, sinks or even "pseudo sinks" needs to be substantiated by showing the ratio between reproduction and mortality (Watkinson and Sutherland 1995).

Lastly, Rodenhouse et al. (1997) suggested that animal populations may be regulated by "site-dependence" in species where (1) breeding habitat is heterogeneous in reproductive output, and (2) habitat is preemptively occupied (some individual will not gain access to high-quality habitat) where high-quality sites are always occupied first. Simulation models showed that demographic rates for the population as a whole decreased progressively as more sub-optimal habitat was occupied. As a result, demographic rates were highest when mainly high-quality habitat was occupied. It seems, that Pacific-slope flycatcher populations may be regulated by "site-dependence". However, this is only a partial test of this model because of the limited nature of the data. First, Pacific-slope flycatchers settle along a habitat quality gradient (deciduous > mixed > coniferous) and habitat is "preemptively' occupied with high-quality habitat being occupied first. Furthermore, fewer territories were occupied in both mixed and coniferous habitat when climatic factors were unfavorable. However, whether population growth rates are higher during years when fewer territories are occupied in low-quality habitat needs to be further investigated.

CHAPTER III: PHYSIOLOGICAL AND BEHAVIORAL FACTORS INFLUENCING ARRIVAL TIME AND TERRITORY ACQUISITION ON THE BREEDING GROUNDS IN A MIGRATORY TYRANNID FLYCATCHER

INTRODUCTION

The Pacific-slope flycatcher (*Empidonax difficilis*), a common non-oscine passerine of western North American forests, is socially monogamous, and males defend multi-purpose territories where mating, nesting and foraging occur within the same territory (Davis et al. 1963). This species follows a "despotic" distribution (Fretwell and Lucas 1970) on the breeding grounds in western Washington, settling according to a habitat quality gradient, defined by reproductive success, that correlates positively with a red alder gradient (*Alnus ruba*): high-quality habitat (high reproductive success and red alder abundance), medium-quality habitat (medium reproductive success and red alder abundance) and low-quality habitat (low reproductive success and red alder abundance; Chapter 2). Males occupying both deciduous and mixed habitat arrive significantly earlier compared to males occupying coniferous habitat, and males occupying deciduous habitat pair significantly earlier than males in both mixed and coniferous habitat, and males in mixed habitat pair earlier than males in coniferous habitat (Chapter 2). Adult males arrive and pair earlier and are found mainly in deciduous and mixed habitat compared to yearling males (Chapter 2). Male densities differ significantly among habitats; they are significantly highest in high-quality habitat, but do not differ between medium and low-quality habitat (Chapter 2). Given this habitat-quality gradient, competition for territories in high quality habitat should be intense. Therefore only males in prime condition should gain access to these territories (Milinski and Parker 1991).

This raises the question: what factors, besides age, affect habitat settlement patterns and territory acquisition in this monogamous migrant songbird?

To verify the critical assumption of competitive exclusion under the "despotic" distribution model, the competitive ability of individuals must be evaluated. The competitive ability of an individual may depend on its relative physical condition and its behavioral strategy (Milinski and Parker 1991). For example, differences in age (Krebs 1971, Zack and Stutchbury 1992, Holmes et al. 1996, Petit and Petit 1996, Hasselquist 1998), and arrival time on the breeding grounds (Lanyon and Thompson 1986, Potti and Montalvo 1991, Petit and Petit 1996, Hasselquist 1998, Brown and Bromberger-Brown 2000, Pearson and Manuwal 2000) have been shown to influence who ultimately will gain access to high-quality territories.

It is well established that testosterone influences territorial behavior and therefore the competitive ability of individuals (for review see Balthazart 1983, Harding 1983, Wingfield et al. 1994, Wingfield et al. 1998, Wingfield et al. 1999a). Testosterone regulates aggressive behavior, stimulates the development of accessory organs and some secondary sexual characteristics, induces morphological and physiological changes necessary for breeding, and activates reproductive behavior and song rates in birds (for review see Wingfield et al. 1987, Wingfield et al. 1990a, Ketterson and Nolan 1994). Despite the importance of high testosterone levels during the early part of the breeding season, elevated testosterone levels in monogamous species (1) reduces reproductive success (Silverin 1980, Hegner and Wingfield 1987, Ketterson et al. 1992, Beletsky et al. 1995), (2) decreases male parental behavior (Wingfield 1984a, Chandler et al. 1994, Saino and Møller 1995, Cawthorn et al. 1998 and references therein), (3) increases parasite loads (for review see Hillgarth and Wingfield 1997a), (4) suppresses the immune system (for review see Hillgarth et al. 1997), and (5) increases the potential for injury and death (Dufty and Wingfield 1986, Wingfield et al. 1990a, Nolan et al. 1992).

Despite recent increases in knowledge of the role of physiological and endocrine factors as well as parasites on territorial and breeding behavior in birds, we know very little how these factors interact to influence settlement patterns and territorial behavior on the breeding grounds (but see Wingfield et al. 1990a, Silverin 1998). In this paper, I investigate how physiology, endocrinology and parasites influence settlement patterns and territorial behavior in male Pacific-slope flycatchers.

Because arrival time on the breeding grounds determines habitat settlement patterns in this species (Chapter 2), I investigated which physiological measures influence arrival time. For example, body size (Petit and Petit 1996, Silverin 1998), fat scores (Silverin 1998), body condition index (Marra et al. 1995), and hematocrit count (i.e., packed cell volume to total volume; Saino et al. 1997) have been shown to influence habitat settlement patterns and/or arrival time in songbirds. Therefore, I predicted that males in high-quality habitat should have higher fat scores, more positive condition indices, and higher hematocrit counts compared to males that arrive later.

If Pacific-slope flycatcher males compete for high-quality territories on the breeding grounds, then males arriving early in high-quality habitat should experience high rates of challenges from later arriving males. Therefore behavioral, physiological as well as endocrine measures should differ among habitat types. First, when males are challenged with a song play back during the territorial phase, they sing more beta songs (i.e., territorial defense song, see methods) ten minutes after the challenge occurred compared to the same period before and during the challenge (Leu and Pearson unpl. data). Therefore, males in high-quality habitat should sing more beta songs. Furthermore, if males in high-quality habitat are repeatedly challenged they should (1) respond more aggressively to simulated territorial intrusions, (2) have higher levels of testosterone as predicted by the "challenge hypothesis (Wingfield et al. 1990a), and (3) have lower ectoparasite prevalence (i.e., number of infected individuals in a population) and intensity (i.e., mean number of parasites) because ectoparasites can physiologically challenge their hosts (for review see Loye and Zuk 1991, Loye and Carroll 1995, Clayton and Moore 1997, Hillgarth and Wingfield 1997b).

METHODS

All data were collected in the Capitol State Forest (Washington Department of Natural Resources; 46^{O} 55' N, 121^{O} 10' W) Southwest of Olympia, Washington between 1997 and 1999. Between 1997 and 1999, I established 11 research sites where different habitat plots (i.e., deciduous, mixed, coniferous habitat; Chapter 2) were directly adjacent to each other. The mean nearest neighbor distance between research sites was 1.47 km (± 0.15 SE). I established research plots that differed in red alder and preferred nest substrate abundance (for detailed habitat description see Chapter 2): high-quality habitat (high abundance), medium-quality habitat (medium abundance), and low-quality habitat (low abundance). Of these research sites, five contained all three habitat types, four contained only mixed and coniferous habitat, one contained deciduous and coniferous habitat, and one consisted of deciduous and mixed habitat.

Male capture — I captured males throughout the breeding season with mist nets using a Pacific-slope flycatcher specimen as mount and a song play back. Upon capture, each male was banded with a USFW aluminum band. I refrained from using color bands for two reasons: (1) color bands cannot been seen in Pacific-slope flycatchers because belly feathers cover the bands and (2) light conditions in the forest environment rendered color identification impossible. Permits to capture flycatchers were issued by the University of Washington's Animal Care Committee (ACC # 2857-06), U.S. Fish and Wildlife Service (Permit # 20337), and the Washington Department of Fish and Wildlife (Permit # WN-0085).

Age classes — Males in their first potential breeding season (yearling male hereafter) were distinguished from older males (adult males hereafter) following Johnson (1974) according to the following characteristics (see Chapter 2): (1) shape of rectrices; (2) differences in plumage wear of rectrices; (3) texture of body plumage (yearling plumage is more lax and less intensive in pigmentation); and (4) patchiness of plumage (yearlings can have up to three generations of feathers); (5) coloration of greater primary covert edges, and (6) skull ossification (most Empidonax flycatchers have not fully ossified skull when one year old, Johnson 1974). Overall, I was able to determine the age in 88.8 % (n = 144) of all males captured.

Arrival and pairing dates — Research plots were sampled each year starting before males arrived (earliest male arrival April 23), to determine arrival and pairing dates. Depending on weather condition, I visited each research plot every second to fourth day and I used mid points between visits to estimate arrival and pairing date. I decided that males were paired when (1) females were present on the territory (males change song type from mainly singing female attracting songs to territorial defense songs), and/or (2) I heard contact notes between males and females (for changes in song frequencies and song type see Johnson 1980, Ainsley 1992). Because arrival and pairing dates differed among years (see Chapter 2), I standardized dates among years by subtracting the yearly mean arrival and pairing date from each arrival and pairing date.

Body condition — I measured body condition in four different ways. First, I estimated feather wear on the crown. Feathers on the crown consisted of two types of feathers: unworn feathers of greenish appearance, and worn feathers of brownish appearance. Old feathers could be easily discerned from new ones, because worn feathers lacked a pointed feather tip and the tip consisted of fewer vanes along the rachis. To estimate feather wear on the head, I employed a feather wear score scale (following Young 1991) ranging from score 1 (0 – 20% brown) to score 5 (80-100% brown). Overall, feather wear scores did not differ among years (Kruskal-Wallis = 1.12, $p = 0.57$) and did not correlate with capture date ($r_S = 0.11$, $p = 0.33$, $n = 83$). I therefore combined the data across years and time of year.

Second, I developed a body condition index for each male by correcting body weight for body size. Following Pyle et al. (1997), I measured male bill and tarsus length with calipers (to nearest 0.1 mm) as well as wing chord and tail length with a ruler (to nearest 0.5 mm). Each male was weighed (to nearest 0.1g) using a portable electronic scale (LS 200, Ohaus Corporation, Florham Park, NJ). Following Marra et al. (1998), bill, tarsus, wing and tail length were used to develop a body index derived by adjusting body mass by body size. These morphological measures were reduced to a single body size score using an unrotated principle component analysis (component loadings: wing = 0.86, bill = 0.45, tarsus = -0.17, tail = 0.81). Factor one explained 40.6% of total variation. The factor one scores were then regressed against weight [Factor score = - 6.07 (± SE of 2.46) + 0.55 (± SE of 0.22) * weight, $r^2_{adj.} = 0.06$, $F = 6.09$, $p = 0.016$] and the resulting residuals were used as the body condition index. Body condition indices did not differ among breeding stages ($F_{4,72} = 0.98$, $p = 0.43$) and year (1998 vs. 1999; t-test = 1.75, df = 75, $p = 0.081$), and there was no correlation between capture date and body index ($r = -0.16$, $p = 0.16$, $n = 65$). I therefore combined the data across breeding stages and time of year for analysis.

Third, I measured fat deposits for each individual following Helms and Drury (1960). Fat scores were significantly higher and more variable in the abdomen ($\bar{x} = 1.04 \pm 0.08$, n =

104) compared to the furculum region ($\bar{x}$ = 0.16 ± 0.05, n = 104; Mann-Whitney U = 89.07, p < 0.0005). Furthermore, fat scores did not correlate between the two body regions (r_s = 0.10, p = 0.30). Because the median furculum fat score was zero, I used only the abdomen fat score for analysis.

Fourth, I measured hematocrit (ratio of packed cells to total blood volume) for each individual where I also collected blood for hormone analysis (described below). Upon capture, I collected a small blood sample (≈ 70-200µl) into heparinized, micro-hematocrit capillary tubes by puncturing the alar vein on the wing with a 26 gauge needle. Blood samples were stored on ice and were centrifuged (at 4000 r. p. m for 10min.) about 2 - 6 hrs. after collection. Hematocrit was measured in one capillary tube (randomly selected if more than one tube) by using a calipers (to nearest 0.1mm) to determine length of packed cells and total length (Saino et al. 1997). Hematocrit levels did not differ among years (Mann-Whitney U = 184.0, p = 0.42, n = 42), therefore, I lumped data across years.

Song data — During the territorial phase (i.e., before female arrival), Pacific-slope flycatchers elicit three main types of vocalizations: alpha song, beta song and a contact note (Fig. 5). These three song types can be easily differentiated in the field. Song behavior in Tyrannid flycatchers seems to be genetically determined (Kroodsma 1984, Kroodsma 1989). When paired, males switch from singing mainly alpha to mainly beta songs (Leu and Pearson unpl. data, Johnson 1980, Ainsley 1992).

During the territorial phase from 1997 - 1999, I counted beta songs and contact notes, using focal sampling, between 06:00 to 10:00 am. In 1997, I measured rates of the two song types for both 10 min. and 15 min. However, the ratio of beta and contact notes did not differ between 15 and 10 min. samples (beta song: Mann-Whitney U = 254.0, p = 0.82; contact note:

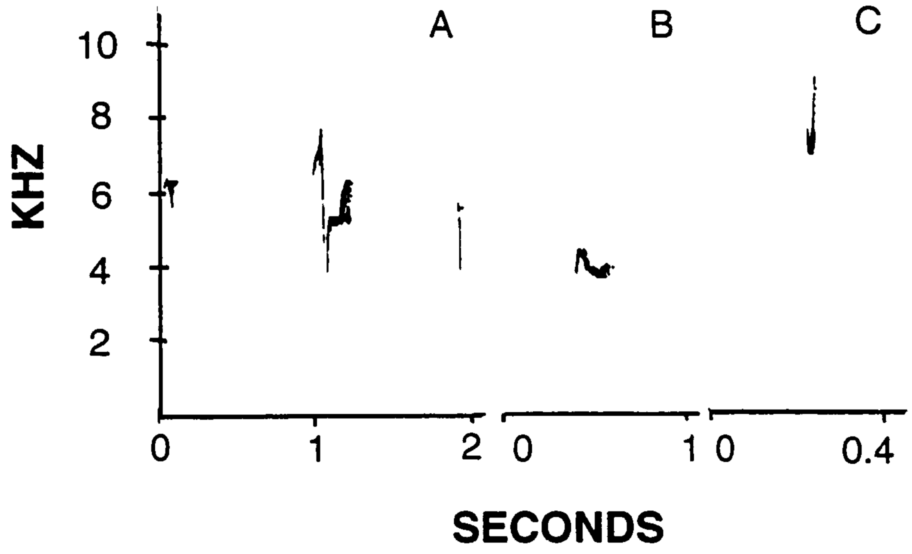

Figure 5: Song types for Pacific-slope flycatchers: a) male alpha song (female attracting song), b) male beta song (territory defense song), and c) male female contact note (male-male and female-male interactions).

Mann-Whitney U = 272.0, p = 0.83). I therefore collected song data for 10 min. during 1998 and1999.

At the habitat scale, using a multivariate regression analysis, there was no relationship between song type (dependent variable) versus year and time of day (independent variables) for beta songs (deciduous: $F_{2,15} = 0.85$, $p = 0.45$; mixed: $F_{2,19} = 3.09$, $p = 0.07$; and coniferous: $F_{2,9} = 0.70$, $p = 0.52$), and contact notes (deciduous: $F_{2,22} = 1.58$, $p = 0.23$; mixed: $F_{2,24} = 1.28$, $p = 0.30$; coniferous habitat: no contact notes). I therefore combined data across years and time of day.

Aggressive behavior — During the territorial phase in 1998 and 1999, I measured the response time of males to simulated territorial intrusions (i.e., song playback and mount) during a 15min. bout. Response time was defined as the lag between a male approaching from 10m to 2m of the mount. A standardized response time measure was necessary because canopy height differed among habitats. For example, males singing in taller canopies would have longer response times compared to males singing in lower canopies. In all trials, I attempted to challenge the males in the center of their territories. A challenge was defined as non-responding when a male failed to appear within 10m of the mount within 15 min.; these were not included in the analysis (n = 3, 4.5 %). Males that came within 10m but never came within 2m of the mount received a score of 15 min.

I verified whether response time correlates with other aggressive behaviors. Following Wingfield and Hahn (1994), I measured number of flights within five meters of the speaker, number of alpha and beta songs, and total time spent within five meters of the speaker of 14 males. These four variables were reduced to one single score of aggression (for review see Pearson 2000) by using unrotated principle factor one loadings derived from a Spearman rank matrix (alpha song = 0.67, beta song = 0.30, number of flights within five meters of speaker = - 0.96, and time spent within five meters of speaker = - 0.96). Overall, factor one explained 59.5 % of total variation. Factor one scores significantly correlated with response time ($r = -0.86$, $p < 0.0005$), indicating that males with negative scores (i.e., more aggressive males) also had a shorter response time. Therefore, I found response time to be a good measure of aggression in Pacific-slope flycatchers.

At the habitat scale, using a multivariate regression analysis, there was no relationship between response time (dependent variable) versus year and time of day (independent variables) for deciduous ($F_{2,6} = 0.25$, $p = 0.74$), mixed ($F_{2,19} = 2.49$, $p = 0.11$) nor for coniferous habitat ($F_{2,13} = 1.00$, $p = 0.39$). I therefore combined data across years and time of day.

Testosterone plasma concentrations — Following Wingfield and Farner (1976), blood samples were collected immediately following capture, centrifuged about 2-6 hrs. after collection and plasma samples were stored at – 20 °C (field season: Capitol Medical Center, Olympia; post field season: University of Washington, Seattle) until assayed. Each fall, plasma testosterone concentrations were determined via direct radioimmunoassays (for description of assay see Wingfield et al. 1992). Prior to extracting hormones, I added approximately 2000cpm of tritiated testosterone to each sample to calculate percent recovery. Intra-assay variation for this assay has been reported to be around 11% (see Hunt 1997). Inter-assay variation was 10.3% ($n = 3$), and mean recovery was 87.7% for 1997 (mean plasma volume: 47.9 ± SE of 4.8 µl, $n = 11$), 84.4% for 1998 (mean plasma volume: 41.0 ± SE of 2.9 µl, $n = 19$), and 87.5% for 1999 (mean plasma volume: 23.2 ± SE of 5.6 µl, $n = 6$).

Overall, testosterone concentrations did not correlate with plasma volume ($r = -0.17$, $p = 0.24$, $n = 36$), capture time (i.e., start of challenge to capture time; $r = -0.16$, $p = 0.27$, $n = 48$), standardized arrival time ($r = -0.28$, $p = 0.19$, $n = 23$), and lag between arrival and capture ($r = -0.09$, $p = 0.61$, $n = 33$). Furthermore, testosterone concentrations did not differ among years (deciduous habitat: $F_{2,5} = 0.36$, $p = 0.71$; mixed habitat: $F_{2,9} = 3.07$, $p = 0.10$; coniferous habitat: $F_{2,12} = 1.45$, $p = 0.25$). I therefore combined data across years.

Ectoparasite loads — To avoid bias, I inspected males for the presence of lice after all morphological measures were completed. In 1997, I checked three regions for lice: head, throat, and breast. This revealed that lice eggs (glued to proximal part of feather shaft) and adult instars were solely found on the throat. Therefore in subsequent years, I only checked the throat region for presence/absence of louse eggs and adults. Following Clayton and Walther (1997), I counted eggs and adult louse using a visor with 2x magnification (Optivisor, Donegan Optical Company, Inc., Lenexa, KS) while lifting approximately five feathers with forceps each time on approximately 10 locations on the throat.

Statistical analyses — I analyzed the data at two levels. First, I tested whether there were differences in male quality among habitat-quality types, lumping age classes. This was necessary because I could not assign all males to an age class (some males were in poor condition but had both adult and yearling plumage characteristics). Second, because adult males occupied mainly high and medium-quality habitat, I captured only two adult males in low-quality habitat, I tested whether male quality differed among adult males in the former two habitat types only. I tested each variable for normality and used appropriate transformations for skewed data. In cases where transformation did not improve normality, I used non-parametric statistics (Zar 1984). To test differences among habitats, I used ANOVA with Tukey post-hoc analysis for normal data and the Kruskal-Wallis test and post-hoc analysis described by Zar (1984) for non-normal data. To test frequency distributions among habitats, I used the G-test (Log-likelihood ratio test, Zar 1984). I used Pearson or Spearman rank correlation analysis (Bonferroni adjusted p-values were used in multiple comparisons) to investigate correlations among variables. I employed multivariate regression analysis and used standardized coefficients to investigate which variables contribute most in explaining arrival time (Wilkinson and Coward 1997). All statistical analyses were done with SYSTAT 7.0 (SYSTAT 1997). All p-values reported throughout this paper represent two-tailed tests. For all analysis, I used $p \leq 0.05$ as the level of statistical significance. Results of tests reporting means are indicated as means ± one standard error (SE).

RESULTS

Crown feather wear — Combining age classes, feather wear scores differed among habitats (Kruskal-Wallis = 16.82, $p < 0.0005$; Fig. 6). Scores were lower in high ($p < 0.0005$) and medium ($p = 0.007$) compared to low-quality habitat; scores were similar in high and medium-quality habitat ($p = 0.16$). Adult males had lower feather wear scores ($\bar{x} = 1.5 \pm 0.12$, $n = 58$) than yearlings ($\bar{x} = 2.7 \pm 0.26$, $n = 17$; Mann-Whitney U = 219.5, $p < 0.0005$). For adults, feather wear scores were lower for males occupying high ($\bar{x} = 1.1 \pm 0.10$, $n = 21$) compared to medium-quality habitat ($\bar{x} = 1.8 \pm 0.18$, $n = 33$; Mann-Whitney U = 220.5, $p = 0.006$). Feather wear scores correlated significantly with standardized arrival dates for age classes combined ($r_S = 0.49$, $p = 0.001$, $n = 60$), showed a trend for adults ($r_S = 0.33$, $p = 0.08$, $n = 45$), but not for yearlings ($r_S = -0.06$, $p = 1.00$, $n = 12$).

Body condition index — Combining age classes, body condition indices differed among habitats ($F_{2,72} = 6.65$, $p = 0.002$; Fig. 6). Body indices were more positive in high than in low-quality habitat ($p = 0.001$), did not differ between high and medium-quality habitat ($p = 0.14$), and approached significance between medium and low-quality habitat ($p = 0.06$; Fig. 6). Not surprisingly, body condition indices differed significantly between age classes (t-test = 3.84,

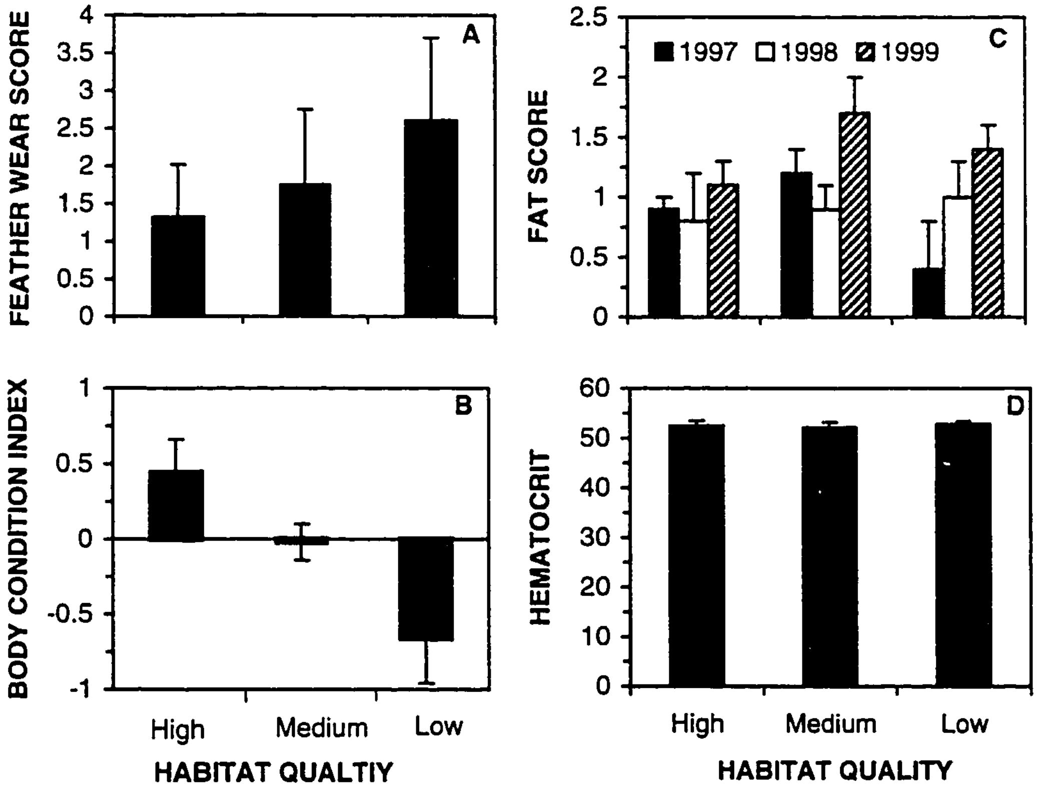

Figure 6: Body condition variables ($\bar{x}$ ± SE) measured during the breeding season in high, medium, and low-quality habitat (sample sizes given in same sequence) for adult and yearling males with regard to **A**) crown feather wear (n = 25, 36, 20); **B**) body condition indices (n = 22, 38, 15); C) abdomen fat scores (1997.: n = 10, 10, 8; 1998: n = 9, 21, 8; 1999: n = 12, 16, 7); and **D**) percent hematocrit (n = 6,20,15).

df = 67, $p < 0.0005$); they were more positive in adults ($\bar{x} = 0.22 \pm 0.11$, n = 57) compared to yearlings ($\bar{x} = -0.86 \pm 0.29$, n = 12). For adult males, condition indices differed significantly between high ($\bar{x} = 0.60 \pm 0.24$, n = 18) and medium-quality habitat ($\bar{x} = 0.017 \pm 0.13$, n = 35; t-test = 2.03, df = 23, p = 0.02). There was a significant correlation between standardized arrival date and body condition index for age classes combined ($r_s = -0.48$, p = 0.001, n = 60), a trend for adult males ($r_s = -0.33$, p = 0.08, n = 45), but not for yearlings ($r_s = -0.057$, p = 1.00, n = 12). Because crown feather wear is also an index of body condition, I tested whether these two variables correlate. There was a significant negative correlation between body condition indices and crown feather wear scores for age classes combined ($r_S = -0.39$, p = 0.01, n = 60), but not for adults ($r_S = -0.32$, p = 0.10, n = 45) and yearlings only ($r_S = 0.37$, p = 0.70, n = 12).

Abdomen fat scores — Fat scores differed among habitat types in 1997 (Kruskal-Wallis = 11.04, p = 0.004; Fig. 6) but not in 1998 (Kruskal-Wallis = 1.00, p = 0.607) nor in 1999 (Kruskal-Wallis = 1.00, p = 0.607; Fig. 6). Abdomen fat scores were higher in high (p = 0.02) and medium (p = 0.001) compared to low-quality habitat, but did not differ between high and medium-quality habitat (p = 0.52). Fat scores differed among years (Kruskal-Wallis = 12.98, p = 0.002). They were significantly higher in 1999 ($\bar{x} = 1.37 \pm 0.14$, n = 37) compared to 1997 ($\bar{x} = 0.86 \pm 0.11$, n = 28; p = 0.031) and 1998 ($\bar{x} = 0.87 \pm 0.14$, n = 39; p = 0.001) but did not differ between 1997 and 1998 (p = 0.69). With regard to male age classes, there was a trend for abdomen fat scores to differ between adults and yearlings in 1997 (Mann-Whitney U = 85.0, p = 0.07), but did not differ in 1998 (Mann-Whitney U = 80.5, p = 0.67) and 1999 (Mann-Whitney U = 95.0, p = 0.72).

Hematocrit — Hematocrit values did not differ among habitat types (Kruskal-Wallis = 0.36, p = 0.84, n = 41; Fig. 6), nor between age classes (adults: $\bar{x}$ = 52.01 ± 0.91, n = 25; yearlings: $\bar{x}$ = 52.08 ± 0.60, n = 11; Mann-Whitney U = 140.0, p = 0.93, n = 36). There was no relationship between hematocrit levels and standardized arrival time and time since arrival ($F_{2,31}$ = 0.54, p = 0.59).

Overall, using a multivariate regression analysis, with standardized arrival date as the dependent variable and crown feather wear, body condition index, abdomen fat score, and hematocrit as independent variables resulted in a significant model ($F_{4,36}$ = 3.07, p = 0.029; r^2_{adj} = 0.17). Using standardized coefficients, both abdomen fat score (0.29) and body condition (-0.27) contribute most in predicting arrival time, followed by crown feather wear score (0.18), and least by hematocrit (0.02). Body condition indices and crown feather wear scores correlated significantly (r_S = - 0.32, p = 0.021, n = 70) whereas abdomen fat scores did not correlate with either variable (crown feather wears: r_S = 0.02, p = 1.00, n = 70; body condition: r_S = - 0.15, p = 0.69, n = 70).

Song data — Number of beta songs ($F_{2,49}$ = 0.06, p = 0.94, Fig. 7) and contact notes ($F_{2,49}$ = 1.20, p = 0.31, Fig. 7) did not differ among habitat types.

Aggressive behavior — Response time did not differ among habitat types ($F_{2,60}$ = 1.35, p = 0.27, Fig. 7) nor between adults and yearlings (adults: $\bar{x}$ = 83.43 ± 13.8, n =30; yearling males: $\bar{x}$ = 60.9 ± 16.53, n = 10; t-test = - 0.52, df = 28, p = 0.58). Furthermore, the number of males not coming within 2m of the mount during territorial intrusions did not differ among habitat types (deciduous habitat = 16.7%, n = 14; mixed habitat = 15.2%, n= 32; coniferous habitat = 13.3%, n = 17; G-test = 0.11, df = 2, p = 0.95). Response time did not correlate with

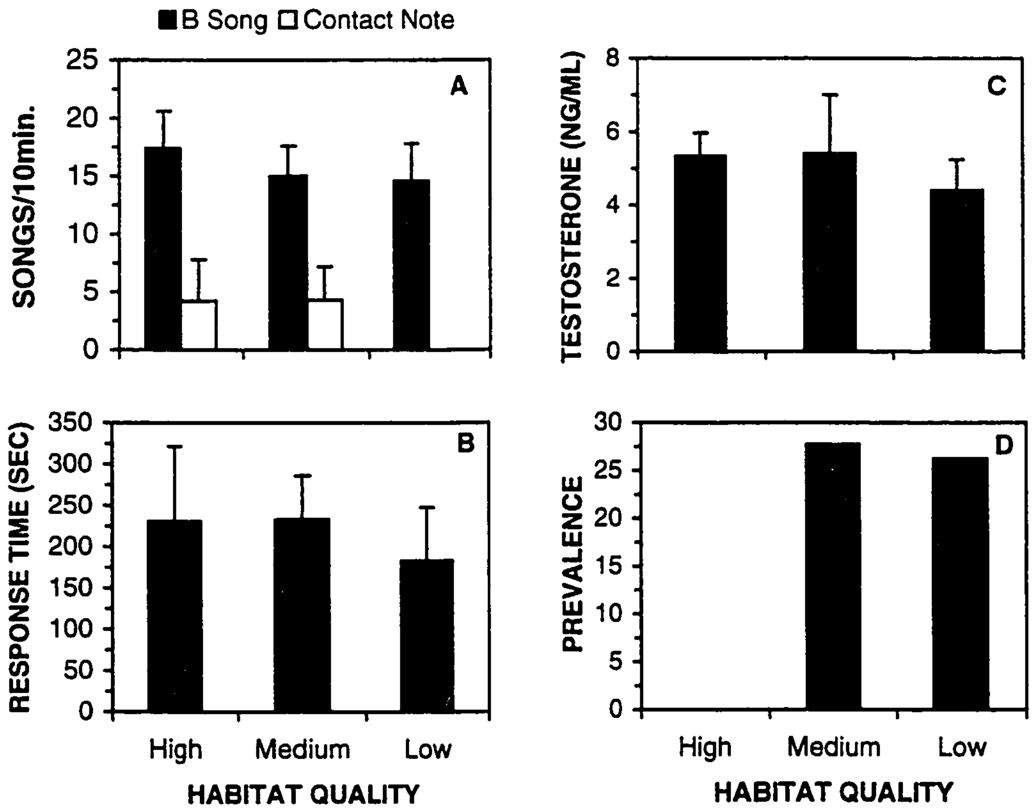

Figure 7: Behavioral and hormonal variables ($\bar{x} \pm$ SE) and lice prevalence (%) measured during the territorial phase in high, medium and low-quality habitat (sample sizes given in same sequence) for adult and yearling males with regard to A) beta songs and contact notes (n = 25, 27, 15); B) response time to territorial intrusions (n = 13, 31, 19); C) testosterone plasma concentrations (testosterone: n = 8, 24, 14); and D) lice prevalence (n = 12, 29, 23).
)

body condition indices ($r_S = -0.08$, $p = 1.00$, $n = 43$), and crown feather wear ($r_S = 0.23$, $p = 1.00$, $n = 43$).

Testosterone plasma concentrations — Testosterone plasma levels did not differ among habitat types ($F_{2,43} = 1.00$, $p = 0.38$, Fig. 7). There was a trend for testosterone concentrations to be higher for adult ($\bar{x} = 6.80 \pm 0.92$ ng/ml, $n = 22$) compared to yearling males ($\bar{x} = 4.97 \pm 1.17$ ng/ml, $n = 10$; t-test = 1.82, df = 30, $p = 0.08$). Combining habitat types, testosterone concentrations did not correlate with response times ($r = 0.14$, $p = 1.00$, $n = 43$), and body condition indices ($r_S = 0.07$, $p = 1.00$, $n = 43$) but showed a trend with crown feather wear scores ($r_S = 0.41$, $p = 0.06$, $n = 43$).

Ectoparasites — Louse prevalence differed among habitat types (G-test = 6.68, df = 2, $p = 0.034$; Fig. 7). It was zero in deciduous habitat, did not differ between mixed and coniferous habitat (G-test = 0.02, df = 1, $p = 0.90$; Fig. 7), but differed between deciduous and combined mixed and coniferous habitat (G-test = 6.62, df = 1, $p = 0.01$). Intensity (i.e., number of eggs per individual) followed a negative binomial distribution; very few individuals were heavily infested with louse eggs (Fig. 8). The frequency distribution of intensity did not differ between mixed and coniferous habitat (Kolmogorov-Smirnov two sample test = 0.20, $p = 1.00$). At the population level, prevalence (i.e., the number of infected individuals) was 23.3 % ($n = 64$). Interestingly, adult lice were found only on 28.6 % ($n = 14$) of infected individuals. Louse prevalence did not differ among years (1997: 30.0 %, $n = 20$; 1998: 17.4 %, $n = 23$; 1999: 19.0 %, $n = 21$; G-test = 1.10, df = 2, $p = 0.58$) nor between adult (24.3%, $n = 37$) and yearling males (21.1%, $n = 19$; G-test = 0.076, df = 1, $p = 0.78$).

I also investigated to what degree mallophagous lice influence individuals behaviorally as well as physiologically. I assessed this at two levels: (1) by combining habitat types; and (2) by combining deciduous and mixed habitat. The latter comparison

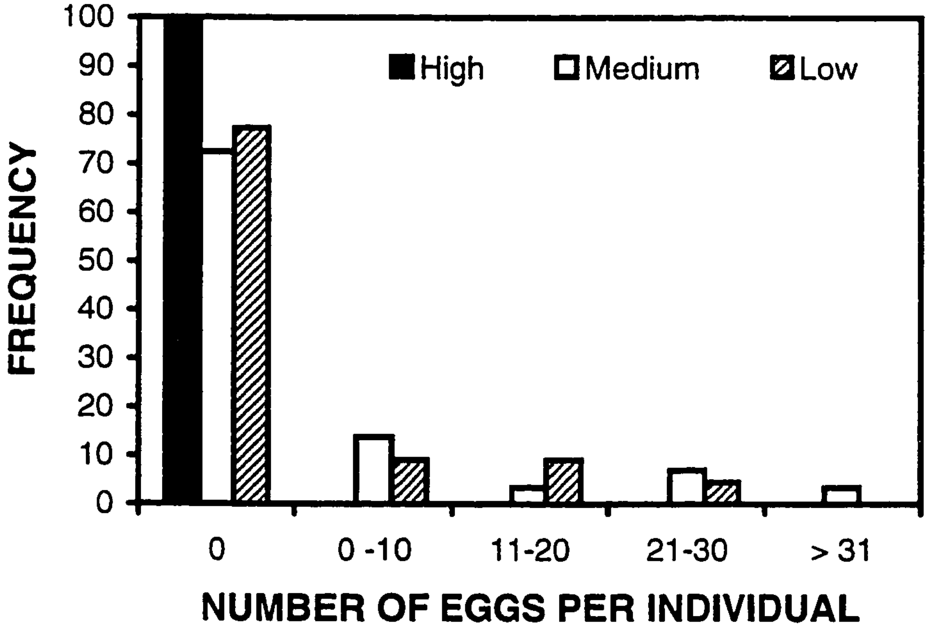

Figure 8: Intensity (i.e., number of eggs per individual) frequency distribution for high (n = 12), medium (n = 29), and low quality habitat (n = 22).

circumvents age-related covariation. With regard to standardized arrival time, there was a trend for unparasitized males to arrive earlier compared to parasitized males when habitats were combined (t-test = - 1.82, df = 42, p = 0.076; Table 6); this trend was significant using data from deciduous and mixed habitat only (t-test = - 1.99, df = 27, p = 0.03). Although response time to territorial intrusions was lower for unparasitized compared to parasitized males, this was not statistically different for habitats combined (t-test = - 0.56, df = 38, p = 0.65; Table 6), nor for deciduous-mixed habitats (t-test = - 0.06, df = 23, p = 0.95). The same was true for testosterone plasma levels. Concentrations were higher for unparasitized than parasitized males, however, this was not statistically different for habitats combined (t-test = 1.51, df = 44, p = 0.36), nor for deciduous-mixed habitats (t-test = 1.15, df = 31, p = 0.26; Table 6). Furthermore, body condition indices as well as abdomen fat score did not differ between parasitized and unparasitized males for habitats combined (body condition index: t-test = 0.54, df = 41, p = 0.59; abdomen fat score: Mann-Whitney U = 358.5, p = 0.40; Table 6), nor for deciduous-mixed habitats (body condition index: t-test = 0.44, df = 26, p = 0.66; abdomen fat score: Mann-Whitney U = 111.5, p = 0.75; Table 6). In contrast, crown feather wear scores were significantly lower for unparasitized compared to parasitized males for habitats combined (Mann-Whitney U = 107.5, p = 0.04, Table 6); this trend approached significance in deciduous-mixed habitats (Mann-Whitney U = 41.5, p = 0.08, Table 6). Lastly, I investigated whether hematocrit counts (i.e., % red blood cells) differed among unparasitized males, males with eggs, and males with adult lice instars and eggs. Hematocrit counts differed significantly among the three groups (Kruskal-Wallis = 8.95, p = 0.01; Fig. 9). Hematocrit counts were significantly lower for males with adult instars and eggs compared to unparasitized males (p = 0.03) and males with eggs (p = 0.006). Hematocrit counts did not differ between unparasitized males and males with eggs (p = 0.23).

Table 6: Mean ± SE (n) standardized arrival time, response time to territorial intrusions (response), plasma testosterone concentration (T), condition index, abdomen fat score, and head feather wear index for males parasitized with lice and unparasitized males for habitat combined (overall effect) and for deciduous and mixed habitat.

	Habitat types combined		Deciduous and mixed habitat	
	Unparasitized	Parasitized	Unparasitized	Parasitized
Arrival time (days)	-2.3 ± 6.1 (37)	6.0 ± 4.2 (7)	-7.4 ± 1.4 (37)	1.5 ± 4.3 (4)
Response (sec.)	73.5 ± 12.6 (32)	85.8 ± 17.9 (8)	89.7 ± 18.0 (19)	91.7 ± 23.7 (6)
T (ng/ml)	5.8 ± 0.7 (73)	3.9 ± 0.4 (9)	6.2 ± 0.8 (27)	3.8 ± 0.3 (6)
Condition index	- 0.06 ± 0.2 (35)	- 0.26 ± 0.4 (8)	0.11 ± 0.2 (22)	- 0.06 ± 0.4 (6)
Abdomen fat scores	1.2 ± 0.1 (48)	0.9 ± 0.2 (13)	1.0 ± 0.2 (26)	0.9 ± 0.3 (8)
Feather wear index	1.8 ± 0.2 (36)	2.6 ± 0.4 (10)	1.4 ± 0.2 (23)	2.3 ± 0.6 (6)

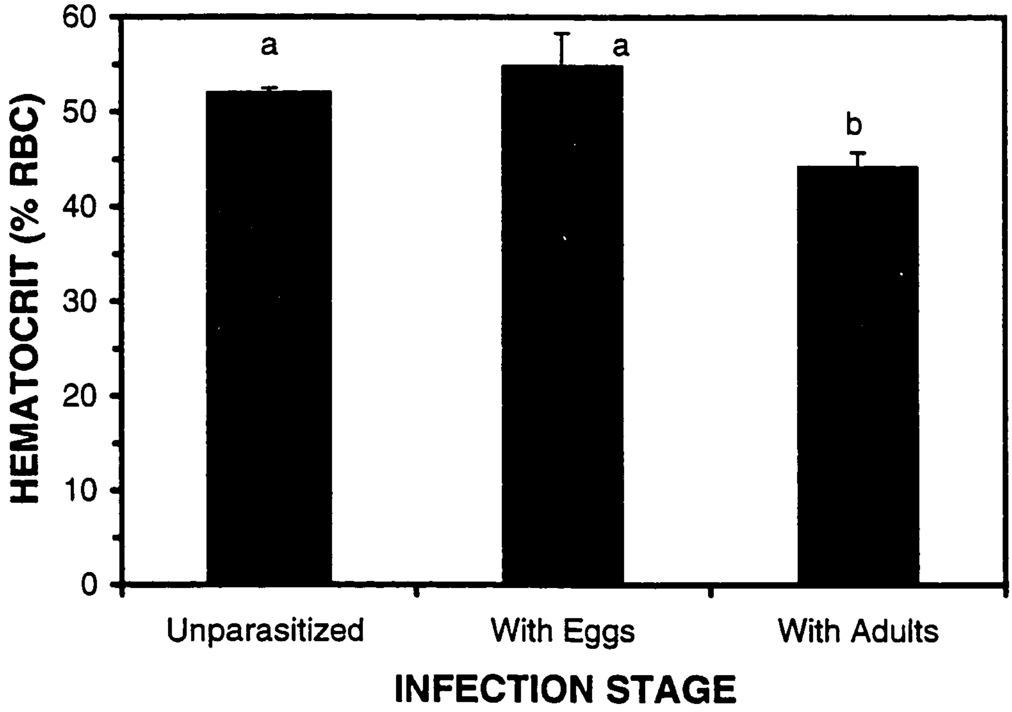

Figure 9: Percent hematocrit ($\bar{x} \pm$ SE) for unparasitized males (n = 45), males with eggs (n = 8), and males with adult lice (n = 3). Data not sharing same letter are significantly different from each other ($p < 0.05$).

DISCUSSION

Arrival time and physiological condition of males

Several studies have clearly demonstrated that arrival time on the breeding ground is an important variable explaining either male or territory quality in songbirds, and ultimately reproductive success (Lundberg and Alatalo 1992, Holmes et al. 1996, Petit and Petit 1996, Hasselquist 1998, Pearson and Manuwal 2000). This is also true for Pacific-slope flycatchers: early-arriving males establish territories in high-quality habitat where reproductive success is significantly higher (Chapter 2). An important question is what physiological factors influence male arrival on the breeding grounds. Both body condition and abdomen fat scores were key in predicting arrival time, followed by crown feather wear. Hematocrit was not important. In contrast, Saino and Møller (1997) found that male barn swallows (*Hirundo rustica*) arriving earlier on the breeding grounds had higher hematocrit levels. Why this difference exists is unclear.

Fat scores were not an important factor indicating territory quality in Pacific-slope flycatchers. Pacific-slope flycatchers arrive on the breeding grounds with low fat deposits; fat deposits were absent in the furculum region and few individuals had fat deposits on the abdomen. Absence of fat deposits during arrival on the breeding grounds has also been found in the hermit (*Dendroica occidentalis*) and Townsend's warblers (*D. townsendi*; Pearson pers. comm.). In Pacific-slope flycatchers, abdomen fat scores differed among habitat types only in one year when lower scores were found in low-quality habitat. Silverin (1998) found that male pied flycatchers occupying optimal habitat had higher furculum fat deposits.

In contrast to fat scores, body-condition indices were an important factor indicating territory quality in Pacific-slope flycatchers. They differed among high and medium-quality habitat in adult males and between age classes. Size differences with regard to habitat quality has also been documented in Prothonotary warblers (*Protonotaria citrea*; Petit and Petit 1996), but not in non-migratory oystercatchers (*Haematopus ostralegus*; Ens et al. 1995), and European jays (*Garrulus glandarius*; Andrén 1990). Therefore, the importance of body size to territory acquisition may be highest in species that undergo long-distance migration where larger individuals can risk leaving the wintering grounds earlier (see Marra et al. 1998) and possibly overcome periods of food shortage during migration and/or when establishing territories on the breeding grounds. Directional selection for larger body size was documented in barn swallows (*Hirundo rustica*) and cliff swallows (*Petrochelidon pyrrhonota*) during arrival on the breeding colonies. During a cold weather spell that lasted six days, larger individuals had higher survival than smaller individuals (Brown and Bomberger-Brown 1998, 1999, 2000). Lastly, body condition indices also may reflect differences in territory quality on the wintering grounds. For example, Marra et al. (1998) found that not only did male American Redstarts (*Setophaga ruticilla*) with higher body condition indices leave the wintering grounds earlier, but the earlier leaving individuals also occupied high-quality habitat on wintering grounds.

Similar to body condition indices, crown feather wear may also reflect differences in territory quality on wintering grounds because plumage condition reflects physiological condition during the molt when the current plumage was acquired (Thompson et al. 1997). Pacific-slope flycatchers undergo their prebasic and prealternate molt on the wintering grounds (Johnson 1963). Given that males with high crown feather wear scores arrive later on the breeding grounds, it is possible that these males occupy sub-optimal habitat on wintering grounds where energetic requirements for a complete molt are not available. Alternatively, feather wear differences may result from foraging behaviors that differ among habitat types. For example lower food availability in low-quality habitat may require foraging behavior that is abrasive to feathers such as hovering (hovering is used by the Pacific-slope flycatcher to find food in moss during cold spells; Leu and Gillen pers. observ.). It is well known that species breeding in abrasive habitats undergo two complete molts during a year compared to one in species that breed in benign habitats (discussed in Willoughby 1992).

Assortive habitat settlement patterns: endocrine measures and territorial behavior

Later arriving males do not appear to challenge males with established territories in high-quality habitat. First, there were no differences among habitat types with regard to response time to simulated territorial intrusions. One could argue that the response time is not an important measure of aggressive behavior. However, the PCA factor scores of four other aggressive behaviors (flights within five meters of the speaker, number of alpha and beta songs, and total time spent within five meters of the speaker) correlated well with response time, indicating that response time is a good measure of aggression in Pacific-slope flycatchers. The similarity in aggressive behavior among males occupying different habitat is further substantiated by the fact that the probability of males flying within 2m of the mount did not differ among habitats. Silverin (1998), however, documented elevated levels of aggressive behavior in male pied flycatchers (*Ficedula hypoleuca*) occupying high-quality habitat where males attacked an intruder more frequently and spent more time near the intruder during simulated territorial intrusions than males in low-quality habitat. Second, I found that beta song rates did not differ among habitat types. This also suggests absence of repeated challenges by later arriving males because when males are challenged during the territorial phase, the beta song rate increased (Leu and Pearson unpl. data). Third, testosterone concentrations did not differ among habitat types. This is interesting because male densities are higher in high-quality habitat compared to the medium and low-quality habitat (Chapter

2). The "challenge hypothesis" (Wingfield et al. 1990a) predicts that males in socially unstable environments should have elevated levels of testosterone. In support of this, testosterone levels were elevated in high-density habitat in polygynous species, such as in red-winged (*Agelaius phoeniceus*) and yellow headed black birds (*Xanthocephalus xanthocephalus*; Beletsky et al. 1992) and pied flycatchers (Silverin 1998), as well as in socially monogamous species, such as in song sparrows (*Melospiza melodia*; Wingfield and Hahn 1994), and European starlings (*Sturnus vulgaris*; Ball and Wingfield 1987).

If males in high-quality habitat are frequently challenged by late arriving males, then testosterone levels should be higher in high-quality habitat. For example, when territorial song sparrow males are removed from their territories, replacement males and their neighbors have elevated levels of testosterone (Wingfield 1985). The data of this study showed no habitat effect with regard to testosterone plasma levels as well as aggressive behavior. However, Hews and Moore (1997) argued that behavioral traits, such as aggressive behavior, are not testosterone dose-dependent, and therefore one should not expect a habitat quality-testosterone gradient. Alternatively, testosterone levels may be at a maximum during the territorial phase and therefore frequent territorial challenges may not increase testosterone plasma levels during this period. Indeed, testosterone plasma levels are significantly higher during the territorial and sexual phase in Pacific-slope flycatchers compared to the parental phase (Leu and Wingfield unpl. data). An interesting question is whether testosterone levels will increase during the parental phase when a male is challenged.

Testosterone concentrations did not correlate with aggressive behavior (i.e., response time to territorial intrusions) in Pacific-slope flycatchers. This contrasts with other studies that found that aggressive behavior correlates with testosterone titers (Moore 1984, Wingfield and Hahn 1994, Johnsen 1998, Silverin 1998). It may be that testosterone levels do not increase after a male was challenged in Pacific-slope flycatchers during the territorial phase. In support of this, there was no correlation between total time challenged and testosterone levels during the territorial phase. Alternatively, elevated levels of testosterone may be more important in maintaining courtship behavior. Pacific-slope flycatchers, as other *Empidonax* flycatchers (Pereyra 1998), engage in aggressive inter-sexual aerial chases (these chases were not observed among males) that can end in both birds fighting on the ground. Pereyra (1998) argued that testosterone may play an important role in courtship behavior in the dusky flycatchers (*Empidonax oberholseri*).

Assortive settlement patterns and ectoparasites

During the territorial phase, louse prevalence was lower in high compared to medium and low-quality habitat. Louse intensity followed a negative binomial distribution (for review see Rékási et al. 1997), typical of parasites infestations, where very few individuals are heavily infested (Hutson 1981, Morbey 1996, Rékási et al. 1997).

Do lice inflict a competitive disadvantage onto males? Infested adult males arrived significantly later and were found exclusively in the medium-quality habitat during the territorial phase (Chapter 2). Combining age classes, there was a strong trend for males infested with lice to arrive later. However, whether parasites affect arrival time in songbirds is equivocal. For endoparasites, Rätti et al. (1993) found that pied flycatchers infested with *Trypanosomes* arrived later on the breeding grounds and established territories in sub-optimal habitat whereas purple martins (*Progne subis*) infested with *Haemoproteus* arrived earlier on the breeding grounds (Davidar and Morton 1993). The influence of *Haemoproteus* on arrival time in purple martins may depend on the virulence of the parasite, where it may be very virulent only in young individuals, whereas adults surviving a chronic parasite infection are superior in mounting an immune response and are therefore in superior condition (Davidar and Morton 1993).

Neither response time to a territorial intrusion, testosterone, nor body condition index differed statistically between males infected with lice and unparasitized males. In contrast, crown feather wear scores were significantly lower in unparasitized males. As discussed previously (Chapter 2), it is conceivable that infected males occupy sub-optimal habitat on the wintering grounds and therefore get a late start on spring migration. Males infested with adult lice had significantly lower hematocrit levels compared to males infested with lice eggs or unparasitized males. Lower hematocrit levels indicate anemia and therefore lower oxygen up take (for discussion see Wingfield et al. 1990b, Potti and Montalvo 1991). Lower hematocrit levels were also found in red jungle fowl (*Gallus gallus*) infected with a nematode (*Ascaridia galli*; Johnsen and Zuk 1998), great tit (*Parus major*) nestlings infected with the hen flea (*Ceratophyllus gallinae*; Richner et al. 1993), and pied flycatcher fledglings infected with mites (*Dermanyssus gallinoides*) but not with blowfly (*Protocalliphora azurea*; Potti et al. 1999).

Conclusions

My study suggests that in Pacific-slope flycatchers arrival time determines habitat settlement patterns on the breeding grounds. Arrival time differed between age classes (yearling males arrived later) and males infected with lice (infected males arrived later). Arrival time seems to be influenced by body condition and fat scores. Larger males arrive earlier compared to smaller males. Once on the breeding grounds, the data suggest that males in high-quality habitat are not repeatedly challenged by males arriving later on the breeding grounds. There was no difference among habitat types with regard to the territorial defense song, testosterone plasma concentrations, and response time during territorial intrusions. However, it is possible that aggressive behavior may differ among eco-regions. Pacific-slope flycatchers occupy breeding habitat from sea level up to 4000ft where abundance seems to decrease with increasing elevation (Lehmkul et al. 1999). Assuming that low elevation forests are the prime habitat for this species, aggressive behavior may not differ within a certain elevation level but may differ along an elevational gradient. This has been documented in Townsend's and hermit warblers and their hybrids where aggressive behavior differed over large spatial scales but not at smaller scales (Pearson and Rohwer 2000).

Because, breeding ground settlement patterns may be influenced by factors occurring on the wintering grounds in Pacific-slope flycatchers, it is conceivable that assortive territory settlement patterns also occurs on the wintering grounds. This phenomenon has been documented in American redstarts (Marra et al. 1998) where adult males exclude females and yearling males from gaining access to optimal habitat on the wintering grounds. Alternatively, it could be that larger males winter further north and therefore have a distance advantage over smaller males. In dark-eyed juncos (*Junco haemalis*), larger males winter further north compared to smaller males (Ketterson and Nolan 1983). It is evident, that in order to understand territory acquisition on the breeding grounds in Neotropical migrants, territorial behavior of these species need to be also studied on the wintering grounds. The few authors that have studied this phenomenon (e.g., Marra et al. 1998) have demonstrated that assortive settlement patterns also exist on the wintering grounds.

CHAPTER IV: IS FEMALE MATE CHOICE DRIVEN BY MALE OR TERRITORY QUALITY: AN EXPERIMENT WITH A MONOGAMOUS CUP-NESTING FLYCATCHER?

INTRODUCTION

Sexual selection in territorial birds may be influenced either by male quality, territory quality, or both. The importance of each in female mate choice is unclear because male and territory quality often correlate (for review see Searcy 1979, Yasukawa 1981, Searcy and Yasukawa 1983, Slagsvold 1986, Andersson 1994, Andersson and Iwasa 1996). For example, in order to maximize fitness, females should pair with males occupying territories where resources critical for breeding, such as high food and/or preferred nest substrate availability, are maximized. In turn, high-quality males may occupy these territories and therefore, whether females select male or territory quality is difficult to discern.

While many studies have identified male traits that distinguish between males that were either selected or rejected by females (Gibson et al. 1991), these traits include age (Alatalo et al. 1984, Studd and Robertson 1989), plumage characteristics (Alatalo et al. 1986, Johnson 1988a, Hill 1990, Palokangas et al. 1992), song repertoire size (Leisler et al. 1995, Catchpole 1996, Buchanan and Catchpole 1997, Hasselquist 1998), tail length (Andersson 1982, Møller 1988, Møller 1991b, Palokangas et al. 1992), body size (Alatalo et al. 1986, Rohwer et al. 1996), and parasite loads (Palokangas et al. 1992), few studies have investigated mate choice based on territory quality. There is evidence that resources such as territory size (Price 1984, Harper 1985, Nagata 1986), habitat characteristics (Lenington 1980), nest box position and quality (Alatalo et al. 1986, Slagsvold 1986, Slagsvold 1987), nest substrate availability and number of nests (Evans 1997), food availability (Nagata 1986), and plant cover on territory (Pleszczynska 1978, Pleszczynska and Hansell 1980) are more important than male quality to explain mating success. While female mate choice has been investigated in socially polygynous dichromatic species (e.g., Pleszczynska and Hansell 1980, Rohwer et al. 1996, Langston et al. 1997), polygynous monochromatic species (e.g., Evans and Burn 1996, Evans 1997), and monogamous-polygynous dichromatic species (e.g., Alatalo et al. 1986, Slagsvold 1986), there are only a couple of studies that evaluated the role of male quality on female mate choice in socially monogamous monochromatic species (Johnson 1988b, Johnson 1988a, Marzluff and Balda 1988) and none, to my knowledge, on territory quality.

In this study, I investigated female mate choice in the Pacific-slope flycatcher (*Empidonax difficilis*), a monochromatic, socially monogamous, suboscine flycatcher, using both a correlational (male quality) and experimental approach (territory quality). The Pacific-slope flycatcher is "despotically distributed" (Chapter 2) on the breeding grounds along a gradient of increasing red alder (*Alnus ruba*) abundance that correlates positively with reproductive success (Chapter 2). This flycatcher species is an ideal species for mate choice studies because song repertoire size is identical among males (Johnson 1980, Kroodsma 1984, Kroodsma 1989) and because number of natural nest sites can be manipulated (discussed below).

In the correlational study, I investigated whether female mate choice is based on female attracting song rate (the alpha song), body size, crown feather coloration, response time to territorial intrusions, and louse intensity (i.e., number of parasites per individual). In the experimental study, I manipulated territory quality by removing potential nest substrates (before males arrived on the breeding grounds) in the high-quality habitat (deciduous habitat), to investigate whether females select this cue to assess territory quality. Because food availability could influence territory selection by females (Nagata 1986), I attempted to control for this by having both treatment and control plots in the same study site (a riparian corridor). By removing adventitious nest substrate, the preferred nest substrate, I was able to investigate the following objective: Do females assess habitat quality at the nest substrate level when they first arrive on the breeding grounds? Because adventitious substrate seems to be a critical factor in territory quality, I predicted that females will settle in control before treatment plots.

METHODS

Study area — All data were collected in the Capitol Forest (Washington Department of Natural Resources; 46^{O} 55' N, 121^{O} 10' W) Southwest of Olympia, Washington between 1997 – 1999 for the correlational study, and in 1999 and 2000 for the experimental study (for habitat description see Chapter 2). Briefly, the Capitol Forest is in the western hemlock zone (Franklin and Dyrness 1988) which consists of a matrix dominated by coniferous species [most common species: Douglas-fir (*Pseudotsuga menziesii*)] interspersed with deciduous species such as red alder (*Alnus ruba*). The topography is defined by hills with steep flanks that are bifurcated by riparian corridors. These riparian corridors consist mainly of red alder, interspersed with western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) in the overstory. The shrub layer, interspersed with late successional conifers (e.g., western hemlock and western red cedar), consists of various *Vaccinium* species, salmon berry (*Rubus spectabilis*), devilsclub (*Oplopanax horridum*), cascara (*Rhamnus purshiana*), and vine maple (*Acer circinatum*).

Research sites — For the correlational study, I established a total of 11 multi-habitat research sites where different habitat plots (i.e., deciduous, mixed, coniferous habitat) were directly adjacent to each other (Chapter 2). The mean nearest neighbor-distance between research sites was 1.47 km (± 0.15 SE). Of these research sites, five consisted of all three habitat plots, four consisted of mixed and coniferous habitat plots, one consisted of deciduous and coniferous habitat plots, and one consisted of deciduous and mixed habitat plots (Chapter 2). For the experimental study, all research sites were located within riparian corridors, consisting of deciduous forest with red alder in the overstory and salmonberry in the understory. The forest directly adjacent on either side of the riparian corridors consisted of coniferous forest with Douglas-fir as the dominant species in the overstory and vine maple in the understory.

Nest site selection — Pacific-slope flycatchers nest in an ideal habitat for treatment manipulation of territory quality because this species typically places their nests in one of two locations on a tree: crotches between the major trunk and lateral branches or behind adventitious branches along the tree trunk. Crotch substrate is found in every single tree, while the adventitious substrate is found only in about 61 % of red alders (Chapter 2). Adventitious substrate, compared to crotch substrate, is a critical territory feature for Pacific-slope flycatchers because 80.9% (n = 47) of all nests I found in high-quality habitat were placed in this substrate.

Male quality — For both studies, as described previously (Chapter 3), I captured males using mist nets and song-play backs during the territorial phase for the correlational study and during the pairing and breeding phase for the treatment study. Upon capture, I assigned age class following Johnson (1974) and I measured culmen, tarsus, wing, tail length, and body mass on each male. These variables were used to develop a body index score, by using residuals derived from regressing weight on factor scores (PCA) of the morphological measurements (Chapter 3, following Marra et al. 1998). For the experimental males, the factor one loadings (including coefficients for standardized factor scores) were as follows:

wing length = 0.78 (0.43), tarsus length = 0.62 (0.34), culmen length = -0.50 (-0.28), and for tail length = 0.75 (0.42). Regressing factor one scores against weight resulted in a significant relationship between the two variables ($F_{1,18} = 5.67$, $p < 0.0005$; $r^2_{adj} = 0.20$). For each male, I also assessed crown feather by assigning a score from ranging from 1 (fresh) to 5 (very worn, Chapter 3) and abdomen fat deposits following Helms and Drury (1960). I also assessed mallophagous louse infestations. Louse presence was determined by checking the throat region of males using watch maker's lenses (2x magnification) and forceps (see Chapter 3). Permits to capture flycatchers were issued by the University of Washington's Animal Care Committee (ACC # 2857-06), the U.S. Fish and Wildlife Service (Permit # 20337), and the Washington Department of Fish and Wildlife (Permit # WN-0085).

Aggressive and song behavior — During the territorial phase from 1997 - 1999, I counted alpha songs, using focal sampling, between 06:00 to 10:00 am. The alpha song consists of three syllables (Fig. 5, Chapter 3) where males usually start with the first syllable but do not necessarily always sing all three syllables in a song (Leu and Delap unpl. data., Johnson 1980). Given this variation, I defined an alpha song if it consisted of at least one song syllable. At the habitat scale, there was no relationship between alpha song (dependent variable) versus year and time of day (independent variables) (deciduous: Multivariate regression $F_{2,22} = 1.35$, $p = 0.28$; mixed: $F_{2,24} = 2.19$, $p = 0.13$; and coniferous: $F_{2,12} = 0.86$, $p = 0.45$). I therefore combined data across years and time of day.

I measured the response time of males to simulated territorial intrusions (i.e., song play back and a mount of a Pacific-slope flycatcher specimen) during a 15min. bout (see Chapter 3) during the territorial phase in the correlational study and during the incubation/parental phase in the experimental study. Response time was defined as the time elapsed from when a male approached the mount from 10m to 2m. In all trials, I attempted to challenge the males in the center of their territories. A challenge was defined as "non-responding" when a male failed to appear within 10m of the mount within 15 min.; these were not included in the analysis (correlational study: n = 3, 4.5%; experimental study n = 0). Males that came within 10m but never came within 2m of the mount received a score of 15 min.

Territory quality manipulations —The experiment was replicated in ten research sites, five in 1999, and five in 2000. Using a paired design, each research site consisted of a randomly assigned treatment (adventitious branches removed) and control plot (adventitious branches retained). In eight research sites, the treatment and control plots encompassed both sides of riparian habitat along a stream and plots were directly adjacent to each other. Because the riparian corridor was extremely wide in two research sites, the treatment and control plots were on one side of the stream only and were of similar width. In each research site, the control and treatment plots were of equal length ($\bar{x}$ = 130.0m ± 7.15, range = 85m – 170m) and similar width (≈ 50-80m). The mean nearest neighbor distance between research sites was 2.4 ± SE of 0.9 km in 1999, and 1.5 ± SE of 0.2 km in 2000. Before males arrived on the breeding grounds (March of 1999 and 2000), I manipulated territory quality on treatment sites by removing all adventitious branches but not in controls. Adventitious branches were removed up to five meters high (95% of all nests in adventitious branches were between 0.82 to 4.80m) on all red alder trees along the riparian corridor (flat terrain) to the distinctive coniferous ecotone (steep terrain).

To verify whether the treatment and control plots differed in number of crotch and adventitious substrates, I randomly selected prior to the treatment, five red alders in each plot and counted the number of possible crotch and adventitious substrates. I repeated the sampling post treatment in each of the treatment plots. The number of crotch and adventitious substrate did not differ between pre-treatment treatment and control plots (adventitious substrate: Wilcoxon = 0.24, p = 0.81, crotch substrate: Wilcoxon = - 0.56, p = 0.57; Fig. 10). However, the treatment significantly removed the number of adventitious substrate (Wilcoxon = -2.80, p = 0.005; Fig.10), but did not change the number of crotch substrate (Wilcoxon = 0.26, p = 0.80; Fig.10).

Territories and experimental plots — Because of the juxtaposition of control and treatment plots, it was possible that males could have their territories overlap (1) the treatment and control plot, (2) the treatment and adjacent unmanipulated habitat, and (3) the control and adjacent unmanipulated habitat. I approached these problems as follows. Because I mapped locations of singing males, I knew the location of each territory in detail. Early arriving males occupied large territories that shrank in size after every possible territory in the plot was occupied. At this point, it became clear whether the territory was within a control or a treatment plot, except in two territories. In one of the territories, the nest was built in the control and I therefore assigned this pair to controls. In the other, detailed habitat use observations of both sexes revealed that this pair spent most of their time outside the control boundary in unmanipulated habitat; I did not use this pair in the analysis. Lastly, as discussed below, five treatment pairs built nests directly adjacent to the treatment boundary ($\bar{x}$ = 6.2 ± SE of 1.6m) in coniferous habitat. These pairs were included in the analysis because all foraging activity and feeding of fledglings took place within the treatment plots; including these pairs made the analysis more conservative.

Breeding phenology — I visited each territory every 2-3 days starting in the beginning of April, well before males arrived. To determine male arrival date and pairing date, I used the mid-point between visits. Because arrival and pairing dates differed among years (1997-1999) in the correlational study, I standardized the dates by subtracting the yearly mean from each

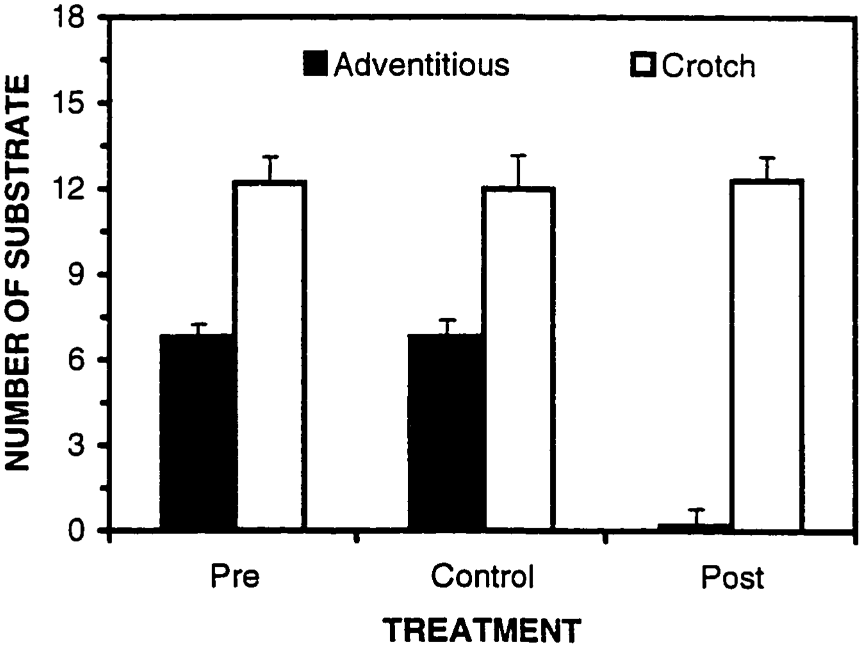

Figure 10: Number of potential adventitious and crotch nest substrate for pre and post habitat treatment (i.e., adventitious nest substrate removed). Shown are mean (± SE) number of substrate in control.(n =10) and before and after removal of adventitious substrate in experimental plots (n = 10).

date (Chapter 2). In the experimental study, arrival dates differed between years (1999: $\bar{x}$ = May 15 ± 1.7, 2000: $\bar{x}$ = April 30 ± 1.2; t-test = 7.25, df = 27, p < 0.0005) and among research sites in 1999 ($F_{4,9}$ = , p = 0.04) and 2000 ($F_{4,10}$ = 8.79, p = 0.0 3). I standardized arrival dates by subtracting the plot mean from the dates. Pairing dates also differed between years (1999: $\bar{x}$ = June 1 ± 2.8, 2000: $\bar{x}$ = May 19 ± 2.8; t-test = 3.02, df = 26, p = 0.006), but only among research sites in 1999 ($F_{4,9}$ = 4.36, p = 0.03) and not in 2000 ($F_{4,9}$ = 2.08, p = 0.17). I also standardized pairing dates as described above.

I considered males paired when females were present on their territories. I determined clutch initiation dates by using the date when the first egg was laid. In cases where nests were found with nestlings, or territories with fledglings (I was unable to check most crotch nests because they were built high up in the canopy), I back-calculated clutch initiation date by using four days for clutch completion (mean clutch size 3.8 = ± 0.06, mode = 4, n = 36), an incubation period of 15 days and a fledgling period of 16 days (Davis et al. 1963). For clutch initiation dates I used dates of first clutches only. Overall, clutch initiation dates did not differ between 1999 (June 14 ± 3.7 days, n = 9) and 2000 (June 8 ± 3.8 days, n = 12; t-test = 1.26, df = 19, p = 0.22), I therefore combined years for analysis.

Breeding success — Because a minimum of 20 nests are required for breeding success analysis (Martin et al. 2000), and because nests of Pacific-slope flycatchers are hard to find (particularly the crotch nests), I measured breeding success in two ways. First, I calculated the percent of nests that fledged at least one nestling by combining first and replacement nests (predation rate did not differ between first and replacement nests Fisher's exact test p = 0.56). There was no bias in nesting success calculations, because I found 21 of 23 nests during the nest building/egg-laying phase. However, over the course of the experiment, I only found 13 nests of control and 10 nests of treatment pairs. Because there are less than 20 nests in each category, nesting success analysis may be biased. As described previously (see Chapter 2), I also estimated breeding success by assigned a breeding index (following Vickery et al. 1992b) to each territory where: 1 = male present > four weeks, 2 = paired, 3 = nesting behavior (e.g., female warning, female carrying nesting material), 4 = adult carrying food (in most cases I found the nest observing this behavior). Breeding success, estimated by percent nests producing at least one fledgling and using Mayfield estimates (Mayfield 1961, Mayfield 1975), correlate with breeding indices (Chapter 2). Overall, breeding indices did not differ between 1999 and 2000 (Mann-Whitney U = 109.0, p = 0.86), I therefore, combined years for analysis.

Data analyses — With regard to male quality and female mate choice along the habitat-quality gradient, I used Spearman rank correlations to test whether number of alpha songs correlate with mean plot pairing date. Because males were not identified individually, I used mean number of songs and mean pairing date per habitat plot (i.e., habitat type) for the analysis. To investigate which male characteristics influenced female mate choice, I used each male only once for analysis. In case where males were captured twice, I used the data collected during the first capture for analysis. I used Spearman rank correlations (Bonferroni corrected for multiple comparisons) to test whether body condition index, response time, crown feather wear, louse intensity, and testosterone correlated with standardized pairing date (i.e., pairing date – yearly mean, Chapter 2). This analysis was done at two levels by combining age classes [age class could only be assigned in 90.6%, (n = 21) of captured males] and for adults only (yearling males were not analyzed separately because only four paired).

For the experimental study, I used paired t-tests (normal data) and Wilcoxon signed rank tests (non-normal data) because each research site, a riparian corridor, contained both a control and treatment plot. This approach controlled for between riparian corridor variation. I used each plot as a data point (plot mean in cases with multiple males or pairs) in arrival date, pairing date, and breeding index analyses. Nesting success, mate loss rates, and nest placement were analyzed using G-tests (log-likelihood ratio test, Zar 1984). To test whether male quality differed between control and treatment plots, I used each male as a data point. Lastly, I used Spearman rank correlations (Bonferroni corrected for multiple comparisons) to test whether body condition index, crown feather wear correlate with standardized pairing date. Both body condition index and crown feather wear did not correlate with captured data and breeding season stage and can therefore be still used for male quality assessment even though males were captured post the territorial stage (see Chapter 3). Louse intensity was not correlated with pairing success because males were captured during the incubation-nestling phase and could have subsequently been infected. All statistical analyses were done with SYSTAT 7.0 (SYSTAT 1997). All p-values reported throughout this paper represent two-tailed tests. For all analyses I used $p \leq 0.05$ as the level of statistical significance. Results of tests reporting means are indicated as means ± SE.

RESULTS

Correlational study

Females did not select males according to alpha song rates ($r_S = 0.43$, $p = 0.031$, $n = 23$; Fig. 11). In the high-quality habitat (i.e., deciduous habitat) where males paired first, these males sang the fewest alpha songs. Crown feather wear, response time to territorial intrusions, and louse egg intensity did not correlate with standardized pairing date (pairing date – yearly mean; Table 7). In contrast, body condition index correlated with standardized pairing dates

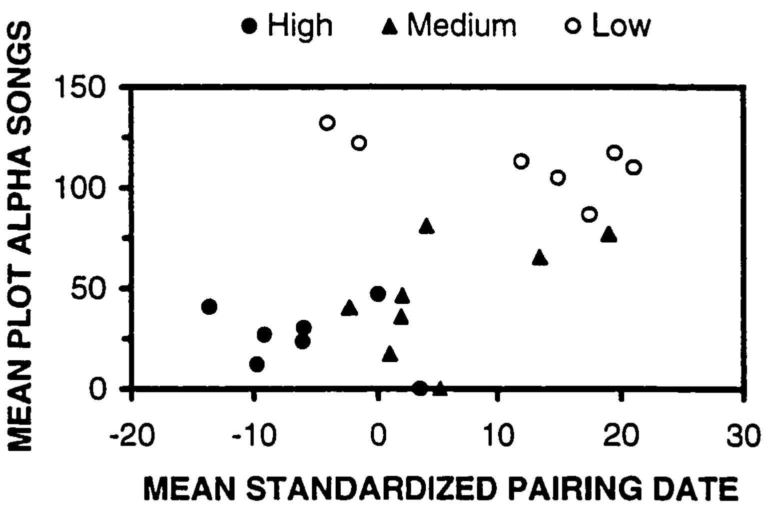

Figure 11: Mean plot alpha song rates versus mean plot standardized pairing dates (i.e., date – mean research plot date) for three habitat types: • = high-quality habitat (deciduous habitat, n = 7 plots); ▲ = medium-quality habitat (mixed habitat, n = 9); and O = low-qualtiy habitat (coniferous habitat, n = 7).

Table 7: Correlation of standardized pairing dates (i.e., all habitats: date – yearly mean; experimental plots: date – plot mean) versus body condition index, crown feather wear, response time, and parasite intensity for males in correlational and experimental study.

	All habitats				Experimental plots	
	All males (n = 21)		Adult males (n = 15)		(n = 19)	
Variable	r_s	p	r_s	p	r_s	p
Body condition index	- 0.64	0.017	- 0.68	0.05	-0.171	1.00
Crown feather wear	0.29	1.00	0.40	1.00	-0.403	0.26
Response time	0.10	1.00	-0.003	1.00		
Louse egg intenstiy	0.11	1.00	-0.07	1.00		

for all males and adult males only (Table 7) indicating that males with positive body condition indices paired earlier compared to male with negative body condition indices.

Treatment study

There were a total of 29 territories, of which 14 (48.2%) were in control plots. Four research sites contained one male in each of the control and treatment plots (40.0 %), two sites (20.0%) contained one male in the control plot and two males in the treatment plot, whereas the reverse was found in one site (10.0%). Lastly, three plots contained two males in each plot (20.0 %).

Arrival and pairing date — Male arrival dates did not differ between control and treatment plots (Paired t-test = - 0.43, df =9, p = 0.68; Fig. 12). Contrary to the predictions, pairing dates also did not differ between control and treatment plots (Paired t-test = - 0.67, df =9, p = 0.52; Fig. 12).

Male quality — With regard to male arrival time, standardized arrival dates (i.e., arrival date – mean plot date) did not correlate with body indices (r = - 0.30, p = 0.20, n = 20). When comparing males occupying treatment and control plots, there was no difference between males with regard to body indices (t-test = 0.67, df = 18, p = 0.51), louse prevalence (G-test = 0.22, df = 1, p = 0.64), louse intensity (Mann-Whitney U = 4.0, p = 0.48), and response time to simulated territorial intrusions (t-test = 0.24, df = 18, p = 0.82; Table 8). With regard to female mate choice, standardized pairing dates did not correlate with body indices or with crown feather wear (Table 7).

Pairing success and mate loss rates — Of the 29 males, 28 paired (96.5%). The only unpaired male was in a treatment plot. This male spent 61 days on the territory before abandoning it. Mate loss rates differed between control and treatment plots (G-test = 5.87, df = 1, p = 0.015). In control plots, none of the males lost a mate (n = 14), compared to 26.6 %

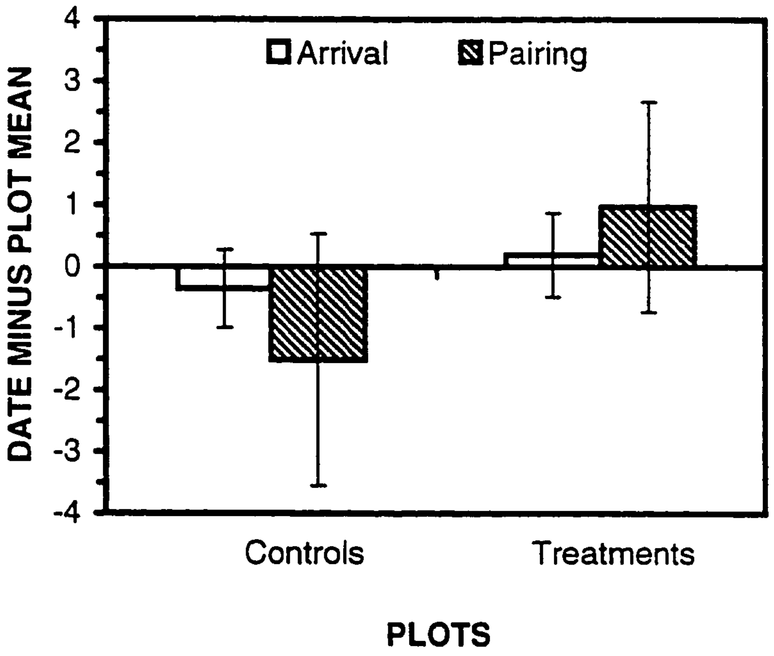

Figure 12: Male arrival and pairing dates with regard to experimental (nest substrate removed) and control plots (nest substrate present). Shown are mean (± SE) standardized arrival and pairing date (i.e., date – mean research plot date) for experimental (n = 10; adventitious nesting substrate removed) and control plots (n = 10).

Table 8: Measures of male quality, clutch initiation date, nest substrate selection, nesting success and breeding index measured in control and treatment plots.

	Control Plot	Treatment Plot	p-value
Male quality:			
Body index scores [a]	0.13 ± 0.33 (10)	- 0.13 ± 0.22 (10)	0.51
Mallophagous lice prevalence [b]	40.0 (10)	33.3 (10)	0.64
Mallophagous lice intensity [a]	8.8 ± 3.9 (4)	13.3 ± 3.9 (3)	0.48
Response time [a]	117.5 ± 50.0 (7)	127.5 ± 53.3 (10)	0.82
Clutch initiation date [a]	June 8 ± 3.0 (12)	June 13 ± 5.1 (12)	0.39
Clutch initiation – pairing date [a]	14.5 ± 1.5 (11)	13.1 ± 1.7 (7)	0.41
Nest location within plot boundaries [b]	100.0 (13)	50.0 (10)	p = 0.001
Nest substrate: % adventitious nests			
All nests combined [b]	84.6 (13)	50.0 (10)	0.09
Inside plot nests only [b]	84.6 (13)	20.0 (5)	0.01
Nesting success [b]	53.8 (13)	30.0 (10)	0.25
Breeding index [a]	4.4 ± 0.2 (14)	3.3 ± 0.4 (15)	0.02

[a] $\bar{x}$ ± SE (n)

[b] % (n)

(n = 15) of males occupying treatments. On average, males lost their females 17.0 ± 3.1 days (n = 4) after pairing. This duration did not differ from the time lag between pairing and clutch initiation date of first clutches ($\bar{x}$ = 14.0 ± 1.1, n = 18; Kruskal-Wallis = 21.5, p = 0.22). Of the males that lost their mate, all but one paired again. On average, males spent 41.3 ± 9.4 days (n = 3) unpaired between losing the female and pairing again.

Nest location and substrate selection — I found a total of 23 nests, of which 20 were first attempts. With regard to first clutches, 12 nests were of pairs occupying control and eight of pairs occupying treatment plots. Of the 20 nests, all but one was built in red alder.

Nest location with regard to plot boundaries differed between control and treatment plots (G-test = 10.22, df = 1, p = 0.001; Table 8). Pairs occupying control plots built all their nests within the plot boundaries whereas only 50.0% (n = 10) of pairs occupying treatment plots built their nests within the plot boundaries (Table 8). Five treatment pairs built their nests outside the treatment boundary in untreated, but medium-quality habitat (mixed coniferous deciduous habitat), where a few alders, containing fewer potential adventitious nest substrates, remained. Of the five nests, four were built in adventitious substrates. The average distance from the plot boundary to these nests was 6.2 ± SE of 1.6m.

Nest substrate of all nests (first and replacement of first nest combined) tended to differ between treatment and control plots when all nests (i.e., nests within and outside of plot boundaries) were combined (G-test = 2.85, df = 1, p = 0.09; Table 8). In control plots, 83.3 % of the nests were in adventitious nest substrate compared to 50.0% of nests in treatment plots (Table 7). Using only nests located within the plot boundaries, significantly more nests were built in adventitious substrate in control compared to treatment plots (G-test = 6.26, df = 1, p = 0.012; Table 8).

Clutch initiation dates — I was able to determine clutch initiation dates on 21 of the 28 territories (in seven treatment territories I never found the nest or observed any fledglings). Clutch initiation dates did not differ between control and treatment plots (t-test = - 0.88, df = 19, p = 0.39; Table 8).

Time lag between pairing date and initiation of first clutches did not differ between control and treatment plots (Mann-Whitney U = 47.5, p = 0.41; Table 7), nor between nests built in adventitious (14 ± 1.2 days, n = 14) and crotch substrate (11.3 ± 1.9 days, n = 3; Mann-Whitney U = 15.5, p = 0.48).

Reproductive success — Nesting success was higher in control pairs compared to treatment pairs, the difference, however was not significant (G-test = 1.33, df = 1, p = 0.25; Table 8). Nests built in adventitious substrate (56.3 %, n = 16) were more successful compared to crotch nests (14.3 %, n = 7; G-test = 24.40, df = 1, p = 0.05). Using each territory as a data point, breeding indices were higher in control compared to treatment plots (Mann-Whitney U = 155.0, p = 0.02; Table 8).

DISCUSSION

Male territory selection — There was no difference in male arrival date between control and treatment plots. In adult Pacific-slope flycatcher males, habitat selection seems to be based on site fidelity, influenced by previous breeding success, because return rates were higher for males occupying high-quality habitat, where breeding success is highest, compared to the absence of returning banded males in the medium and low-quality habitat (Chapter 2). In yearling males habitat selection may be based on knowledge of habitat supporting high-densities of females [i.e., yearling males scouting for high female density habitat during their first year on the breeding grounds (see Zack and Stutchbury 1992)]. I documented a habitat switch between years in a male that was captured in low-quality habitat as a yearling and in medium-quality habitat as an adult in the following breeding season (Chapter 2). Therefore it could be, as shown in other bird species (Manuwal 1974, Hill 1988), that yearling males possibly gain knowledge about locations of habitat containing high females densities during their first breeding season, subsequently returning to these location during the next breeding season (for review see Zack and Stutchbury 1992).

Female territory selection — If females select habitat according to territory quality (i.e., presence of preferred nest substrate) then females should pair earlier with males on territories containing adventitious nest substrate. Interestingly, pairing dates did not differ between control and treatment plots. Given that there was a lot of variation in pairing dates in both experiment and treatment plots, power of the statistical analysis is suspected to be low (post-hoc sample size analysis with power = 0.90 revealed that the smallest significant difference at $p = 0.05$ was four times larger than the observed difference and that a sample size of 134 research sites is required to acquire significance). In contrast, there is ample evidence that female mate choice occurs at the territory quality in songbirds. For example, females selected territories by nest box attractiveness (upright vs. tilted nest boxes, Slagsvold 1986), nest box quality (diameter of entrance hole, Alatalo et al. 1986), number of vacant nests (Evans 1997), and food availability (Nagata 1986). Because I placed both treatment and control plots in the same location within a riparian corridor, food availability should not differ between control and treatment plots within an experimental research site. However, microclimatic factors and juxtaposition to other habitat types can influence insect availability in forest habitat (Whitaker et al. 2000). If experimental research sites differed in insect availability, then pairing dates should have differed among experimental research sites. However, pairing dates only differed among experimental research sites in one of the two years (see methods). This suggests that insect availability very likely did not influence territory quality and therefore female mate choice in this experiment.

So what cues do female Pacific-slope flycatchers use to chose among potential mates or territories on the breeding grounds? Correlational data suggests that females use presence of red alder as a cue. Females arrived first in deciduous habitat (high-quality habitat, Chapter 2) and settled later in medium-quality habitat (medium quality habitat) and last in coniferous habitat (low quality habitat). Pairing date correlated also with male body condition but not with alpha song rate, response time to territorial intrusions, color of crown feather, and louse infestation. But, male body condition indices also differed among habitat types (Chapter 3). They were highest in the high-quality habitat among adult males. Therefore, it is unclear whether females select territories according to presence of red alder or male body condition. Furthermore, in the experimental study, body condition indices did not correlate with pairing date nor were they different between control and treatment males.

What other cues could females potentially use to select a potential mate? First, recent studies have shown that a previously classified sexually monochromatic species, the blue tit (*Parus caeruleus*), is dichromatic on the crown patch in the ultraviolet spectrum. In mating trials, female blue tits selected males with brighter crowns (Hunt et al. 1997, Andersson et al. 1998). It would be interesting to investigate whether male Pacific-slope flycatchers also differ in some plumage characteristics in the ultraviolet spectrum, for example on the crown patch, because males erect crown feathers during male-female interactions (Leu and Pearson pers. observ.). Second, because the alpha song of Pacific-slope flycatchers contains three syllables, and variation exists in the syllable sequence among males (Leu and Delap unpl. data), it would be interesting to investigate whether females cue in on syllable sequence. Third, because both sexes engage in fighting flights when pairing (see also Pereyra 1998), resulting in both partners being on the ground in the extreme case, it is possible that females select males according to male vigor. This has been shown in pied flycatchers where males were experimentally handicapped by removing a limited number of wing and tail feathers (Lifjeld and Slagsvold 1988) resulting in females preferring control over treated males. In turn, male vigor could be "maintained and orchestrated" by testosterone (Wingfield et al. 1994, Pereyra 1998). Therefore it would be interesting to investigate testosterone plasma levels during this period when the inter-sexual chases take place.

Female mate choice model — It could be argued for cup nesting migratory passerines, a combination of male and habitat cues, temporally separated, influence female settlement patterns. For example, in the great reed warbler (*Acrocephalus arundinaceus*), females seem to select males according to both habitat quality (i.e. length of reed/water edge) and male quality (larger song repertoire size and lower aggression; Leisler et al. 1995). Do females use these traits in concert when selecting a male or do they use them at different times during pair formation? I suggest that females use a hierarchical approach when choosing among potential mates and territories where certain cues are important at time of arrival and some during pairing. Furthermore, these two events are temporally separated in migratory species where as in resident species these two events may overlap. This approach is similar to the "hierarchical decision-making process" by Neotropical migrants selecting habitat on the wintering grounds proposed by Hutto (1985) where habitat selection at the macro scale may be genetically determined whereas at the micro scale, local factors, such as food availability, influence habitat choice. This approach also incorporates the hierarchical process of cues involved that prepare organisms for reproduction (for review see Wingfield et al. 1999b). For example, "initial predictive cues" such as photoperiod, activate the secretion of hormones important for reproduction, whereas "supplementary cues", such as temperature or presence of nesting substrate, fine-tune hormone-behavior relationships (Wingfield et al. 1999b). For migratory cup nesting songbirds, I suggest that a female's body condition reflects arrival time, and if habitat is occupied "preemptively" (Fretwell and Lucas 1970), habitat settlement of later arriving females will be influenced by the presence of females in optimal habitat (Fig. 13). How do early arriving females select a male? I suggest that they use a combination of "supplementary factors", both at macro and micro scales, and social cues (i.e., male or female presence) to assess territory quality (Fig. 13). Upon arrival, females may use macro supplementary factors, such as presence of deciduous habitat (the high-quality habitat), and presence of a male or other females (i.e., the social cue) for territory quality assessment. As females settle on their territories, hormones associated with breeding will increase and therefore there is an increase in behaviors important for breeding, such as building a nest (for review see Wingfield et al. 1999b). At this point, females switch from using habitat-social cues to micro supplementary factors, such as presence of nest substrate or food availability. In the absence of such resources, females can, among others, (1) compete with other females for another territory within the optimal habitat, (2) mate with an already paired male in the optimal habitat, (3) stick it out and make the best of a bad situation (e.g., nest in sub-optimal nest substrate thereby increasing chance of predation), or (4) settle in sub-optimal habitat (if habitat is settled preemptively) and increase fitness by extra pair fertilization with male in adjacent high-quality habitat (Fig. 13). For later arriving females, the only way to increase fitness will be to seek extra-pair copulations with males that are more fit than the male a female is paired with (Fig. 13). However, females in the medium-quality habitat may move to sub-optimal habitat.

What evidence is there to support this hypothesis? First, the data suggest that upon arriving on the breeding grounds, female Pacific-slope flycatchers selected (1) territories in

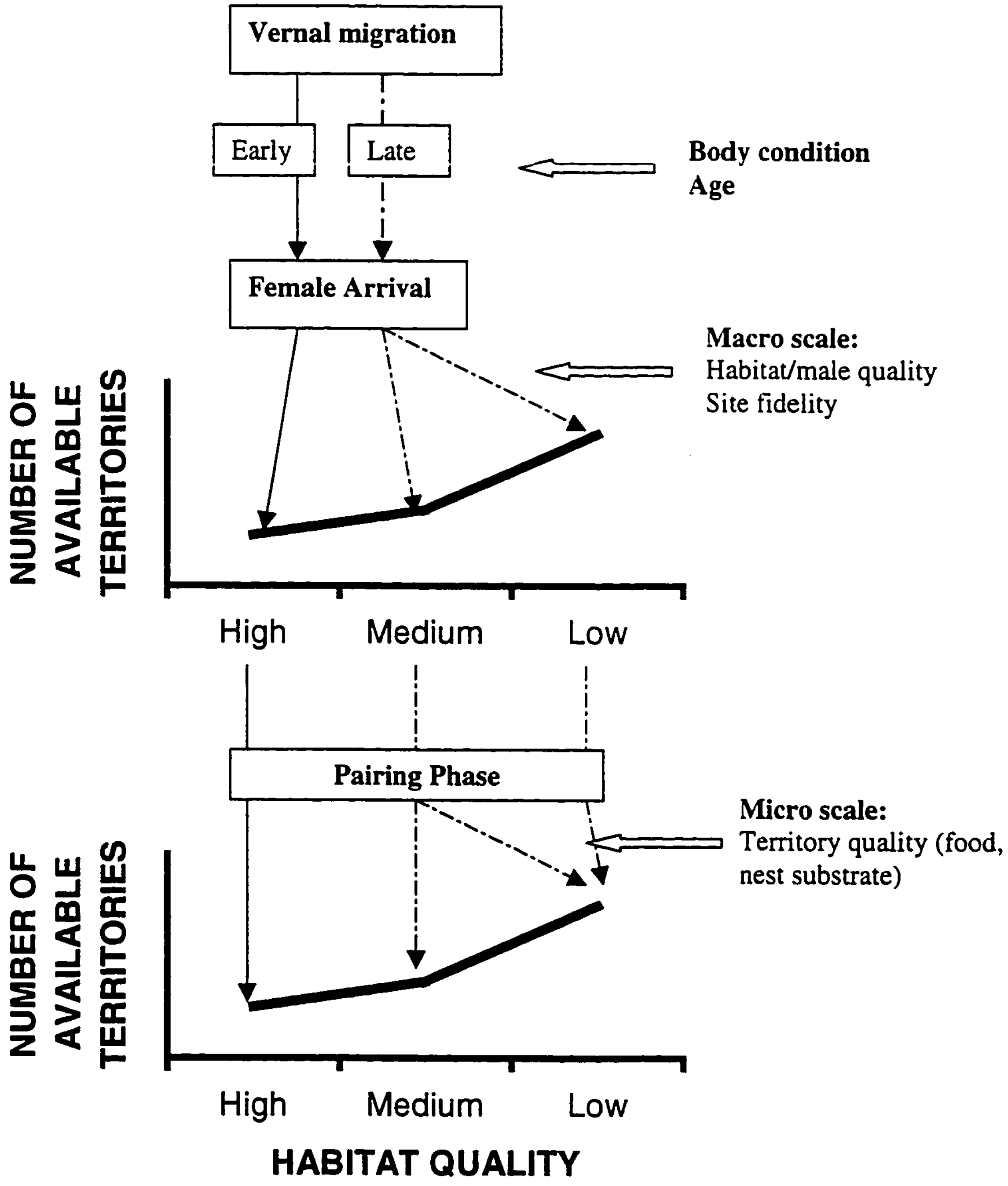

Figure 13: Female settlement patterns on the breeding ground in relationship to body condition. Early females select males according to macro factors (e.g., habitat/male quality) during arrival on the breeding grounds and according to micro factors (e.g., food, nest substrate) during the pairing phase. See text for further explanations.

deciduous habitat first, and (2) larger males. Within the high-quality habitat, as shown in the experiment, females did not select males according to body size or territory quality (i.e., presence of preferred nest substrate). This suggests that females will use the habitat as a macro supplementary cue (high versus medium abundance of alder) and presence of males (i.e., social cue), but that nest site presence/absence does not play a role. Alternatively, within high-quality habitat, females may select territories according to site fidelity as shown in robins (*Erithacus rubecula*; Harper 1985), presence of other females as shown in marsh wrens (*Cistothorus palustris*; Leonard and Picman 1988), or mate with males randomly.

Second, when females arrive on the breeding grounds, they possibly undergo a physiological transitory phase switching from the migratory to the breeding "life-history stage" (Jacobs 1996, Jacobs and Wingfield 2000). In Pacific-slope flycatcher females, time lag between pairing and clutch initiation is on average 16 days. Interestingly, this period does not differ among habitat types and years (Chapter 2). During this period, hormones "initiated and orchestrated" morphological changes and behavior associated with breeding (for review see Logan and Wingfield 1995, Garcia et al. 1996, Sreekumar and Sharp 1998, Lormée et al. 1999, Wingfield et al. 1999b). In turn, the secretion of these hormones may be regulated by initial predictive (e.g., photoperiod), supplemental and social cues (Wingfield et al. 1997, Hau et al. 1999, Wingfield et al. 1999b, Jacobs and Wingfield 2000) but also by differences in migration distance between wintering and breeding grounds (Silverin and Viebke 1994). For example, female turkeys (*Meleagris gallopavo*), held at warmer temperatures and with access to nesting boxes had shorter time spans between onset of photosimulation and sexual maturity and onset of incubation compared to females held at cooler temperatures and with no access to nest boxes (El Halawani et al. 1984). Furthermore, photosimulated white-crowned sparrow females (*Zontrichia leucophrys pugatensis*) held at warm temperature had larger yolky follicles compared to females held at cooler temperatures. This effect, however, was only present in females housed near males (Wingfield et al. 1997). Therefore, both supplemental and social cues are necessary to induce morphological and behavioral changes necessary for breeding. In addition, females may need to build up fat reserves depleted during migration, before hormones associated with breeding reach a critical threshold above which behavior associated with breeding is maintained (Wingfield and Jacobs 1999, Wingfield et al. 1999b). Indeed, most Pacific-slope flycatcher males arrive with little or no fat reserves on the breeding grounds and when females arrive weather patterns are still unpredictable (Chapter 2).

Third, as breeding hormones increase and therefore associated behavior necessary for breeding, females may fine tune habitat selection by using micro supplementary cues such as presence of adventitious nesting substrate. Therefore, if this nesting substrate is absent on a territory, females should abandon the current male. This is supported by the data from this experiment; I found a higher mate loss rate among males occupying territories on treatment plots. Females abandoned territories at the time when they started building nests because the time lag between pairing and mate loss date did not differ from the time lag between pairing and clutch initiation of pairs within the treatment and control plots. Alternatively, females could make the best of a bad situation by staying on the territory and by building a nest in sub-optimal habitat. If only nests were included that were within the boundaries of the plots, then nest substrate selection differed among treatment and control plots. Significantly more nests were built in adventitious substrate in control compared to treatment plots. However if all nests were included in the analysis, then nest substrate selection did not differ between treatment and control plots. Indeed, only 50% of all nests were built near the boundaries of the treatment plots; in contrast, all nests in controls were within the plots. This indicates that females selected adventitious nest substrate and searched for such substrate in sub-optimal habitat, directly adjacent to the treatment plots. In fact, nests were very close to the treatment boundary (average distance = 6.2m). Overall, nesting success was higher in adventitious nests compared to crotch nests and breeding success was higher, measured by a breeding index (breeding index correlates with other breeding success estimates, Chapter 2), for pairs occupying control plots. Therefore, the lack of adventitious nest substrate may have induced the higher mate loss in males occupying treatment plots.

Conclusions — The results of this experiment suggest that when Pacific-slope flycatcher females arrive on the breeding grounds, they possibly use presence of red alder as a first supplementary cue and then switch to another supplementary cue, such as nest sites, further along in the reproductive cycle. Furthermore, this experiment suggests that females are not locked into the territory they first settled on, but that habitat quality is re-evaluated as the breeding season progresses and that females switch territories if resources important for breeding are absent. This phenomenon obviously needs further investigation. What mechanisms operate at the female level with regard to habitat and mate choice? Arrival dates of females vary extensively since males in coniferous habitat pair at the time when pairs in the optimal habitat have nestlings (Chapter 2). Are these females that already attempted breeding but abandoned males after their first breeding attempt failed? Circumstantial evidence points to this, females with unsuccessful nests in the first breeding attempt abandoned nest males in the medium-quality habitat but not in the optimal habitat (Leu unpl. data). Is body condition also an important factor in influencing female arrival on the breeding grounds? What are the levels of hormones associated with breeding when females first arrive on the breeding grounds and at a week post arrival?

CHAPTER V: CONCLUSIONS

My study suggests that the Pacific-slope flycatcher (*Empidonax difficilis*) follows a "despotic" distribution (Fretwell and Lucas 1970) on the breeding grounds because fitness related measures, such as pairing success, reproductive success, and number of breeding attempts, differed among habitat types (Table 5, Chapter 2). Deciduous habitat is the high-quality habitat because breeding success and number of breeding attempts were highest in this habitat. In deciduous habitat, red alder densities are highest and red alders provide the adventitious nest substrate which is the preferred nesting substrate for Pacific-slope flycatchers. Furthermore, nests were initiated earliest and breeding success was highest in adventitious nest substrate.

The "despotic" distribution predicts that later arriving individuals will be excluded from gaining access to optimal habitat (Fretwell and Lucas 1970, Bernstein et al. 1991). Therefore, there should be intense competition for breeding territories in high-quality habitat because competition increases in heterogeneously distributed resources important for breeding (Milinski and Parker 1991). Although there was an age effect (yearling males occupied poorer habitat), the data suggest that once on the breeding grounds, later arriving males do not challenge established males in high-quality habitat (Chapter 3). There were no differences among habitat types with regard to territorial defense song rates, aggressive behavior, and testosterone plasma levels. As a result, the data suggest that breeding territories are occupied "preemptively" and that later arriving males seem to recognize the "keep out signs" of already established males (Davies and Houston 1984).

My data suggests that prior breeding experience (discussed in Chapter 2) and arrival time determine habitat settlement patterns of male Pacific-slope flycatchers on the breeding grounds. Arrival dates differed between age classes (yearling males arrived later) as did degree of louse infestation. Arrival time seemed to be influenced by body condition and fat deposit where males with large positive body condition indices arrived earlier compared to males with negative body condition indices. Therefore, breeding ground settlement patterns could be influenced by factors occurring on the wintering grounds in Pacific-slope flycatchers. It is conceivable that assortive territory settlement patterns also occur on the wintering grounds which could influence body condition and therefore departure time form the wintering grounds and arrival time on the breeding grounds (see Marra et al. 1998). However, because males in high-quality habitat leave the breeding grounds later than males breeding in medium and low-quality habitat (Leu unpl. data), how do these males establish territories in optimal habitat on the wintering grounds where optimal territories are possibly already occupied by males that left the breeding grounds earlier? It is possible that intense competition occurs on the wintering grounds for high-quality habitat not only at the intraspecific but also at the interspecific level and/or that there is a geographic separation of wintering grounds (Ketterson and Nolan 1983). Clearly, there is a need to study how Neotropical migrants distribute themselves on the wintering grounds.

The data from this study further suggest that females select habitat at different scales, temporally separated, when arriving on the breeding grounds (Chapter 4). Upon arrival, females selected habitat first at the macro habitat scale, that is, females settled first in deciduous habitat (high-quality habitat). However, because larger males also occupied deciduous habitat first, it remains to be determined whether females select male or habitat quality. Within high-quality habitat, the experiment suggested that females did not select males on territories that contained preferred nest substrate over those males occupying territories where preferred nest substrate was experimentally removed and female mate choice was not based on male size, color of crown patch, or aggressive behavior. This suggests that females either pair randomly with a male in high-quality habitat, base their choice on site fidelity (Harper 1985) or on the presence of other females (Leonard and Picman 1988), or select males according to characteristics not measured in this study (e.g., male vigor). As the breeding season progresses, females may select territories at the micro-habitat scale (e.g., the nest substrate scale). Females abandoned territories more frequently in treatments and placed their nests in sub-optimal habitat compared to females in controls.

Implications to conservation biology — As pointed out by Van Horne (1983) and Vickery et. al. (1992a), density of individuals is not an adequate measure of habitat quality for a species. In this study, I found that densities of males were higher in high (deciduous habitat) compared to medium (mixed habitat) and low-quality habitat (coniferous habitat). However, because males in low-quality habitat have the highest song rates, abundance estimates derived for example, from point counts (acoustic sampling), could possibly infer that coniferous habitat had the highest abundance of males and is therefore the high-quality habitat. For this reason, density estimates should only be used as a habitat quality measure if accompanied by fitness related measures. For example, pairing success can be relatively easily assessed and has been shown to be a good indirect measure of fitness in passerines (Chapter 2, Slagsvold 1986, Potti and Montalvo 1991, Petit and Petit 1996). Alternatively, because nests of most passerine species are hard to find, another approach is to estimate fitness by employing the Vickery reproductive index (following Vickery et al. 1992b). Although this reproductive index has been developed for songbirds breeding in grassland, this study documented that it can be adapted for forest dwelling songbird species as well. Both the reproductive indices and Mayfield breeding success estimates (Mayfield 1961, Mayfield 1975) showed the same trend with regard to habitat-quality. Using Vickery indices (Vickery et al. 1992b) circumvents the time consuming approach of finding nests.

My study also indicated that low-quality habitat on the breeding grounds may still be valuable for yearling males. While most studies on the conservation of endangered species focus on habitat where adults establish territories, habitat occupied by yearling males is rarely identified (but see Holmes et al. 1996, Petit and Petit 1996). However, this might be important for species conservation. If non-breeding yearling males need a breeding season to learn where high-quality habitat is located (discussed in Zack and Stutchbury 1992), then a heterogeneous habitat of low and high-quality habitat facilitates this process to take place. In Pacific-slope flycatchers, yearling males set up territories in low-quality habitats that can be found directly adjacent to high-quality habitat. Furthermore, if yearling individuals establish territories in unsuitable habitat where survival rates are low, then the recruitment of yearlings into older and reproducing cohorts may be small. This could have a major impact on population regulation.

Lastly, this study showed that habitat selection needs to be studied in a variety of habitats. Studies that do not encompass all possible habitats occupied by a species may bias definitions of optimal habitat. For example, if I had studied Pacific-slope flycatchers only in mixed (medium-quality habitat) and coniferous habitat (low-quality habitat), then I would have concluded that the medium-quality habitat (i.e., breeding success is higher) is the optimal habitat. However this is clearly not the case because breeding success was higher in deciduous habitat. Studying habitat selection in only a part of a species' habitat spectrum may lead to a limited understanding of nest site selection. Clearly, most species use multiple nest substrates but their relative importance may not be fully understood if the scope of a habitat selection study is limited to only a few of the possible habitat types.

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