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ACTIVITY PATTERNS OF WHITE-THROATED SWIFTS IN CALIFORNIA

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ABSTRACT: We investigated the daily and seasonal activity patterns of the White-throated Swift and related these patterns to seasonal changes in day length and variation in environmental conditions. The time of morning exit from the roost fluctuated more with daily variation in the weather than by season, occurring later after sunrise when temperatures were cool, particularly during winter. Exit time was delayed if temperatures rapidly exceeded the optimal range for aerial insect activity shortly after sunrise. Exit times were also delayed by rain. The evening return of White-throated Swifts to their roost fluctuated more predictably with season, although entry times were also influenced by weather. Entry time was delayed when temperatures were cold and occurred earlier when they were warm or hot or during rain. The pattern of group entry varied by season. In winter, evening roost entry was clumped, with large numbers of swifts entering together. In spring, entry was scattered, with smaller groups entering over a longer period. The pattern of morning exit was clumped year round, with most swifts exiting together as a group.

The White-throated Swift (*Aeronautes saxatalis*) is common but surprisingly little studied. Previous observations of its activity patterns or how environmental conditions affect these patterns have been few (Pickwell 1937). Most published accounts involve brief periods of observations and, while descriptive, draw few conclusions.

As widely reported, White-throated Swifts spend the night in communal roosts located in cracks and crevices of rocky cliffs, sea cliffs, rock quarries (Hanna 1909, 1917, Bent 1940, Anderson 1943, Dobkin et al. 1986) or man-made structures such as buildings (Collins and Johnson 1982), freeway overpasses, and bridges (Ryan and Collins 2000). Some individuals use these seasonal roosts as nest sites during the breeding season. Only during the nesting season do White-throated Swifts return to solid surfaces intermittently during the day to feed their young (Ryan and Collins 2000).

Pickwell (1937) found that in winter White-throated Swifts leave their roost site in the morning and forage on the wing, not returning to the roost until late afternoon or early evening. Entry and exit times vary through the year. Cold weather may affect these behaviors and lead to mortality. Hanna (1917) also noted that cold temperatures delay or prevent the morning exit from the roost.

Detailed studies of the activity patterns of the Chimney Swift (*Chaetura pelagica*) during the nesting season found that the birds exit their roost before sunrise and return after sunset (Michael and Chao 1973, Zammuto and Franks 1981). Roost entry and exit times are associated more closely with sunrise and sunset time than with temperature, wind speed, or cloudiness (Zammuto and Franks 1981). These authors found that morning exit takes place at a wider range of light intensities than does evening entry and that the birds leave the roost significantly later and enter it significantly earlier on colder days. Activity patterns have also been studied in migratory Common Swifts (*Apus apus*) and Alpine Swifts (*Apus melba*) in Europe (Koskimies 1950, Lack and Lack 1952, Lack 1956, Church 1956) and resident Little Swifts (*Apus affinis*) in India (Razack and Naik 1965).

The goal of this study is to document the daily and seasonal activity patterns of the White-throated Swift and to relate these to seasonal changes in day length and variation in environmental conditions. Interpreting the activity patterns of swifts, however, requires an understanding of their primary foraging habitat, the air column. All organisms that occur here are either adapted for flight or are passively swept into the air column by wind and are often referred to as "aerial plankton" (Glick 1939). Swifts forage on the arthropod component of aerial plankton, most of which belongs to the insect orders Diptera (flies), Hemiptera (bugs), Coleoptera (beetles), and Hymenoptera (bees and wasps) or the class Arachnida (spiders) (Glick 1939). Most swifts forage in both the terrestrial zone (0–300 m above ground), where the density of aerial plankton is highest, and the aeroplankton zone (>300 m above ground), where most arthropods are driven passively by air currents (Berland 1935, Glick 1939). Most swifts feed without any apparent selection on all arthropods of adequate size (Koskimies 1950, Collins 1980, Rudalevige et al. 2003).

Swifts appear to spend the majority of their time in the air foraging. Church (1956) went so far as to assume that all time spent away from the roost is spent foraging. Such habits make swifts indicators of events taking place within the air column. The birds' reactions to changes in day length and weather provide insight into the effects of these variables on this assemblage of prey organisms. Swifts react not only to the conditions that limit their ability to fly, such as darkness and adverse weather, they react to a wider variety of conditions that limit their prey. The times at which they exit and enter the roost reflect time spent foraging and, therefore, time when aerial plankton is sufficient to support the swifts' foraging effort. In this study, we use time spent in and away from the roost to investigate how various environmental conditions influence the White-throated Swift's activity.

STUDY AREA AND METHODS

Ryan observed roosts at Santiago Oaks Regional Park (Santiago Oaks) near the city of Villa Park and at Caspers Wilderness Park (Caspers Park) about 13 km northeast of the city of San Juan Capistrano, Orange County, California, from December 1993 to March 1995. Observations at these two inland sites were augmented by those made by Collins at a coastal site in the city of Rancho Palos Verdes (Palos Verdes), Los Angeles County, from November 1968 to September 1973.

At Santiago Oaks, the roost was in a 1.5-m vertical crack approximately 30 m above the base of a 40-m northeast-facing cliff on "Rattlesnake Ridge." At Caspers Park the flock used two roosts, shifting from one to the other in January 1994. The two sites were on sandstone cliffs about 250 m apart, with the second being on the adjacent Santa Margarita Ranch. The first roost was in a 3-m crack approximately 16 m from the top of a 20-m cliff; the second roost was in a vertical crack 2.5 m long and 18 m from the base of a 20-m cliff. The Palos Verdes roost, in an abandoned rock quarry at the end of Forrestal Road, was in a nearly horizontal crack about 5 m below the top of a west-facing 30-m cliff.

During each month of our study, we visited each site in the morning and evening when swifts exited and entered their nightly roosts. In the evening, we began observations at least two hours before the expected entry time and terminated them 15 minutes after the last swift entered the roost. The following morning, we began observation one hour before the expected exit time and ended 30 minutes to two hours after the last swift exited the roost. We determined when the last swift exited from the previous evening's total count. We combined observations at the two inland sites (Santiago Oaks and Caspers Park) but analyzed these data separately from those from the coastal site (Palos Verdes) because of the time between observation periods and differences in local conditions.

We analyzed the swifts' daily schedule in terms of "mean exit time" for the morning and "mean entry time" for the evening, expressing these times in minutes before or after sunrise or sunset. We recorded the number of swifts entering or exiting by minute (e.g., 23 entered during 16:12, 12 during 16:13, etc.) during each watch. For each morning and evening we generated a mean entry or exit time, then compared this mean to the official Pacific Standard Time of sunrise or sunset. Because of the speed at which these events take place, the numbers of swifts in large groups (>30 individuals) are estimates.

We analyzed mean exit and entry times by month and season, comparing them by four categories of temperature and four of weather. The four temperature categories were cold (<15.5° C), mild (15.5–21° C), warm (21°–27° C), and hot (>27° C). The four weather categories were clear (0–20% cloud cover), partly cloudy (20–80% cloud cover), cloudy (80–100% cloud cover), or rainy. We also investigated the effects of light intensity, measured in foot candles (fc) with a small hand-held light meter pointed toward vegetated hills.

During our observations, we recognized two distinct entry and exit patterns: clumped and scattered. We defined a clumped entry/exit as >3/4 of individuals present entering or exiting the roost within a five-minute period and the event taking less than one hour. We defined a scattered entry/exit as <1/2 of the swifts entering or exiting the roost within any five-minute period and the whole event spanning more than one hour. We considered events falling between these two categories as intermediate. We limited our analysis of patterns of aggregation to observation periods during which we recorded at least 10 birds.

Coastal southern California has a Mediterranean climate characterized by cool, intermittently rainy winters, cool and overcast springs, and hot, dry summers. Using 30-year precipitation and temperature records (Ryan 1996), we delimited three seasons for our comparisons, winter (October to March), spring (April to June), and summer (July to September).

Using a chi-squared contingency table we tested differences among clumped, scattered, and intermediate entries and exits for significance. The level of rejection was at $P = 0.05$. Statistical analysis of other observations is presented in Ryan (1996).

RESULTS

Seasonal Patterns

At all sites we found seasonal patterns of exit and entry to be parallel. Exits occurred mostly after sunrise: later during winter, earlier during spring, and later during summer (Table 1, Figure 1). The evening return to the roost occurred mostly before sunset: later during winter, earlier during spring and summer (Figures 1 and 2).

Environmental Influences

The influence of temperature on exit time differed by site. At Caspers Park and Santiago Oaks swifts exited earliest when the temperature was mild, slightly later when it was cold or warm, and latest when it was hot (Table 1). At Palos Verdes swifts exited later during cold temperatures, at an intermediate time during mild temperatures, and earlier during warm temperatures. At this site, during our study, the temperature did not reach the hot category (Table 1). We observed later mean entry times during cold temperatures, intermediate under mild temperatures, and earliest during warm and hot temperatures.

The influence of weather on the swifts' exit times was similar at all sites: the birds exited later under rainy conditions, earlier under clear skies, and at intermediate times under cloudy and partly cloudy skies (Table 1). At all sites swifts returned to the roost earliest during rain; there was no clear pattern among the three sites for return under cloudy, partly cloudy, or clear conditions.

White-throated Swifts exited the roost under a wide range of light intensities. They tended to exit at lower light intensities during summer (July 59 fc, August 90 fc, and September 91 fc) and at higher light intensities during winter (October 160 fc, November 286 fc, December 267 fc, and February 250 fc). All of the exits during light intensities of <100 fc took place during cloudy and foggy conditions, which are frequent during spring and summer. These differences coincide with differences in time of day. On average, the swifts exited their roosts at light intensities much higher than those at which they entered.

Table 1 Mean Exit Times of White-throated Swifts from Roosts at Caspers Park, Santiago Oaks, and Palos Verdes[a]

	Caspers Park/Santiago Oaks	Palos Verdes
Month		
January	164.2 ± 0.22 (20)	83.5 ± 1.62 (856)
February	94.4 ± 2.41 (48)	93.5 ± 2.19 (510)
March	148.9 ± 3.35 (118)	52.0 ± 3.46 (212)
April	132.0 ± 6.00 (78)	−4.9 ± 4.24 (14)
May	115.2 ± 4.37 (113)	32.2 ± 6.52 (62)
June	78.0 ± 5.46 (54)	138.2 ± 7.20 (10)
July	93.7 ± 3.74 (97)	111.5 ± 2.69 (99)
August	179.5 ± 1.01 (143)	48.9 ± 2.36 (227)
September	105.9 ± 2.18 (252)	71.2 ± 8.72 (60)
October	105.6 ± 1.33 (181)	136.4 ± 1.56 (422)
November	114.0 ± 1.74 (81)	115.4 ± 0.99 (684)
December	101.2 ± 10.42 (12)	104.5 ± 0.96 (925)
Season[b]		
Winter	119.4 ± 32.1 (460)	100.6 ± 0.73 (3609)
Spring	112.3 ± 51.1 (245)	38.5 ± 6.37 (86)
Summer	124.9 ± 46.5 (492)	68.6 ± 2.46 (385)
Temperature[c]		
Cold	116.1 ± 4.32 (163)	105.8 ± 0.90 (1525)
Mild	106.5 ± 0.97 (755)	86.2 ± 1.37 (1458)
Warm	126.9 ± 7.88 (72)	22.8 ± 1.77 (109)
Hot	169.4 ± 2.47 (163)	N/A
Weather[d]		
Rainy	172.2 ± 2.30 (81)	178.4 ± 3.92 (51)
Cloudy	120.6 ± 3.25 (202)	117.7 ± 2.82 (281)
Partly cloudy	124.0 ± 2.17 (390)	132.9 ± 2.18 (300)
Clear	106.5 ± 1.70 (457)	87.6 ± 0.86 (2527)

[a]Values represent minutes after sunrise (negative if exit was before sunrise) and are expressed as mean ± standard error (number of recorded exits).

[b]Winter, October–March; spring, April–June; summer, July–September.

[c]Cold, <15.0° C; mild, 15.5–21.0° C; warm, 21.5–27.0° C; hot, >27.0° C.

[d]Rainy, any precipitation during observation period; cloudy, >80% cover; partly cloudy, 20–80% cover; clear, <20% cover.

White-throated Swifts entered their roosts during light intensities ranging from 400 to 2.5 fc. Swifts entered at higher mean light intensities in July (114 fc) and August (147 fc), at lower mean light intensities in September (25 fc), October (10 fc), November (77 fc), and December (40 fc).

Group Entry and Exit

The frequency of clumped and scattered exits did not differ significantly by season ($\chi^2 = 4.33$, $P > 0.25$), although most exits were clumped. Entries were clumped during the winter and scattered during the spring. This difference was significant ($\chi^2 = 23.02$, $P < 0.001$).

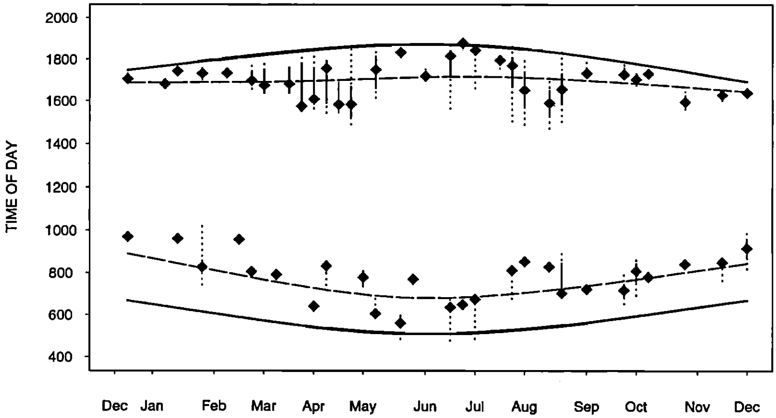

Figure 1. Activity of White-throated Swifts at Caspers Park and Santiago Oaks roosts, 1994–95. Data are represented as weekly averages from winter solstice to winter solstice. Diamonds represent the median times of exit from the roost and entry into it for the week. Solid vertical lines represent the range from the first to third quartile. Dashed vertical lines represent the total range of exits and entries. Dashed horizontal lines represent a fitted curve of the mean entry and exit times. Solid horizontal lines represent times of sunrise and sunset.

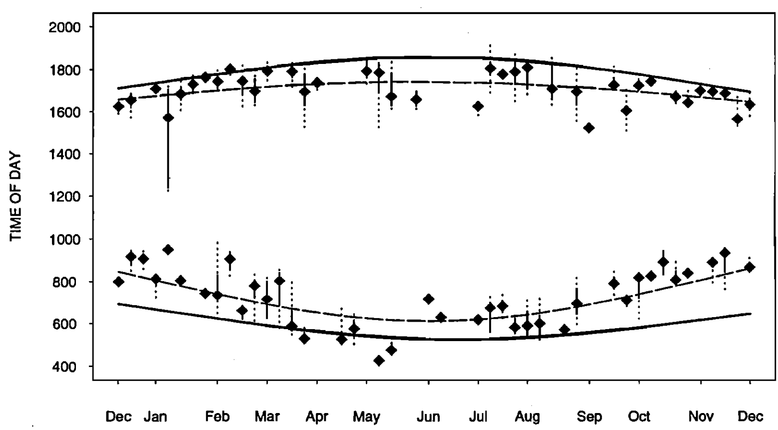

Figure 2. Activity of White-throated Swifts at Palos Verdes roost, 1968–73. Data are represented as weekly averages from winter solstice to winter solstice. Diamonds represent the median times of exit from the roost and entry into it for the week. Solid vertical lines represent the range from the first to third quartile. Dashed vertical lines represent the total range of exits and entries events. Dashed horizontal lines represent a fitted curve of the mean entry and exit times. Solid horizontal lines represent times of sunrise and sunset.

DISCUSSION

Seasonal Patterns

At all seasons most White-throated Swifts exit the roost after sunrise; our only exception was one morning in April at Palos Verdes (Table 1). In India, resident Little Swifts behave similarly, exiting their roost between 1.25 and 3.25 hours after sunrise (Razack and Naik 1965). The Alpine Swift, a migratory species, also exits after sunrise (Arn-Willi 1960). Conversely, the Common Swift, another migrant that spends less time on its breeding grounds, exits the roost well before sunrise in Germany and Finland, with exit times being earlier at higher latitudes where the extended twilight increases light intensity well before the actual sunrise (Scheer 1949). Therefore, the post-sunrise departure among swifts at lower latitudes may be a result of less ambient light prior to sunrise, mild climate, and an extended breeding period. The length of the delay also appears to be influenced by temperature and weather, particularly during the winter.

White-throated Swifts enter the roost close to or after sunset during the winter, before sunset during the spring and summer (Table 2, Figures 1 and 2). Michael and Chao (1973) found entry times of the Chimney Swift, a migratory species, to be most strongly related to sunset time and more directly to light intensity. Weather conditions had some influence with swifts entering later, just before dark, on days less favorable for foraging, earlier on days with wind and rain in the late afternoon. Common Swifts return to the roost substantially after sunset; Alpine Swifts return to the roost close to but slightly before sunset (Arn-Willi 1960). Later entry times at higher latitudes may be a response to the need to maximize foraging time during a shortened breeding season and extended twilight. Without the pressure of a limited breeding season and subsequent migration, White-throated Swifts appear to optimize their foraging time to match times when aerial insects are most abundant in the air column, entering the roost site well before sunset during the breeding season and later, closer to sunset, in the winter (Figures 1 and 2).

While the ultimate cause of these patterns may be fluctuations in prey abundance, temperature, and day length, one difficult question is, "what are the proximate causes?" What are the White-throated Swift's cues to exit from the roost? Prior to exiting, swifts moved from deeper within the roost to nearer the opening, where they often remained for extended periods. This behavior may be an attempt by the swifts to assess conditions outside the roost before exiting. Furthermore, on rainy mornings, and particularly on cold mornings, individuals and small groups exited the roost, briefly circled the area, and then re-entered the roost. We suspect the swifts may be detecting changes in temperature, light, and humidity, by means of visual (rain and clouds) and possibly tactile cues (wet conditions), or some combination of these factors, to determine if conditions outside are suitable for foraging.

Environmental Influences

Variations in the pattern of exit and entry at White-throated Swift roosts also appear attributable to changes in temperature and weather. At Palos Verdes White-throated Swifts exited later during cold and mild temperatures,

Table 2 Mean Entry Times of White-throated Swifts to Roosts at Caspers Park, Santiago Oaks, and Palos Verdes

	Caspers Park/Santiago Oaks	Palos Verdes
Month		
January	1.5 ± 1.86 (32)	6.8 ± 0.55 (880)
February	19.6 ± 0.45 (191)	1.2 ± 0.89 (577)
March	69.7 ± 1.74 (208)	7.3 ± 2.20 (206)
April	101.5 ± 4.33 (169)	54.0 ± 6.39 (54)
May	95.6 ± 7.17 (104)	66.8 ± 6.36 (59)
June	118.0 ± 8.33 (32)	152.5 ± 7.30 (10)
July	52.4 ± 3.71 (79)	89.0 ± 10.60 (73)
August	71.0 ± 3.73 (155)	58.5 ± 2.13 (303)
September	44.0 ± 2.79 (552)	55.3 ± 3.75 (293)
October	-6.6 ± 0.84 (171)	8.9 ± 3.68 (209)
November	46.1 ± 1.78 (120)	3.3 ± 0.70 (633)
December	5.1 ± 1.39 (140)	26.6 ± 0.70 (1496)
Season		
Winter	27.2 ± 1.14 (862)	12.9 ± 0.44 (4031)
Spring	101.3 ± 3.54 (305)	68.1 ± 4.78 (123)
Summer	50.2 ± 2.15 (786)	60.4 ± 2.26 (669)
Temperature		
Cold	17.7 ± 2.73 (175)	14.6 ± 0.77 (2263)
Mild	25.1 ± 0.91 (817)	26.4 ± 0.86 (1640)
Warm	88.4 ± 2.63 (437)	41.6 ± 1.78 (290)
Hot	47.9 ± 2.94 (474)	100.1 ± 1.24 (37)
Weather		
Rainy	128.0 ± 5.06 (105)	406.6 ± 0.69 (106)
Cloudy	8.1 ± 2.20 (189)	32.0 ± 2.50 (379)
Partly cloudy	12.2 ± 1.85 (311)	18.1 ± 2.00 (471)
Clear	50.3 ± 1.40 (1519)	20.2 ± 0.52 (4164)

[a]Values represent minutes before sunset (negative if exit was after sunset) and are expressed as mean ± standard error (number of recorded entries).

[b]Winter, October–March; spring, April–June; summer, July–September.

[c]Cold, <15.0° C; mild, 15.5–21.0° C; warm, 21.5–27.0° C; hot, >27.0° C.

[d]Rainy, any precipitation during observation period; cloudy, >80% cover; partly cloudy, 20–80% cover; clear, <20% cover.

earlier during warm temperatures, with no observations at temperatures above 27° C. At Caspers Park and Santiago Oaks, they exited later under cold, warm, and hot conditions and earlier under mild conditions (Table 1). Most observations at Palos Verdes (88%) were during winter. When we restricted analysis of observations at Caspers Park and Santiago Oaks to winter alone, we found the pattern at all sites to be similar, of swifts exiting later in cold temperatures. The Common, Little, and Chimney Swifts also exit later at lower temperatures (Koskimies 1950, Razack and Naik 1965, Zammuto and Franks 1981).

White-throated Swifts can go into torpor during periods of cold temperatures (Bartholomew et al. 1957). Arousal from torpor to normal body temperature can occur at environmental temperatures as low as 4° C. It is likely that on cold mornings torpid swifts require more time to warm themselves to a body temperature at which they can become normally active (Bartholomew et al. 1957). Thus later exit times are likely due, in part, to a delay caused by recovery from torpor and/or reduced activity by insects at colder temperatures.

Torpor is a plausible explanation of delays following extremely cold nights, but, at the elevations of our study sites, on few winter nights in southern California does the temperature drop below 10° C. Delays on mornings following mild but cool nights may be a learned behavioral reaction to a reduction in prey at these temperatures.

Both low and high temperatures affect the activity level of aerial arthropods (Holm and Edney 1973, Romoser and Stoffolano 1994). Reduced activity results in a reduction in the passive and active recruitment of arthropods into the air column. The optimal temperature range for aerial arthropods at a height of 60 m above the ground is between 22° and 38° C. Glick (1939, 1957) found that abundance of aerial arthropods decreases considerably at temperatures below 18° C and is very low at temperatures below 15.6° C.

If insect activity drops at colder temperatures, swift activity should drop as well. Common Swifts have been observed not to leave the roost until the air temperature was high enough for "normal" numbers of flying arthropods to be available (Koskimies 1950). The temperature at the first outward flight of Common Swifts varies from 13° to 17° C, with a mean of 15° C, corresponding to expected increases in insect availability (Koskimies 1950).

The temperature at ground level influences the activity of arthropods in the air column, although this influence may be delayed. Few insects fly at temperatures under 15° C, so few are available to be wafted aloft (Koskimies 1950). When temperatures are extremely cold or remain cold after sunrise, dispersal of arthropods into the air is delayed. This may be a primary reason that cold temperatures delay morning exit times of White-throated Swifts.

White-throated Swifts entered the roost later during cold temperatures, earlier during mild, warm, and hot conditions (Table 2). Earlier entry under warmer conditions may be a response to high insect abundance throughout the day providing the birds enough food to meet their demand for energy. The stable, predictable conditions of the southern California summer—long, warm days, rare stormy weather, high abundance of aerial arthropods—provide the swifts with ample food and time to forage earlier in the day. Even while nesting, the Barn Swallow (*Hirundo rustica*) requires as few as six hours of foraging to meet both its own needs and those of its nestlings (De la Cueva and Blake 1997).

On extremely hot days, however, fewer prey may be available. Summer afternoons in southern California regularly exceed 30° C from May to early October. Daily temperatures generally peak in early afternoon (12:00–15:00). Temperatures above 30° C have been shown to reduce aerial insect abundance, particularly in the early afternoon when combined with convection (Koskimies 1950). This reduction lowers prey abundance in the late afternoon and early evening. Early entry in summer may be the swifts' response to reduced aerial insect abundance due to high heat later in the day. Additionally, delays in exiting nocturnal roosts after warm nights followed by a rapid rise in temperature after sunrise may be a reaction to decreased prey abundance caused by continuous warm temperatures.

At all sites rain also delayed the swifts' morning exit. Other studies have shown that variations in weather affect exit times of swifts similarly. Cloudy weather and rain cause several species of swifts to exit their roost later (Koskimies 1950, Lack and Lack 1952, Razack and Naik 1965, Michael and Chao 1973, Zammuto and Franks 1981). Weather affects arthropod abundance in the air column (Glick 1939), sometimes immediately: raindrops knock arthropods out of the air (Koskimies 1950). However, insect abundance drops during long dry spells and increases immediately following rain (Glick 1939). The immediate effect of rain on the White-throated Swift is a drop in prey abundance during the rain and delayed exit times on rainy mornings.

White-throated Swifts return to the roost earlier during rain (Table 2). We observed swifts entering roost sites early in the afternoon, immediately before or close to the beginning of rain showers. We did not observe swifts outside the roost during heavy rain. Adverse conditions such as fog and rain elicits an early return to the roost in several species of swift (Lack and Lack 1952, Church 1956, Razack and Naik 1965, Zammuto and Franks 1981). Common and Chimney Swifts return to the roost immediately before and shortly after the start of rainstorms (Lack and Lack 1952, Zammuto and Franks 1981). Common Swifts dodge local patches of rain (Lack and Lack 1952). This avoidance behavior may account for Church's (1956) seemingly contradictory statement that weather has no effect on the Common Swift.

Light Intensity

Church (1956) attributed the Common Swift's exit times to changes in light intensity alone. We, however, found White-throated Swifts exiting at a wide range of light intensities, which tended to be lower during the summer and higher during the winter.

Roosting time is correlated with sunlight intensity in several species of swifts (Koskimies 1950, Razack and Naik 1965, Michael and Chao 1973, Zammuto and Franks 1981). However, sunlight intensity at the time of the return to the roost varies with the weather. Chimney Swifts enter the roost at higher light intensities during colder months (Michael and Chao 1973).

In southern California, White-throated Swifts vary greatly in the timing of their return to the roost in relation to light intensity and sunset. They enter at higher light intensities during the early summer, at lower light intensities during the later summer and winter. The Chimney Swift differs, entering at lower light intensity in warmer months, at higher light intensity during colder months (Michael and Chao 1973). From this, it seems that temperature and its influence on prey abundance is more of an influence on swift activity than light intensity by itself. Light intensity, however, does set ultimate limits to swift flight and foraging and is often correlated with the influences of temperature on these activities.

Patterns of Group Entry and Exit

The evening return to the roost is an impressive spectacle described for several species of swifts (Lack and Lack 1952, Church 1956, Razack and

Naik 1965, Michael and Chao 1973). Entries have been characterized as large, dramatic events with large numbers of swifts pouring into a roost within a few minutes (Linton 1924, Pickwell 1937, Church 1956, Razack and Naik 1965, Michael and Chao 1973); such "clumped" entries are typical in winter. During spring, however, the White-throated Swift has a more "scattered" pattern of entering and exiting in smaller groups over a more extended period.

At all three roost sites we studied White-throated Swifts were most numerous during winter. The swifts gathered close to the roost for an hour or more before entering, frequently in one large flock. Often, the flock formed screaming parties that circled close to the opening of the roost site, vocalizing loudly. They then scattered into the air above the roost, possibly to feed, between successive close approaches. They often repeated this behavior several times. As sunset approached, the swifts slowly increased elevation, spiraling upward until they were almost out of sight. In so doing, they remained in sunlight even after the sun had dropped below the horizon at ground level. This may have been an attempt to stay warm long as possible before roosting, as Tomback (1978) reported for Clark's Nutcracker (*Nucifraga columbiana*). Eventually, an individual dived toward the roost and others followed, with the majority of the group entering the roost within minutes. We observed as many as 140 swifts entering their roost within one minute. Frequently, one to five stragglers remained outside the roost for several more minutes before entering.

Roost entries were more scattered during the spring. Small groups converged on the roost site, often circling it repeatedly. They entered the roost in even smaller groups, spaced widely apart. Rarely were the numbers entering uniform; groups of two to six individuals were most common, but the size of flocks entering roosts in spring still ranged up to 60. During these months, the populations at Caspers Park and Santiago Oaks were generally lower; and the weather tended to be milder.

Summer entries were scattered, clumped, or intermediate in no distinct pattern. Contributing to this variation was the smaller number of swifts using the roosts, which resulted in the deletion of several observations from the analysis (see Study Area and Methods).

We were also unable to detect a distinct pattern in exits at all seasons. Exits tended to be clumped. The exit of the main group usually took longer than the entry, with 25–35 individuals exiting per minute; a maximum of 63 individuals exited in one minute at Caspers Park.

CONCLUSIONS

In summary, the roosting behavior of the White-throated Swift varies seasonally in numbers of individuals (Ryan and Collins 2003a), entrance and exit patterns, and sociality (Ryan and Collins 2003b). Although entrance and exit times show some linkage to ambient light conditions, the related variables of temperature and weather and, in turn, their effect on the swift's aerial food supply, seem to be the stronger predictors of roosting behavior. Parallel studies of swifts elsewhere under different environmental regimes may provide additional clues as to the most important variables influencing their behavior.

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