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Breeding biology of Dusky Flycatchers in a southern Utah mixed conifer-aspen woodland

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ABSTRACT. Dusky Flycatchers (*Empidonax oberholseri*) nesting in a mixed conifer-aspen woodland in southern Utah occurred at a breeding density of 0.44 territories/ha. Females began laying first clutches 1–26 June; adults fed nestlings (in renesting attempts) as late as mid August. Mean clutch size was 3.8 eggs in first clutches and 3.6 eggs overall. Incubating females spent 90% of daylight hours on the nest, where they were fed by males 1.1 times/hour. Incubation lasted 14–16 d; nestlings remained in the nest 15–17 d. Thirteen of 32 nests (40.6%) were successful in producing at least one fledgling, with successful nests producing 2.7 young/nest. Based on exposure, probability of a nest surviving from egg laying to fledging was 0.40. Predation accounted for 84.2% of nest failures; brood parasitism by a Brown-headed Cowbird (*Molothrus ater*) occurred at one nest.

SINOPSIS. **Biología reproductiva de *Empidonax oberholseri* en arbolados mixtos de coníferos y álamo temblón en la parte sur de Utah**

Se encontró una densidad reproductiva de 0.44 territorios por hectáreas de una población reproductiva de *Empidonax oberholseri* en arbolados mixto de coníferos y de álamo temblón en la parte sur de Utah. Las hembras comienzan la primera camada de 1 al 26 de junio; los adultos alimentaron pichones (en intentos de reanidamiento) hasta mediados de agosto. El tamaño promedio de la primera camada fue de 3.8 huevos y de 3.6 en general. Las hembras que incubaron invirtieron el 90% de las horas de luz en los nidos en donde fueron alimentadas por los machos. 1.1 veces/hr. El periodo de incubación fue de 14–16 días y los pichones permanecieron en el nido de 15–17 días. Un 40.6% (13/32) de los nidos fueron exitosos (producir al menos un pichón). Los nidos exitosos produjeron un promedio de 2.7 pichones/nido. La probabilidad de un nido de mantenerse activo desde la puesta de huevos hasta que el pichón deja el nido fue 0.40. El 84.2% de los nidos que fracasaron fueron a mano de depredadores y en un nido hubo parasitismo por parte de *Molothrus ater*.

Key words: breeding biology, Dusky Flycatcher, *Empidonax oberholseri*, life history, nest success

The Dusky Flycatcher (*Empidonax oberholseri*) is a common migratory species that breeds throughout much of montane western North America, from Yukon south to Arizona and from California east to western South Dakota (American Ornithologists' Union 1998). Breeding habitat consists of open or patchy coniferous, aspen, and montane riparian woodlands, and a variety of open shrubby habitats, including oak scrub, willow thickets, and montane chaparral (Sedgwick 1993a; American Ornithologists' Union 1998). Although Dusky Flycatcher populations appear to be increasing and may benefit from forestry practices that create openings in coniferous forest (Sedgwick 1993a), such generalizations are based on abundance of breeding birds (e.g., Breeding Bird Survey data), which may not necessarily reflect breeding productivity (e.g., Van Horne 1983). For example, although Dusky Flycatchers in British Columbia readily colonized low-quality habitat resulting from one particular forest management regime, birds there experienced greatly reduced nesting success compared with birds nesting in control areas (Easton and Martin 1998). These data suggest that the Dusky Flycatcher may exhibit source-sink population dynamics (Pulliam 1988) and emphasize the importance of understanding variation in life history traits and demographic factors among habitat types and geographic areas.

Despite the species' general abundance and large range, Dusky Flycatcher breeding biology remains largely undocumented outside of the Pacific Northwest (Bowles and Decker 1927; Sedgwick 1993b; Campbell et al. 1997; Easton and Martin 1998, 2002; Liebezeit and George 2002) and the Sierra Nevada of California (Johnson 1963; Morton and Pereyra 1985; Oppenheimer et al. 1996; Pereyra and Morton 2001; Cain and Morrison 2003). Without information on nesting ecology and demographic

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variables from throughout the species' range, our understanding of the life history and population biology of the Dusky Flycatcher remains limited. Detailed information on the species' natural history is lacking completely from the southern Rocky Mountains-Colorado Plateau region (i.e., Utah, Colorado, Arizona and New Mexico). Here I describe the breeding biology of Dusky Flycatchers in a mixed conifer-aspen woodland in southern Utah, thus providing the first detailed life history information from the southern interior portion of the species' breeding range. I place this information in a range-wide context and evaluate the extent and potential importance of geographic variation in Dusky Flycatcher breeding biology.

STUDY AREA AND METHODS

I observed Dusky Flycatchers nesting 0.2–2.5 km east of Duck Lake (37°31′N, 112°42′W) and north of State Route 14, in Dixie National Forest, Kane County, southern Utah. Elevation of the study area was 2580 m and topography was mostly level with scattered small lava knolls. Habitat was open-canopy, regenerating trembling aspen (*Populus tremuloides*) woodland with interspersed Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*) trees. The area was a transition zone between spruce-fir forest, which was confined to a mesic corridor along Duck Creek, and mixed conifer forest, the dominant forest type in the area. Using aerial photographs, I calculated the area of the study site to be 32.0 ha.

I observed Dusky Flycatchers and their nests from early May to late August, 2000 and 2001. I traversed the study area at least twice weekly to monitor all pairs and find as many nests as possible. In this species, males (only) sing frequently throughout nest-building, egg-laying, and incubation, and females alone construct nests and incubate eggs (Johnson 1963; Sedgwick 1993a); I found no contradictory evidence and thus assumed that singing birds were males and that nest-building or incubating birds were females. I located Dusky Flycatcher nests by following adults carrying nesting material (females) or food (males during incubation, both sexes during nestling period) to nests and, based on other behavioral cues, by searching vegetation. I found nests (N = 32) primarily during nest-building (66% of nests), but also during egg-laying (17%), incubation (14%), and nestling (3%) periods. By knowing general territory boundaries (see below) and searching for renests immediately following failure, I was able to distinguish between first and subsequent nesting attempts.

Male Dusky Flycatchers use preferred song perches, often located near their nests, and counter-sing with neighboring males. Males and females interact and call back and forth when females are away from nests. By spending equitable amounts of time in all portions of the study area each week, knowing the locations of most nests and making consistent observations of male singing behavior and male-female use of the area around nests, I was confident in grouping unmarked pairs into general territory boundaries. I used landmarks and aerial photographs to map general territory boundaries and calculate territory density.

I monitored nests every 3–5 d, but only approached nests closely during egg-laying/early incubation, to determine clutch completion and clutch size, and late in incubation to determine hatching date and hatching success. Also, at a small sample of nests (N = 5), I used dial calipers and a 50-g Pesola scale to measure 9–10 d old nestlings. Following nest failure or fledging, I measured nest and nest-site characteristics with ruler (cm) and tape-measure (m); I estimated tree height from measurements made with a clinometer.

I documented adult behavior at nests by videotaping nests with a camera placed 10–20 m away and concealed by vegetation or, occasionally, by observing nests directly from a concealed location (without a blind) 25–30 m away. Adults did not appear to alter their behavior in response to the presence of the video camera or observer. In order to obtain a sample representative of population-level behavioral variation, I observed as many nests as possible and avoided observing any nest more than once during each stage of the nesting cycle (i.e., laying, incubation, and nestling). Nest observations (65.1 h total) averaged 1.76 h (range, 1.0–3.1 h) in duration and occurred during nest-building (12.6 h at five nests), egg-laying/incubation (25.9 h at nine nests), and nestling (26.6 h at 13 nests) stages, mainly between 06:00 and 13:00. From videotapes and field notes, I quantified nest visitation rates during all nesting stages, time spent incubating and duration of incubation attentive periods (i.e., female at nest) and inattentive periods (i.e., female away from nest), and incubation-feeding rates (i.e., males feeding females at nest). During the nestling stage, I quantified time spent brooding (i.e., females covering young), duration of brooding attentive periods, and fecal sac removal rates.

I considered a nest successful if it fledged least one young. In addition to measuring apparent nest success (percentage of nests with known outcome that were successful), I estimated nest survival and its variance based on exposure days (Mayfield 1961, 1975; Johnson 1979). I considered a failed nest to be the result of predation if nest contents disappeared before the latter part of the nestling period, if the nest material was disheveled, or if the nest was on the ground. Nest success was almost always confirmed by observing fledglings or adults carrying food in the immediate vicinity of a recently active nest. Other signs used to infer successful fledging included fecal material in the nest cup or on the nest rim and a flattened area on the nest rim, on which nestlings perch immediately prior to fledging.

Prior to all statistical analyses, I confirmed that data met parametric assumptions of normal distribution and homoscedasticity. I used *t*-tests to test for differences in nest site characteristics between nest substrates and simple linear regression to examine relationships between parental care and nestling age. I compared daily nest survival rates between egg and nestling stages and between years using the program CONTRAST (Hines and Sauer 1989). Nest success did not differ significantly between years (e.g, daily survival rates: $\chi^2_1 = 0.77$, $P = 0.38$), so I combined data from both years for analyses.

RESULTS AND DISCUSSION

Breeding phenology. Male and female Dusky Flycatchers began arriving on the study site during the first and second weeks of May, respectively. Males established territories upon arrival. Aspens were generally bare when females began arriving, but had 70–90% of their leaves by the time most females began nest building. Breeding density, which varies substantially across the species' range and nesting habitats, was 0.44 territories/ha (44 territories/km^2) at the southern Utah site, and thus similar to the 41, 40, 30, and 45 territories/km^2 reported for mixed coniferous forest and montane chaparral in California (Sedgwick 1993a).

The first females began nest building 20–22 May in 2000, about one week after arriving. The mean date the first egg was laid in first nesting attempts was 12 June (range, 1 June–26 June; $N = 13$ nests). The mean hatching date (first egg in clutch) was 30 June for first nests (range, 20 June–13 July; $N = 9$), and the mean fledging date was 19 July (range, 12 July–28 July; $N = 5$) for first nests. Dusky Flycatchers did not attempt second broods, but renested up to three times following nest failure. The mean date the first egg was laid in renesting attempts was 3 July (range, 18 June–18 July; $N = 14$). The mean hatching date was 19 July (range, 10 July–5 August; $N = 11$), and the mean fledging date was 4 August (range, 27 July–18 August; $N = 5$) for renests.

Egg dates in southern Utah (1 June–5 August) were generally similar to those reported from western Montana (31 May–21 July; Sedgwick 1975), but there are exceptionally early egg (24 May) and nestling (10 June) records from British Columbia (Campbell et al. 1997). Dusky Flycatchers in southern Utah appear to breed later into the season than more northern birds; renesting pairs often had nestlings during August, as late as mid August, compared to late nestling records of 26 July in British Columbia (Campbell et al. 1997), 28 July in western Montana (Sedgwick 1975), and 5 August in Colorado (Sedgwick 1998).

Nest site. Dusky Flycatchers built nests ($N = 32$) in trembling aspen (78%), Engelmann spruce (16%), common juniper (3%), and Douglas-fir (3%). Nests in aspen were placed primarily in crotches of sapling stems or vertical forks of branches in larger trees. In one case, a nest was placed on a shelf of bark peeling away from a small aspen snag. Nests built in Engelmann spruce were saddled on drooping horizontal branches of mature trees, located well away from the main stem, and supported by numerous small supporting branches (Table 1). Compared to spruce nest sites, nests in aspen tended to be in smaller trees (often saplings), located closer to the main stem, and supported by fewer, but larger branches (Table 1). The

Table 1. Descriptions of Dusky Flycatcher nest sites in trembling aspen and Engelmann spruce substrates.

Nest site variable	Mean ± SE: Trembling aspen (N = 25)	Mean ± SE: Engelmann spruce (N = 5)
Nest height (m)	1.72 ± 0.37	1.73 ± 0.10
Substrate height (m)[a]	4.05 ± 0.47	10.7 ± 1.08
Distance from trunk (cm)[a]	0.86 ± 0.61	79.4 ± 10.1
Number supporting branches[b]	2.4 ± 1.22	4.6 ± 0.60
Diameter supporting branches (cm)[c]	2.08 ± 0.27	0.69 ± 0.11

[a] $P < 0.0001$.
[b] $P < 0.01$.
[c] $P < 0.05$.

mean nest height was similar in aspen and spruce nests, despite clear differences in height between aspen and spruce substrates (Table 1). The nest in Douglas-fir was unique in that it was built among six small (0.55 cm mean diameter) hanging dead branches, 16.5 cm from the main trunk of the 13.6-m tall tree. Overall, mean (± SE) nest height was 1.67 ± 0.29 m (range, 0.44–9.7; N = 32).

Southern Utah nest substrates, primarily deciduous saplings and shrubs and less often coniferous shrubs or trees, were consistent with the species' range-wide trend (Sedgwick 1993a; Easton and Martin 2002; Liebezeit and George 2002). Mean nest height in southern Utah was similar to that reported for limber pine (*Pinus flexilis*)-mountain juniper (*Juniperus scopulorum*) woodland in western Wyoming (1.33 m, N = 34; Kelly 1993) and open coniferous forest in western Montana (1.50 m, N = 25; Sedgwick 1975, 1993b), but substantially lower than that found in riparian woodland in western Montana (3.64 m, N = 40; Banks and Martin 2001).

In 2001, a pair of Dusky Flycatchers successfully fledged young from a nest site that was also used (unsuccessfully) in the previous year; it is unknown whether the same pair built both nests. Although not noted previously in the Dusky Flycatcher (Sedgwick 1993a), nest-site reuse appears to be widespread among *Empidonax* flycatchers (Poole and Gill 1993–1997, 1998–2002).

Nest. Females appeared to build nests without male assistance, generally in 5–8 d for first nesting attempts. Building females took material to nests 19.9 ± 2.24 times/h during morning observations (range, 12–27; N = 7 observations [10.6 h total] at five nests); females worked on nests less frequently during the afternoon (1–7 nest visits/h; N = 2 observations [2.0 h] at two nests). Females were present at nests 27.2 ± 3.0 s/visit (range, 2–112; N = 6 observations [9.6 h] at five nests) during nest building, similar to observations by Banks and Martin (2001) in riparian woodland in western Montana. Sedgwick (1975) noted that building females visited nests less frequently (approximately 10 times/h) and remained at nests longer (45–60 s/visit) in open coniferous forest in western Montana.

Dusky Flycatcher females began nest-building by placing spider webbing, followed by a shallow base of vegetative material, on a substrate. Females then built the walls of the nest cup, and hence the bulk of the structure, before completing the bottom of the nest and, finally, lining the cup. Throughout nest building, females collected and used spider webbing both to fasten nest material together and to the substrate. Upon arriving at a nest during building, a female typically perched briefly on the rim to add new material to the nest, then immediately sat low in the cup, often rotating to face different directions, to arrange material with her bill and shape the interior of the nest with her body. Females frequently reached over the rim of the nest and, with sweeping motions of the bill, pulled spider webbing up from the exterior of the nest to secure fresh material. Before flying from a nest, the female typically remained sitting in the nest and performed a series of stretching motions, shaping the interior of the nest cup by arching her back, with slightly raised wings and lowered tail, and pressing her breast deeply into the floor and walls of the cup.

Nests were small, open cups (outer diameter, 7.64 ± 0.24 cm, N = 7; inner diameter, 4.8 ± 0.2 cm, N = 5; cup depth, 3.6 ± 0.13 cm, N = 5; outer nest height, 6.44 ± 0.2 cm, N = 7), composed primarily of shredded grasses and strips of aspen bark, thin forb stems, spruce and pine needles, and various plant fibers (e.g., plant down). Less common materials incorporated into nests included small woody twigs, aspen leaves, foliose lichens, small pieces of string, tissue paper, and cellophane. Females lined nest cups with coniferous bud scales, mammal hairs, and feathers of locally breeding species (e.g., Gadwalls [*Anas strepera*], Spotted Sandpipers [*Actitis macularia*], Steller's Jays [*Cyanocitta stelleri*], Black-headed Grosbeaks [*Pheucticus melanocephalus*]). Nest-building behavior and nest structure and composition in southern Utah were very similar to descriptions from California (Johnson 1963) and Montana (Sedgwick 1975, 1993b).

Renesting females typically moved all nesting material from depredated nests to new nest sites if (and only if) the depredated nest had not fallen to the ground; similar behavior has been observed in Montana (Sedgwick 1975) and California (Liebezeit and George 2003). Females built renests in 3–6 d, moving an average of 38.6 ± 6.46 m (range, 13.5–61.5; N = 7) between nest sites.

Interspecific interactions appeared to occur most frequently during nest building, at which time I observed numerous chases between Dusky Flycatchers and Western Wood-Pewees (*Contopus sordidulus*) and between Dusky Flycatchers and Warbling Vireos (*Vireo gilvus*). Any competitive relationships between Dusky Flycatchers and Warbling Vireos or Western Wood-Pewees is speculative, but it is notable that all three species overlap in the type of material used in nest construction. Indeed, I once observed a female Dusky Flycatcher make regular trips to steal nesting material from a Warbling Vireo nest.

Eggs. After lining the nest, females often waited 1–2 d before laying the first egg and occasionally sat on empty nests during this period, as observed by Bowles and Decker (1927). Females typically laid one egg/day on consecutive days, but skipped 1–2 d between eggs at four of eight nests monitored closely during laying (see Sedgwick 1993b; Oppenheimer et al. 1996). Although Dusky Flycatcher eggs are occasionally marked with light brown dots (Bowles and Decker 1927), they are otherwise reported as white or creamy white (Bent 1942; Sedgwick 1993a). All eggs inspected in southern Utah (83 eggs at 25 nests) were white and unmarked. Mean clutch size was 3.56 ± 0.15 eggs (range, 2–5; N = 23 clutches) overall and, thus, within the species' typical range of three to four eggs (Bent 1942; Morton and Pereyra 1985; Sedgwick 1993a). Mean clutch size declined from 3.78 ± 0.15 eggs (range, 3–5; N = 14 clutches) in first nesting attempts to 3.22 ± 0.27 eggs (range, 2–4; N = 9 clutches) in renesting attempts.

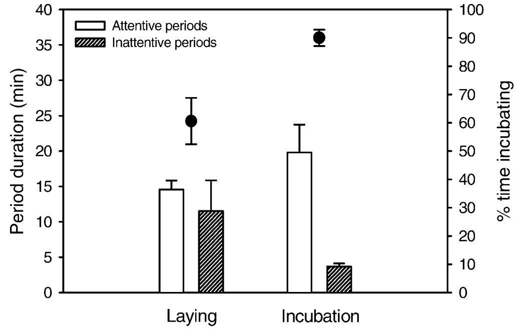

Fig. 1. Duration of attentive and inattentive periods (bars, left ordinate) and percent time spent on the nest (circles, right ordinate) by female Dusky Flycatchers prior to (egg-laying) and following (incubation) clutch completion.

Incubation. No evidence suggested that males participated in incubation. The onset of incubation varied from the first to last egg, but incubation behavior tended to become more regular with laying of the penultimate or ultimate egg, as documented by Morton and Pereyra (1985). Females spent more time on the nest, with longer attentive periods and shorter inattentive periods, after the clutch was complete than before (Fig. 1). Following clutch completion, females spent 90.0 ± 2.87% of daylight hours incubating (N = 9 observations [16.8 h] at eight nests), which is higher than that observed in the Sierra Nevada (75.8%; Morton and Pereyra 1985) and western Montana (86.0%; Sedgwick 1975). Mean attentive and inattentive periods were 19.79 ± 3.93 min and 3.68 ± 0.44 min (N = 7 observations [13.5 h] at six nests), respectively. Attentive periods in southern Utah were thus remarkably similar to those documented in the Sierra Nevada (19.3 min; Morton and Pereyra 1985) and Montana (21.0 min; Sedgwick 1975, 1993b); inattentive periods in Utah were notably shorter than in the Sierra Nevada (6.8 min) and Montana (6.6 min). Variation in climatic conditions (e.g., temperature, solar radiation) due to elevation or latitude may explain variation in inattentive periods among the Utah, Sierra Nevada, and Montana sites. For example, if temperatures are warmer at the Utah study area, which is lower in elevation than the Sierra Nevada study area and farther south than the Montana study area, the cooling rate of eggs may be slower, thereby allowing females to spend more time away from nests per inattentive period.

Males fed incubating females at the nest 1.1 ± 0.39 times/h (range, 0–5; $N = 13$ observations [25.9 h] at nine nests), spending 2.46 ± 0.67 s (range, 1–7; $N = 8$ observations [16.0 h] at seven nests) at the nest per visit. Males fed incubating females less frequently before (0.36 ± 0.23 feeds/h) than after (1.43 ± 0.52 feeds/h) clutch completion. The mean rate of incubation feeding in southern Utah was much lower than that recorded in western Montana (5.38 ± 0.76 feedings/h; Sedgwick 1993b). Incubation feeding, however, was more widespread in Utah, where eight of nine males (88.8%) fed incubating females, than in Montana where only seven of 13 males (53.8%) carried food to incubating females (Sedgwick 1993b). Utah males may feed incubating females less frequently because females in Utah spend more time foraging per inattentive period than females in Montana.

Hatching rate was 90%, with 49 of 54 eggs in active nests hatching successfully. At nests surviving to hatching in western Montana, Sedgwick (1975) found that 95% of eggs (62 of 65) hatched. The incubation period, defined as the day the last egg was laid to the day the first egg hatched, averaged 14.1 ± 0.11 d (range, 14–15; $N = 9$ nests). Reflecting variation in the onset of incubation, eggs hatched synchronously or asynchronously, with clutches hatching over a 1–3 d period. Thus, following Sedgwick (1993a) in defining incubation as the day the last egg was laid to the day the last egg hatched, the incubation period varied from 14–16 d, as noted in other areas of the species' range (Sedgwick 1993a).

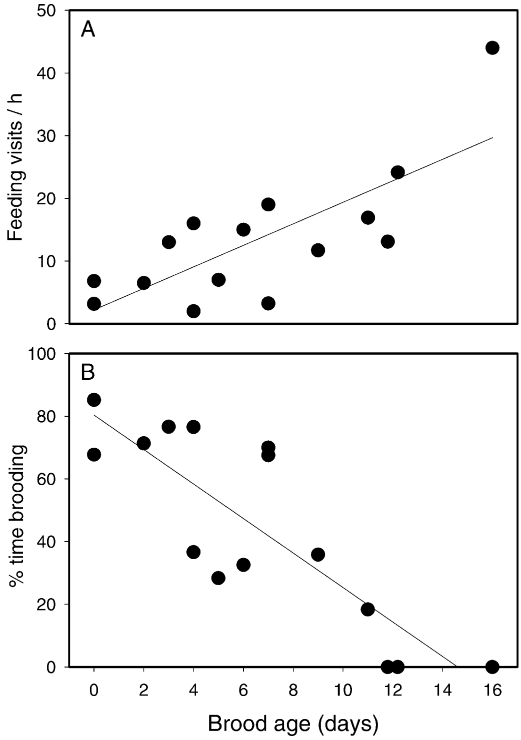

Fig. 2. Variation in Dusky Flycatcher (A) nestling feeding rate (males and females combined) and (B) percent time spent brooding (females only) over the nestling stage. Feeding rate increased ($y = 2.208 + 1.718x$, $r^2 = 0.58$, $P = 0.001$) and time spent brooding decreased ($y = 80.393 - 5.506x$, $r^2 = 0.71$, $P < 0.0001$) as nestlings aged.

Nestlings and parental care. Primary pin feathers broke sheaths when nestlings were 9–10 d old, at which time nestling mass was 10.7 ± 0.16 g (range, 9.8–11.3) and tarsus length was 16.0 ± 0.17 mm (range, 15.0–16.6; $N = 10$ nestlings, five nests). These data are consistent with those of Pereyra and Morton (2001) for the Sierra Nevada.

Both parents fed nestlings at the nest, averaging 13.4 ± 2.74 feeds/h (range, 1.96–44.0; $N = 15$ observations [26.6 h] at 13 nests) or 4.87 ± 0.81 feeds/nestling/h (range, 1.62–14.66) throughout the nestling period. Nestling feeding rate increased and brooding attendance decreased as nestlings aged (Fig. 2). Females brooded young up to 87% of the time early in the nestling period, but not at all in the 3–4 d

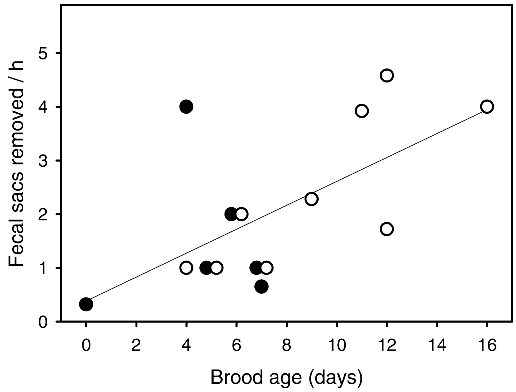

Fig. 3. Adult Dusky Flycatchers disposed of nestlings' fecal sacs by eating them at the nest (closed circles) or carrying them away from the nest (open circles). Fecal sac removal rate increased as nestlings aged ($y = 0.596 + 0.233x$, $r^2 = 0.37$, $P = 0.021$).

preceding fledging. In western Montana, adult feeding rate (2.06 feeds/nestling/h overall) increased over the first half of, but apparently not throughout, the nestling period; brooding attendance declined from 65.8–71.6% during first six days of the period to 35.9% after day seven (Sedgwick 1975). Brooding was performed by females alone, as observed by Sedgwick (1975, 1993a) and Pereyra and Morton (2001), and occurred in periods averaging 9.62 ± 0.97 min (range, 0.1–32.1; $N = 12$ observations [22.9 h] at 12 nests). During extremely hot conditions (e.g., mid-day in late July), females occasionally shaded nestlings (and eggs) by perching on the nest edge with wings spread.

Adults often collected nestlings' fecal sacs after feeding (males and females) or brooding (females only), disposing of an average 2.18 ± 0.49 fecal sacs/h (range, 0.0–4.58; $N = 14$ observations [25.6 h] at 11 nests) over the entire nestling period. Fecal sac removal rate increased as nestlings aged (Fig. 3), presumably reflecting an age-related increase in fecal sac production by nestlings. Adults tended to eat fecal sacs at the nest early in the period, but shifted to carry fecal sacs away from the nest when nestlings were 4–7 d old (Fig. 3), as observed by Sedgwick (1975). This pattern is consistent with the trend documented to date among other altricial, temperate zone songbirds (Hurd et al. 1991).

Nest material was infested with blowfly (Diptera: Calliphoridae) puparia at one nest, suggesting that nestlings are at least occasionally parasitized. Boland et al. (1989) reported that Dusky Flycatchers, along with "Western" and Willow flycatchers, are known hosts of the blowfly *Protocalliphora cuprina*.

Females flushed from nests by humans did not perform distraction displays, but dived inconspicuously over the edge of the nest and flapped their wings only when near the ground and moving away from the nest site. Adults responded strongly to nestling distress calls (high-pitched, shrill calls), given when handled by humans, by diving at the intruder, bill-snapping and alarm-calling. An adult responded similarly to a chipmunk (*Tamias* sp.) that was within one meter of a nest containing nestlings, diving at the chipmunk repeatedly and eventually chasing it out of the area.

Fledgling stage. The average nestling period, defined as the day the first egg hatched to the day the last nestling fledged, was 16.4 ± 0.4 d (range, 15–17; $N = 5$ nests). Pereyra and Morton (2001) also reported that fledging generally occurred on day 16 or 17 in the Sierra Nevada, and Sedgwick (1993b) found an average nestling period of 17.5 d for eight nests in western Montana.

Immediately prior to fledging, young birds were very active, standing on the rim of the nest and support branches outside of the nest, flapping wings, preening, and climbing over each other when anticipating adult arrival. Nestlings also scratched their heads at this age, raising a foot over a lowered wing. During this time, adults often perch within a meter of the nest, with food, giving solicitation ("d-d-d") calls (following Sedgwick 1993a), seemingly to encourage nestlings to leave the nest. Brood separation occurred in a brood of four fledglings, all of which left the nest between 10:00 and 12:00 on the same day. This brood immediately divided into two groups of two, located ca. 15 m apart and fed by both parents. Both adults continued feeding both groups of fledglings, located ca. 80 m apart, the day after fledging. By day nine, one group of young remained within 30 m of the nest and appeared to be fed by one adult alone, while the other adult appeared to care exclusively for the other group, located ca. 170 m away. Extended observations of the foraging adults suggested that neither moved between the two groups of fledglings. At a second nest extensively observed following fledg-

Table 2. Documented variation in Dusky Flycatcher nesting success.

Location	Habitat	*N*	Nesting success Apparent[a]	Mayfield[b]	Source
California					
Northwestern	ponderosa pine	167	29.3%	0.28	Liebezeit and George 2002
Sierra Nevada	mixed conifer	67	34.3%	—	Siegel and DeSante 2003
Sierra Nevada	riparian/meadow	37	48.6%	0.43	Cain and Morrison 2003
British Columbia	mixed conifer	10	50.0%[c]	0.51[c]	Easton and Martin 1998
Montana	mixed conifer	24	58.9%	0.38	Sedgwick 1993b
Wyoming	pine-juniper	32	40.6%	0.35	Kelly 1993
Utah	conifer-aspen	32	40.6%	0.40	this study

[a] Percentage of nests producing ≥1 fledgling.
[b] Mayfield (1961, 1975).
[c] Control plots only.

ing (i.e., eight days), brood separation did not occur, despite one of three fledglings leaving the nest a day after its siblings. Behavior of fledglings was generally similar to that described by Sedgwick (1993a).

Nest success. Thirteen of 32 nests (40.6%) fledged at least one young bird, with successful nests producing 2.7 ± 0.27 young. Nest predation was the most important cause of nest failure, accounting for 16 of 19 failed nests (84.2%). Two nests (10.5% of failures) failed because adult females disappeared (presumably died), and one nest (5.3%) failed as a result of brood parasitism by a Brown-headed Cowbird (*Molothrus ater*), with the flycatcher nestlings dying in the nest and the cowbird fledging successfully. Predation was also the most important cause of nest failure for Dusky Flycatchers in western Wyoming (Kelly 1993), the Sierra Nevada (Cain and Morrison 2003), and northern California (Liebezeit and George 2002), where 89.5%, 94.7%, and 96% of nest failures, respectively, were due to predators.

Using the exposure method of calculating nesting success (Mayfield 1961, 1975), the probability of a southern Utah nest surviving from egg-laying to fledging was 0.40. The probability of nest survival declined from 0.67 during the egg stage (egg-laying and incubation combined) to 0.60 during the nestling stage, a trend also reported from northern California (Liebezeit and George 2002) and Wyoming (Kelly 1993). Daily survival rates in southern Utah, however, did not differ significantly between egg (0.977 ± 0.008) and nestling (0.970 ± 0.011) stages ($\chi^2_1 = 0.28$, $P = 0.60$).

Mayfield estimates of Dusky Flycatcher nesting success (throughout the nesting cycle) range from 0.28 to 0.51, with no clear geographic or habitat-related pattern (Table 2). Additional data, albeit confined to the nestling stage, come from Idaho and Montana aspen forest, where Rotella et al. (2000) reported apparent nesting success of 78.4% and a Mayfield daily survival rate of 0.971 during the nestling stage. Following Mayfield (1961, 1975), the probability of a Rotella et al. (2000) nest surviving the nestling stage was 0.60 (assuming a 17.5-d nestling period; Sedgwick 1993b), which is similar to what I observed during the nestling stage in southern Utah.

Brown-headed Cowbirds were uncommon and brood parasitism was low (5.3%) at the southern Utah site, which appears to be the trend throughout the Dusky Flycatcher's range (Sedgwick 1993a). Brood parasitism may vary as a function of landscape features within geographic regions, as in western Montana (Tewksbury et al. 1998), where rates range from 11.1% in open coniferous forest (Sedgwick 1993a) to 27% in riparian forest (Banks and Martin 2001). Nevertheless, even where parasitism rates are relatively high, the Dusky Flycatcher appears to be much less susceptible than co-existing open-cup nesting species (Tewksbury et al. 1998; Banks and Martin 2001).

CONCLUSIONS

General behavior, clutch size, parental care, and nest success of Dusky Flycatchers in southern Utah were consistent with information currently available from elsewhere in the species' range. Nevertheless, several aspects of Dusky Flycatcher breeding phenology and incubation behavior in southern Utah showed potentially important deviations from range-wide patterns, which generally represent more northern populations. Dusky Flycatchers in southern Utah occasionally had active nests as late as mid August, which is later than that observed in more northern areas. This may indicate that southern birds have greater renesting opportunities, possibly because of reduced temporal constraints on migration-related behavior. Compared to Dusky Flycatcher females in Montana, Utah females appeared to have longer inattentive periods during incubation and be fed less frequently by males during attentive periods. These patterns may indicate that environmental conditions in southern areas allow females improved foraging opportunities during incubation. For example, higher ambient temperatures could reduce egg cooling rates and thereby allow females to spend more time away from the nest per inattentive period.

Given the broad array of woodland and shrub habitat types occupied by the generalist Dusky Flycatcher across its large breeding range, its reproductive ecology remains relatively poorly sampled. Nevertheless, data show that Dusky Flycatcher reproductive success varies among habitats, on both large (Table 2) and small scales (e.g., Easton and Martin 1998). The life history of the southern Utah population described here is largely consistent with that described for the Dusky Flycatcher range-wide, but also shows variation that may be due to region- or habitat-specific effects. Local breeding density, habitat structure, and predation pressure may interact in complex ways within and among populations, such that large-scale patterns may only be recognized once adequate sampling is attained. Results presented here contribute to our understanding of geographic and habitat-related variation in life history and demography of the Dusky Flycatcher. Additional information on the breeding biology of Dusky Flycatchers in previously unstudied areas (e.g., in isolated populations at the edge of the species' range) and habitats (e.g., those representing extremely high and low breeding densities) may further our understanding of this species' habitat relationships, life history, and demography.

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