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EFFECTS OF SNOW-RELATED ENVIRONMENTAL VARIATION ON BREEDING SCHEDULES AND PRODUCTIVITY OF A HIGH-ALTITUDE POPULATION OF DUSKY FLYCATCHERS (*EMPIDONAX OBERHOLSERI*)

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Abstract.—Reproductive schedules of Dusky Flycatchers (*Empidonax oberholseri*) at Tioga Pass, in the central Sierra Nevada of California, varied considerably among years. Dates of earliest laying ranged from 29 May to 1 July and varied with snow depth, melt dates, and other factors associated with snowpack. A small apparent advance in laying date over the course of the study (0.52 days year^{-1} over 15 years) was associated with extremes in winter snowpack and spring melt that were related to wet–dry cycles in the Sierra Nevada. Spring snowpack acted on reproductive timing through direct and indirect effects of temperature, melt schedule, and phenological changes in habitat availability. The influence of these variables on laying dates was greatest on the first females to lay (most in early June) and declined through mid-July, when breeding terminated. Clutch size and fledgling production varied between years of heavy and light snowpack as a direct consequence of delayed egg laying in years of heavy snow. In years of light snowpack, females that laid eggs by mid-June produced larger clutches, fledged more young per nest, and were more likely to renest if nest failure occurred. Only two females attempted two broods in a single season, and both were among the first to breed. Seasonal declines in sensitivity to local environmental conditions may constrain the ability of Dusky Flycatchers to adjust breeding schedules to match phenological delays produced by changes in winter temperature, precipitation, and snowpack, and may limit range expansion to areas with arid winters and earlier spring melt. *Received 8 June 2010, accepted 1 August 2011.*

Key words: behavioral plasticity, climate change, clutch size, Dusky Flycatcher, *Empidonax oberholseri*, environmental factors, reproductive success, Sierra Nevada, snowpack, timing of breeding, tyrant flycatchers, warming.

Efectos de la Variación Ambiental relacionada con la Nieve sobre la Fenología Reproductiva y Productividad de una Población de Altura de *Empidonax oberholseri*

Resumen.— La fenología reproductiva de *Empidonax oberholseri* en el paso de Tioga, en la Sierra Nevada central de California, varía considerablemente entre años. Las fechas del inicio de la puesta variaron entre el 29 de mayo y 1 de julio, y variaron con la profundidad de la nieve, fechas de derretimiento de la nieve, y otros factores asociados con la acumulación de nieve. Un pequeño y evidente adelanto en la fecha de puesta a lo largo del estudio (0.52 días año^{-1} por 15 años) se asoció con los extremos de acumulación de nieve en el invierno y con el derretimiento de primavera que estuvieron relacionados con los ciclos de humedad-sequedad en la Sierra Nevada. La acumulación de nieve en la primavera actuó sobre el momento de reproducción a través de efectos directos e indirectos de la temperatura, cronograma del derretimiento y de los cambios fenológicos en la disponibilidad de hábitat. La influencia de estas variables en las fechas de puesta fue mayor para las primeras hembras en poner (la mayoría a principios de junio) y disminuyó hasta mediados de julio, cuando terminó la reproducción. El tamaño de la nidada y la producción de volantones varió entre años de acumulación de nieve pesada y leve como una consecuencia directa del atraso en la puesta de los huevos en años de fuertes nevadas. En años de acumulación leve de nieve, las hembras que pusieron huevos hasta mediados de junio produjeron nidadas mayores, tuvieron más volantones por nido y fueron más propensas a volver a anidar después de un fracaso de anidación. Sólo dos hembras criaron dos nidadas en una sola temporada, y ambas estuvieron entre las primeras hembras en comenzar la reproducción. Las disminuciones estacionales en la sensibilidad a las condiciones ambientales locales pueden limitar la capacidad de los individuos de *E. oberholseri* de ajustar las fechas de la reproducción para que coincida con los retrasos fenológico producidos por los cambios de la temperatura invernal, las precipitaciones y el acumulo de nieve; y esto puede limitar la expansión del área de distribución a áreas con inviernos áridos y con derretimiento de primavera más temprano.

Birds that breed at high latitude and high elevation are often highly responsive to variation in temperature, precipitation, and other cues that normally mark the transition from winter to spring (Wingfield and Farner 1980, Crick et al. 1997, Crick and Sparks 1999, Wingfield 2008). In most species, reproductive development is stimulated by increasing photoperiod, but other

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factors can modulate the actual onset of breeding. In migrants, for instance, warmer springs can trigger earlier departure from wintering areas, permit more rapid migration, and allow earlier settlement and nesting (Both and Visser 2001, Cotton 2003, Wilson and Arcese 2003, Gordo et al. 2005), whereas cool, wet springs can delay nesting. Changes in temperature and precipitation patterns in locations across the Northern Hemisphere have altered snowfall and rates of spring snow melt, leading to earlier leafing and earlier breeding by birds in many, but not all, areas (Inouye et al. 2000, Møller 2008).

Where winter precipitation is dominated by snow, as in the alpine and subalpine, spring and summer conditions can vary widely among years at comparable dates (Morton 1978, Hahn et al. 1995, Martin and Wiebe 2004, Meltofte et al. 2007). The timing of egg laying in these highly seasonal environments is a critical determinant of the degree of synchrony between energetically demanding phases of the nesting cycle and the resources necessary to support them, a phenomenon reflected in temporal changes in clutch size and reproductive success (Thomas et al. 2001, Drent 2006). Given that early clutches are often larger and more successful than clutches produced later in the season (Kluijver 1951, Perrins 1970, Murphy 1986, Verhulst et al. 1995), and more likely to produce future breeders (Dolan et al. 2009), the selective pressure to nest as early as local conditions permit appears to be strong in most species. In some years, however, late spring storms and erratic food supplies can cause widespread mortality in early migrants (Eckhardt 1977, Brown and Brown 1998) or the death of embryos or nestlings in existing nests (Whitmore et al. 1977, Brown and Brown 2000, Morton 2002). Consequently, the stimulatory influence of one set of conditions on reproductive behaviors (e.g., warmer temperatures, decreased snow cover, habitat development) may be negated occasionally by effects from other variables (e.g., wind, rain, snowfall) to determine the actual timing of laying (Wingfield et al. 1992, Wingfield and Farner 1993, Wingfield 2008).

Much evidence indicates that global warming has resulted in earlier spring conditions and phenological advancements in locations across the Northern Hemisphere (Walther et al. 2002, Parmesan 2006). However, an additional outcome of warming is greater environmental variability, manifested in part by wider extremes in temperature and precipitation, including snowfall (Intergovernmental Panel on Climate Change 2007). Lower temperatures and the strong seasonality that define high-altitude areas make them ideal locations for investigating the effects of proximate factors on the timing of reproduction, and the physiological and behavioral responses that permit or limit reproductive success in such highly variable environments. Studies of sedimentation rates and pollen distributions along the eastern side of the Sierra Nevada mountains indicate that temperature and precipitation patterns in this region have fluctuated widely over the past 18,000 years, with at least four major cold–warm oscillations during the most recent period of glacial retreat (Benson et al. 1997). Changes in Sierran temperatures and precipitation patterns have also occurred in the more recent historical past, and more are predicted under various regimes of future warming (Cayan et al. 2008). With this in mind, I attempted to identify the environmental factors that exert the greatest influence on reproductive timing and offspring production of a high-altitude population of Dusky Flycatchers (*Empidonax oberholseri*). Dusky Flycatchers are Nearctic–Neotropical migrants, widely distributed at higher elevations in western North America (Johnson 1963, Sedgwick 1993). Evidence indicates an increase in their distribution and abundance in some interior (Johnson 1965, 1974) and northern mountain ranges during the past century (Campbell et al. 1997, Eckert 1998), which suggests that populations may be "niche tracking" (Tingley et al. 2009), wherein shifts in range accompany geographic changes in the physical conditions that define their ecological niche.

Relatively long reproductive cycles and exposed nests make Dusky Flycatchers potentially vulnerable to changes in weather and resource abundance that are closely associated with variable spring conditions. Because snow is the dominant form of precipitation at higher elevations and snow conditions can vary extensively in the Sierra Nevada, I investigated the relationship among timing of breeding, clutch and brood size, and fledgling production in relation to annual variation in snowpack, temperature, and habitat phenology over a 15-year period, and herein examine the implications that these findings may have for demographic changes in this species.

Methods

Study area.—I studied a population of Dusky Flycatchers at Tioga Pass (37°N, 119°W; elevation 2,900–3,500 m) in the eastern Sierra Nevada of California, from 1981 through 1995. Birds generally arrived on the study area in late May and early June and began departure for wintering grounds in central Mexico in late July (Pereyra 1998). Dusky Flycatchers are socially monogamous, and females build open-cup nests in shrubs and small trees. Nesting territories at Tioga Pass are established along steep, brush- and tree-covered mountainsides wherever potential nest sites are available. In the Sierra Nevada, the trees most often used for nesting include willows (*Salix* spp.), Quaking Aspen (*Populus tremuloides*), Lodgepole Pine (*Pinus contorta*) and Whitebark Pine (*P. albicaulis*) (Johnson 1963, Sedgwick 1993, Pereyra 1998, Cain and Morrison 2003). The study site was censused every third day from the third or fourth week of May onward to detect the settlement of new Dusky Flycatchers. I was able to closely monitor the reproductive activities of individual females over the entire season to document timing of breeding, clutch and brood size, nest success, and renesting behavior because most breeding birds were banded and color-marked (30–60 individuals year^{-1}).

Timing of breeding.—Most nests were discovered during the initial stages of construction or during laying. Once found, each was visited every third day until either the young fledged or the nest failed. Exact clutch-initiation dates, starting with the first egg, were known for most nests or could be determined by measuring daily increases in the size of the air cell on the blunt end of the egg (Pitts 1995, Oppenheimer et al. 1996) or by back-calculating from hatch dates. Because females tended to reuse their nest materials if a nest failed, I was able to associate replacement nests (i.e., renests) with specific females by following them as they carried material between their initial and subsequent sites. Efforts to raise a second brood after successfully fledging chicks from a first effort (i.e., double broods) were rare (2 females in 15 years [2 of 791 nests; 0.25%]), and therefore annual productivity was based on the production of one nest per female.

Environmental data.—I recorded daily precipitation and air temperature with portable rain gauges and hygrothermographs, respectively, located at opposite ends of the study area, to evaluate

the effects of weather on laying schedules. Daily minimum and maximum temperatures were also obtained from two weather stations located along the crest of the Sierra Nevada (Twin Lakes and Echo Summit; NOAA National Climatic Data Center). The correlations between (1) the average minimum temperature for Twin Lakes and Echo Summit and data collected locally at Tioga Pass ($r = 0.892$, $n = 411$, $P < 0.0001$) and (2) the average maximum temperature for the two sites and Tioga Pass ($r = 0.907$, $n = 408$, $P < 0.0001$) were highly significant. I therefore used the averaged minimum and maximum temperatures from Twin Lakes, Echo Summit, and Tioga Pass for the months of May, June, and July to describe weather patterns. The use of data from official weather stations, in conjunction with data from the study site, helped ensure that patterns accurately reflected prevailing conditions in the Sierra Nevada, as well as the conditions that Dusky Flycatchers would be experiencing locally. Daily precipitation recorded in rain gauges was similarly averaged with data available from the NOAA Climatic Data Center for Ellery Lake.

The amount of snow that remained on the study site in late May was a function of winter snow accumulation (through April) and temperatures in April and May. Therefore, as measures of spring snow conditions, I used 1 April snow depth, density (% water), and water content (SWE, snow water equivalent, cm^3; Table 1). These data are collected annually at a network of sites, including Tioga Pass, by the California Cooperative Snow Survey on 1 April, when seasonal snow accumulations typically peak (Howat and Tulaczyk 2005). Snow depth and SWE are two characteristics of snowpack that influence the amount and extent of spring runoff, and ambient temperatures through June (Cayan 1996). Snow density is a function of temperature conditions and crystal structure during snowfall and of the pressure exerted by total accumulated overburden (Roebber et al. 2003). Dense snows are heavy, unstable on steep slopes, prone to avalanche, and slower to melt in spring. To assess the effects of snowpack on breeding habitat, at weekly intervals I visually estimated the percentage of snow cover that remained on the largest meadow at Tioga Pass from late May onward. This provided an index of snow melt and the availability of newly emergent habitat for nesting and foraging.

Leafing and flowering phenologies of alpine and subalpine flora are strongly affected by snow conditions (Morton 1978, 1994; Høye and Forchhammer 2008; Inouye 2008). The annual flowering schedule of Swamp Onion (*Allium validum*), a conspicuous and abundant wildflower that emerges from wet marshy areas as the snow recedes, is an easily assessed indicator of herbaceous development used in other avian studies at Tioga Pass (Morton 1994, Hahn et al. 2004). Following the method of Morton (1994), I used the annual date on which full flowering occurred in several centrally located patches of *Allium*. *Allium* is pollinated primarily by insects (Currah and Ockendon 1978), and flowering is synchronous within patches (Morton 1994). Because insect emergence is tied to leafing and flowering, and both can be limited by snow melt, *Allium* flowering dates should reflect overall availability of insects for breeding birds. Dusky Flycatchers are primarily aerial insectivores but also take insects from the ground and from vegetation. I monitored seasonal changes in the biomass of flying insects by collecting weekly samples of insects caught in a network of six yellow dishpan traps (36 × 29 × 13 cm) that were filled with a dilute solution of soapy water (3 or 4 drops per tub) and distributed along the central axis of the study area. Insects were strained from the soap solution every 5 days and stored in 70% EtOH. Each sample was later dried and weighed to the nearest 0.01 g. The 5-day mass of insects collected per tub was then used to construct a seasonal profile of relative aerial insect abundance in relation to plant phenology (as represented by *Allium* flowering date). In order to describe variation in phenology, I used as benchmarks the Julian dates of 0% snow cover (annual melt date), *Allium* flowering, and those on which the insect traps yielded 100% of peak aerial insect biomass. The insect profiles reflected changes in the abundance of potential food items available, but because of the diversity of foraging sites and feeding modes used by Dusky Flycatchers, they should not be viewed as indicative of the actual food items selected by individual birds.

Table 1. Description of the environmental variables used in analyses to test for the effects of snow conditions (snowpack), temperatures, and phenological conditions on laying dates of Dusky Flycatchers at Tioga Pass, California. See text for complete explanation of measurements, computations, and sources.

Temperature and precipitation variables	
Ta-min	Mean minimum daily temperatures for month of May, June or July (°C)
Ta-max	Mean maximum daily temperatures for month May, June or July (°C)
Precipitation	Total monthly precipitation for June (expressed in cm)
Snowpack characteristics (for Tioga Pass)	
Snow depth	Snow depth (cm) on 1 April, at maximum seasonal accumulation
Snow density	Density of ice crystal packing (%)
SWE	Snow water equivalent (cm^3) of a given volume of snow, if melted
Annual melt date	Julian date of 0% snow cover on central meadow (= annual melt date)
Phenological indicators	
Peak insect date	Julian date at which 100% of peak insect biomass was captured in traps
Allium flowering date	Date of *Allium* bud break (>75% of flower buds open) on central meadows

Statistical Analyses

Early spring conditions.—Because annual snowpack has pervasive influences on many aspects of the environment, I first analyzed the relationship among 1 April snowpack at Tioga Pass, monthly minimum and maximum temperatures, and precipitation (April–July), and then their combined effects on annual spring melt dates (date of 0% snow cover). I used Pearson product-moment correlations to generate a correlation matrix, from which variables with significant *a priori* potential to affect phenological conditions during the laying period were selected for use in further analyses. These included snowpack characteristics (depth, density, and snow water equivalent), June monthly minimum (Ta-min) and maximum temperatures (Ta-max), June precipitation, and annual melt date (date of 0% snow cover). To place the results in the context of winter snowfall over a longer time course, I used, as points of reference, the long-term mean snow depth at this

location (California Cooperative Snow Survey data, 1927–1995), and monthly temperature norms from National Climatic Data summaries for Ellery Lake, Twin Lakes, and Echo Summit (May–August). Annual departures from the long-term values for mean snow depth and mean monthly temperature were obtained by subtracting annual values for the years of the study from the long-term climatic norms computed for each station by the National Climatic Data Center.

Laying date.—To describe annual variation in laying dates for each year, I extracted the earliest 10%, middle 80% (hereafter "mean annual laying date"), and latest 10% of clutch starts and used backward stepwise multiple regression to examine each (dependent) in relation to a subset of environmental variables (independents) selected from the previously described correlation analysis (see Table 1 for a full description of variables). Predictors entered into the full model included snow depth, annual melt dates (0% snow cover), ambient temperatures (June Ta-min, Ta-max) and total monthly precipitation during June. Two indicators of phenological development (*Allium* flowering dates and peak insect biomass) were also included. Conditions in May and July (Ta-min and Ta-max) were also correlated with snow conditions but were not included in the final analyses as they were outside of the main laying period.

Because multiple regression requires that each dependent variable be modeled as a direct function of two or more independent variables, but cannot specifically address indirect effects through mediating variables, I also performed a path analysis in AMOS, version 19 (SPSS, Chicago, Illinois) on the variables extracted from the original correlation matrix. These were used to construct a model of potential pathways through which laying dates in Dusky Flycatchers might be influenced directly or indirectly by snowpack characteristics, melt dates, and phenological indicators. Path analysis allows for both direct and indirect effects of an independent on a dependent variable, and a given factor can act as both a dependent and independent variable in the same model (annual melt date, for example), depending upon the specified pathway. April snow depth, SWE and June temperatures (Ta-min and Ta-max), and precipitation were included as exogenous, correlated variables ($P < 0.03$). Snow density, another attribute of snowpack, and precipitation can influence snow melt, so both were included as additional exogenous, but uncorrelated, variables. Log likelihood values for this model, with all of the specified pathways, did not indicate significant departure of the data from the specified model at saturation ($\chi^2 = 14.323$, df = 15, $P = 0.501$), or after reduction by sequential exclusion of nonsignificant pathways ($\chi^2 = 27.681$, df = 24, $P = 0.274$). Path coefficients (standardized regression coefficients, β) were considered to represent a potentially significant causal effect between one variable and another if $P < 0.05$.

Reproductive output.—I tested for an influence of timing of breeding on breeding productivity by comparing dates of the onset of laying, clutch size, brood size, and nest success (percentage of nests that fledged at least 1 nestling) between years of light or heavy snowpack. For the latter analyses, I separated years into those with a winter snowpack that was below or above the long-term (78-year) mean. Additional analyses of the influence of snow depth on reproduction were based on *Z*-scores of annual snowpack in which years were classified as light (*Z*-score < −0.5), moderate (*Z*-score between −0.5 and +0.5), or heavy (*Z*-score > 0.5).

Most statistical analyses (linear and stepwise multiple regression, Pearson-product correlation analyses, GLM procedures) were performed using SPSS software. The path analysis was conducted using AMOS. Most variables met the necessary assumptions for the use of parametric statistics. Those that did not (e.g., insect biomasses) were log-transformed as necessary to normalize their distributions or, in the case of clutch size and brood size, were tested using nonparametric tests (SPSS exact tests; Mehta and Patel 1996). Means ± SE are reported for all comparisons, and standardized β values are reported in lieu of, or along with, raw regression coefficients to better enable comparisons of effect among significant predictor variables.

Results

Laying schedules of Dusky Flycatchers varied significantly among years ($F = 14.351$, df = 14 and 693, $P < 0.0001$), with evidence of a small advance in mean laying date over the course of the study (0.52 days year^{-1} over a 15-year period, $n = 708$ nests, 1981–1995; standardized $\beta = -0.172$, $t = -4.426$, $P < 0.0001$; Fig. 1A). The wide range in mean laying dates for first clutches, from 16 June to 9 July (overall mean = 26 June ± 11 days, $n = 544$ first clutches; analysis of variance, $F = 22.845$, df = 14 and 530, $P < 0.0001$), suggested a strong influence of one or more environmental factors on laying date.

Annual variation in spring conditions.—Environmental conditions that could influence laying date—temperatures, precipitation, and snowpack characteristics (depth, SWE, and density)—all varied from year to year, but without consistent increase or decrease over the years of the study (April snow depth, Fig. 1B; April–June temperatures, Fig. 1C–E; $F \leq 0.1$ for comparisons across 15 years, $P > 0.1$). Over shorter time spans, snow depth and temperature varied in relation to wet and dry cycles along the west coast. Annual April snow depths ranged from 90.9 to 375.7 cm (mean = 187.2 ± 22.8, $n = 15$ years; Fig. 2A), with exceptionally heavy snowpacks occurring in 1982, 1983, and 1995 (Fig. 2A) but significant shortfalls in the years between 1983 and 1994. A significant decline in April snow depths during this period (snow depth = −13.62 [year] + 27256, $\beta = -0.627$, $t = -2.66$, $P = 0.021$) and mean monthly June temperatures from 1985 through 1995 (June Ta-min, $F = 23.282$, df = 1 and 9, $P < 0.001$, $r^2 = 0.721$, slope = −0.472 ± 0.098, $\beta = -0.849$) corresponded to several years of persistent drought. Within this pattern, Ta-min (May–July) were negatively correlated with annual snow depth (May: $r = -0.627$, $P = 0.012$; June: $r = -0.660$, $P = 0.007$; July: $r = -0.567$, $P = 0.027$), and increased snow depth was associated with delayed annual melt dates (melt date = 137.9 + 0.245 [snow depth]; $r^2 = 0.88$, $P < 0.001$, $n = 15$ years). Increased snow depth, density, snow water equivalent, and annual melt date were, in turn, correlated with delayed flowering and insect emergence (Table 2).

Association of environmental factors with timing of the earliest 10%, middle 80%, and latest 10% of clutches.—Annual departures above and below the long-term average snow depth (Fig. 2A,B) were strongly associated with variation in the timing of breeding and overall laying schedule of Dusky Flycatchers (Fig. 2C). Over 90% of first clutches were initiated by the last week of June in years of low snowpack, but fewer than half of

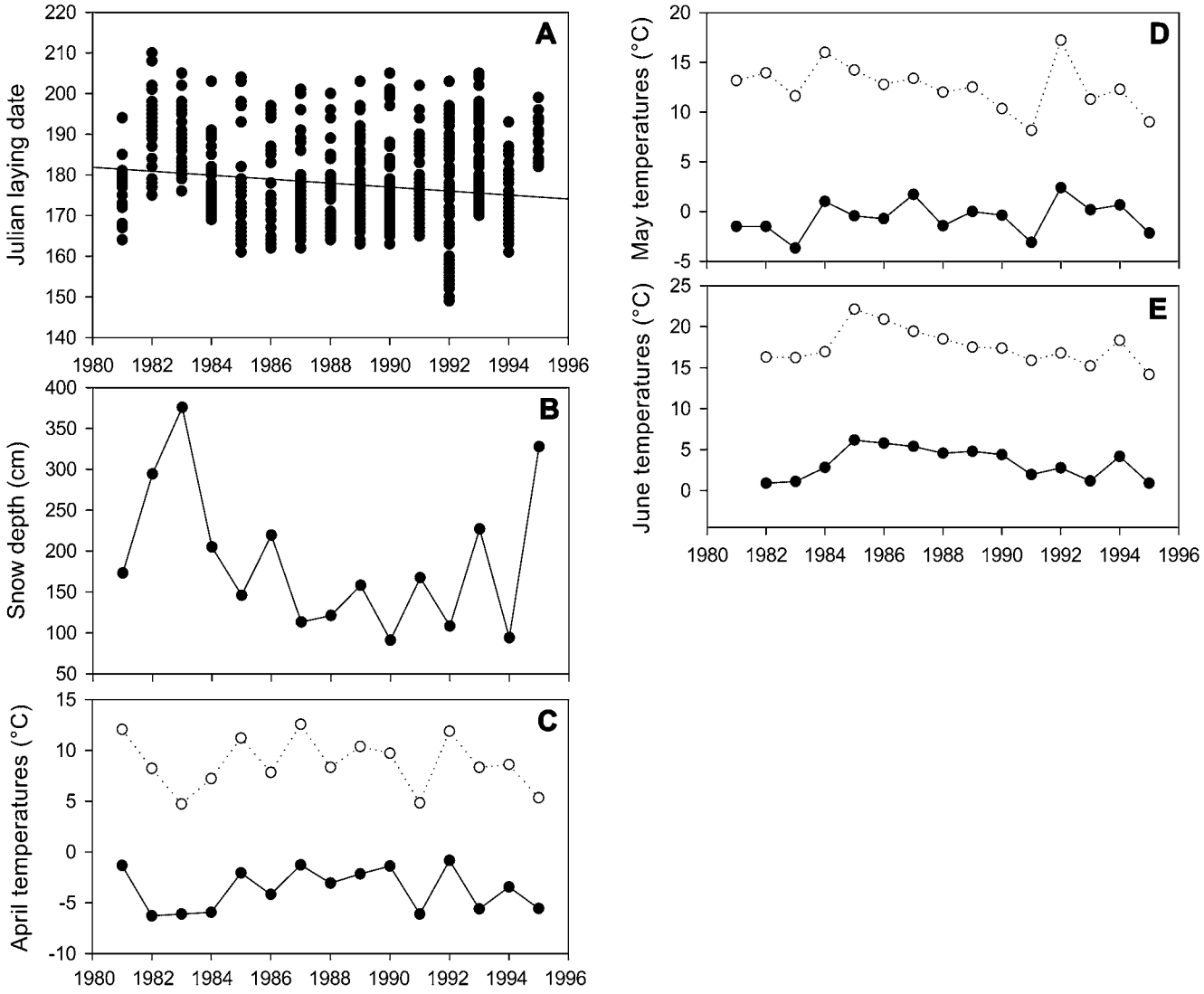


Fig. 1. Variation in Dusky Flycatcher laying dates at Tioga Pass, in the eastern Sierra Nevada of California, in relation to climatic conditions during the study period (1981–1995). Each solid black circle (panel A) represents a clutch start (regression equation for mean laying dates of clutch starts across years: $y = -0.518$ (year) + 1207, $F = 19.587$, df = 1 and 707, $P < 0.001$). Snowpack conditions are represented by 1 April snow depths at Tioga Pass (panel B) during the study period. Temperature data consist of monthly minimum (solid black circles) and maximum values (open circles) for April (panel C), May (panel D), and June (panel E) averaged among sites along the Sierra Nevada (see text). Regressions for each variable with time, across all 15 years, were not significant (F values < 0.1 and P values > 0.1); however, snowpack declined from 1983 to 1994 and June temperatures from 1985 to 1995 (see text).

nests contained eggs by this date in years of heavy snow (Fig. 2C; Kolmogorov-Smirnov $Z = 5.17$, $P < 0.0001$).

Although snow depth alone accounted for 85% of the variation in annual mean laying dates of the middle 80% of first clutches (mean laying date = 0.065 [snow depth] + 166.44 $r^2 = 0.845$; $F = 61.30$, df = 1 and 13, $P < 0.0001$), other variables—such as temperature and phenological conditions, which correlated with snow conditions (Table 2)—also contributed (Table 3). Using backward stepwise multiple regression, significant predictors of variation in annual laying date for the first two portions of the schedule (earliest 10%, middle 80%) included snow depth, annual melt date, and date of peak insect biomass (Table 3). Temperature and *Allium* flowering dates were also significant predictors, but only for the first 10% of clutches. For mean annual laying dates (middle 80%), precipitation replaced temperature as a predictor (Table 3). For the last 10% of laying dates, none of these variables made significant contributions in either full or reduced multiple regression models (Table 3).

Although dates of *Allium* flowering and peak insect biomass were significant predictors of variation in the initial 10% and middle 80% of annual laying dates, they too were delayed by deeper snow (Table 2 and Fig. 3A). Because annual laying dates generally

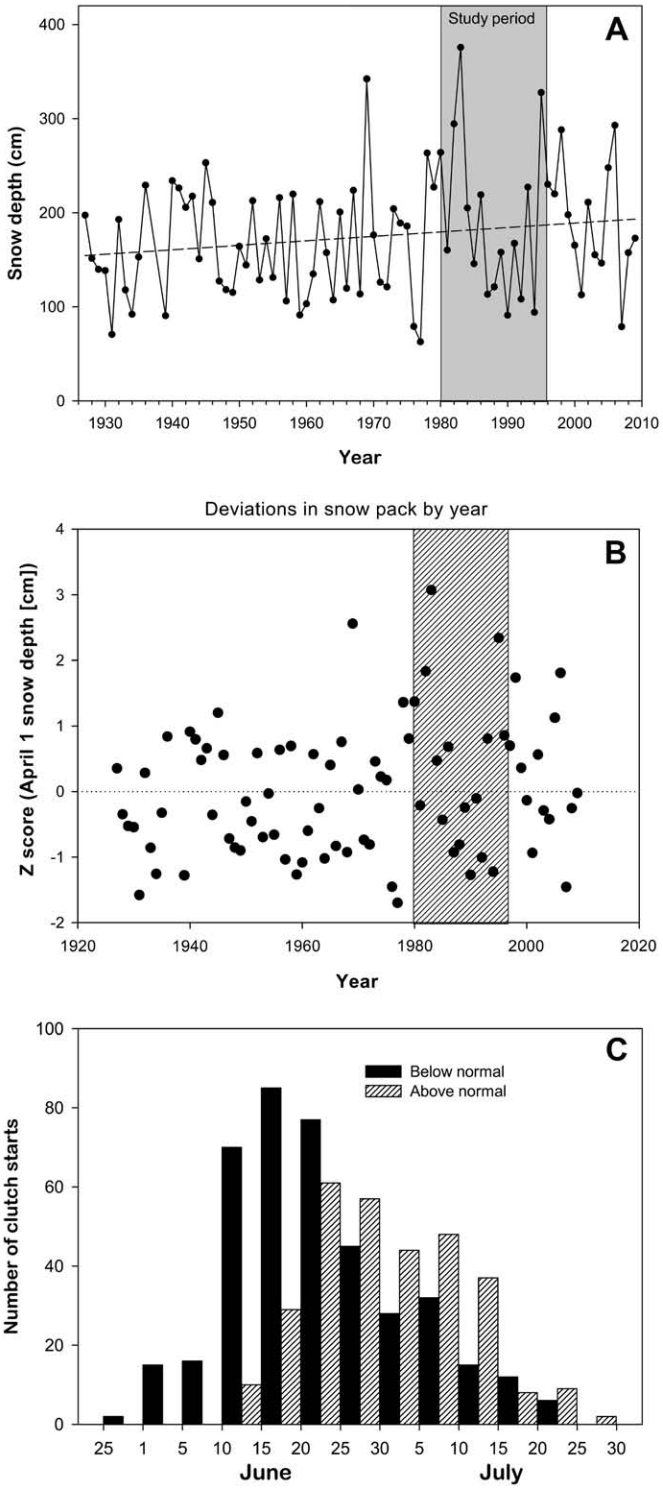


Fig. 2. Snow depths on 1 April at Tioga Pass, California, between 1981 and 1995 (A, shaded area) in relation to 78 years of long-term California Cooperative Snow Survey data (A, unshaded area), deviations from long term mean (B) and seasonal distribution of clutch starts (C) for Dusky Flycatchers in years of below-normal versus years of above-normal snowpack for nests in which clutch initiation dates were known.

Table 2. Pearson product-moment correlation coefficients (r) between annual snowpack characteristics (snow depth, SWE, density), June minimum and maximum temperatures, and melt schedule (as represented by Julian date of complete snow melt), and their correlation with Julian dates of *Allium* flowering and peak insect abundance between 1981 and 1995 at Tioga Pass, California. The date of peak insect abundance and *Allium* flowering date represent the Julian dates at which seasonal peak biomass (dry weight) of captured insects [g]) and peak flowering occurred. Snow depth (cm), SWE (cm^3), snow density (% water) measurements are for 1 April (source: California Cooperative Snow Survey). Mean minimum and maximum temperatures were regional means for several high-elevation sites along the crest of the Sierra Nevada (see text). Correlation coefficients and associated P values that were significant ($P < 0.05$) are in bold.

	Annual melt date r (P)	*Allium* flowering date r (P)	Date of peak insect abundance r (P)
Snow depth	**0.935 (<0.001)**	**0.927 (<0.001)**	**0.800 (0.003)**
SWE	**0.944 (<0.001)**	**0.894 (<0.001)**	**0.644 (0.022)**
Snow density	**0.601 (0.019)**	0.366 (0.121)	**0.892 (<0.001)**
June Ta-min	**–0.659 (0.010)**	**–0.790 (0.001)**	–0.148 (0.352)
June Ta-max	–0.329 (0.148)	**–0.574 (0.025)**	0.111 (0.388)
Annual melt date		**0.903 (<0.001)**	**0.859 (0.001)**

preceded dates of flowering (mean difference from earliest 10% to flowering: 42.3 ± 2.1 days) and dates of peak insect biomass (earliest 10% to peak: 30.8 ± 5.4 days), it was unlikely that the regression results reflected a direct effect of either of these variables on laying date. Annual mean laying dates overlapped with dates of peak insect biomass only in years of below-normal snowpack (Fig. 3A) and were increasingly out of synchrony with phenological indicators as snow depth increased (Fig. 3B). The difference between the Julian dates of laying and Julian dates of peak *Allium* flowering and insect emergence increased with snow depth (time to *Allium* flowering: $r = -0.604$, $P = 0.017$; time to peak insect biomass: $r = -0.835$, $P < 0.001$), which suggests that the apparent effects of these phenological indicators on timing of breeding were actually indirect consequences of their mutual, but unequal, dependence on snowpack.

To help distinguish between direct and indirect effects of snowpack on laying dates, I constructed a model specifying a set of pathways through which snowpack (depth, density, SWE), temperature (June Ta-min, Ta-max), and precipitation (June total) could either directly or indirectly influence mean annual laying dates (Fig. 4). Significant path coefficients positing direct effects of temperature, snow depth, and density on earliest 10% and mean annual (middle 80%) laying dates (negative for Ta-max, indicating earlier onset with warmer temperatures; positive for snow depth and density, indicating delayed laying with heavier snowpack; Table 4) supported the hypothesis that these factors influenced laying behavior directly (Fig. 4). Path coefficients linking laying dates to snow depth, density, and temperature (June Ta-min) through the mediating effects of melt date were also significant (Fig. 4). In contrast to the multiple regression analyses (Table 3), the path analysis of the last 10% of clutches revealed subtle effects of seasonal conditions, most notably the effects of extended snow melt (via SWE) and June precipitation on annual variability in laying (Table 4).

Table 3. Multiple regression models predicting annual laying dates in Dusky Flycatchers for the first 10%, middle 80%, and last 10% of clutch starts in relation to environmental conditions at Tioga Pass, California, between 1981 and 1995. Response variables (annual laying dates) were regressed on annual 1 April snow depth, melt date (date of 0% snow cover), June temperatures (monthly minimum [Ta-min], maximum [Ta-max]), total June precipitation (ppt), and two phenological indicators (*Allium* flowering date, date of peak insect biomass). Results include regression statistics for full model with all predictors included, and the model containing a reduced (best) set of predictors, after backward stepwise removal of variables that did not meet tolerance for further inclusion. Correlation coefficients for each variable in the model include Pearson's correlation, partial correlation, controlling for the effects of other independent variables in the model, and part correlation, reflecting the unique effect of the independent variable on the response variable. *P* values that were significant ($P < 0.05$) are in bold.

								Correlations (*r*)		
	Predictors	Slope	SE	β	*t*	*P*	r^2	Pearson's	Partial	Part
Full model	(constant)	357.371	52.555		6.800	**<0.0001**	0.941			
(first 10%)	Snow depth	0.185	0.042	2.066	4.386	**0.003**		0.841	0.856	0.404
	Melt date	0.401	0.108	1.213	3.708	**0.008**		0.842	0.814	0.341
	June Ta-min	0.375	1.594	0.093	0.235	0.821		–0.622	0.089	0.022
	June Ta-max	–1.658	0.997	–0.467	–1.663	0.140		–0.533	–0.532	–0.153
	June ppt	–0.339	0.500	–0.095	–0.679	0.519		0.266	–0.249	–0.063
	Allium flowering date	–0.989	0.275	–1.544	–3.592	**0.009**		0.761	–0.805	–0.331
	Peak insect date	–0.336	0.109	–1.115	–3.074	**0.018**		0.725	–0.758	–0.283
Reduced	(constant)	357.626	47.149		7.585	**<0.0001**	0.935			
	Snow depth	0.188	0.038	2.093	4.889	**0.001**		0.841	0.852	0.415
	Melt date	0.427	0.095	1.294	4.501	**0.001**		0.842	0.832	0.382
	June Ta-max	–1.202	0.401	–0.339	–2.998	**0.015**		–0.533	–0.707	–0.255
	Allium flowering date	–1.029	0.225	–1.606	–4.565	**0.001**		0.761	–0.836	–0.388
	Peak insect date	–0.363	0.090	–1.202	–4.017	**0.003**		0.725	–0.801	–0.341
Full model	(constant)	222.548	30.869		7.209	**<0.0001**	0.967			
(middle 80%)	Snow depth	0.105	0.025	1.488	4.234	**0.004**		0.908	0.848	0.291
	Melt date	0.169	0.063	0.650	2.661	**0.032**		0.856	0.709	0.183
	June Ta-min	–0.063	0.936	–0.020	–0.067	0.948		–0.803	–0.025	–0.005
	JuneTa-max	–0.348	0.586	–0.124	–0.593	0.572		–0.653	–0.219	–0.041
	June total ppt	0.447	0.293	0.159	1.523	0.171		0.467	0.499	0.105
	Allium flowering date	–0.207	0.162	–0.411	–1.281	0.241		0.915	–0.436	–0.088
	Peak insect date	–0.240	0.064	–1.009	–3.729	**0.007**		0.729	–0.816	–0.256
Reduced	(constant)	178.031	7.532		23.635	**<0.0001**	0.955			
	Snow depth	0.083	0.015	1.179	5.652	**0.000**		0.908	0.873	0.381
	Melt date	0.137	0.052	0.528	2.662	**0.024**		0.856	0.644	0.179
	June ppt	0.579	0.207	0.205	2.788	**0.019**		0.467	0.661	0.188
	Peak insect date	–0.216	0.045	–0.910	–4.860	**0.001**		0.729	–0.838	–0.327
Full model	(constant)	129.768	102.839		1.262	0.247	0.357			
(last 10%)	Snowpack	–0.026	0.083	–0.493	–0.318	0.760				
	Melt date	0.055	0.211	0.281	0.261	0.802				
	June Ta-min	1.365	3.120	–0.572	–0.438	0.675				
	June-Ta-max	1.492	1.951	0.707	0.765	0.469				
	June ppt	0.986	0.978	0.463	1.009	0.347				
	Allium flowering date	0.289	0.539	0.758	0.536	0.609				
	Peak insect date	–0.094	0.214	–0.523	–0.438	0.674				
Reduced	(constant)	174.157	20.670		8.426	0.000	0.000			
	Allium flowering date	0.131	0.099	0.344	1.320	0.210				

To what extent might Dusky Flycatchers adjust the end of the breeding schedule to compensate for later onset of breeding and later phenological development to maintain a breeding season of constant length? If shifts in the timing of the onset of breeding are matched by concomitant shifts in time of breeding termination, separate linear regressions relating either the first or last 10% of laying dates to annual snow depth (Fig. 5A, B) would be expected to change in parallel. Alternatively, converging lines would suggest that sensitivity to prevailing environmental factors differs between start and end of breeding. The slope of the regression line for the laying date of the earliest 10% of clutches was significantly steeper than that for the latest 10% (Fig. 5A, B; difference between slopes = 0.215, $t = 5.663$, $P < 0.0001$), indicating a progressive reduction in the length of the breeding season as spring snow depth increased (difference between earliest and latest laying dates vs. 1 April snow depth, $r = -0.653$, $P = 0.008$, $n = 15$). Overall, the duration of the laying season was a month or less in heavy snow years (mean duration = 30.3 days, range: 14–35 days, $n = 6$) as compared with years at or below normal in snowpack (mean duration: 39.2 ± 7.0 days, range: 35–54, $n = 9$; *t*-test, $t = 2.234$, df = 13, $P = 0.044$).

Association of environmental factors with clutch size, brood size, and potential productivity.—Differences in mean laying

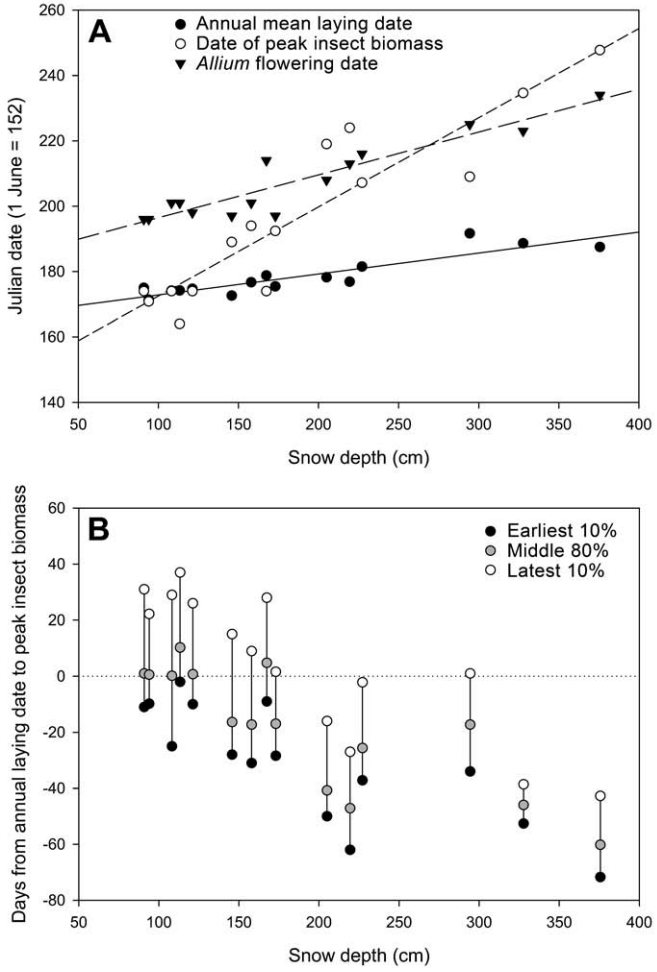


Fig. 3. Mean annual laying date (middle 80% of clutch starts) of Dusky Flycatchers (black filled circles) and annual dates of peak insect biomass (open circles) and *Allium* flowering (black filled triangles) in relation to April snow depth at Tioga Pass, California (panel A), and number of days from annual laying dates (earliest 10%, middle 80%, latest 10% of clutch starts) to date of peak insect biomass (panel B) as a function of snow depth. Annual laying schedules below the zero-line (date of peak insect biomass) were laid in advance of the peak in that year, and positive values after the peak.

dates among years of light, moderate, and heavy snowpack (Fig. 6A) translated into small but statistically significant differences in mean initial clutch size (Fig. 6B; 3.59 ± 0.02, n = 492; Kruskal-Wallis, H = 7.122, df = 2, P = 0.028). Mean clutch size was significantly larger in years of light snowpack than in years of moderate to heavy snowpack (Jonckheere-Terpstra test, standardized J-T statistic: -2.744, P = 0.006). Consequently, more young fledged per nest in years of below-normal snowpack (3.3 ± 0.06 fledglings nest^{-1}, n = 197 nests) than in years of above-normal snowpack (2.8 ± 0.08 fledglings nest^{-1}, n = 148 nests; Mann-Whitney U, Z = –2.491, P = 0.013).

Because mean annual clutch size declined as mean annual snow depth increased (Spearman's r = –0.676, P < 0.0001, n = 15), the number of fledglings produced annually by the population also declined as snow depth in April increased (Spearman's r = –0.438, P = 0.036). This was due, in part, to shorter breeding seasons in years of deep April snowpack and to the positive relationship between length of laying season and the total number of fledglings produced (Spearman's r = 0.724, P = 0.002). The number of breeding territories varied little among years (45–50 territories), but in the heaviest snow years, fewer clutches were produced by the first 2 weeks of July. The percentage of nests to produce at least one fledgling was modestly, but not significantly, higher in years of below-normal (212 of 402 nests, 52.7%) than in years of above-normal snowpack (132 of 291 nests, 45.3%; χ^2 = 3.673, df = 1, P = 0.065). However, the likelihood that a failed nest would be replaced declined through June and into July, and very few replacement nests were built after 15 July (Fig. 7). Thus, the combined effects of an elevated number of young produced per nest in years of light snowpack (see above) and increased probability of renesting in early years of light snowpack resulted in two-thirds more young being produced by the population in years of light (82.6 ± 9.5, n = 9) than in years of heavy snowpack (49.3 ± 10.9, n = 6; t = 2.25, df = 13, P = 0.042).

Discussion

Highly variable annual breeding schedules of Dusky Flycatchers at Tioga Pass, and a slight, but statistically significant, trend toward an earlier onset of breeding between 1981 and 1995 suggest that Dusky Flycatchers are highly sensitive to one or more of the environmental variables that were measured, and that some of these may have changed in a consistent manner. Arrival and settlement times, which have advanced in some migrants (Mason 1995, Butler 2003, Marra et al. 2005), occurred at comparable dates from year to year (Pereyra 1998), which suggests that laying schedules were largely shaped by responses to local conditions rather than changes in migration schedules. Two climatic conditions that have undergone recent change in many mountain ranges of western North America and Europe are temperature and snowfall (Diaz and Bradley 1997, Mote et al. 2005). Winter precipitation in the Sierra Nevada has become more variable, in part because of warmer autumn and winter temperatures (Dettinger and Cayan 1995, Christy et al. 2006). At low to moderate elevations (below 1,500 m) this has led to more rainfall, lighter winter snowpacks, and earlier spring snow melt (Stewart et al. 2005, Maurer et al. 2007). At higher elevations, where temperatures change more slowly, subfreezing temperatures ensure that most precipitation falls as snow. Snowfall accumulations, which can be extreme in these environments, are generally more strongly related to anomalous precipitation events than to changes in temperature (Cayan 1996, Hamlet et al. 2005, Knowles et al. 2006).

For Dusky Flycatchers breeding at Tioga Pass (3,000 m), spring snowpack (depth, density, SWE) and ambient temperatures were the factors that affected laying schedules most strongly. Inclement spring weather, including both rain and snowfall, was common and can delay laying in some females (Pereyra and Wingfield 2003), but spring precipitation was not a significant predictor of annual variation in laying schedules across years. In relation to snow depth and density, earliest and mean annual laying dates in Dusky Flycatchers were later in years of heavy spring snowpack

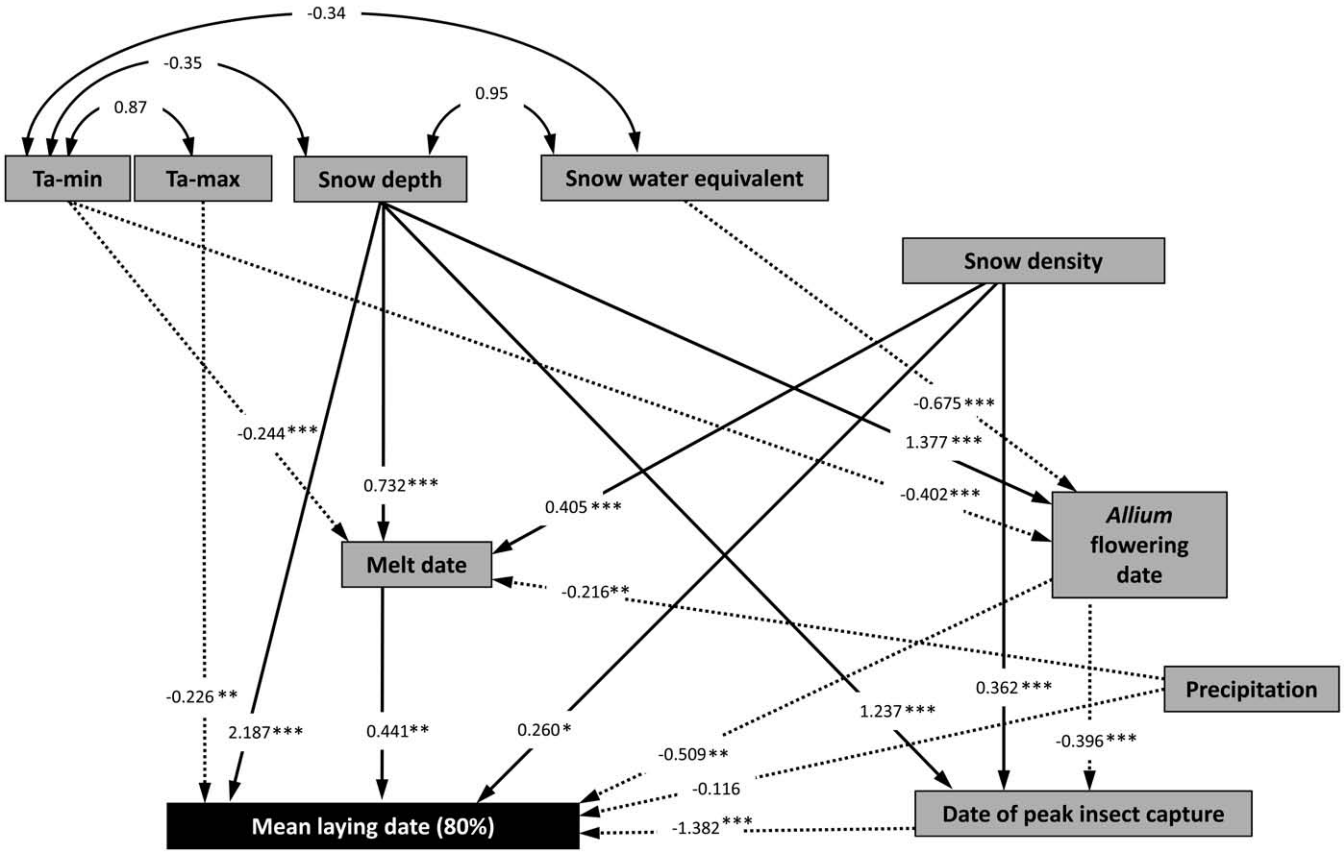


Fig. 4. Path analysis model of potential pathways through which environmental factors (snow depth, snow water equivalent, density, June maximum and minimum temperatures, June precipitation, annual melt date, and phenological indicators such as *Allium* flowering date and date of peak insect biomass) could directly or indirectly influence mean annual laying date of Dusky Flycatchers at Tioga Pass, California. Statistically significant path coefficients that were positive are indicated with solid black arrows, and those that were negative are indicated with dashed arrows. The absence of an arrow between two variables indicates a pathway that was tested but found to be nonsignificant and, hence, subsequently omitted from the final model. Standardized regression coefficients (β) for statistically significant pathways ($P \leq 0.05$) are indicated on their respective arrows (absence of asterisk, $P = 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Table 4. Results of path analysis (unstandardized regression coefficients [± SE], standardized regression coefficients [β], and *P* values) performed on the model in Figure 4. Standardized path coefficients linking environmental variables (snow characteristics [snow depth, water equivalent, density], June temperature, precipitation, annual melt date, and phenological indicators [*Allium* flowering date, date of peak insect biomass]) to annual laying dates of Dusky Flycatchers at Tioga Pass, California (first 10%, middle 80%, last 10%), that were significantly different from zero are in bold, as are significant *P* values.

Independent variable	First 10%			Middle 80%			Last 10%		
	Coefficient ± SE	β	*P*	Coefficient ± SE	β	*P*	Coefficient ± SE	β	*P*
SWE	–0.248 ± 0.131	**0.501**	**0.000**	0.010 ± 0.029	0.070	0.744	0.300 ± 0.078	**2.632**	0.000
Ta-min	1.948 ± 0.561	**0.444**	**0.000**	–0.207 ± 0.620	–0.064	0.738	0.526 ± 1.651	0.196	0.750
Ta-max	–1.409 ± 0.307	**–0.413**	**0.000**	–0.571 ± 0.191	**–0.226**	**0.003**	1.806 ± 0.568	**0.882**	**0.001**
Snow depth	0.054 ± 0.019	**1.183**	**0.004**	0.139 ± 0.022	**2.187**	**0.000**	–0.240 ± 0.059	**–4.648**	**0.000**
Melt date	0.532 ± 0.065	**1.357**	**0.000**	0.114 ± 0.044	**0.441**	**0.010**	0.073 ± 0.117	0.362	0.534
Density	–0.776 ± 0.120	**–0.590**	**0.000**	0.241 ± 0.111	**0.260**	**0.031**	0.273 ± 0.296	0.358	0.356
Precipitation	0.131 ± 0.163	0.036	0.421	0.295 ± 0.153	–0.116	0.054	0.731 ± 0.342	**0.354**	**0.032**
Allium date	–0.753 ± 0.122	**–1.147**	**0.000**	–0.257 ± 0.086	**–0.509**	**0.003**	0.899 ± 0.255	**2.195**	**0.000**
Insect date	–0.157 ± 0.081	–0.472	0.053	–0.320 ± 0.055	**–1.382**	**0.000**	–0.197 ± 0.148	–1.144	0.185

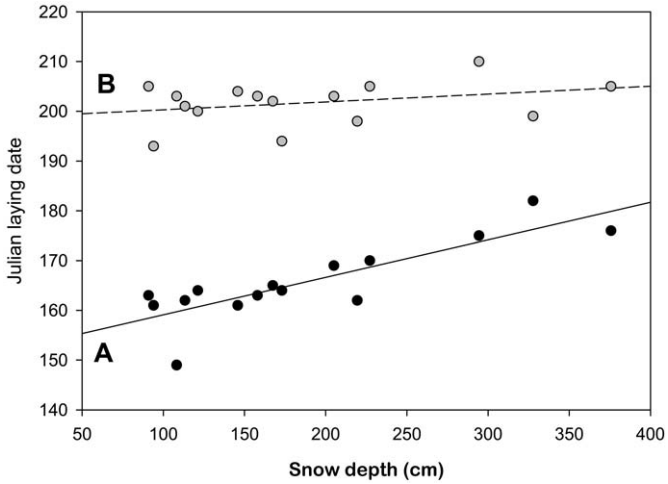


Fig. 5. Relationship between April snow depth and annual laying dates and length of the laying season of Dusky Flycatchers at Tioga Pass, California (represented as the distance between the regression lines), over the 15 years of the study (1981–1995). Points represent annual laying dates for (A) earliest (solid black circles, solid regression line) and (B) latest (gray circles, dashed regression line) 10% of clutches laid in each season with respect to 1 April snowpack measurements at Tioga Pass.

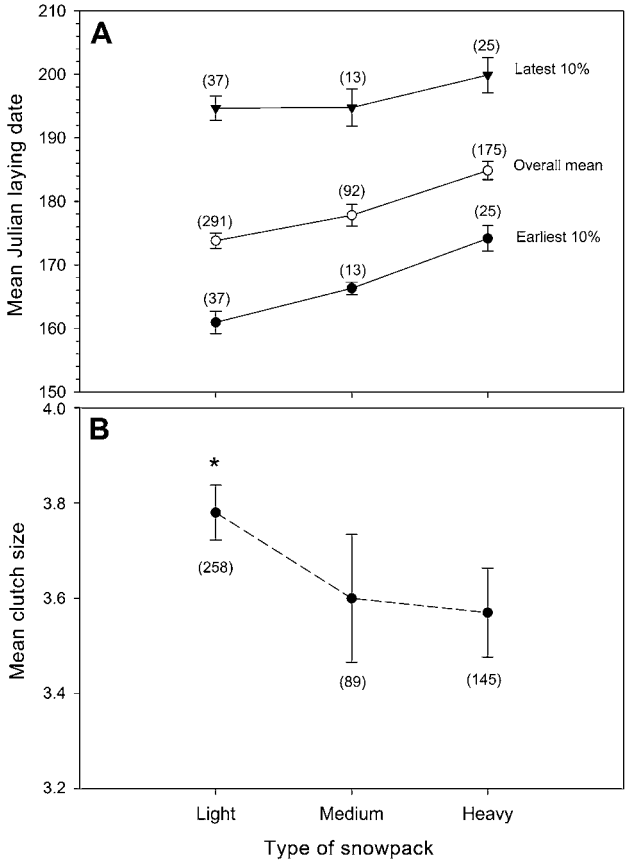


Fig. 6. Mean laying date and clutch size (± 2 SE) of Dusky Flycatchers at Tioga Pass, California, between 1981 and 1995 with respect to snowpack conditions (light, medium or normal, and heavy snow years) in the Sierra Nevada. Mean laying dates for earliest and middle 80% of clutches differed significantly between years of light, medium, and heavy snow ($P < 0.001$), but not for the latest 10%. Latest laying dates were only marginally delayed in heavy snow years, and significantly only between heaviest and lightest years ($P < 0.05$).

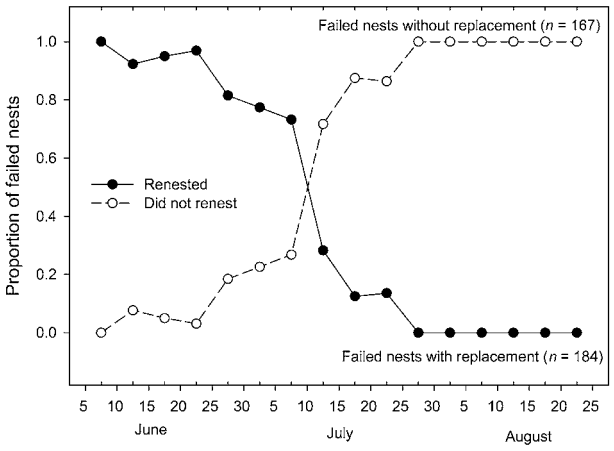


Fig. 7. Proportion of Dusky Flycatcher nests at Tioga Pass (1981–1995) that failed in each 5-day seasonal interval that were either replaced (solid black circles) or not replaced (open circles). Nests that failed after 15 July were generally not replaced.

and low temperatures, and earlier in years of light snowpack and high spring temperatures. Snow depth and density influenced laying dates directly, as well as indirectly through the mediating influence of melt date. Melt date, in turn, was influenced by June mean minimum temperatures and total monthly precipitation (both rain and snow). Surprisingly, the effects of snow-related variables on flowering dates and time of peak insect abundance, which were both correlated with annual laying dates, appeared to be exerted through the suppression of phenological development by snow itself, rather than through melt date ($\beta \approx 0$ in both cases). Temperature and phenological indicators are correlated with laying dates in other species (Winkler et al. 2002, Thomas et al. 2010, Wiebe and Gerstmar 2010), and in Dusky Flycatchers these together accounted for a significant proportion of the variation in timing of laying. However, correlations became weak or nonsignificant after controlling for the effects of snow depth, and in many years clutches were laid well in advance of leafing or flowering and before substantial numbers of flying insects were captured in pan traps. Hence, females were not dependent on some critical threshold of phenological development in plant and insect communities to initiate laying.

Snow cover often retards the onset of laying among birds that nest on or close to the ground (Morton 1978, 1994, 2002; Hahn et al. 1995, 2004). Dusky Flycatchers are probably less directly affected by snow cover because they nest above ground in shrubs and trees. Nonetheless, snow cover retarded phenological development in some of their preferred habitat. On some heavily snow-laden territories, portions of habitat remained covered for most of the season, and some female Dusky Flycatchers on those territories failed to lay eggs despite their construction of a nest (M. E. Pereyra unpubl. data). In heavy snow years, conditions that would normally be encountered in June may not occur until mid- to late July, or even August (e.g., see fig. 1A and 1B in Hahn et al. 2004 and plate 1 in Morton 2002). For Dusky Flycatchers, the emergence of

suitable conditions by mid-July, when most females ceased to renest, had little if any stimulatory effect on further laying, and there was little evidence that the laying season could be extended to take advantage of ameliorating conditions.

Potential fitness consequences of variation in reproductive timing.—In many birds, including other tyrannids, clutch sizes decline steadily over the course of the season (Murphy 1983, 1986). Maximum clutch sizes early in the breeding period presumably reflect strategies that optimize success under conditions of strong environmental seasonality (Cody 1966, Morton 1976, Hannon et al. 1988). Early clutches are often more successful (Perrins 1970, Verhulst et al. 1995, Arnold et al. 2004, Verhulst and Nilsson 2008), and at Tioga Pass clutch sizes declined rapidly from mid-June onward (Morton and Pereyra 2004). In years of heavy snow, delayed laying in Dusky Flycatchers resulted in small but significant reductions in the number of young fledged per female and the total number of fledglings produced on the study area. The percentage of clutches that fledged at least one chick did not differ between years of light and heavy snowpack, but the likelihood that a failed nest would be replaced was greatest early in the season and declined precipitously after the first week of July. A delayed start to breeding thus resulted in substantially lower productivity for individual females and the entire population.

Physiological capacity for evolutionary shifts in response.—Natural selection should favor females that initiate clutches early and produce replacement clutches quickly, particularly where growing seasons are brief and nest failure is common (Martin and Wiebe 2004). Many successful alpine, subalpine, and subarctic passerines exhibit these behaviors, and conditions that delay nesting in these species may only moderately affect their ability to complete one or more nesting cycles before the season ends.

However, for passerines like Dusky Flycatchers that have longer periods of postnatal development and parental care (Pereyra and Morton 2001), even small shifts in timing may create constraints that strongly influence success. The wide distribution of Dusky Flycatchers across the mountains of western North America and evidence of recent northward range expansions (Campbell et al. 1997, Eckert 1998) suggest that, despite their relatively long reproductive cycle, Dusky Flycatchers are well adapted to the extreme conditions of high-elevation environments. The dominant factor influencing timing of breeding, and ultimately individual productivity, is snowpack. In the absence of inhibition by extensive snow cover or associated conditions, factors such as warmer temperatures and rapid phenological development may accelerate the onset of laying, but there is little evidence that laying can be substantially extended beyond the current date at which laying ends.

The sensitivity of the underlying neuroendocrine system to stimulatory cues changes seasonally in birds (Ball 1993, Dawson and Sharp 2007, Dawson 2008, MacDougall-Shackleton et al. 2009), such that factors that might stimulate reproductive activity early in the season are no longer effective at the end, which in Dusky Flycatchers appeared to occur in mid-July. Declines in responsiveness to stimulatory cues, through the development of photorefractoriness, help to end reproduction before conditions become unfavorable for survival of nestlings and fledglings (e.g., Dolan et al. 2009) or for completion of postreproductive activities, including migration. Although this relatively rigid termination schedule presumably confines breeding to a brief and optimal period, it may also make birds less able to adjust to favorable environmental conditions that lie outside of this period and, in particular, may constrain responses when reproduction is delayed. Paradoxically, a warmer, wetter climate in western North America may lead to hotter, drier conditions in summer and fall, more winter precipitation falling as rain rather than snow at moderate elevations (1,300–2,000 m) where mean temperatures are close to freezing (Cayan 1996), but heavier winter snowpacks and delayed spring melt at higher elevations (e.g., ≥2,800 m; Howat and Tulaczyk 2005, Maurer et al. 2007). Even small reductions in clutch size and fledgling production because of delayed reproduction at higher elevations might be expected to favor birds that select habitats at lower elevations or other locations that consistently experience an earlier melt of winter snow. This suggests the potential for regulatory processes such as photorefractoriness to canalize ecophysiological responses to changing conditions that could, in turn, influence distributional patterns.

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