Great Basin Naturalist

Volume 54 | Number 4 Article 10

10-25-1994

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Recommended Citation
Morton, Martin L. (1994) "Comparison of reproductive timing to snow conditions in wild onions and White-crowned Sparrows at high altitude," *Great Basin Naturalist*: Vol. 54 : No. 4 , Article 10.
Available at: https://scholarsarchive.byu.edu/gbn/vol54/iss4/10

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Great Basin Naturalist 54(4), © 1994, pp. 371–375

COMPARISON OF REPRODUCTIVE TIMING TO SNOW CONDITIONS IN WILD ONIONS AND WHITE-CROWNED SPARROWS AT HIGH ALTITUDE

Martin L. Morton[1]

ABSTRACT.—Timing of reproduction was assessed for wild onions and White-crowned Sparrows in relation to snow conditions on the same subalpine meadow in the Sierra Nevada for 21 years. Flowering date and clutch initiation date were both highly correlated with snow conditions, being later as snowpack was deeper. Interannual variation in schedule was 46 days for onions and 33 days for sparrows. There was nearly a fivefold difference in snowpack depth, and date of snow disappearance varied interannually by 72 days. Compensation for late-lying snows occurred in both species but was greater in sparrows than in onions because the nest-building behavior of sparrows was flexible. In years of deeper snow, sparrows were able to lay eggs earlier because they built more nests than usual in trees and shrubs rather than waiting for groundcover to develop.

Key words: Allium, Zonotrichia, *snowpack, high altitude, proximate factors, reproduction.*

Montane settings are useful for the study of environmental adaptation in organisms because their brief, sharply delimited growing seasons and variable climates can be potent agents of natural selection. Diurnal and seasonal cycles of abiotic factors, principally air temperature (Ta), moisture, and wind speed, shift in level and amplitude as elevation increases (Rosenberg 1974). The resulting decrease in mean Ta, high winds, decreased availability of soil moisture due to freezing, and variable snowpack can greatly influence the phenology, distribution, and productivity of plants (Billings and Bliss 1959, Scott and Billings 1964, Weaver and Collins 1977, Ostler et al. 1982). Annual schedules of reproduction and survival of hibernating mammals (Morton and Sherman 1978) as well as reproductive success of both sedentary (Clarke and Johnson 1992) and migratory birds (Morton 1978, Smith and Andersen 1985) also are known to be affected, especially by spring storms and snowpack depth. It follows that long-term studies of the annual rhythm of reproduction of organisms at high altitude should provide valuable information for understanding the pathways and scope of adaptations to climatic conditions and for determining the efficacy of environmental variations to act as cues or proximate factors in the control of reproduction schedules. Such studies are few, however, and, to my knowledge, there are none that have compared plants and animals on the same study area. Herein I present 21 seasons of data that index reproductive schedules of the wild onion (*Allium validum*) and the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) at the same location in the Sierra Nevada in relation to interannual variations in snow conditions.

MATERIALS AND METHODS

The study site, Tioga Pass Meadow (TPM), is a subalpine meadow with an area of about 50 ha (0.5 × 1.0 km) and elevation of 3000 m located in the upper end of Lee Vining Canyon, Mono County, California. It is bounded by Tioga Lake on the northern edge and the boundary of Yosemite National Park at Tioga Pass on the southern edge. *Allium validum,* which grows in large clumps in wet meadows at elevations of 1200–3350 m in the Sierra Nevada, is usually 0.5–1.0 m in height and has numerous small (6–10 mm) flowers organized into terminal umbels (Munz 1970). For 21 summers, 1968–70, 1973, 1976, and 1978–93, when I was on TPM daily, I kept notes on the flowering schedule of one particular, fairly compact patch of *A. validum* that covered an area of about 0.1 ha (25 × 40 m) near the center of TPM and that usually

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contained about 1200 umbels. Technically, flowering includes the period from floral bud initiation through floral persistence (Rathcke and Lacey 1985), but I use the term to describe the date on which buds opened to reveal the mass of flowers within. In any given year this date varied by 2 wk or more among the various patches of *A. validum* scattered across TPM, but flowering within a particular patch, including the study patch, was highly synchronous, occurring within a 3-d period for most individuals. The last day of this opening period was noted every year and is the datum used in this analysis.

The primary focus of my field studies on TPM was the reproductive biology of *Z. l. oriantha*, a migratory finch that winters in Mexico and breeds in montane meadows of the western United States. Individuals arrive at breeding areas in May and June and depart for wintering grounds in September and October. Wet subalpine meadows like TPM are a preferred breeding ground habitat, but more xeric locations at lower elevations are sometime utilized (Morton and Allan 1990). Nests are built only by females and are placed on the ground or in shrubs, such as willows (*Salix* sp.), or in small trees. Data gathered on banded females included the date they laid their first egg of the season, i.e., the clutch initiation date. Herein I use the mean date of the first 10 clutch initiations on TPM each season to indicate the onset of reproduction in *Z. l. oriantha*. Most nesting data were obtained from females that were frequently observed and trapped (each had a unique combination of color bands), allowing me to follow changes in their behaviors, body weights, and brood patches. This was important to data quality because females quickly renested if a nest was lost from storms or predation.

Information on snow conditions was available because, first, I estimated from direct observations the snowcover on TPM as the season progressed up to the day when all patches of snow had disappeared—the date of 0% snowcover. Second, information on snow depth in TPM could be obtained because it is a site traditionally used by the State of California Department of Water Resources to measure snow depth in order to predict water storage and runoff. Maximum snowpack occurs about 1 April, and this measurement is published in their bulletin 120.

RESULTS

During this study snow depths ranged from a low of 79.0 cm in 1976 to a high of 375.7 cm in 1983. The earliest 0% snowcover date was 1 June 1992, and the latest 11 August 1983, a range of 72 d. The earliest date for onion flowering was 6 July 1968 and 1976, and the latest was 21 August 1983, a range of 46 d. The earliest mean date for clutch initiations, based on the first 10 nests of the season, was 27 May 1992, and the latest mean date was 29 June 1983, a range of 33 d (Table 1). Thus, reproductive schedule in relation to snowpack was affected more in onions than in sparrows. In both species, however, timing of reproduction was highly correlated ($P < .001$) with maximum snowpack (Fig. 1). The final disappearance of snow (0% snowcover) was tightly coupled to snow depth, and flowering and clutch initiation schedules were related accordingly to time of snow disappearance (Table 2). Slope values for the relationship of flowering to both measures of snow conditions (snow depth and 0% snowcover) were about twice those observed for clutch starts in relation to these same two measures (Table 2). Slopes for both comparisons were significantly different (*t* tests, $P < .001$).

DISCUSSION

Reproduction was delayed by deep, late-lying snow more so in *A. validum* than *Z. l. oriantha*, but there was a compensatory mechanism operating to lessen the temporal impact of heavy snows even in the onion. When flowering date was regressed on snow disappearance date, the slope was 0.53, far less than 1.0 (Table 2). How then does the onion adapt? Only three major physical environmental factors have been identified as cues that initiate flowering: temperature, moisture, and photoperiod (Rathcke and Lacey 1985). Photoperiod-responsive or long-day plants are relatively unaffected by snowpack because they flower and are pollinated late in the summer. In contrast, nonphotoperiod-responsive plants tend to bloom in spring or early summer, and phenophases may be affected by as much as 6 wk by temperature and moisture conditions (Owen 1976). Some plants can "catch up," at least somewhat, by condensing or telescoping phenophases when delayed by overlying snow (Billings and Bliss 1959, Scott and Billings

TABLE 1. Twenty-one years of data on snow conditions, time of flowering in *A. validum*, and mean of clutch initiations and nest locations in *Z. l. oriantha*. The first 10 nests of the season were used to calculate mean date of clutch initiation, and all nests found in a given season were used to calculate percentage of those built aboveground. Number of nests found per season: mean = 59.6, S.D. = 21.9, range = 18-100, total of all years = 1252.

Year	Snow depth (cm)	0% snowcover (Julian day)	Onion flowering (Julian day)	Clutch initiation (mean Julian day)	Aboveground nests (%)
1968	113.5	175	188	160.6	40.0
1969	342.1	215	233	170.1	72.3
1970	176.3	183	198	158.3	34.9
1973	204.2	181	207	163.1	59.3
1976	79.0	158	188	153.8	10.9
1978	263.4	215	222	177.2	50.8
1979	227.1	191	207	160.7	43.6
1980	262.6	214	217	177.0	52.4
1981	173.0	167	197	156.4	25.3
1982	294.4	216	225	169.0	43.8
1983	375.7	224	234	181.3	32.1
1984	205.0	197	208	158.3	44.6
1985	145.8	172	197	156.8	25.5
1986	243.3	213	213	160.9	56.9
1987	113.3	163	201	152.5	18.6
1988	121.2	170	198	161.3	11.1
1989	158.0	176	201	156.2	39.4
1990	90.9	172	196	157.4	30.0
1991	167.4	181	214	164.7	46.7
1992	108.2	152	201	146.8	37.0
1993	227.1	199	216	169.5	49.2

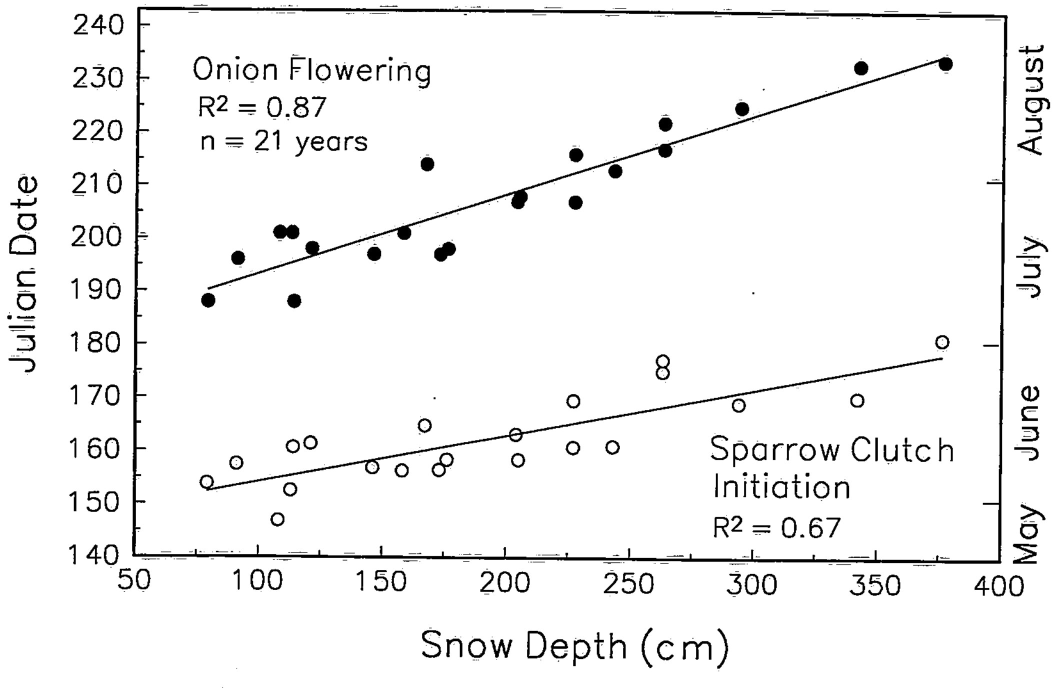

Fig. 1. Date of flowering in *A. validum* and mean clutch initiation in *Z. l. oriantha* as a function of snow depth on 1 April at Tioga Pass Meadow.

TABLE 2. Slopes and coefficients of determination (R^2) for linear regressions involving date of flowering in *A. validum* and mean date of clutch initiation and percentage of nests placed in sites off the ground in *Z. l. oriantha* in relation to snow conditions (snow depth on 1 April and date of 0% snowcover) at Tioga Pass Meadow. $N = 21$ years.

Y	X	Slope	R^2 (%)	P
0% snowcover	Snow depth	0.25	86.1	<.001
Flowering date	Snow depth	0.15	86.9	<.001
Flowering date	0% snowcover	0.53	76.1	<.001
Clutch initiation date	Snow depth	0.09	68.9	<.001
Clutch initiation date	0% snowcover	0.34	75.7	<.001
Aboveground nests	Snow depth	0.12	40.2	.002
Aboveground nests	0% snowcover	0.47	42.4	.001

1964, Weaver 1974, Weaver and Collins 1977). Alpine plants often store large quantities of carbohydrate in underground organs; mobilization of these reserves to shoots can occur even before snowcover is gone. Relatively high carbohydrate levels are then maintained in the shoot portion until after fruiting, whereupon a return of peak reserve levels to underground parts occurs at the beginning of fall dormancy (Mooney and Billings 1960). The mechanism whereby events in the growing season can be accelerated has not been studied to my knowledge, but this seasonal cycle of transport and utilization of stored energy must be a vital constituent.

A puzzling aspect of *A. validum*'s flowering response is that it was strongly affected by snow conditions, typical of nonphotoperiod-responsive plants that usually flower in May or June. *A. validum* flowers in July or August, a time that is more typical of plants cued by long days (Owen 1976). Perhaps *A. validum* has seasonal changes in its photoresponsivity and is following a mixed strategy energetically, using stored reserves early in the season and then later switching to a greater reliance on photosynthate of the current year, the latter being a trait common to photoperiodic species (Mooney and Billings 1960).

The lessened impact of snow conditions on reproductive schedule in *Z. l. oriantha*, as compared to *A. validum*, appears to occur because the bird has flexible nest-building habits. Only about 11% of all nests constructed at TPM in dry years, such as 1976, were placed in aboveground sites (Table 1). In wet years, such as 1969, when snowpack was unusually heavy, this increased to 72% (Table 1). The 1983 data seem anomalous, but hot spring weather induced rapid snowmelting, and more nests were placed on the ground than might have been otherwise expected. The main point here is that when groundcover was adequate for hiding nests, females seemed to prefer nesting on the ground. When plant growth and development were impeded by late-lying snow, they did not wait a long period for this cover to develop, but instead built a greater proportion of their nests aboveground, usually in pines (*Pinus* sp.) and willows. Thus, behavioral plasticity in selection of nesting sites allowed *Z. l. oriantha* to proceed with rearing young with less delay than might be predicted from snow conditions or even from plant phenophases.

In summary, this correlative study presents temporal indices of reproductive schedules during 21 years in a plant and an animal occupying the same high-altitude environment, thus permitting a comparison of their responses to a proximate or environmental factor experienced in common, namely interannual variation in snowpack. Both organisms were affected by this factor and both exhibited compensatory adjustments of their schedules. The adjustment was greater in the animal because it possesses a basic trait, not present in the plant, that can be acted on by natural selection, its behavior.

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Received 5 April 1993
Accepted 9 March 1994