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SEASONAL VARIATION IN NEST PLACEMENT OF ABERT'S TOWHEES

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Several meteorological variables are known to influence the heat budgets of nesting birds (e.g., Walsberg and King 1978a, b). Such factors include air temperature, incident radiation, wind, and humidity. If the microclimate of the nest is unfavorable, parent birds may become inattentive, exposing eggs or nestlings to excessive heat or cold. They may then desert the nest and their offspring may die. To improve the probability of nesting successfully, many Old World desert birds place their nests so as to receive morning sunlight (Maclean 1976). Several investigators have demonstrated nonrandom orientation of hole entrances of New World cavity-nesting birds (Ricklefs and Hainsworth 1968, Inouye 1976, Inouye et al. 1981), but few have tested for the significance of nonrandom placement or variation in placement between seasons of open nests. Maclean (1976) indicated that larks in the Kalahari Desert oriented their nests to receive shade in summer and sun in winter. Balda and Bateman (1970) predicted that Pinyon Jays (*Gymnorhinus cyanocephalus*) in Arizona may place first nests of the season on the sunny sides of ponderosa pines (*Pinus ponderosa*), but that they may orient later nests more randomly. They showed that these trees in March were 3°C warmer on the south side than on the north side, and that the jays selected nest sites to gain more heat: all jay nests, regardless of season, had a significant southward orientation. I report here a second test of Balda and Bateman's (1970) hypothesis, using data for a bird of hotter climates, the Abert's Towhee (*Pipilo aberti*). This sedentary species inhabits only desert riparian regions of the southwestern United States, whereas the mobile Pinyon Jay occupies a greater elevational and latitudinal range, though breeding chiefly in foothills and lower mountain ranges. Because nests of the Abert's Towhee are typically exposed to higher spring and summer temperatures than those of the Pinyon Jay, a second test of Balda and Bateman's prediction may demonstrate greater seasonal variation in nest placement.

The study was conducted in honey mesquite (*Prosopis glandulosa*) habitat on the Colorado River Indian Reservation 10 km north of Ehrenberg, Arizona. From January to July 1980, I spent 15 h each week (84 5-h searches) looking for nests on, or near a gridded study plot of 20 ha. Field work terminated in July when no new nests were started.

The Abert's Towhees in my study area built their open nests in mesquite, willow (*Salix goodingii*), exotic salt cedar (*Tamarix chinensis*), saltbush (*Atriplex lentiformis*), in-

kweed (*Suaeda torreyana*), arrowweed (*Tessieria sericia*), and mistletoe (*Phoradendron californicum*), a parasite of mesquite (Finch 1981a). Nests built in March were constructed of mesquite bark, saltbush, salt cedar and arrowweed leaves, grasses and even newspaper. Later nests were made predominantly of mesquite leaves, which became available in April (Finch 1981a).

Compass direction of the nest with respect to the main trunks of mesquites, willows and salt cedars was recorded for 52 nests. I did not include nests built in small shrubs because compass directions were difficult to determine accurately. Nests were allocated to early and late seasons by dividing in half the number of days of the observed breeding season (118 days from first to last nest initiated). The Rayleigh Z test (Batschelet 1965) was used to test for randomness of nest concentration of early and late nests, and Batschelet's (1965:33) parametric two-sample test applying the F-statistic was used to test for a difference in mean direction between early and late nests. Information on solar paths and prevailing wind directions in the lower Colorado River valley was provided by the Laboratory of Climatology, Arizona State University, Tempe.

The results indicate that the placements of early nests were more concentrated than late nests (Table 1). Their distribution was significantly unimodal with a preferred southeast direction, whereas the distribution of late nests had a nonsignificant northwestward orientation. The mean directions of early and late nests were significantly different ($F_{(1,50)} = 14.82, P < 0.001$). Because the distribution of late nest orientations was nonsignificant, the value of this two-sample test may be lessened. The Rayleigh tests nevertheless confirm the difference in the distributions of nest orientations. The circular distributions of early and late nests are shown in Figure 1.

These results suggest that Abert's Towhees place their nests in response to environmental factors that are important only during the first half of the breeding season. In the lower Colorado River valley, the sun rose at 89° (almost due East) in March 1980 and traversed the south-

TABLE 1. Orientation of Abert's Towhee nests with respect to the main trunk of the tree.

Season	Number of nests	Nest concentration ^a	Rayleigh's Z test ^b	Mean direction ^c
Early	24	0.367	3.23	130° ± 69°
Late	28	0.205	1.18	321° ± 72°

^a A value of 1 indicates all nests were placed in precisely the same direction, and a value of 0 indicates a uniform distribution.

^b Rayleigh's Z test (Batschelet 1965) shows that the distribution of early nests was significantly unimodal ($P < 0.05$), whereas the distribution of late nests was random ($P > 0.05$).

^c Standard deviation is included.

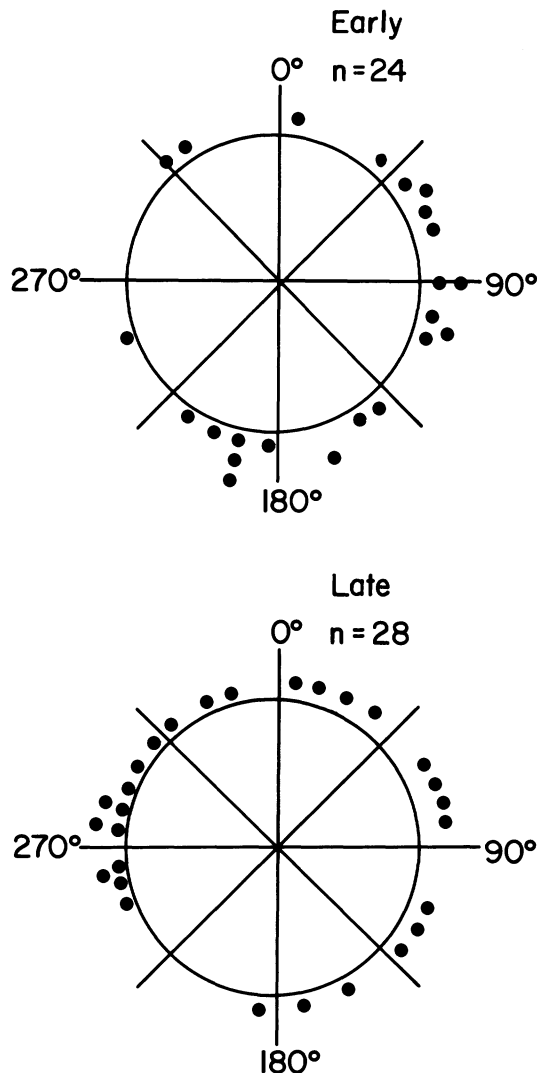


FIGURE 1. Compass orientation of early and late nests in the lower Colorado River valley.

ern hemisphere of the sky; the elevation of the sun from the horizon was only 58° at solar noon. In June, the sun rose at 61°NE and was almost directly overhead (81° from closest horizon) at solar noon. Early nests of Abert's Towhees that were placed on the southeast sides of trees received maximum incident radiation in the morning, when the air was cool. As the breeding period progressed to August, mean maximum air temperatures rose from 23.8°C to 42.9°C (Finch 1981a), and nest placement that allowed rapid heat gain presumably became less adaptive. Late in the season, nests tended to be placed northwestwardly although the distribution was not significant. Warmer, southeastern nests may reduce adult and nestling energy expenses early in the season, whereas later, northwestern nests may protect embryos from potentially lethal radiant heat (Bennett and Dawson 1979) and/or prevent high evaporative water losses from parents and offspring.

Wind direction may also influence nest placement of Abert's Towhees. A nest on the lee side of a tree may be better protected from cooling or destructive winds. From March through May of 1980, the prevailing wind directions were from west-northwest, but from June through September the prevailing winds were from south-south-

east. Southeastwardly placed nests in spring were shielded from the greatest proportion of winds (in contrast, see Balda and Bateman's 1970 study). Summer nests were apparently placed randomly with respect to wind direction. For a dark-plumaged bird like an Abert's Towhee, convective heat loss via feather erection in wind may even be a principal means of cooling during the desert summer (Walsberg et al. 1978).

Early nests of Abert's Towhees were therefore placed advantageously relative to both solar radiation and prevailing winds. The relative importance of either of these factors was not determined. Because concentration of late nests was not significantly different from random, it seems likely that either (1) air temperature and wind did not influence nest site selection and nesting success late in the season (e.g., air temperature may have been identical on all sides of the tree as indicated by Balda and Bateman 1970), (2) the probability of reproductive success was independent of nest site placement, or (3) towhees used other, less obvious, methods of selecting nest sites (e.g., Walsberg 1981).

Nesting success of the towhees decreased during the season (Finch 1981a), associated with an influx of Brown-headed Cowbirds (*Molothrus ater*). The pressures of cowbird parasitism or predation (Finch 1981b, 1982a) may have overridden decisions to place nests primarily with regard to microclimatic conditions (see Best and Stauffer 1980:153). As the season progressed, towhees spent less time locating and constructing nests (Finch 1981a) and even built some nests that fell apart (pers. observ.). In addition, they confiscated abandoned nests of their own or other species (Finch 1982b). This apparent inclination to "save time" at the end of the breeding period suggests that they took less care in selecting nest sites. When compared with an overwhelming probability of nesting failure caused by predation and brood parasitism (approximately 95%; Finch 1981a), a less-than-satisfactory microclimate at a late nest may have negligible effect on the productivity of Abert's Towhees in the lower Colorado River valley.

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FLIGHT SONG AND SONG FLIGHT IN THE ORANGE-CROWNED WARBLER

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Birds of many species commonly sing while flying. The behavior is characteristic of many open-country species, such as larks, pipits, and Bobolinks (*Dolichonyx oryzivorus*) and also occurs among some woodland species, including several wood warblers (Parulidae; Ficken and Ficken 1962). In some of these warbler species, both the song given during flight, and the flight itself, are distinctly different from perch song and "normal" direct flight. Ficken and Ficken described such songs as "usually a variable warbling [accompanied by a] rising flight on slowly flapping or quivering wings [and] typically a direct and silent descent."

Workers have reported "flight songs" and "song flights" occurring in several species of *Vermivora*, including the Tennessee Warbler (*V. peregrina*; Bowdish and Philipp 1916), Nashville Warbler (*V. ruficapilla*; Bowles and Bowles 1906, and Thayer, reported in Chapman 1907), Bachman's Warbler (*V. bachmanii*; Howell 1924, reported in Bent 1953), and Blue-winged Warbler (*V. pinus*; Pitelka 1939). The songs and flights described for these species, however, appear to be less modified than those described by the Fickens for non-*Vermivora* warblers.

I observed flight songs and song flights occurring in the Orange-crowned Warbler (*V. celata*) during behavioral studies of the species in its typical nesting habitat in Contra Costa County, central coastal California. I followed the behavior of unmated territorial males prior to 12:00, during March, April, and May of 1980, 1981, and 1982. Although I may have overlooked the behaviors, I did not observe flight songs and song flights in unmated birds during late February, June, and early July, nor among mated birds during any month. Populations of these warblers were relatively dense in my study areas, with all males having at least two territorial neighbors. Territorial disputes were common.

Most flight songs I heard were begun in mid-flight, and completed on a perch. Occasionally the entire song was rendered in the air. I could detect, by ear, no difference between songs sung during flight and those sung entirely while perched. When in song flight, the wings of a warbler characteristically "fluttered" or "quivered" in a way I never saw in normal direct flight. I observed nothing resembling the rising flight and direct descent described by the Fickens. I noted nine instances of birds singing while in

flight during 260 min of observation in which the individual Orange-crowned Warblers were in sight. Since these birds usually sang four to six songs per minute, it is apparent that flight songs occurred much less frequently than perch songs. Flight songs and song flights apparently occurred at random, and I noticed no associated special circumstances, such as the presence of a female or a competing male.

The flight songs and song flights I observed in Orange-crowned Warblers differed from those described by the Fickens. They generally resembled those described for other species of *Vermivora*, although the fluttering in song flight has hitherto been reported only for the Nashville Warbler (Bowles and Bowles 1906). I am aware of only two reports of song and flight behavior resembling those I have reported here occurring in parulids other than species of *Vermivora*. The American Redstart (*Setophaga ruticilla*) apparently has an "unmodified" flight song and song flight often associated with encounters with females or rival males (Ficken 1962). The Kirtland's Warbler (*Dendroica kirtlandii*) also has such songs and flights, but they do not seem to be associated with any special environmental context (Mayfield 1960:133).

Relatively unmodified flight song and song flight now are reported for the majority of North American *Vermivora*, suggesting that these forms of behavior are characteristic of the genus.

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