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FACTORS INFLUENCING WINTER DISTRIBUTION AND ABUNDANCE OF TOWNSEND'S SOLITAIRE

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In winter, Townsend's Solitaire (*Myadestes townsendi*) is among the most specialized of all North American birds, since it depends almost entirely on the fleshy cones of junipers (*Juniperus*) for food (Lederer 1977a, b; Salomonson and Balda 1977). *Juniperus* spp. is widespread throughout North America (Elias 1980), but the solitaire is restricted in winter to only a portion of that range (A.O.U. Check-list Com. 1957). Many other birds feed upon juniper cones, both in- and outside the solitaire's range, but none appears to be so specialized. The purpose of this study was to attempt to explain why this most specialized juniper-seed predator does not or cannot occupy all regions where its winter food is available.

Grinnell (1914) noted that birds are common only in certain parts of their ranges, which he called centers of abundance. Species' centers of abundance may coincide with areas of maximum resource abundance and diversity. This would be most readily testable in the case of resource specialists, for which the abundance and variety of available resources could be most easily measured. For example, the Acorn Woodpecker (*Melanerpes formicivorus*) is a highly specialized acorn predator, whose centers of abundance coincide with regions of high oak (*Quercus*) species richness and abundance in western North America (Bock and Bock 1974). Presumably a greater variety of available resources increases the probability that at least one will produce a sufficient food crop each year. Acorn Woodpeckers do not normally occupy areas in the west with only one oak species.

In this study, I tested the hypothesis that winter abundance of Townsend's Solitaire is positively correlated with juniper species density and overall abundance. A related hypothesis is that variability in solitaire numbers from year to year would be negatively correlated with juniper species density, because higher resource diversity should reduce the frequency of population declines or emigrations caused by food shortages.

METHODS

Christmas Bird Count (CBC) data on Townsend's Solitaire for the winters of 1962–63 through 1971–72 were combined into 55 latitude-longitude blocks (Fig. 1A), and means and standard deviations of solitaire numbers counted per party-hour per block were computed for the 10-year period. Total CBC sample size for this study was 8129. Distribution maps for 12 species of North American *Juniperus* (from Elias 1980) were superimposed on a single map to determine regional patterns of juniper species density. Abundance of juniper was more difficult to measure. Junipers frequently are mixed as subdominants in various com-

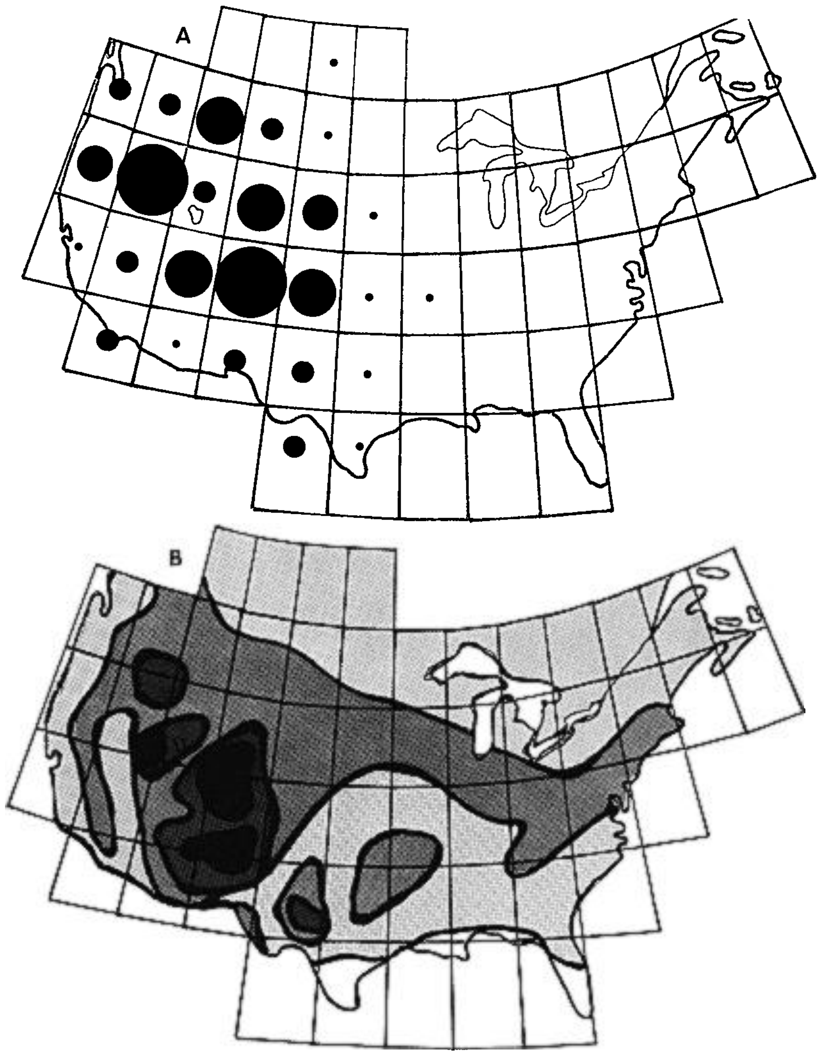

FIG. 1. A. Winter abundance pattern of Townsend's Solitaire, based upon Christmas Bird Count data for 1962–63 through 1971–72. Five sizes of dots represent <0.01 but >0.0, 0.01–0.09, 0.10–0.19, 0.20–0.39, and ≥0.40 birds/party hour. B. Species density of *Juniperus* spp., based upon maps in Elias (1980). Four degrees of shading indicate occurrence of one to four species.

TABLE 1

CORRELATIONS AND PARTIAL CORRELATIONS AMONG SOLITAIRE WINTER ABUNDANCE, JUNIPER SPECIES DENSITY, AND JUNIPER ABUNDANCE

Comparison	Correlation
A. Solitaire abundance vs juniper species density	0.639**
B. Solitaire abundance vs juniper abundance	0.473*
C. Juniper species density vs abundance	0.662**
D. A, with juniper abundance held constant	0.494*
E. B, with juniper species density held constant	0.087

* $P < 0.05$, ** $P < 0.01$.

munity types, but habitat descriptions of CBC circles usually give no indication of their presence or abundance. As an alternative, I calculated the percentage of each 5° block which Küchler (1964) designated as having juniper as dominant or co-dominant potential vegetation.

Pearson product-moment correlation coefficients were calculated comparing the variables (1) mean solitaires per party-hour per block, (2) coefficient of variation of solitaire abundance per block (standard deviation/mean), (3) maximum juniper species density per block, and (4) juniper abundance per block. Sample size was the 26 five degree blocks which recorded solitaires during the 10-year period. Because variables 3 and 4 were highly correlated, partial correlations were computed to look for the independent relationships between solitaire variables and juniper species density vs juniper abundance.

RESULTS AND DISCUSSION

Fig. 1A shows the winter abundance pattern of Townsend's Solitaire, while Fig. 1B shows juniper species density. Correlations between solitaire numbers and junipers are presented in Tables 1 and 2.

Within the range of Townsend's Solitaire, its numbers were significantly higher and significantly less variable as juniper species density increased (Tables 1, 2), supporting both initial hypotheses. Partial correlations among solitaire numbers and variability and juniper abundance

TABLE 2

CORRELATION AND PARTIAL CORRELATIONS AMONG VARIABILITY OF SOLITAIRE ABUNDANCE, JUNIPER SPECIES DENSITY, AND JUNIPER ABUNDANCE

Comparison	Correlation
A. Solitaire variability vs juniper species density	−0.603**
B. Solitaire variability vs juniper abundance	−0.402*
C. Juniper species density vs juniper abundance	0.662**
D. A, with juniper abundance held constant	−0.491*
E. B, with juniper species density held constant	−0.005

* $P < 0.05$, ** $P < 0.01$.

were near 0 (Tables 1, 2). These results suggest that resource diversity is an important factor influencing both the distribution and abundance of Townsend's Solitaire, perhaps more important than resource abundance. Doubtless juniper abundance is important to solitaires on a local scale, but I was unable to measure this relationship with CBC data.

As with the equally specialized Acorn Woodpecker (Bock and Bock 1974), winter abundance of Townsend's Solitaire probably is influenced by both the abundance and the variety of its resources. This principle should apply to all species, namely, that centers of abundance (Grinnell 1914) are coincident with areas where resources are predictable as well as common. More generalized species should be subject to these same biogeographical constraints, but the relationship will be less clear because the variety of suitable resources is greater and difficult to measure. Such generalized species can be expected to have larger and more diffuse centers of abundance.

The winter abundance pattern of Townsend's Solitaire does not fit perfectly with that of juniper species density. In general, the birds appear to be more common in the northwestern portion of the area of high juniper species density than in the south (Fig. 1A, B). Several factors may be responsible for this result. The first is the relationship of the breeding and winter ranges. Solitaires nest north through western Canada to Alaska (A.O.U. Check-list Com. 1957). These northern breeders probably come south in fall only as far as is necessary to find juniper cones in good numbers, thereby accumulating most winters in the northern part of their range. Also, junipers may produce cones more regularly in northern latitudes (R. P. Balda, pers. comm.). Other bird species may influence the winter abundance patterns of the solitaires by competing with them for juniper cones. Competitors include American Robins (*Turdus migratorius*) and bluebirds (*Sialia* spp.) (Lederer 1977a, b; Salomonson and Balda 1977). CBC data show that these species have southerly winter abundance patterns. Mountain Bluebirds (*Sialia currucoides*) are particularly abundant in west Texas (Andrews and Bock 1979), an area of high juniper species density and comparatively low solitaire numbers (Fig. 1A, B).

A final factor which may influence solitaire distribution is juniper palatability. Benedict (1981) has found that solitaires in the Front Range of Colorado greatly prefer cones of *Juniperus scopulorum* over those of the sympatric *J. communis*. Solitaires rarely winter in parts of Canada where only *J. communis* is found, suggesting that cones of this species alone may not represent a suitable food supply. There is evidence that other junipers in the Southwest and Pacific Coast may not produce cones palatable to Townsend's Solitaire (R. P. Balda, pers. comm.).

One null hypothesis for the present study is that the relationship between solitaire abundance and juniper species density is a coincidence—that the solitaire's winter range is an ecological and evolutionary consequence of some other variable such as climate, competition, or proximity to the breeding range. Correlative studies such as this one cannot rule out this possibility. However, such speculations only beg the fundamental question. Why, among the variety of North American birds which feed on juniper cones, is Townsend's Solitaire alone so specialized? Why are juniper cones in the eastern U.S. eaten only by more generalized frugivores such as robins, bluebirds, waxwings (*Bombycilla* spp.), and Evening Grosbeaks (*Hesperiphona vespertina*)? The only explanation for this, other than historical accident, would seem to be that junipers elsewhere in North America are an unreliable food source upon which to specialize, presumably because the one or two species present fail to produce cones over large areas in large numbers every year.

SUMMARY

Townsend's Solitaire (*Myadestes townsendi*) is a specialized juniper-seed predator. Winter abundance of this species is positively correlated with species density of *Juniperus* spp., while variability in numbers is negatively correlated with the same factor. These results support the hypothesis that species' ranges and centers of abundance are coincident with areas of diverse as well as abundant resources, because such diversity assures that the food supply will be predictable as well as abundant.

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