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NESTING PHENOLOGY AND PRODUCTIVITY OF BIRDS IN THE WHITE AND INYO MOUNTAINS, CALIFORNIA, AS ASSESSED WITH NEST-BOXES

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ABSTRACT.—Nest-boxes were monitored from 1988 to 1992 on 5 grids in the pinyon-juniper (*Pinus-Juniperus*) woodlands of the White and Inyo Mountains, California, to determine breeding phenology and productivity of cavity-nesting birds, and characteristics of used and non-used nest-boxes. We found a total of 112 nests of 6 species. Bewick's Wrens (*Thryomanes bewickii;* 64 nests), Mountain Chickadees (*Poecile gambeli;* 18), Ash-throated Flycatchers (*Myiarchus cinerascens;* 12), and Juniper Titmice (*Baeolophus ridgwayi;* 11) were the most common species utilizing the boxes. Nest phenology and numbers of young were similar to values reported elsewhere in the literature for the species, although nesting success for Mountain Chickadees appeared lower in our study. Chickadees were associated with relatively dense, mature vegetation on southern slopes. Juniper Titmice used areas with tall juniper shrubs and generally sparse vegetation. Bewick's Wrens used areas with short trees, sparse vegetation, and many stumps. Nest-boxes were underutilized (<15% use) by most species relative to their availability and relative to detected abundances of the species. We suggest that nest-boxes can provide valuable breeding biology information and can potentially increase the productivity of rare and cavity-limited species.

Key words: Thryomanes bewickii, Poecile gambeli, Myiarchus cinerascens, Baeolophus ridgwayi, Sialia currocoides, Sitta carolinensis, *limiting factor, nest-boxes, nesting success, White Mountains, Inyo Mountains.*

Studies of nest-box use by secondary cavity-nesting birds have traditionally been conducted to gather basic natural history information (e.g., Brandt 1951:429–433, Munro and Rounds 1985), including productivity (and population limitation), fecundity, and nesting phenology (Brawn 1988, Finch 1989). Nest-boxes also have been used to test hypotheses about whether birds select nest-boxes based on vegetative, food, predator, or competitive factors in their environment (Munro and Rounds 1985, Gutzwiller and Anderson 1987, Brawn 1988, Finch 1989).

As part of a long-term ecological research project started in the White and Inyo Mountains, California, in 1988 (Morrison 1988, Hall et al. 1991), we collected information on the use of nest-boxes by birds in pinyon-juniper (*Pinus monophylla–Juniperus osteosperma*) woodland vegetation. Our objectives were to (1) describe the reproductive characteristics of the species in the White and Inyo Mountains, (2) describe the vegetation around nest-boxes to elucidate any patterns of nest-box selection, and (3) determine if nest sites were limiting to cavity-nesting birds.

STUDY AREA

The White Mountains (1515–4245 m elevation) are located east of the city of Bishop, Inyo County, California, and north of Westgard Pass. The Inyo Mountains are joined with the Whites at the vicinity of Westgard Pass but extend south and rise from 1515 m to >3000 m elevation. The dominant vegetation between 2090 m and 2725 m elevation in both ranges is pinyon-juniper woodland, which is an arid, high-desert environment with sparse vegetative cover.

The average March–May (spring) temperature in the White Mountains from 1988 to 1992 was 5.7°C; the average June–August (summer) temperature was 14°C (unpublished data). In typical years, snowcover and rainfall last from November through May, and afternoon thunderstorms occur in late summer. Average fall and winter temperatures are 3.7°C and 0.4°C, respectively (unpublished data).

The only tree species in the woodland are singleleaf pinyon and Utah juniper. Dominant perennial shrubs are big sagebrush (*Artemisia tridentata,* with 3 varieties), bitterbrush (*Purshia*

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glandulosa and *P. tridentata*), rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*), Mormon tea (*Ephedra viridis*), and cactus (*Opuntia* and *Echinocereus*). Annual plants include about 5 grass genera and 20 forb genera (Hall 1992).

METHODS

We established 5 nest-box grids during the winters of 1988 (2 grids), 1989 (2 grids), and 1990 (1 grid) in the White and Inyo Mountains. All grids were established within 1 km of a road, for access purposes, and then randomly within areas of homogeneous pinyon-juniper vegetation. Grids ranged in elevation from 2120 m in the Inyo Mountains to 2575 m in the White Mountains, which enabled us to sample the pinyon-juniper woodland environments from their lowest elevational occurrence to their upper limit. Grids were 2.5 to 17 km apart.

Each grid consisted of 5 parallel lines with 5 nest-boxes each (25 boxes per grid). To place the boxes, we determined a random compass bearing upon arriving at the proposed site and set 5 boxes at 50-m intervals along the bearing line. This was repeated for the remaining 4 parallel lines, for a total grid area of 4 ha. We placed boxes in the most vigorous (i.e., well-vegetated) and closest pinyon tree to the 50-m mark. Each box was hung on the trunk, amidst branches >2 m high, but about midway up the tree. To minimize the potential effects of hot summer sunlight on nesting birds, nest-boxes were faced from the north to the west.

Each box, made of construction-grade redwood, was 25 cm tall × 13 cm wide, thus allowing all known secondary cavity-nesting species access to the interior. Because Mountain Bluebirds (*Sialia currocoides*) are the largest known cavity-nesting bird in the White and Inyo Mountains, entrance holes of 38 mm diameter were designed to fit them (Yoakum et al. 1980, Hall et al. 1991).

We always checked nest-boxes in early spring (February–May) to make sure they were free of rodent nests, old bird nests, and debris, so that nesting birds would have empty, unused sites from which to choose. Starting in early April, when the different bird species began to form pairs, we checked all nest-boxes weekly, and this continued until the end of the breeding season in mid-August. We also removed rodent nests from the boxes during the breeding season to make the boxes continually available to birds.

We summarized nest-box data from 1988 to 1992 into 11 variables (Table 1) describing nest construction, general phenology, productivity (i.e., number of eggs, young, and fledglings), and spatial relationships with conspecifics and other secondary cavity-nesting bird species. In some instances we had to back-calculate from known dates (e.g., those of fledging, hatching) to determine nest initiation and egg-laying dates. Only data on complete nests (i.e., those with a lined cup at some point during a season) were analyzed. We converted all dated variables into Julian day numbers to facilitate statistical analyses.

In 1992 we sampled nest-box–centered vegetation plots at all 125 boxes. Thirty-four vegetation and topographic measures were made in a 15-m-radius plot (0.07 ha), with some measurements made within the whole plot and others made along a 30-m-long transect bisecting the plot (Appendix). We measured variables that described characteristics of nest-box placement, the nest tree, number of natural cavities available in the nest plot (as a means of evaluating nest-site limitation), cover by shrubs and trees in the plot, and aspect and slope of the area around the nest-box (Appendix). Because these variables remained constant over the duration of the project, we assumed they reflected characteristics experienced by birds throughout the study period.

We conducted general descriptive statistics to describe bird-nesting phenology. Because of low use of nest-boxes, we combined data across years. We conducted 2- and 3-way analyses of variance (Zar 1984:163) to evaluate differences in reproductive variables among species, years, and grids, with subsequent Tukey's multiple comparison tests (Zar 1984:185). Before conducting multiple regression analyses (Zar 1984:329), we conducted correlations (Zar 1984:328) among all vegetation variables to look for high multicolinearity. Only 3 variables (height of pinyon, juniper, and sagebrush shrubs; Appendix) were highly correlated (i.e., $r^2 \geq 0.67$). We did not choose to remove any of these variables from subsequent analyses, however, because we saw that they were measuring different components of the vegetation. We conducted multiple regression analyses only for Bewick's Wrens (*Thryomanes*

TABLE 1. Phenological characteristics of complete nests of 5 cavity-nesting bird species in the White and Inyo Mountains, California, 1988–1992.

Species Variable	Mean (± *s*)	No. of nests
Bewick's Wren		
First nest construction day	6 May (± 25.3 days)	64
Final nest construction day	18 May (± 26.4 days)	64
First day of egg-laying	21 May (± 23.4 days)	43
Final day of egg-laying	27 May (± 24.0 days)	42
Total no. dead and alive eggs	5.4 (± 1.1)	43
Total no. of probable fledglings	3.4 (± 2.3)	42
Approximate failure day of nest	9 Jun (± 24.0 days)	11
Approximate fledging date of young	25 Jun (± 23.4 days)	30
Total no. dead eggs and/or chicks	2.1 (± 2.4)	42
Distance to nearest conspecific nest	86 (± 43.8 m)	61
Distance to nearest nest of another bird	71 (± 28.1 m)	64
Mountain Chickadee		
First day of egg-laying	17 May (± 12.9 days)	18
Final day of egg-laying	23 May (± 12.7 days)	18
Total no. dead and alive eggs	6.1 (± 1.3)	18
Total no. of probable fledglings	2.4 (± 2.4)	18
Approximate failure day of nest	8 Jun (± 9.3 days)	7
Approximate fledging date of young	27 Jun (± 16.3 days)	10
Total no. dead eggs and/or chicks	3.3 (± 2.8)	18
Distance to nearest conspecific nest	94 (± 33.1 m)	10
Distance to nearest nest of another bird	74 (± 30.7 m)	18
Ash-throated Flycatcher		
Final nest construction day	29 May (± 0.0 days)	1
First day of egg-laying	2 Jun (± 14.8 days)	12
Final day of egg-laying	6 Jun (± 14.9 days)	12
Total no. dead and alive eggs	4.4 (± 0.5)	12
Total no. of probable fledglings	3.0 (± 1.9)	12
Approximate failure day of nest	27 Jun (± 2.0 days)	3
Approximate fledging date of young	5 Jul (± 17.1 days)	9
Total no. dead eggs and/or chicks	1.4 (± 1.8)	12
Distance to nearest conspecific nest	50 (± 0.0 m)	2
Distance to nearest nest of another bird	71 (± 50.2 m)	12
Juniper Titmouse		
Final nest construction day	2 May (± 3.5 days)	2
First day of egg-laying	11 May (± 15.3 days)	11
Final day of egg-laying	16 May (± 15.1 days)	11
Total no. dead and alive eggs	5.5 (± 1.2)	11
Total no. of probable fledglings	4.2 (± 1.8)	11
Approximate failure day of nest	12 Jun (± 0.0 days)	1
Approximate fledging date of young	18 Jun (± 17.0 days)	9
Total no. dead eggs and/or chicks	1.3 (± 2.1)	11
Distance to nearest conspecific nest	50 (± 0.0 m)	2
Distance to nearest nest of another bird	70 (± 26.8 m)	11
Mountain Bluebird		
Final nest construction day	2 Jun (± 0.0 days)	1
First day of egg-laying	14 May (± 27.8 days)	6
Final day of egg-laying	18 May (± 27.3 days)	6
Total no. dead and alive eggs	4.7 (± 0.5)	6
Total no. of probable fledglings	3.7 (± 2.0)	6
Approximate failure day of nest	26 Jun (± 0.0 days)	1
Approximate fledging date of young	13 Jun (± 19.9 days)	5
Total no. dead eggs and/or chicks	1.0 (± 2.0)	6
Distance to nearest conspecific nest	128 (± 31.8 m)	4
Distance to nearest nest of another bird	63 (± 24.2 m)	6

bewickii) and Mountain Chickadees (*Poecile gambeli*) because they had the largest sample sizes (64 and 18 nests, respectively). The dependent variable for all analyses was the number of fledglings; independent variables included all those measured in nest-box plots except direction the nest-box faced and aspect of the vegetation plot (Appendix). These factors were assessed versus number of fledglings by 1-way ANOVAs for each species separately.

To determine if the bird species used nest-boxes non-randomly, we used *t* tests (Zar 1984: 126) to compare vegetative characteristics of boxes with nests and characteristics of boxes that were never used, for each species. These comparisons were made only for those species with ≥11 nests (i.e., Bewick's Wrens, Mountain Chickadees, Ash-throated Flycatchers [*Myiarchus cinerascens*], and Juniper Titmice [*Baeolophus ridgwayi*]).

For all analyses we used SPSS-PC+ software (Norusis 1990) and considered *P*-values ≤ 0.05 to be significant.

RESULTS

Sixty-four complete Bewick's Wren nests were found among the 5 grids from 1988 to 1992, as well as 18 Mountain Chickadee nests, 12 Ash-throated Flycatcher nests, 11 Juniper Titmouse nests, 6 Mountain Bluebird nests, and 1 White-breasted Nuthatch (*Sitta carolinensis*) nest. Most nests were found on our "Cedar Flat" grid at 2210 m elevation; this grid and the 2 other medium-elevation grids (at 2150 and 2270 m elevation) had a total of 70 nests. Most wren (n = 18), flycatcher (5), titmouse (10), and nuthatch (1) nests were found on the medium-elevation grids, whereas most chickadee nests (9) were found on our highest elevation grid (2575 m), and most bluebird nests (3) were found on our lowest elevation grid (2090 m).

Numbers of young fledged did not differ among species, years, or grids ($F_{13,76}$ = 1.42, P = 0.17), although the number of eggs did differ among species ($F_{13,98}$ = 2.5, P = 0.01; species main effect F = 4.6, P = 0.001), with chickadees having the most eggs per clutch and flycatchers having the fewest. Nesting phenology (as measured by first day of egg-laying, last day of egg-laying, and fledging date) differed significantly among species and years (*P*-values ≤ 0.01; Table 1). Across all years, nuthatches constructed nests first, followed by chickadees, titmice and bluebirds, wrens, and then flycatchers. Titmice, bluebirds, and nuthatches fledged their young first, followed by wrens and chickadees, and then flycatchers.

There were 525 nest-boxes available on the 5 grids over the 5 years of the study, and an additional 7 natural cavities were detected in the nest plots. Of 560 total sites thus available to birds over the 5 years, Bewick's Wrens used 8–15% of available cavities; Mountain Chickadees, 1–7%; Ash-throated Flycatchers, 0–4%; Juniper Titmice, 0–3%; Mountain Bluebirds, 0–4%; and White-breasted Nuthatches, 0–1%.

Bewick's Wren

Of 64 total wren nests found, only 43 (67%) contained eggs at some point during a breeding season. Nest construction by wrens occurred in mid-May; clutches were laid in late May, with an average of 5.4 eggs; and young birds fledged by late June, with an average of 3.4 birds fledging successfully. An average of 2.1 young died in the nest before fledging (Table 1). Eleven of 43 nests with eggs failed from 1988 to 1992; thus, nesting success was 74% (32 of 43 nests with eggs). Most failures (4) occurred on Midway between 16 June and 2 July. The distance from a wren's nest to a conspecific's nest averaged 86 m (n = 61 nests), and the distance from a wren's nest to the nest of a bird of another species averaged 71 m (n = 64); these values differed significantly from each other (Welch's t = 2.3, P = 0.03).

The number of fledglings from wren nests was negatively associated with juniper cover and tree diameter (adjusted R^2 = 0.14, P = 0.003). There were no differences in number of fledglings by aspect or by orientation of the nest-box (ANOVA *P*-values ≥ 0.22). Average height of trees in plots with used nest-boxes was significantly less than average height in plots with non-used boxes (t = 2.2, P = 0.03), but there were more stumps in used than non-used plots (t = 2.0, P = 0.05) and a greater distance to plants in the 2nd quarter of used plots than non-used plots (t = 2.1, P = 0.04).

Point counts conducted from 1989 to 1991 in the pinyon-juniper zone (Morrison et al. 1993) demonstrated that Bewick's Wrens were the most common species breeding in the study area ($\bar{x}$ = 0.87 detections/point). Based on this value averaged across the 150 point-count stations sampled each year, wrens averaged about 131 birds in the study area, or about 65 pairs. Thus, the ratio of the number of pairs detected (65) to the number of complete nests (43) was 1.51.

Mountain Chickadee

All 18 chickadee nests that we found contained eggs at some point during a breeding season. Nest construction by chickadees occurred in early May; clutches were laid mid-May, with an average of 6.1 eggs; the young birds fledged by late June, with an average of 2.4 birds fledging successfully; an average of 3.3 young died in the nest before fledging (Table 1). Six nest failures occurred between 31 May and 18 June; thus, nesting success was 67% (12 of 18 nests). The distance from a chickadee nest to a conspecific's nest averaged 94 m ($n = 10$), and the distance from a chickadee nest to the nest of a bird of another species averaged 74 m ($n = 18$); these values did not differ significantly from each other (Student's $t = 1.6$, $P = 0.12$).

The number of fledglings from chickadee nests was negatively associated with distance to plants in the 1st quarter of the nest plots, but was positively associated with number of pinyon trees >3 m tall and <6 m tall, and the height of the nest-box (adjusted $R^2 = 0.83$, $P = 0.001$). The number of fledglings from chickadee nests also differed among aspect categories: more young were fledged from boxes with southerly than easterly aspects ($F_{3,12} = 4.1$, $P = 0.03$). There were no differences in vegetative characteristics between used and non-used plots (t-test P-values ≥ 0.10).

Mountain Chickadees were the 2nd most common breeding species in the White and Inyo Mountains ($\bar{x} = 0.57$ detections/point). Based on the average number of detections across the 150 point-count stations sampled each year, chickadees averaged about 86 individuals, or roughly 43 pairs in the study area. Thus, the ratio of pairs detected (43) to complete nests (18) was 2.39.

Ash-throated Flycatcher

All 12 flycatcher nests we found contained eggs at some point during a breeding season. Nest construction by flycatchers occurred in mid- to late May; clutches were laid in early June, with an average of 4.4 eggs; the young birds fledged by early July, with an average of 3.0 birds fledging successfully; an average of 1.4 young died in the nest before fledging (Table 1). Three nest failures occurred between 25 June and 29 June; thus, nesting success was 75% (9 of 12 nests). The distance from a flycatcher nest to a conspecific's nest averaged 50 m ($n = 2$ nests). The distance from a flycatcher nest to the nest of a bird of another species averaged 71 m ($n = 12$); these values did not differ significantly from each other (Welch's $t = 1.5$, $P = 0.18$).

The number of fledglings from flycatcher nests did not differ by aspect, nest-box orientation, or tree vigor (ANOVA P-values ≥ 0.29). There were no significant differences in vegetation characteristics between used and non-used plots (t-test P-values ≥ 0.06).

Ash-throated Flycatchers were counted relatively uncommonly in the White and Inyo Mountains ($\bar{x}$ abundance = 0.20 detections/point). This abundance equated to about 30 individuals, or 15 pairs, in the pinyon-juniper woodland. The ratio of pairs detected (15) to complete nests (12) was 1.25.

Juniper Titmouse

All 11 titmouse nests that we found contained eggs at some point during a breeding season. Nest construction occurred in early May; clutches averaging 5.5 eggs were laid in mid-May; young birds fledged by mid-June, with an average of 4.2 birds fledging successfully, but an average of 1.3 young dying in the nest before fledging (Table 1). The only nest failure occurred on 12 June; thus, nesting success was 91% (10 of 11 nests). Distance from a titmouse nest to a conspecific's nest averaged 50 m ($n = 2$ nests), whereas the distance from a titmouse nest to the nest of a bird of another species averaged 70 m ($n = 11$); these values differed significantly from each other (Welch's $t = 2.5$, $P = 0.03$).

There were no differences in the number of titmouse fledglings by aspect, nest-box orientation, or tree vigor (ANOVA P-values ≥ 0.28). Height of juniper shrubs was greater in plots with used nest-boxes than in plots with non-used boxes ($t = 2.4$, $P = 0.04$), and distance to plants in the 1st quarter of the nest plot was also greater in used vs. non-used plots ($t = 2.3$, $P = 0.04$).

Titmice were counted relatively uncommonly in the pinyon-juniper woodland ($\bar{x}$ abundance = 0.21 detections/point). This abundance equated to about 32 individuals, or 16 pairs, in the study area. The ratio of pairs detected (16) to complete nests (11) was 1.45.

Mountain Bluebird

All 6 bluebird nests that we found contained eggs at some point during a breeding season. Nest construction occurred in early May; clutches were laid in mid-May, with an average of 4.7 eggs; young birds fledged by mid-June, with an average of 3.7 birds fledging successfully; an average of 1.0 young died in the nest before fledging (Table 1). The single nest failure occurred on 26 June; thus, nesting success was 83% (5 of 6 nests). Distance from a bluebird nest to a conspecific's nest averaged 128 m (n = 4), and to the nest of a bird of another species, 63 m (n = 6); these values differed significantly from each other (Student's $t = 3.7$, $P = 0.006$).

Mountain Bluebirds were also relatively uncommon in the study area ($\bar{x}$ = 0.21 detections/point). Their abundances equated to about 32 individuals, or 16 pairs, in the study area. The ratio of pairs detected (16) to complete nests (6) was thus 2.67.

White-breasted Nuthatch

The 1 nuthatch nest we found was constructed in late April. The clutch of 7 eggs was laid by 11 May, and 6 young fledged on 19 June. This nest was located 70 m from the nearest nest of another species.

Nuthatches were counted very infrequently during point counts in the study area ($\bar{x}$ = 0.14 detections/point), which equated to about 21 individuals, or about 10 pairs. The ratio of pairs detected (10) to complete nests (1) was thus 10.0.

DISCUSSION

Breeding Biology

Bewick's Wrens used our nest-boxes most commonly, followed by Mountain Chickadees, Ash-throated Flycatchers, and Juniper Titmice. During our study the medium-elevation grids (i.e., 2150–2270 m) had the greatest nest-box usage of all our study grids, with the most wren, flycatcher, titmouse, and nuthatch nests occurring there. Mountain Chickadees nested most commonly on our highest elevation grid. None of these findings were unexpected when compared with abundance data collected on the same species from 1989 to 1991 in the study area (Morrison et al. 1993; see also Ryser 1985), which showed that these birds were most abundant in this middle-elevation range. One surprising finding, however, was that Mountain Bluebirds nested most commonly on our lowest elevation grid (2090 m), although they exhibited greater abundances at higher elevations (Morrison et al. 1993).

Our findings on the reproductive characteristics of the bird species in the White and Inyo Mountains paralleled information published previously for the species in other regions of the Great Basin. Mountain Chickadees laid the most eggs (6.1) of all species involved in our study, whereas Ash-throated Flycatchers laid the fewest (4.4). Baicich and Harrison (1997) noted a range of 6–12 eggs for Mountain Chickadees, and Johnsgard (1979) noted a range of 3–7 eggs for Ash-throated Flycatchers. Juniper Titmice averaged slightly fewer eggs (5.5) during our study than Johnsgard (1979) noted (i.e., range of 6–8). Bewick's Wren and Mountain Bluebird nests, and our single White-breasted Nuthatch nest, all fell within ranges of eggs noted by Bent (1964:78), Dickey (1935:150), Johnsgard (1979:322), Pravosudov and Grubb (1993), and Kennedy and White (1997) for these species in the Great Basin. Nesting success for all species (except nuthatches) ranged from 67% (for chickadees) to 91% (for titmice). Li and Martin (1991) found a 72% success rate for Mountain Chickadee nests in natural cavities in central Arizona; thus, although chickadees laid the most eggs in our study, they may have been exhibiting a relatively low success rate. The fledging rate (number fledglings/number eggs laid) of Bewick's Wrens has been estimated to be between 51% and 70% (summarized in Kennedy and White 1997); in our study 74% of nests fledged young. The average fledging rate for 1st- and 2nd-brood eggs of Mountain Bluebirds has been estimated at 81% (Power and Lombardo 1996); in our study 83% of the nests fledged young. A study of Ash-throated Flycatchers in the western Great Basin from 1984 to 1987 demonstrated that 79% of all flycatcher nests in nest-boxes successfully fledged young (Dunning and Bowers 1990), which also was similar to the success rate we found (75%). Annual and lifetime reproductive success for White-breasted Nuthatches is essentially unknown (Pravosudov and Grubb 1993), probably due to the fact that the species primarily nests in natural cavities or old woodpecker holes rather than nest-boxes.

Distances from used nest-boxes to conspecifics' nests varied among the species we observed, with Ash-throated Flycatchers and Juniper Titmice nesting closest to their conspecifics, followed by Bewick's Wrens, Mountain Chickadees, and Mountain Bluebirds, in ascending order (overall range = 50–128 m). Distances between nesting birds of other species showed a different pattern: on average, each species (except nuthatches) nested about 70 m from the other species (range = 70–74 m); the 1 nuthatch nest we found was located 63 m from the nest of a neighbor. Thus, wrens, chickadees, and bluebirds nested closer to other species than they did to their own kind, whereas flycatchers and titmice nested closer to their own kind than they did other species. These results are not unexpected: the territories of Bewick's Wrens are known to vary in shape and size depending on the distribution of vegetation, amount of open space, and density of birds in the vicinity (Kennedy and White 1997), but male wrens are also known to exhibit spacing among conspecifics (Johnsgard 1979:322). When Mountain Bluebirds do not have close conspecifics, the territories of these birds may not have obvious boundary points (Power and Lombardo 1996), thus indicating their breeding season territoriality. And finally, Mountain Chickadees are also known to defend breeding territories against conspecifics (Brennan 1989:87). Ash-throated Flycatchers and Juniper Titmice could be more tolerant of their own kinds for many reasons; for example, Mountain Bluebirds may compete for nest sites with Ash-throated Flycatchers in the western Great Basin (Simpkin and Gubanich 1991).

Bewick's Wrens were the only species of the 6 we observed that appeared to build nests that they never used. Male Bewick's Wrens are known to be bigamous, and in some instances polygynous (Johnsgard 1979:322), and male House Wrens (*Troglodytes aedon*) have been shown to fill multiple cavities with twigs, or even to build complete nests that are never used by a female (Finch 1989). Thus, it is possible that at least some of the 21 wren nests we found that never contained eggs were "extra" male wren nests, although Kennedy and White (1997) asserted that while males do often place some material in more than one nest-box at a time, they do not produce multiple dummy nests.

Physical Characteristics of
Nest-Boxes and Nest Plots

Vegetation, topography, and nest-box characteristics explained 14% and 83% of the variation in Bewick Wren and Mountain Chickadee fledgling numbers, respectively. Mountain Chickadee fledging success in our study was strongly associated with relatively dense, mature vegetation, on warm slopes. Brennan et al. (1999) also found that Mountain Chickadees on the west side of the Sierra Nevada, California, used nest-boxes in areas with moderate amounts of tree canopy closure and density. Chickadees also used plots with a more southerly aspect in their study. None of these characteristics differed between used and non-used nest-boxes in our study, however, so apparently chickadees were using the boxes in proportion to their availability.

Bewick's Wrens and Juniper Titmice, on the other hand, appeared to select boxes disproportionately: titmice used nest plots with greater juniper shrub height and sparser vegetation around the nest; wrens used plots with shorter overall tree height, sparser vegetation around the nest, and more stumps. Numbers of wren fledglings were also associated with sparser juniper cover and small-dbh trees. We could not locate any habitat selection information for Juniper Titmice, but our findings for Bewick's Wrens corresponded with other information available for the species. In our study the use of plots with more stumps was also similar to that seen in other studies, including the observation that these wrens are known to nest in stumps, knotholes, and cavities of fallen or live trees, and in dense brush piles. They will also nest in old buildings, under boards, in the headlights of old cars, in plant watering pots, and behind awnings (Bent 1964:177, Dickey 1935:150, Johnsgard 1979: 322), demonstrating their extreme nesting versatility.

Cavity Availability

A very small percentage (range = 0% to 15%) of the available nest-boxes and natural cavities during our study were used by the nesting species we monitored. It is likely, of course, that we did not locate other non-cavity nesting sites (e.g., broken limbs, rock outcrops). Because so few boxes were occupied, it is unlikely that nest sites were limiting for the species we studied.

Nest-boxes can be a useful management tool for increasing population sizes of cavity-nesting bird species, especially for species nesting in areas lacking natural cavities. However, based on our study, we suggest that it may not be worthwhile to provision nest-boxes unless a population has already been determined to be limited by the availability of cavities. We think that nest-boxes remain, however, a useful tool for assessing breeding characteristics of secondary cavity-nesting species.

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APPENDIX. Vegetation and topographic variables describing characteristics of nest-boxes on grids in the White and Inyo Mountains, California, 1988–1992.

Variable	Unit
Height of nest-box in tree	meters
Direction that box entrance faced	degrees
Height of tree with nest-box	meters
Diameter at breast height of nest-box tree	centimeters
Distance to edge of tree canopy from entrance of nest-box	meters
Position of nest-box plot on slope, from 0.0 (gully bottom) to 1.0 (top of hill)	rank
Slope of land at center of nest-box plot	percent
Aspect of nest-box plot, measured from center	degrees
Total number of natural cavities present in plot	number
Total number of stumps present in plot	number
Total number of standing, dead trees in plot	number
Total number of pinyon trees >1.5 m tall and ≤ 3 m tall	number
Total number of pinyon trees >3 m tall and ≤ 6 m tall	number
Total number of pinyon trees >6 m tall	number
Total number of juniper trees >1.5 m tall and ≤ 3 m tall	number
Total number of juniper trees >3 m tall and ≤ 6 m tall	number
Total number of juniper trees >6 m tall	number
Number of hits of pinyon along point-intercept line	number
Number of hits of juniper along point-intercept line	number
Number of hits of sagebrush along point-intercept line	number
Number of hits of bitterbrush along point-intercept line	number
Number of hits of rabbitbrush along point-intercept line	number
Number of hits of Mormon tea along point-intercept line	number
Mean height of pinyon shrubs (<1.5 m tall) in plot	meters
Mean height of juniper shrubs (<1.5 m) in plot	meters
Mean height of sagebrush shrubs (<1.5 m) in plot	meters
Mean height of bitterbrush shrubs (<1.5 m) in plot	meters
Mean height of rabbitbrush shrubs (<1.5 m) in plot	meters
Mean height of Mormon tea shrubs (<1.5 m) in plot	meters
Distance from nest-box to nearest shrub or tree in 1st quarter of circle (PQ1)	meters
Distance from nest-box to nearest shrub or tree in 2nd quarter of circle (PQ2)	meters
Distance from nest-box to nearest shrub or tree in 3rd quarter of circle (PQ3)	meters
Distance from nest-box to nearest shrub or tree in 4th quarter of circle (PQ4)	meters
Mean of PQ1 + PQ2 + PQ3 + PQ4	meters