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Author(s): David F. DeSante
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THE ROLE OF RECRUITMENT IN THE DYNAMICS OF A SIERRAN SUBALPINE BIRD COMMUNITY

David F. DeSante*

Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970

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The role of recruitment of young in the dynamics of bird populations, although often suggested as being of critical importance (see, e.g., Andrewartha and Birch 1984), has only recently been quantitatively investigated, primarily through studies of lifetime reproductive success (McCleery and Perrins 1988; J. Smith 1988; van Noordwijk and van Balen 1988). These studies have shown that variations in the rate of recruitment of young into the breeding population, acting primarily through variations in the first-year survival of young birds, may well be the most important factor affecting lifetime reproductive success. Therefore, year-to-year variations in the rate of recruitment among coexisting populations probably play a major role in the dynamics and stability of avian communities.

Although theoretical treatments of community stability have existed for more than two decades (see Goodman 1975 for a review) and considerable debate still exists regarding the major factors that influence the dynamics and stability of avian communities (see, e.g., Wiens 1983, 1984; Grant 1985; Noon et al. 1985; Dunning 1986; Ricklefs 1987; Wiens and Rotenberry 1987), relatively few field studies have monitored the dynamics and stability of an entire land-bird community over a long period of time (Wiens 1973; Holmes and Sturges 1975; Wiens and Rotenberry 1981*a;* Williamson 1983; Svensson et al. 1984; Holmes et al. 1986). Even fewer studies have provided data on the long-term productivity of an entire land-bird community. These have relied on indirect means of estimating productivity, such as timed transects measuring the increase in numbers of birds between early summer and midsummer (Holmes and Sturges 1975) or standardized mist netting during the breeding season measuring the ratio of young to adults (DeSante and Geupel 1987). Indeed, nearly all information on annual variations in land-bird productivity and recruitment has arisen from intensive single-species studies (e.g., Perrins and Moss 1975; Nolan 1978; Petrinovich and Patterson 1983; Woolfenden and Fitzpatrick 1984; Bryant 1988; Harvey et al. 1988; McCleery and Perrins 1988; J. Smith 1988; van Noordwijk and van Balen 1988). This is the first long-term study of an entire breeding-bird community that has attempted to moni-

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* Present address: The Institute for Bird Populations, P.O. Box 554, Inverness, California 94937.

Am. Nat. 1990. Vol. 136, pp. 429–445.

tor directly the productivity of all breeding species and to investigate the effects of recruitment of young on community dynamics.

Here, I provide data on the number of breeding territories and the production of fledglings in each territory for all breeding species in a 1-km^2 Sierran subalpine study area for each of seven summers from 1979 to 1985. I also provide rough estimates of adult winter survival, based on return rates of banded adults. These data suggest that recruitment (or lack of recruitment) of young, rather than productivity or adult survival, is the major factor controlling the population and community dynamics of subalpine birds. These results are in accordance with the important role that recruitment has been shown to play in affecting lifetime reproductive success in land birds and in regulating the dynamics of marine fish and invertebrate communities (Cushing 1977; Gaines and Roughgarden 1987). Other aspects of this study, including an analysis of the microhabitat correlates of productivity and in-depth analyses of the nesting success of select species, will be presented elsewhere.

STUDY AREA AND METHODS

The 1-km^2 study area is located in the Harvey Monroe Hall Research Natural Area of the Inyo National Forest on the eastern slope of the Sierra Nevada in Mono County, California, and includes about two-thirds of the subalpine habitat of Slate Creek Valley, one of the headwater tributaries of Lee Vining Creek. The study area's elevation ranges from 3,000 to 3,200 m.

About half of the study area is on the south-facing slope of the valley and is dominated by a more or less continuous, mature lodgepole pine (*Pinus murrayana*) forest, about 20–25 m in height, interspersed with several dry, open, rocky areas and with a few moist subalpine meadows and willow (*Salix* sp.) thickets. A rich, moist ground cover of numerous species of forbs, grasses, and sedges, along with scattered shrubs and subshrubs (primarily *Ribes, Artemisia, Salix,* and *Phyllodoce*), characterizes the eastern two-thirds of the south-facing slope, while the western third has a similar but much sparser and drier ground cover and shrub layer. A few whitebark pines (*Pinus albicaulis*) are scattered throughout the south-facing slope.

The other half of the study area is on the north-facing slope of the valley and is dominated by a patchy woodland of whitebark pine about 8–15 m in height, interspersed with extensive open areas and several willow thickets. On the eastern two-thirds of the north-facing slope, these open areas are primarily dry, grassy or rocky areas, but on the western third they are mostly moist meadows. A few lodgepole pines and a very few mountain hemlocks (*Tsuga mertensiana*) are scattered along the lower elevations of the north-facing slope. The study area is bordered on the north primarily by talus slopes and steep cliffs; on the south and southwest by talus slopes, alpine fell fields, and several small lakes; and on the east and northwest by habitat roughly similar to that of the study area.

The study area was divided into six contiguous plots of 16–17 ha orthogonally gridded at 40-m intervals. The 625 grid points were marked with small rock cairns and 60-cm-tall garden stakes with red or yellow flags. In most years, six observers were responsible for an intensive program of spot mapping and nest monitoring, one for each 16–17-ha grid. In 1982, 1983, and 1985, however, three observers were each responsible for two grids. In most years, detailed spot-mapping censuses were run on each grid on about four mornings per week for about 5 h per morning during the 10-wk period from about June 16 through August 24. During the two heavy-snowfall years, 1982 and 1983, and in 1985, the starting time was delayed about 2 wk, to the beginning of July. A concentrated effort was made during these spot-mapping censuses to locate and monitor nests of all species in all territories for which more than 5% of the territory was contained within the study area. From 485 to 1,060 person-hours were spent each year spot mapping the birds and monitoring their nests.

Because the amount of experience, both with subalpine birds and in the study area itself, varied among the observers, checks were made midway through and at the end of each season to ensure the accuracy of the spot-mapping and nest-monitoring efforts. These checks each consisted of three parts. First, I spent one day with each observer on his or her grid, ensuring that the data were being collected consistently and accurately. Second, summary territory maps and single-paragraph accounts of the current status and results of each breeding territory were written by each observer for each grid. Third, the territory maps completed by each observer were compared and any discrepancies or irregularities thoroughly investigated. Furthermore, each evening, all observers communally wrote a daily journal, recording the current breeding status and results for each species, along with other interesting observations. Thus, all observers kept abreast of developments in the study area.

The data considered here are the total number of breeding territories (or home ranges) of all breeding species (scientific names are given in table 1) for which more than 5% of the territory was included within the 1-km^2 study area, as well as the production of fledglings in each of these territories, for each of the seven summers from 1979 to 1985. At least one nesting attempt qualified a territory as a breeding territory; unmated territorial males and nonbreeding individuals of both sexes were excluded. Territorial boundaries were determined by the spot-mapping method. Productivity (the mean number of young birds fledged per breeding territory) was determined by the detailed monitoring of nests or, in those cases where nests were not found, by counting fledglings.

Counting fledglings was an effective way of monitoring productivity in a given territory because the dependent fledglings remained in, or near, the territory of their parents for most of their post-fledging dependent period (most species) or at least for the first 3–4 days of post-fledging dependence (woodpeckers, American robins, and fringillids). Moreover, the relatively low breeding-bird density and species richness characteristic of the subalpine avian community, along with the relatively open and easily accessible habitat, facilitated counting the fledglings. Nevertheless, at least one nest was found and monitored for 52.8% of the 1,135 breeding territories considered here.

Winter survival of adults was estimated from the return rate each year of 96 breeding adults of 11 species individually color-banded in 1979 (27 dusky flycatchers, 12 mountain chickadees, 1 white-breasted nuthatch, 1 brown creeper, 16

TABLE 1

Number of Breeding Territories and Productivity of Young in a Sierran Study Area of One Square Kilometer

	1979		1980		1981		1982		1983		1984		1985		Mean	
Species	*N*	*Y*	*N*	*Y*	*N*	*Y*	*N*	*Y*	*N*	*Y*	*N*	*Y*	*N*	*Y*	*N*	*Y*
Falconiformes:																
Northern goshawk																
Accipiter gentilis	1	1.0	1	1.0	1	1.0	1	0							.6	.7
Charadriiformes:																
Spotted sandpiper																
Actitis macularia	1	1.0	1	0	1	4.0					2	2.0	1	1.0	.9	1.7
Apodiformes:																
Calliope hummingbird																
Stellula calliope	1	0			1	2.0					1	0			.4	.7
Piciformes:																
Hairy woodpecker																
Picoides villosus													1	2.0	.1	2.0
Northern flicker																
Colaptes auratus			1	1.5							1	3.5	1	3.0	.4	2.7
Passeriformes:																
Dusky flycatcher																
Empidonax oberholseri	**34**	**1.9**	**22**	**2.0**	**24**	**3.0**	**25**	**1.9**	**14**	**1.3**	**20**	**2.3**	**23**	**2.1**	**23.1**	**2.1**
Clark's nutcracker																
Nucifraga columbiana	**7**	**2.1**	**3**	**2.3**	**6**	**2.0**	**5**	**2.0**	**7**	**2.5**	**9**	**2.0**	**8**	**2.3**	**6.4**	**2.2**
Mountain chickadee																
Parus gambeli	**17**	**2.9**	**11**	**2.1**	**15**	**1.9**	**8**	**1.8**	**6**	**3.6**	**10**	**2.2**	**12**	**3.1**	**11.3**	**2.5**
White-breasted nuthatch																
Sitta carolinensis	2	2.0	2	2.3	2	2.0									.9	2.1
Brown creeper																
Certhia americana	1	6.5			1	0							1	3.0	.4	3.2
Rock wren																
Salpinctes obsoletus	1	0	1	0	1	2.0							2	.7	.7	.7
American dipper																
Cinclus mexicanus	2	1.5			2	.7							1	1.5	.7	1.2

Golden-crowned kinglet																
Regulus satrapa					1	5.0									.1	5.0
Ruby-crowned kinglet																
Regulus calendula					1	0									.1	0
Mountain bluebird																
Sialia currucoides	1	0			1	0									.3	0
Townsend's solitaire																
Myadestes townsendi					1	0							1	3.0	.3	1.5
Hermit thrush																
Catharus guttatus	**14**	**1.1**	**7**	**2.7**	**10**	**3.2**	**8**	**1.7**	**7**	**1.3**	**9**	**2.7**	**11**	**1.9**	**9.4**	**2.0**
American robin																
Turdus migratorius	**7**	**1.3**	**5**	**2.1**	**11**	**1.4**	**2**	**1.0**	**4**	**2.0**	**4**	**1.3**	**5**	**2.1**	**5.4**	**1.6**
Yellow-rumped warbler																
Dendroica coronata	**13**	**1.7**	**16**	**2.7**	**20**	**2.6**	**18**	**1.9**	**12**	**1.7**	**25**	**2.0**	**28**	**2.3**	**18.9**	**2.2**
Wilson's warbler																
Wilsonia pusilla	4	1.7	3	2.7									4	2.4	1.6	2.2
Chipping sparrow																
Spizella passerina	3	0			5	.6							11	.9	2.7	.7
White-crowned sparrow																
Zonotrichia leucophrys	**19**	**1.5**	**18**	**2.0**	**18**	**2.4**	**11**	**2.1**	**7**	**2.1**	**13**	**1.4**	**17**	**1.4**	**14.7**	**1.8**
Dark-eyed junco																
Junco hyemalis	**37**	**2.4**	**42**	**2.0**	**47**	**2.2**	**33**	**1.9**	**29**	**2.1**	**41**	**2.0**	**44**	**2.6**	**39.0**	**2.2**
Rosy finch																
Leucosticte arctoa							1	2.5	1	3.5	1	2.5			.4	2.8
Pine grosbeak																
Pinacola enucleator					1	0					1	2.0	1	2.5	.4	1.5
Cassin's finch																
Carpodacus cassinii	**30**	**.6**	**18**	**.3**	**33**	**.3**	**11**	**1.4**	**5**	**.7**	**16**	**.7**	**19**	**.9**	**18.9**	**.6**
Pine siskin																
Carduelis pinus					14	.9	8	1.6			1	2.0	4	1.5	3.9	1.2
Subtotal of dominant species	178	1.7	142	1.9	184	2.0	121	1.9	91	1.9	147	1.9	167	2.1	147.1	1.9
Subtotal of rare species	17	1.3	9	1.7	33	1.0	10	1.5	1	3.5	7	2.0	28	1.5	15.0	1.4
Total	195	1.7	151	1.9	217	1.8	131	1.8	92	1.9	154	1.9	195	2.0	162.1	1.9

NOTE.—*N*, The total number of breeding territories, any part of which touched the 1-km^2 study area. *Y*, The number of young fledged per breeding territory. Dominant species are indicated by boldfaced type. Rare species are in lightface type.

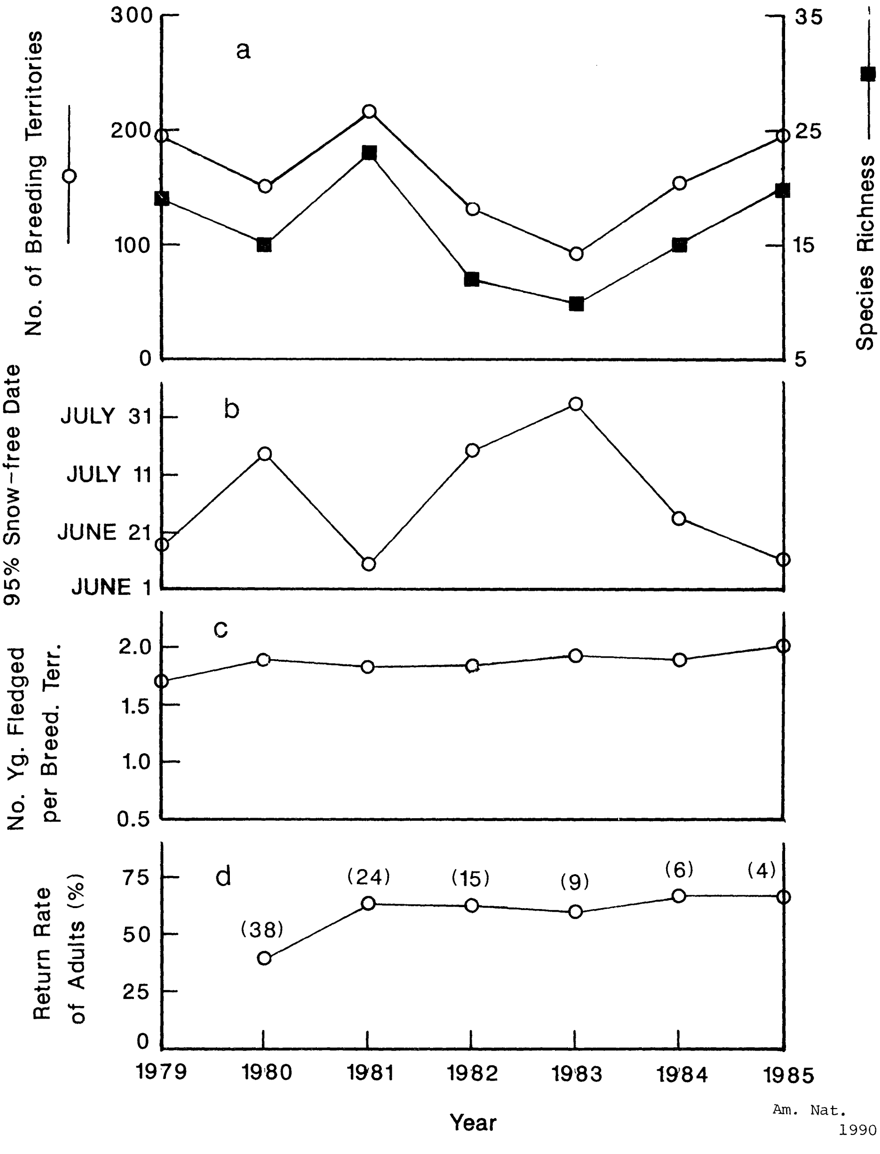

FIG. 1.—*a*, Number of breeding territories of all species combined (*open circles*) and species richness (*solid squares*) in a 1-km^2 Sierran subalpine study area for the seven summers 1979 through 1985. *b*, 95% snow-free date for these same seven summers. *c*, Productivity (number of young fledged per breeding territory) for these same seven summers. *d*, Adult overwintering survival (return rate of adults) for the 6 yr 1980 through 1985; numbers in parentheses indicate the number of adults, of the original 96 banded in 1979, that returned each year.

hermit thrushes, 2 American robins, 4 yellow-rumped warblers, 3 Wilson's warblers, 2 chipping sparrows, 6 white-crowned sparrows, and 22 dark-eyed juncos). No additional birds were color-banded after 1979. Thirteen individually color-banded Cassin's finches were excluded from these calculations because certain individuals did not return in 1982 or 1983 but did return in subsequent years. No instance of skipping years by any color-banded individual was recorded for any of the other 11 species.

Environmental conditions each year at the start of the breeding season were characterized by the timing of snowmelt. This was determined each year as the 95% snow-free date, the date on which 95 of 100 grid-point cairns on a 16-ha reference grid on the south-facing slope first became entirely free of snow.

Bird-species diversity was calculated as $H' = -\Sigma p_i \log p_i$, where p_i is the proportion of the ith species in the total of n species. Evenness was calculated as $J = H'/H'_{\max}$, where $H'_{\max} = \log n$, where n is the species richness.

RESULTS

In total, 27 breeding species were recorded during the seven summers from 1979 to 1985 (table 1). The 9 dominant species, which had average densities equal to or greater than five territories per square kilometer and were present in every year, were the dusky flycatcher, Clark's nutcracker, mountain chickadee, hermit thrush, American robin, yellow-rumped warbler, white-crowned sparrow, dark-eyed junco, and Cassin's finch. The remaining 18 rare species, with average densities of fewer than five territories per square kilometer, were each absent in at least two of the seven summers.

The great majority of the 27 breeding species are at least partially migratory: 8 are long-distance migrants wintering primarily or entirely in the tropics, and 13 are short-distance migrants wintering elsewhere in the temperate region or at lower elevations in the Sierra. Only 6 species are permanent residents in Sierran subalpine habitat (hairy woodpecker, Clark's nutcracker, mountain chickadee, white-breasted nuthatch, rosy finch, and pine grosbeak), and all of these are subject to some degree of winter movement or down-mountain drift, presumably as a function of winter snow conditions and food supply (unpublished data).

The number of breeding territories of all species combined varied dramatically over the seven summers (coefficient of variation, CV = 26.7%), from a high of 217 in 1981 to a low of 92 in 1983 (fig. 1*a*). Species richness varied in a similar manner (CV = 28.3%), from a high of 23 species in 1981 to a low of only 10 species in 1983 (fig. 1*a*). Richness was positively correlated ($r = 0.98$, $P < .001$) with the number of breeding territories, as was bird species diversity ($r = 0.97$, $P < .001$). Diversity, however, showed considerably less variation (CV = 7.5%), from a high of 2.46 in 1981 to a low of 2.03 in 1983. Evenness also varied little (CV = 4.3%), from 0.88 in 1983 to 0.79 in 1981; it was inversely correlated with the number of breeding territories ($r = -0.90$, $P < .01$). Comparisons of species lists between successive years (table 1) clearly indicate that variations in species richness were due to the loss and reappearance of rare species. Roughly synchronous variations in the number of breeding territories, however, were characteristic of all species, including both dominant and rare species. As expected, dominant species showed less variation from year to year (CV = 22.5%) than did rare species (CV = 77.8%).

Environmental conditions in the study area at the start of the breeding season, as indicated by the timing of snowmelt, also varied dramatically over the seven years (fig. 1*b*). Snowmelt occurred as early as early to mid-June following winters of relatively average snowpack, as in 1978–1979, 1980–1981, and 1984–1985. It occurred as late as late July to early August following winters of extremely heavy snowpack, as in 1981–1982 and 1982–1983, when an El Niño southern oscillation (ENSO) disrupted weather patterns worldwide (Philander 1983).

Both the number of breeding territories and the species richness were inversely correlated with the timing of snowmelt ($r = -0.96$, $P < .001$, and $r = -0.94$, $P < .005$, respectively), suggesting that ENSO conditions produced major effects upon this ecosystem more than 300 km from the Pacific Ocean.

Despite the fact that species richness and the total number of breeding territories varied substantially during the study, productivity, measured as the mean number of young fledged per breeding territory, remained essentially constant (fig. 1*c;* CV = 5.6%), even during ENSO years. The major effect of heavy snowfall and late snowmelt years on productivity was to delay the initiation of breeding.

Clark's nutcracker was the first species in each year to fledge young, usually in early to mid-June. American robins and dark-eyed juncos were next, typically fledging first broods in early July in years of early snowmelt. Young were fledged before July 1 in only six robin territories and nine junco territories during the entire seven summers. Young were fledged before July 1 in only two other territories (one each of hermit thrush and white-crowned sparrow). The peak of fledging typically occurred from mid- or late July to early August. For virtually all species, fledging dates were 3–4 wk later in years of heavy snowpack and late snowmelt.

Because of the short breeding season in the subalpine, most pairs of most species bore single broods, although several renesting attempts often occurred for pairs that suffered nest predation early in the season. Second brood attempts (after successfully fledging a first brood) were recorded for only six species, and then usually only in years of early snowmelt. In total, only 33 of 1,135 breeding territories of all species combined (2.9%) attempted second broods in any of the seven summers of the study: brown creeper (1 of 3 breeding territories), hermit thrush (3 of 66), American robin (2 of 38), yellow-rumped warbler (4 of 132), white-crowned sparrow (3 of 103), and dark-eyed junco (20 of 273).

No significant correlation existed between the number of breeding territories in a given year and productivity in the preceding year for dominant species ($r = 0.04$, $P \gg .10$), rare species ($r = -0.08$, $P \gg .10$), or total species ($r = 0.34$, $P \gg .10$), thereby suggesting that population densities in a given year were not primarily controlled by productivity in the preceding year.

No significant correlations existed, for either total species or dominant species, either between productivity in a given year and the number of breeding territories that year ($r = -0.20$, $P \gg .10$, and $r = 0.11$, $P \gg .10$, respectively) or between productivity in a given year and species richness that year ($r = -0.12$, $P \gg .10$, and $r = 0$, $P = 1$, respectively). These results suggest, at least for dominant species, that productivity did not strongly depend on either density or species richness and, therefore, did not strongly depend on either the potential intraspecific or interspecific competitive regime.

For rare species, however, marginally significant negative correlations were found between productivity in a given year and both the number of breeding territories that year ($r = -0.73$, $.05 < P < .10$) and the species richness that year ($r = -0.76$, $P < .05$), suggesting that productivity may be inversely related to density and species richness in these species. Moreover, the correlation between the productivity of rare species in a given year and density that year was improved when the total number of breeding territories of all species combined were considered ($r = -0.84$, $P < .02$). These results, however, should be viewed with caution. Eliminating 1983—the year when only one rare species, the normally alpine-inhabiting rosy finch, bred in the study area—caused the loss of significance in the correlations between the productivity of rare species and the number of breeding territories of rare species ($r = -0.76$, $.05 < P < .10$), the total number of breeding territories of all species ($r = -0.71$, $P > .10$), and the species richness (either of rare species or of total species, since the species richness of dominant species was constant; $r = -0.70$, $P > .10$).

It is also of interest, though perhaps not unexpected, that dominant species produced slightly more young per territory (1.9) than did rare species (1.4). Excluding 1983, when only a single territory of rare species existed (a rosy finch territory that produced 3 or 4 young), this difference was found to be statistically significant (matched-pairs *t*-test, $t = 2.88$, $P < .05$). Cassin's finches were unusual among dominant species in that they showed poor productivity (an average of only 0.6 young per territory). When Cassin's finches were eliminated, the above difference became more significant (2.1 young per territory for dominant species vs. 1.4 for rare species; $t = 3.50$, $P < .02$).

Overwintering survival of adults for all species combined, as indicated by the return rate each year of breeding individuals color-banded in 1979, also appeared to have remained constant from 1981 through 1985 (CV = 4.5%; $\chi^2 = 0.15$, $P > .90$) and averaged 63.8% (fig. 1*d*). The low return rate of adults in 1980 (39.6%) was probably a consequence of including first-year breeders among the birds color-banded in 1979. First-year breeders have been shown to have lower site fidelity than older breeders in a number of passerine species, including *Turdus merula* (European blackbird; Greenwood and Harvey 1976), *Riparia riparia* (bank swallow; Freer 1979), *Parus cinctus* (Siberian tit; A. Järvinen 1982), *Fringilla coelabs* (chaffinch; Mikkonen 1983), and both *Melospiza melodia* (song sparrow) and *Zonotrichia leucophrys nuttalli* (Nuttall's white-crowned sparrow; unpublished data).

No significant correlation was found between the overwintering survival (return rate) of adults in a given year and the number of breeding territories that year ($r = 0.60$, $P > .10$), suggesting that breeding densities did not strongly depend on adult overwintering survival. Moreover, no significant correlation was found between the number of breeding territories in a given year and the overwintering survival (return rate) of adults the following year ($r = -0.33$, $P \gg .10$), suggesting that adult overwintering survival did not strongly depend on the potential competitive regime, although the negative sign of the correlation should be noted.

DISCUSSION

Limitations on the interpretation of the results of this study, posed by its methodology, warrant some discussion. First, different observers worked in different parts of the study plot and in different years. Some variation in techniques was inevitable, and the quality of the data was thus uneven. A concerted effort was made, however, to check the results of the observers in order to minimize this unevenness (see the section "Study Area and Methods," above). Moreover, the two grids on the south-facing slope that together accounted for more than half of the breeding territories were surveyed most consistently with respect to observers (one grid entirely by me and the other by only three observers, one of whom worked for four consecutive years). Thus, the unevenness in data quality present in the study probably did not substantially affect the ability to draw accurate inferences from the results.

Second, only about half of all breeding attempts were monitored directly, the results of the other half being inferred from counts of the number of fledglings. The estimated number of young fledged from known nests was probably biased high, because some young could have died after the last nest check but before or during fledging. However, the estimated number of young fledged from territories for which nests were not found was probably biased low, because some young could have died before the fledglings were found and counted or some fledglings could have been missed. Since nests were found for about half of the territories, these biases probably tended to cancel each other, thus producing a relatively unbiased estimate of the number of young successfully fledged. In addition, the percentage of territories in which nests were found varied somewhat from species to species: dusky flycatcher, 72.8; mountain chickadee, 72.2; American robin, 65.8; Cassin's finch, 61.4; hermit thrush, 57.8; dark-eyed junco, 45.4; yellow-rumped warbler, 43.9; white-crowned sparrow, 38.8; and Clark's nutcracker, 28.9. Since these percentages remained relatively constant from year to year, the results were probably not biased to any significant degree by these variations.

Third, the study lasted only seven summers, still relatively long compared with many land-bird studies. Thus, the statistical analyses reported here, particularly when a year represents a data point, are tests of low statistical power. Failure to reach conventional levels of statistical significance, therefore, should be interpreted as indicating either the absence of a relationship between the variables studied or a weak relationship that was undetectable.

Fourth, estimates of adult survival were based on return rates of birds banded in a single year, 1979. Anderson et al. (1985) have shown that such methods produce highly biased estimates of actual adult survival. Furthermore, the same individuals were involved in the calculations for each year, and they may well represent a biased group of individuals with higher survival rates than most birds. These difficulties are partially overcome since we are more interested in the annual variations in adult survival rates than in their actual values. Nevertheless, other difficulties arise, the most important of which is that the sample size, which was declining progressively, became very small in later years, leading to coarse estimates of survival rates after 1982. Thus, conclusions based upon the apparent constancy of adult return rates must be interpreted with extreme caution.

Fifth, only one habitat type (subalpine) and breeding-bird community were studied. Thus, the results may not be strictly applicable to other habitats. The study area itself, however, is quite large (1 km^2) compared with those used in many avian studies, and it occupies about two-thirds of the subalpine habitat in the particular headwater valley. Moreover, the habitat of the study area is representative of subalpine habitat throughout the Sierra Nevada (although whitebark pines are replaced by foxtail pines [*P. balfouriana*] in the southern Sierra), and the composition of the bird community was, with minor differences, representative of subalpine bird communities throughout western North America, including the Cascades and both the northern and central Rocky Mountains (personal observation). The results, therefore, are likely to be characteristic of other subalpine breeding-bird communities throughout montane western North America and possibly throughout the world.

Finally, an unusual ecological event (a 100-yr ENSO in 1982 and 1983) exerted a dominant influence on the community structure. Nevertheless, the major results of the study held, even when these two years were eliminated from the data and only the remaining five summers were considered. Specifically, both the number of breeding territories and the species richness varied considerably over the five summers (CV = 15.8% and 18.7%, respectively), whereas bird species diversity and evenness varied less (CV = 6.7% and 3.1%). Variations in species richness were caused by the loss and reappearance of rare species. Dominant species showed less variation in the number of breeding territories (CV = 11.3%) than did rare species (CV = 60.9%). Both species richness and bird species diversity were positively correlated with the number of breeding territories ($r = 0.99$, $P < .005$, and $r = 0.97$, $P < .01$, respectively), whereas evenness tended to correlate inversely with the number of breeding territories ($r = -0.79$, $P \approx .10$). Both the number of breeding territories and species richness tended to be inversely correlated with the timing of snowmelt ($r = -0.87$, $P \approx .05$, and $r = -0.83$, $P \approx .08$). Productivity remained relatively constant over the five summers (CV = 6.7%) and was not correlated with either the number of breeding territories ($r = 0.02$, $P \gg .10$) or the species richness ($r = 0.14$, $P \gg .10$). The number of breeding territories did not correlate strongly with productivity in the preceding year ($r = 0.48$, $P \gg .10$), and the overwintering survival (return rate) of adults was essentially constant (CV = 3.1%). This indicates that the mechanisms affecting the dynamics of subalpine breeding-bird communities may be similar both in relatively normal years and in years of extreme environmental variation.

The annual variations over seven summers in the number of breeding territories (CV = 26.7%) and in species richness (CV = 28.3%) were greater than those reported for most avian communities; they were most similar to those reported for grassland and alpine or tundra habitats (Wiens 1973; O. Järvinen 1979; Wiens and Rotenberry 1981*a;* Noon et al. 1985). For example, Holmes and Sturges (1975) found annual variabilities over 5 yr of only 13.9% for the number of breeding individuals and 6.9% for species richness in a northern hardwood ecosystem at the Hubbard Brook Experimental Forest in New Hampshire. In contrast, Svensson et al. (1984) found annual variabilities over 20 yr of 17.7% and 37.1%, respectively, for the number of breeding territories in a low-elevation and high-elevation tundra in southern Swedish Lapland and of 14.1% and 21.8% for species richness at the two elevations. Similarly, O. Järvinen and Väisänen (1976) reported annual variabilities over 10 yr of 20.1% for density and 20.7% for species richness in a Fennoscandian subalpine birch forest. When the two unusual ENSO years were removed from the Sierran data set, the Sierran variabilities dropped to 15.8% for the number of breeding territories and 18.7% for the species richness. Thus, the annual variations in the Sierran subalpine habitat were roughly similar to other subalpine or low-elevation-tundra habitats studied, but with added variability due to the presence of an unusually severe ENSO event during the study.

Species turnover was entirely due to the disappearance and reappearance of rare species. Similar results were reported by Williamson (1983) for a 1-km^2 Welsh island. The rare species that disappeared as breeders from the Sierran subalpine study area during the ENSO years of 1982 and 1983, and reappeared during the recovery years of 1984 and 1985, were primarily species at or near the upper altitudinal limit of their breeding range. This indicates that weather conditions can affect the upper altitudinal limit, moving it up in years of light snowpack and down in years of heavy snowpack. Of further interest is the fact that one alpine species, the rosy finch, which typically breeds higher than the subalpine, nested in the study area from 1982 to 1984. This suggests that weather conditions can affect the lower altitudinal limit of the breeding range of montane species in a similar way.

Productivity and survival rates are two of the major factors affecting population densities (Caughley 1977). It is of considerable interest, therefore, that productivity, as estimated by the mean number of young fledged per breeding territory, appeared to remain relatively constant in the subalpine bird community studied here, even during the ENSO years (CV = 5.6%). This contrasts with data from Hubbard Brook (Holmes and Sturges 1975) that suggest that pronounced annual variations in avian productivity (CV = 35.2%) occurred over a 5-yr study period, presumably in response to outbreaks of caterpillars of *Heterocampa* moths. Annual variations in productivity of 11.4% over a 10-yr period from 1976 to 1985 were found in coastal-scrub and mixed-evergreen-forest habitats in central coastal California in a mediterranean climate that was influenced by the same ENSO event (DeSante and Geupel 1987). The major effect of the ENSO (and the depth of the snowpack and timing of snowmelt in general) on productivity in the subalpine was to delay the onset of breeding. Similar delays due to snowpack were previously reported in montane habitats for white-crowned sparrows (Morton 1976, 1978) and dark-eyed juncos (K. Smith and Andersen 1985).

The fact that productivity of the 9 dominant species in the subalpine tended to be higher and more constant than the productivity of the 18 rare species suggests that the dominant species are the true subalpine species and that the rare species, which are more characteristic of lower elevations, are not as well adapted to subalpine conditions. Since roughly synchronous variations in population density occurred among all species, both dominant and rare, and no strong correlations existed between productivity and population levels or species richness, the subalpine breeding-bird community may be an assemblage of species responding similarly, but relatively independently, to environmental conditions.

Data on the annual return rates of adults in the subalpine study area suggest, with the limitations discussed above, that adult overwintering survival, at least of adults 2 yr old or older, may also have remained relatively constant, even during the ENSO years. This is not completely unexpected, since most individuals breeding in the subalpine migrate to the tropics or to lower elevations in temperate regions, where the impacts of winter weather and particularly the ENSO might be expected to be less than in the subalpine.

Since productivity, and possibly adult overwintering survival, appeared to remain constant, the decreased numbers of breeding territories in 1982, 1983, and probably 1980 had to result from dramatically lowered recruitment rates of new breeders. This can be deduced from the number of breeding territories in 1982 and 1983, which were only 60.4% and 70.2%, respectively, of the number during the preceding year, values close to the estimated average adult return rate of about 60%. Thus, it is likely that few new breeders settled in the study area during those two years. Moreover, because the study area is representative of most of the Sierran subalpine habitat, probably few new breeding birds were recruited anywhere in the subalpine during those years. This suggestion is supported by other work on subalpine populations of dusky flycatchers and white-crowned sparrows some 5–8 km southeast of the study area. These populations also experienced declines during the ENSO years (M. L. Morton, personal communication). Thus, it is unlikely that movements within the subalpine accounted for the pronounced changes in the numbers of breeding territories and breeding species recorded in the study area.

Furthermore, because high breeding-site fidelity among color-banded individuals was found for most dominant species in the study area, at least after their second breeding season (data to be presented elsewhere), most new recruits into the breeding populations can be assumed to be second-year birds in their first breeding season or, to a lesser extent, third-year birds in their second breeding season. What, then, dramatically lowered recruitment rates of second-year (and possibly third-year) birds in heavy snowpack years? I suggest two causes. First, high mortality (low overwintering survival) could have occurred among these younger, less-experienced birds during the severe ENSO winters. Second, these younger birds may not have settled in the study area because of unfavorable conditions (extremely heavy snowpack) at the start of the breeding season. In all likelihood, both these effects occurred, but a lack of settling in the study area was the predominant mechanism. This is suggested by the fact that the average yearly decrease during 1982 and 1983 in the number of long-distance migrants, whose overwintering survival would be expected to be minimally affected by the ENSO, was 28.5%, slightly greater than the analogous decrease in residents (20.8%) but somewhat less than the analogous decrease in short-distance migrants (41.3%). None of these differences, however, was significant.

Since younger birds did not appear to settle in the subalpine during these years of exceptionally heavy snowpack, where did they settle? Since they could not have settled at higher elevations than the subalpine, they must have settled at lower elevations, if indeed they settled at all. These data therefore suggest that natal dispersal and, probably to a lesser extent, breeding dispersal may involve an altitudinal component in montane species, such that individuals produced at the upper altitudinal limit of a breeding range do, under the adverse weather conditions of extremely heavy snowpack and extremely late snowmelt, disperse to lower elevations for breeding.

The converse also appears to be true. Using the number of young fledged per breeding territory in 1983 (1.93) and setting the winter survival of young from fledging to equal the return rate of adults from 1983 to 1984 (0.67; it is probably considerably less), the 1983 population (92 breeding territories) could not have increased above 241.0 birds (120.5 breeding territories) in 1984. In fact, however, 154 territories were actually present in 1984. The 67.4% increase in the number of breeding territories in 1984, therefore, could not have been caused by recruitment from the subalpine alone and must have depended on increased recruitment from lower elevations. Thus, the natal, and possibly breeding, dispersal of montane species may also involve an altitudinal component that can, under favorable weather conditions, disperse individuals for breeding to elevations beyond the local upper altitudinal limit of the current breeding range.

These data do not necessarily indicate that fewer young birds visit the higher elevations in years of heavy snowpack. Relatively constant numbers of young birds may visit the subalpine each year, but fewer may attempt, or be able, to establish territories and settle in years of heavy snowpack; this is presumably because less habitat is relatively free of snow, and thus available, when young birds are attempting to settle. Furthermore, the territorial behavior of established older birds, which usually arrive earlier than young birds on their breeding grounds, may play an important role in preventing the settlement of young birds, at least in habitat that is relatively free of snow. Territoriality may therefore limit the amount of natal, and perhaps breeding, dispersal in years of heavy snowpack.

Hejl et al. (1988), working in true-fir forests at lower elevations in the Sierra, also found depressed populations in 1983 and a highly significant linear recovery in 1984 and 1985. Drawing to some extent on the results reported here, they suggested that populations inhabiting montane habitats may exhibit a "source-sink" structuring (Wiens and Rotenberry 1981*b*), such that lower elevations harbor source populations and individuals unable to establish breeding territories at lower elevations move upslope into less suitable sink habitats during crowded years. I suggest that source populations actually occur at optimal elevations for each species and that dispersing individuals, especially young, may move up or down depending on environmental conditions. If this is indeed the case, results of the type reported here may be expected to occur throughout all elevations in montane environments.

Although recruitment has long been recognized as an important factor in regulating marine fish and invertebrate communities, where life-history patterns are different from those of birds (Cushing 1977; Gaines and Roughgarden 1987), the role of recruitment in affecting avian communities has received little prior attention. Only recently has the importance of individual variations in the recruitment rate of offspring, through variations in the survival rates of first-year birds, been appreciated as a major component of lifetime reproductive success (McCleery and Perrins 1988; J. Smith 1988; van Noordwijk and van Balen 1988). It is of considerable interest, therefore, that variations in the recruitment rate of Sierran subalpine birds, through probable variations in the altitudinal component of natal and breeding dispersal, appear to wield a major influence on the population dynamics of these birds. I suggest that similar results are typical of most avian populations on both the geographical and ecological edges of their ranges (MacArthur 1972). Because the subalpine lies at the ecological edge of the range of many species, and because both environmental conditions and the structure of the avian community are highly variable there (O. Järvinen and Väisänen 1976; this study), the subalpine should prove an excellent location for further studies of avian population ecology and community dynamics.

Finally, I would like to suggest several improvements that could be made in this and other similar studies. First, estimates of adult survival (return rates) could be improved by color-banding large numbers of breeding adults during each year of the study. The effort involved in such an attempt, however, would be considerable. Second, the ages of birds newly recruited into the breeding population should be ascertained. This would allow for the determination of whether variations in natal dispersal or breeding dispersal (or both) are driving the population dynamics of the avian community. Unfortunately, it is often extremely difficult to determine the ages of birds in the spring and summer, even in the hand, after their skulls are fully pneumatized. Pyle et al. (1987) presented numerous suggestions for aging passerine birds by feather shape, wear, and color. These suggestions need to be evaluated critically and tested on known-aged populations. The ability to age passerine birds accurately in the spring would provide an important tool for advancing the understanding of avian ecology and population dynamics.

SUMMARY

The species richness and number of territories of all species combined in a 1-km^2 Sierran subalpine study area fluctuated dramatically over the seven summers of 1979–1985 and were highly correlated with the timing of snowmelt. Over the same period, productivity (as determined by the number of young fledged per breeding territory) remained relatively constant, with dominant species tending to show higher and more constant productivity than did rare species. No significant correlations were found, at least for dominant species, between productivity and either the total number of breeding territories or species richness, suggesting that productivity did not strongly depend on either the potential intraspecific or interspecific competitive regime. Data collected annually on the return rates of 96 breeding adult birds banded in 1979 failed to detect changes in their winter survival rates. These patterns suggest that the recruitment of new breeders, particularly young, is a major factor controlling the population dynamics of subalpine birds and that natal and breeding dispersal may involve an altitudinal component dependent upon environmental conditions at the start of the breeding season.

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