Long-term studies of bird populations in California mountains are conspicuously absent from the literature. While distribution of summer resident species is generally well known, population changes through the summer and fall need study. This is certainly the case in the Yolla Bolly Mountains of the interior north coast ranges of California. Hemphill (1952) presents a fairly complete account of species occurrence in the southern Yolla Bolly Mountains during the summer. A banding project carried out in the Yolla Bollys 15 June to 6 October 1973 afforded us the opportunity to observe seasonal changes in bird populations. This paper is a summary of data collected on a closely interrelated group of species, the wood warblers (Parulidae).

LOCATION OF STUDY

The base of our research activity was a cabin at Howell’s Camp (elevation 6200 feet, USGS Anthony Pk. quadrangle) in the Mendocino National Forest 10 miles east of the southeast corner of the Yolla Bolly-Middle Eel Wilderness Area, and 30 airline miles west of Corning, Tehama County. This site is located on the first major north-south ridge west of the Sacramento Valley. Steep topography is a prominent feature of the Yolla Bollys and the rise from the valley floor to Howell’s Camp is rapid. There is a broad zone of interdigitation between yellow pine forest and chaparral. The ridge top around Howell’s Camp is covered by yellow pine forest dominated by White Fir (Abies concolor), with Incense Cedar (Libocedrus decurrens), Ponderosa Pine (Pinus ponderosa), Sugar Pine (Pinus lambertiana), and mats of Ceanothus cordulatus, Ribes lobbii and R. roezlii with some Bitter Cherry (Prunus emarginata). On the slopes of the ridge grow Ponderosa Pine, Douglas-Fir (Pseudotsuga mensiesii), Black Oak (Quercus kelloggi) and Oregon Oak (Q. garryana). Chaparral occurs to 4,500 feet elevation on the slopes of Thomes Creek Canyon several miles to the south.

The banding site is located on a meadow with two large thickets of Mountain Alder (Alnus tenuifolia) and scattered elderberry (Sambucus caerulea) shrubs. A spring in the meadow fills a small reservoir. To the
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west lie the high ridges of the Yolla Bollys with several peaks near 8,000 feet above sea level. Extensive Red Fir (Abies magnifica var. shastensis) forests with Jeffrey Pine (Pinus jeffreyi), White Pine (Pinus monticola) and locally Foxtail Pine (Pinus balfouriana) is a major habitat not present close to Howell’s Camp. High elevation vegetation including White Fir dominated yellow pine and Red Fir community types is referred to as the boreal zone (after Hemphill 1952). Plant species and community-type classification are based on Munz (1968). A detailed vegetational analysis of the region is provided by Keeler-Wolf and Keeler-Wolf (1974).

METHODS

One mist-net was operated an average of eight hours per day on 35 days between 2 July and 5 October. During this period nearly 1500 birds were caught; 964 were warblers. Due to the absence of summer rain and scarcity of surface water, the spring and elderberries of the meadow were powerful attracters of birds. Many species of passerines, hummingbirds, and woodpeckers were seen feeding on the elderberry nectar and berries. The net was located next to a dripping water trough in an alder thicket. Birds could be seen descending from the sky in numbers into the thicket. The net was nearly as high as the thicket and caught most of the birds going to drink or bathe. The banding sample was a good representation of the species proportions observed in the meadow. Age of warblers was determined by degree of skull ossification, plumage characters, and presence or absence of primary and secondary molt.

To supplement our banding data sight observations were made during our stay 15 June to 5 October 1973. Most observations were made in the Howell’s Camp area, but our knowledge of the status of many species was increased by extended trips in 1973 and in the two previous years into the wilderness area, including the Red Fir forest region of North and South Yolla Bolly Mountains.

RESULTS

A summary of species banded by time period is presented in Table 1. The warbler flocks in the meadow were composed of mixed species whose relative abundance varied. To avoid placing undue stress on hourly fluctuations the data has been grouped into more meaningful sample sizes. To illustrate long-term trends we have organized our data
Table 1. Species composition of warblers banded at Howell's Camp, Yolla Bolly Mountains, Tehama County, California between 2 July and 5 October 1973.

<table>
<thead>
<tr>
<th>BANDING DATES</th>
<th>SAMPLE SIZE</th>
<th>ORANGE-CROWNED</th>
<th>NASHVILLE</th>
<th>YELLOW</th>
<th>YELLOW-RUMPED</th>
<th>BLACK-THR. GRAY</th>
<th>HERMIT</th>
<th>TOWNSEND'S</th>
<th>MacGILLIVRAY'S</th>
<th>WILSON'S</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-9 Jul</td>
<td>25</td>
<td>17</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>10-13 Jul</td>
<td>33</td>
<td>21</td>
<td>4</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
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<td>23-25 Jul</td>
<td>64</td>
<td>51</td>
<td>6</td>
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<td>0</td>
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<tr>
<td>30-31 Jul &amp; 5 Aug</td>
<td>87</td>
<td>53</td>
<td>22</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>4</td>
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<tr>
<td>10-16 Aug</td>
<td>179</td>
<td>90</td>
<td>36</td>
<td>0</td>
<td>38</td>
<td>1</td>
<td>7</td>
<td>0</td>
<td>2</td>
<td>5</td>
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<tr>
<td>21 &amp; 23 Aug</td>
<td>90</td>
<td>44</td>
<td>11</td>
<td>0</td>
<td>28</td>
<td>0</td>
<td>5</td>
<td>0</td>
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<tr>
<td>29-30 Aug</td>
<td>38</td>
<td>13</td>
<td>4</td>
<td>0</td>
<td>14</td>
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<td>7-9 Sept</td>
<td>28</td>
<td>15</td>
<td>1</td>
<td>1</td>
<td>9</td>
<td>0</td>
<td>2</td>
<td>0</td>
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<td>0</td>
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<tr>
<td>12-16 Sept</td>
<td>173</td>
<td>28</td>
<td>0</td>
<td>8</td>
<td>118</td>
<td>3</td>
<td>11</td>
<td>1</td>
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<tr>
<td>17, 21 &amp; 23 Sept</td>
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<td>1</td>
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<td>5</td>
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<td>3</td>
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<tr>
<td>1-2 Oct</td>
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<td>1</td>
<td>129</td>
<td>4</td>
<td>3</td>
<td>6</td>
<td>0</td>
<td>1</td>
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<tr>
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<td>33</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>29</td>
<td>0</td>
<td>1</td>
<td>0</td>
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<td>Totals</td>
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<td>344</td>
<td>88</td>
<td>15</td>
<td>434</td>
<td>11</td>
<td>40</td>
<td>7</td>
<td>8</td>
<td>17</td>
</tr>
</tbody>
</table>
Figure 1. Relative abundance of four most frequently caught warbler species, 2 July-5 October 1973, in Yolla Bolly Mtns., California. Points plotted represent mean dates of banding periods given in Table 1.
into sampling periods of irregular length. The data cannot be used to estimate the size of the populations sampled due to the transient nature of the population. Only four warblers (0.4%) were recaptured: 1 Yellow-rumped Warbler (*Dendroica coronata auduboni*) and 3 Orange-crowned Warblers (*Vermivora celata*). Three recaptures were made over three weeks after the original capture. It is clear that large nomadic populations were being sampled. In Figure 1, data from Table 1 has been converted to relative frequency for Orange-crowned Warbler, Nashville Warbler (*Vermivora ruficapilla*), Yellow-rumped Warbler and Hermit Warbler (*Dendroica occidentalis*). Data points are plotted at mean date of time period, given in Table 1. This graphically shows the change in species composition of the banding sample over time. Trends of the data are discussed below.

**SPECIES ACCOUNTS**

The Lutescent Orange-crowned Warbler (*V. celata lutescens*), a common chaparral breeder, was present in large numbers throughout the boreal regions at the beginning of the study in June. This species increased in abundance through July and began dropping in abundance slowly in August then rapidly in September. All of the birds banded were born that year and going through postjuvenal molt. The percentage of birds having completed postjuvenal molt (except crown where molt was completed last) increased through summer and fall as follows: 2-25 July, 5.6% (n=89); 30 July-14 August, 15.8% (n=95); 15-23 August, 57.0% (n=79); 29 August-5 October, 91.8% (n=49). Orange-crowned Warblers were abundant in scrub and thickets ranging commonly into coniferous forests, often high in the canopy. A maximum of 50 was banded 11 August. A small number of birds which appeared to be of the northern races (*V. celata orestera* or *V. c. celata*) were present from 16 September to 2 October. Orange-crowned Warblers were more abundant in 1973 than in the previous two years.

Nashville Warblers were heard singing in lower elevation yellow pine forest during June, but were not observed around Howell’s Camp and other alder thickets until early July. Flocks of this species associated with Orange-crowned Warblers. As summer progressed Nashville Warblers became relatively and absolutely more numerous, but they dropped in abundance earlier than Orange-crowned Warblers and were nearly absent in late August. Nashville Warblers banded were all hatching year birds in various stages of postjuvenal molt. The percentage of birds having completed postjuvenal molt (except crown where molt was completed last) increased through the summer as follows: 9-24 July, 14.3% (n=14); 31 July-11 August, 44.2% (n=43); 1 August-7 September, 78.3% (n=23). The maximum banded was 34 on 11 August.

Yellow Warbler (*Dendroica petechia*) immatures were seen and banded in small numbers during September and early October. A maximum of 4 was banded on 12 and 17 September. They were always observed in the meadow alder thickets.

Audubon’s Yellow-rumped Warblers were still nesting during June and July when large flocks of *Vermivora* were moving through the boreal region. The Yellow-rumped Warbler is one of the most abundant breeders in the boreal region. Singing was common in June, but stopped almost entirely in early July and was
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replaced by intense nesting activity. Very few Yellow-rumped Warblers were
captured in July; from 2-12 July only 4 adults and 5 young were banded. However,
41 juveniles and 5 adults were caught between 23 July and 18 August. Late sum-
mer juveniles were in heavy body molt. After this, Yellow-rumped Warbler re-
maind common in the banding sample, but only 7 adults were banded. During
late July and throughout August large flocks of Yellow-rumped Warblers were
found, especially in coniferous forests in association with Dark-eyed Juncos (Junco
hyemalis oreganus) and Chipping Sparrows (Spizella passerina). Another large
influx occurred in September. This, coupled with rapid drops in Vermivora abun-
dance, made Yellow-rumped Warbler the dominant fall warbler, with a maximum
of 83 banded on 1 October. During the fall a few Myrtle Yellow-rumped Warblers
(D. c. coronata) were banded.

Black-throated Gray Warbler (Dendroica nigrescens) is a common nesting species
in the Ponderosa Pine dominated yellow pine and Digger Pine (Pinus sabiniana)
belts, but a few were caught and seen in the White Fir dominated yellow pine
forests from late August through early October. We observed only a few birds
above 5,000 feet elevation before August. All birds banded were hatching-year
birds with little conspicuous molt. A maximum of three was banded on 1 October.

Townsend's Warblers (Dendroica townsendi) were seen and banded in small
numbers in late September and early October. They were generally found in coni-
ferous forests in associations with Yellow-rumped Warbler, Dark-eyed Junco, Moun-
tain Chickadee (Parus gambeli), and other mountain winter residents. A maximum
of two was banded on 7 October.

Hermit Warblers breed commonly in mountains to the north and west (Harris
1973 and pers. obs.). This species is an uncommon breeder in the dry and logged
coniferous forests of most of the Yolla Bolly Mountains, but singing males were
commonly found in June in more mesic Abies dominated and mixed evergreen
forests. Immatures were seen and caught in small numbers from late July through
September with a major influx in late August and early September. None banded
were in heavy molt. A maximum of five was banded on 23 August.

MacGillivray's Warbler (Oporornis tolmiei), a common breeder in the moun-
tains to the north and west (Harris 1973 and pers. obs.), was found to be com-
mon in Ceanothus and manzanita dominated scrub only from 5 August through
early September. This species was more common at this time than the banding
data indicate. It was seldom caught because they rarely leave the scrub habitat.
Hemphill (1952) indicated it was a summer resident in the southern Yolla Bol-
lys, but in three years we have found only one before late July. The 8 birds
banded were immatures without sign of molt. A maximum of two was caught on
11 August.

Wilson's Warblers (Wilsonia pusilla) nest in alder thickets in other areas of the
Yolla Bollys. They are particularly common around North Yolla Bolly Mountain.
In the Howell's Camp area no singing males were heard, but immatures were seen
and caught in small numbers from July through September. A maximum of three
was caught on 24 July.

DISCUSSION

Breeding warblers of the Yolla Bolly Mountains show distinct habi-
tat and feeding station preferences. However, flocks of young birds are
nomadic and far less restricted in their distribution. The less nomadic nature of the adult populations is demonstrated by the low capture rates of adults of locally breeding species (e.g., Yellow-rumped Warbler). This is true of other locally nesting passerines including Chipping Sparrow and Dark-eyed Junco. This can be attributed to the territorial associations of breeding pairs. What happens to adult populations after breeding is a question unanswerable from our data. The presence of flocks of young in the boreal zone is a result of dispersal of various nesting populations. While an overview of the different dispersal strategies of the different species is out of the scope of this paper, these strategies may be inferred in part from the species' occurrence in the area of study. Young can come from three sources: 1) up-mountain movement (dispersal from plant communities at lower elevations in the same range), 2) dispersal from local populations, and 3) migration from other geographical areas.

The following is a speculative analysis of seasonal variation in species abundance in terms of the different possible sources of the dispersal populations. Large populations of Orange-crowned Warblers and Nashville Warblers are the result of up-mountain movement. Orange-crowned Warblers moving up from the chaparral are followed by Nashville Warblers coming from the Ponderosa Pine dominated yellow pine belt. It seems reasonable that birds at higher elevations would disperse later than those from lower elevations. Populations of these two species are in the process of molting from juvenal to immature plumage which we would not expect in birds in the process of long-distance migration. Grinnell and Miller (1944:423) noted a period of vagrancy preceding migration in V. c. lutescens; in all races of Orange-crowned Warbler except V. c. sordida (resident southern California race) postjuvenal molt takes place before long-distance migration (Foster 1971). Yellow-rumped Warblers in July and August dispersed from local breeding populations. The small number of Wilson's and Hermit Warblers present during this period were short distance migrants from other areas of the Yolla Bollys. The bulk of young Hermit and MacGillivray's warblers occurring in late July and August were migrants from breeding populations, presumably from mountains to the north. In September and early October the up-mountain migrants disappear and are replaced by long distance migrants. The major influx of this period comes from Audubon's Yellow-rumped Warblers, but small numbers of many other species and races occur. These include: Orange-crowned (several races?), Yellow, Myrtle Yellow-rumped, Hermit, Black-throated Gray, and Townsend's warblers. Northern races of Orange-crowned Warbler, Myrtle Yellow-rumped Warbler, and Townsend's Warbler can be definitely assigned to the long distance migrant category. It is interesting that Black-throated Gray Warbler does not follow the same pattern of occurrence found in other species breed-
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ing at lower elevations in the Yolla Bollys. This difference is probably an inherent difference in dispersal strategies. Why young of some species disperse up-mountain and one young of one species do not is an interesting point of speculation. A possible reason is avoidance of intense competition with the summer resident cogeners, Yellow-rumped and Hermit warblers. Where juvenal Black-throated Gray Warblers disperse is an interesting question.

We observed large flocks of first-year warblers, occurring with many other species of passerines, made up of independently assorting species-flocks. The seasonal abundance of different species varied with the different stages in each species' life history which high mountain occurrence represents. As the season progressed, species composition shifted as the young from different populations dispersed into the boreal region. First to occur are the up-mountain dispersers, then come the local breeders, and last come the migrants from geographically distant areas.

Regardless of dispersal strategy, at least four species maintain large populations of first year birds in the boreal zone of the Yolla Bollys in feeding associations with many other species. This indicates that this region might be highly productive at this time of year and a good place for psychological and physiological preparation for long distance migrations. This would include molt, fat deposition, and collection of experience in a benign environment. The separation of juvenal and adult populations may also result in reduced competition between age classes.

Juveniles, however, will be competing with other juveniles of the same and different species and adults of local breeding species. A good example of the latter is the occurrence of flocks of juvenile Vermivora in the boreal region at the height of the Yellow-rumped Warbler breeding season. However, if food resources are high then competition will be relatively unimportant, as will the incredibly high activity of avian and mammalian predators.

The period during which young disperse and begin to migrate is a critical period in the life history of migratory passerines. It is often a confusing period for bird students as it is difficult to distinguish post-breeding wandering by young from clearly defined migration. Several of the species discussed in this paper have long been noted to have periods of vagrancy and up-mountain movements (Grinnell and Miller 1944). The focus of this paper has been on the community of warblers dispersing young into the boreal region. This problem could alternatively be approached more from the standpoint of dispersal strategies of the various species. It would be interesting to see how much dispersal patterns are determined at the species level and how much they are response to local communities and environments. More intensive banding in mountains may shed light on the nature of the seemingly nomadic movements of young birds. Finally, more observation of resource utilization
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and habitat selection will help determine how benign the boreal region is in summer and fall and the extent of interspecific competition.

SUMMARY

Warbler populations in the boreal region of the Yolla Bolly Mountains were studied by observation and banding. Large nomadic populations comprised mainly of first-year birds inhabit the boreal zone from June through early October. Seasonal peaks of relative abundance differ between species. Orange-crowned Warbler dominates during the summer with large numbers of Nashville Warblers, some Audubon’s Yellow-rumped Warblers and a few Wilson’s Warblers. The peaks for Hermit and MacGillivray’s Warblers are in the late summer. Audubon’s Yellow-rumped Warbler dominates the fall flocks with a few migrant forms occurring in small numbers: Orange-crowned Warbler (northern races), Yellow Warbler, Myrtle Yellow-rumped Warbler, Black-throated Gray Warbler, Hermit Warbler and Townsend’s Warbler. Probable origins of the various populations and timing of dispersal into the boreal zone are discussed.

ACKNOWLEDGMENTS

Sam and Charlotte Wolf generously allowed us the use of their cabin. The critical aid of J. Van Remsen and Joseph Greenberg was enlisted in the preparation of the manuscript and criticisms by Tim Manolis, Bruce Webb, and Alan M. Craig were extremely valuable. A special thank you to Patti Greenberg for drawing the figure.

LITERATURE CITED

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Sketch by Dave Winkler