

the birds were well fluffed out. Insulation values probably did not increase significantly from this point on. Therefore, physiological development probably accounts for increasing thermoregulatory ability after 4 hr of age. Yarbrough (1970) and Lagerspetz et al. (1966) suggest that ability to thermoregulate may be related to a state in neural development. By comparing heat loss of wet and dry duckling carcasses, it is apparent that evaporative cooling plays an important part in heat loss in wet downy young as was shown by Nye (1963). Birds at hatching and 1 hr after are wet or damp and lose heat by heat transfer and evaporative cooling. Newly hatched, wet ducklings can regulate body temperature somewhat because they maintain higher body temperature than dead, wet carcasses. They not only must overcome the evaporative cooling, affecting the wet carcass, but also are probably losing more heat by heat transfer because of peripheral blood circulation. Dry carcasses lose less heat than birds 2 and 4 hr of age for the same reason (fig. 1). Herried and Kessell (1967) found conductance greater for nearly naked nestlings than for dead, defeathered birds, as did Yarbrough (1970) in nestling Gray-crowned Rosy Finches (*Leucosticte tephrocotis*).

SUMMARY

Precocial young of waterfowl must be able to thermoregulate for short feeding periods as no direct parental help in feeding occurs. Reasonable stable body temperatures are maintained within 24 to 48 hr of hatching in Mallard ducklings. At hatch ducklings

have some ability to maintain body temperature. Further physiological development of thermoregulation seems to occur in steps.

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DISPERSION OF FEMALE BLUE GROUSE DURING THE BROOD SEASON

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East of the crest of the Cascade Mountains in Oregon, Washington State, and British Columbia, many Blue Grouse (*Dendragapus obscurus*) move from wintering areas in montane coniferous forests to grassland or shrub-grassland breeding ranges at lower elevations. These areas are in high demand for grazing of domestic livestock, which alters the environment and may affect numbers of Blue Grouse (Marshall 1946; Zwickel 1958; Buss 1960; Hamerstrom and Hamerstrom 1961; Mussehl 1963; Zwickel et al. 1968). In the summer of 1968, an assistant and I studied Blue Grouse on heavily grazed and ungrazed areas in the Methow Valley, Washington, being interested mainly in the effect of different environments on numbers. The present paper is concerned with the dispersion of brood and lone (broodless) females on grazed and ungrazed areas, as patterns of dispersion may have important theoretical implications.

METHODS

Our general approach was to systematically search two areas, one *grazed* and one *ungrazed*, with trained pointing dogs from mid-May to early August. We recorded locations of all sightings of brood and lone females, with data from June, July, and August forming the basis of this paper. This period was chosen because it represents the brood period, peak hatch

having occurred in the last 7-10 days of May. Sightings in June are compared to those for July and August combined because we noted a distinct shift in the distribution of birds in early July, during a short period of very hot, dry weather. My assistant and I alternated study areas each day.

Ideally, a study of dispersion should be time specific, but this is nearly impossible with most species of vertebrates in natural populations. Data presented here represent, in each case, composite sighting locations over at least a month-long period. These represent a minimum of 19 different banded hens on the ungrazed area and 14 on the grazed, with an unknown number of unbanded hens on each. We were not able to reidentify individual hens so some repeat sightings of the same individuals are likely included in the analysis.¹ Densities of breeding birds were essentially the same on the two areas (Zwickel 1972).

One of our main observations concerns an analysis of the distribution of birds in relation to grassland, shrub-grassland, and thickets. For this analysis, any individual or group of Ponderosa Pine (*Pinus ponderosa*), Aspen (*Populus tremuloides*), or Wild Cherry (*Prunus* spp.) trees over 2 m high were considered as thickets. Birds were classified as associated with thickets if within 15 m of them. Shrub-grassland is referred to as *grassland* for purposes of analysis. Statistical analyses concerning the distribution of birds in relation to thickets were done with *Fisher's Exact Test* (Sokal and Rohlf 1969).

¹ The use of composite sightings of unidentified individuals over at least month-long periods makes the assumption that the samples were generally representative of the use of the environment by the respective populations during the time periods specified.

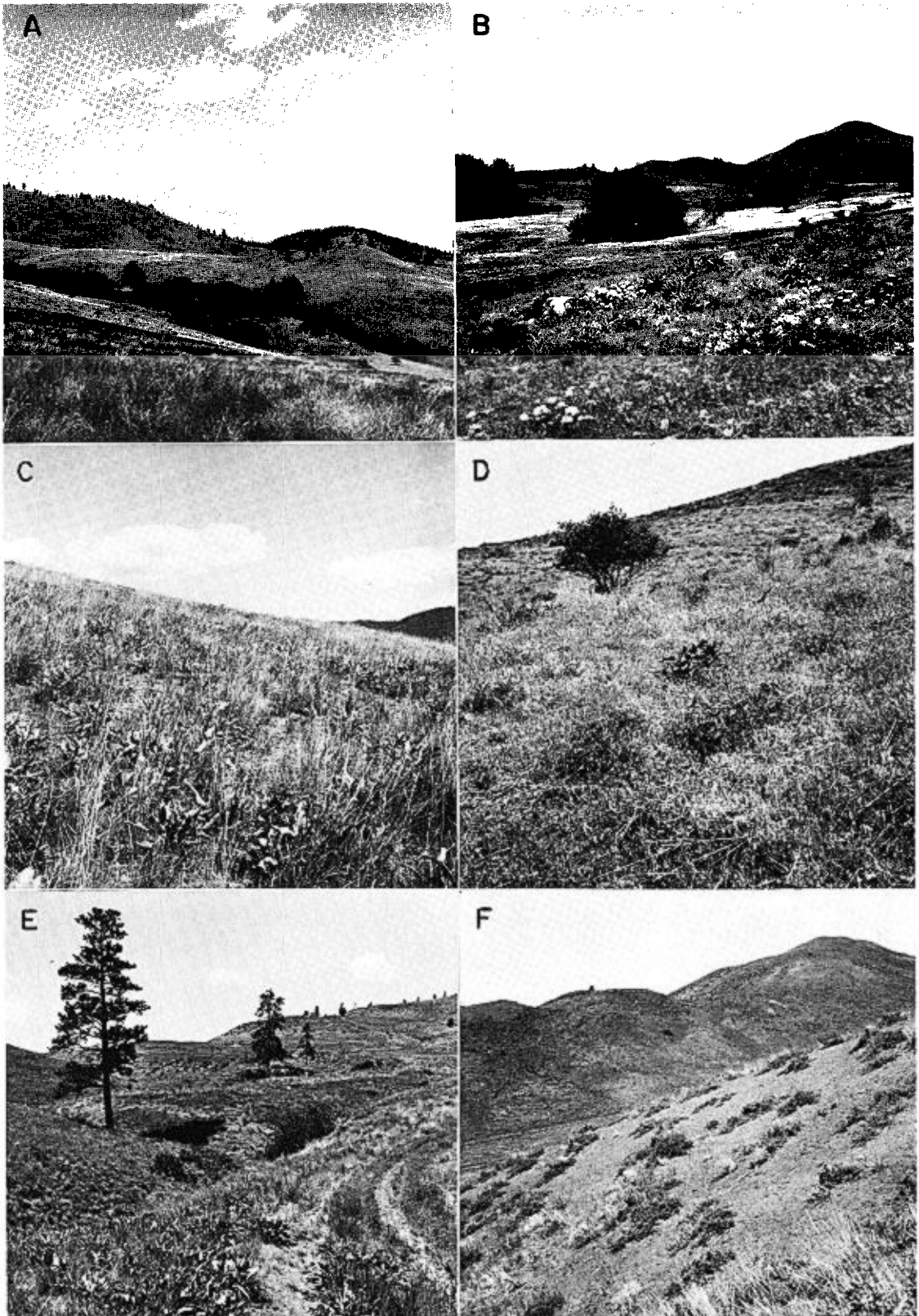


FIGURE 1. Study areas; (A) general view of part of Frazer Creek study area; the study area extended only to the crest of the grass-covered ridge in mid-background, (B) general view of part of Balky Hill study area, (C) Bunchgrass hillside at Frazer Creek, (D) Cheatgrass hillside at Balky Hill—note high-lining on Wild Cherry thicket, (E) Bunchgrass slopes and scattered Ponderosa Pine at Frazer Creek, (F) eroding ridge crest at Balky Hill; also note croding ridges on the far hill.

Since the use of composite samples over month-long periods almost certainly includes repeated sightings of some individuals, the assumption of statistical independence is likely violated to some degree in the use of this test. The effect of this nonindependence is to increase the probability of saying that a real difference exists when it does not. To the best of my knowledge, and that of statistical consultants, no other test is more appropriate, considering the nature of the data. In spite of the above problem, consultants inform me that if values are very low, a real difference almost certainly exists. Thus, exact probabilities are presented, where appropriate, so the reader may judge the likelihood of differences being significant for himself.

STUDY AREAS

Both study areas were in foothills of the Cascade Mountains. One, in the Frazer Creek drainage of the state-owned Methow Game Range, was about 260 ha (640 acres) in size and had been largely ungrazed by domestic livestock since 1940 (Zwickel et al. 1968). The other was a privately owned pasture of about 235 ha (580 acres) in the Bally Hill region, some 5 km (3 miles) to the west. This area had been heavily grazed by cattle for many years. General views of parts of these areas can be seen in figure 1.

Both study areas were in the wheatgrass-bluegrass zone (Daubenmire 1946). Structurally, they were dominated by grasses and two species of shrub, Bitterbrush (*Purshia tridentata*) and Big Sagebrush (*Artemisia tridentata*). Scattered thickets of Aspen or Wild Cherry were common, occurring mainly in or near the bottoms of gullies (fig. 1A,B). Ponderosa Pine occurred as isolated lone trees or as small groves of trees. Some "oldfields" were present on both areas but generally were little used by Blue Grouse.

Grasslands at Frazer Creek were approaching climax condition (fig. 1C,E). The most conspicuous plants were Bluebunch Wheatgrass (*Agropyron spicatum*) and Sandberg's Bluegrass (*Poa secunda*). Bitterbrush, Big Sagebrush, Balsamroot (*Balsamorhiza sagittata*), and Lupine (*Lupinus* spp.) were common, varying in abundance from site to site. Occasional small patches of Cheatgrass (*Bromus tectorum*) persisted on areas that had not fully recovered from heavy grazing prior to 1940, but generally grasslands were relatively homogeneous throughout the study area. Most Aspen thickets had a lush understory of shrubs and herbs.

Domestic cattle grazed the Bally Hill area throughout the period of study, with the grazing season beginning in early May and running to late August. In the summer of 1968, this area was stocked with 100 yearling cattle and 12 adult cows with calves. According to the owners, this was an average stocking rate for this pasture, and is heavy for this class of rangeland. As a result, bare ground and erosion were common, especially on ridges (fig. 1F). Extensive areas were dominated by stands of dense Cheatgrass (fig. 1D) or Big Sagebrush with an understory of Cheatgrass. Only on steeper slopes and other limited areas of light use by cattle did reasonable stands of Bluebunch Wheatgrass and Bluegrass persist. Because of differential use of specific areas by cattle, the grasslands were more heterogeneous than at Frazer Creek. Most thickets were high-lined by cattle (fig. 1D) and had relatively sparse understoreys. Clearly, there were striking differences between Bally Hill and Frazer Creek.

TABLE 1. Distribution of sightings of brood and lone females in relation to thickets or grassland at Frazer Creek and Bally Hill in 1968. Birds considered as associated with a thicket if within 15 m of it.

	Brood females	Lone females	Total
Frazer Creek			
June			
Thicket	3	5	8
Grassland	42	31	73
	45	36	81
July-August			
Thicket	15	9	24
Grassland	37	7	44
	52	16	68
Bally Hill			
June			
Thicket	4	32	36
Grassland	35	16	51
	39	48	87
July-August			
Thicket	31	7	38
Grassland	8	1	9
	39	8	47

Scattered natural springs were available on both areas throughout the period of study. Most, on both areas, became dry by the end of the study.

RESULTS

Locations of all sightings of brood and lone females observed at Frazer Creek and Bally Hill in June and July-August are shown in figures 2 and 3. These data suggest that the dispersion of birds was different on the two areas and between time periods on each area. Differences in dispersion seemed related, in some cases, to the presence of thickets. All birds were therefore classified as being associated with thickets (within 15 m) or grassland and these data are presented in table 1. Results of statistical analyses of these data, within and between areas, can be summarized as follows:

Within Areas

1) At Frazer Creek, brood and lone females were not distributed differently in June (ns = no significant difference; $P = 0.48$).

2) At Bally Hill, brood females were mainly in grassland in June, while lone females were associated with thickets (s = significant difference; $P = 1 \times 10^{-7}$).

3) Brood and lone females were not distributed differently at either area in July-August (ns; $P = 0.09$ at Frazer Creek and 1.00 at Bally Hill).

Between Areas

1) In June, lone females were mainly in grassland on both areas (ns; $P = 0.84$).

2) In June, lone females were mainly in grassland at Frazer Creek but associated with thickets at Bally Hill (s; $P = 2 \times 10^{-6}$).

3) In July-August, brood females were mainly in grassland at Frazer Creek but in or around thickets at Bally Hill (s; $P = 3 \times 10^{-6}$).

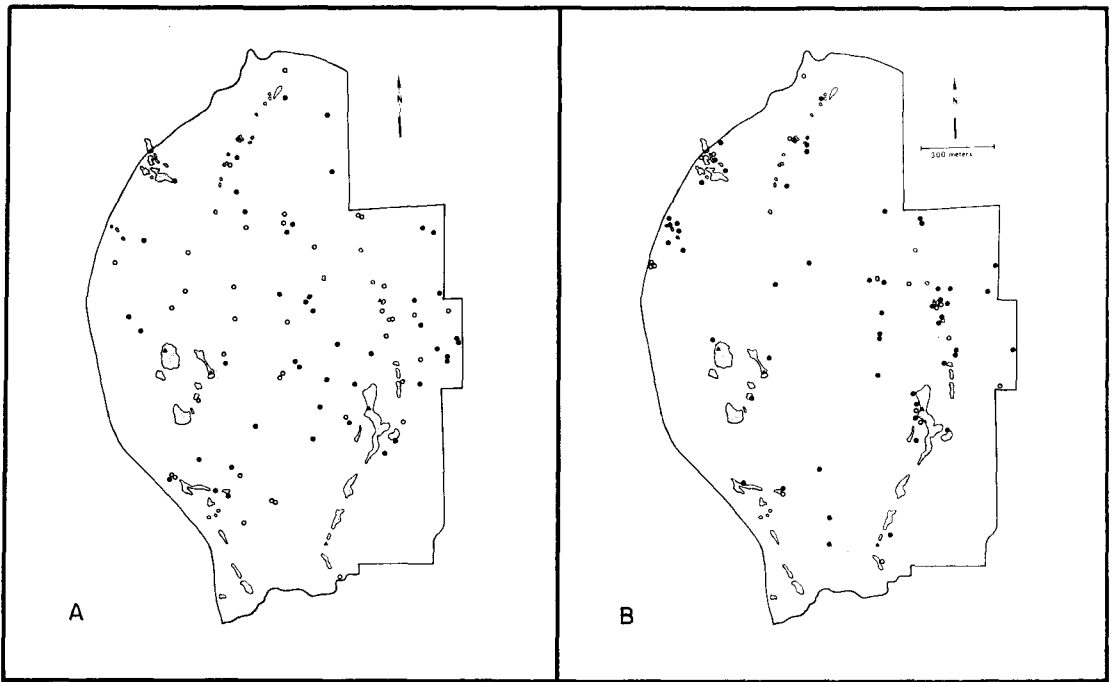


FIGURE 2. Dispersion of sighting locations of females at Frazer Creek; (A) in June, and (B) in July–August. Solid circles represent brood females and open circles represent lone females. Thickets are stippled and solid triangles represent areas with free water that was available during most of the study.

Referring to figures 2 and 3, one can see certain patterns of dispersion beyond those shown by the thicket analysis. For instance, all sightings except those for lone females at Balky Hill were widely, and relatively evenly, dispersed over the study areas in

June. Sightings for both lone and brood females were much more aggregated on both areas in July–August. Thus, visual analysis of the distribution of sightings indicates that birds were either widely dispersed over the study areas in general or clumped.

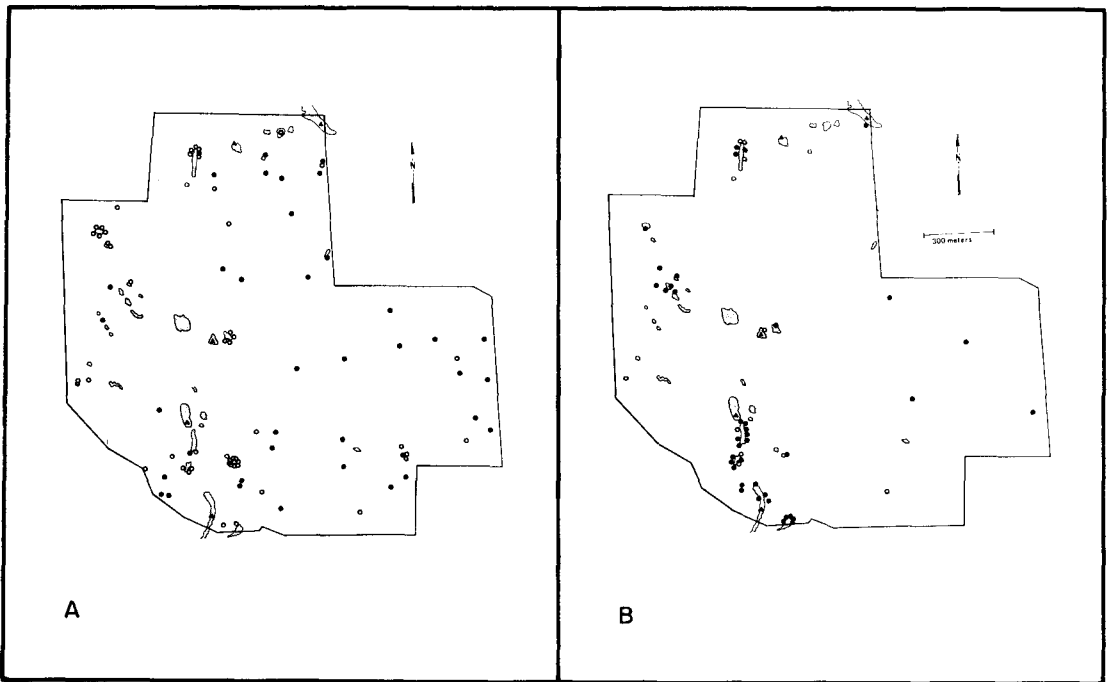


FIGURE 3. Dispersion of sighting locations of females at Balky Hill; (A) in June, and (B) in July–August. Symbols are the same as in Figure 2.

DISCUSSION

Patterns of dispersion may have theoretical implications to numbers of animals (Wynne-Edwards 1962). However, most studies of dispersion in birds have dealt with territorial males only. While this may be relevant to numbers in a monogamous species, it is difficult to see the same relevance in a promiscuous species such as Blue Grouse. Thus, if spacing behavior is important to numbers in a promiscuous species then it may operate independently on males and females, or females could be most important in setting limits to density.

Now, what are some of the implications of the dispersion patterns we observed? The main points of interest here are: (1) in June, brood females were widely dispersed at both areas; (2) in June, lone females were widely dispersed at Frazer Creek, but not at Balky Hill; (3) in July–August, all categories of birds tended toward clumping; and (4) most, but not all, clumping seemed to be associated with an attraction toward thickets.

These data suggest then that brood females remained dispersed on both areas in June, when they had young chicks, even though there was a strong attraction of lone females toward thickets at Balky Hill. Perhaps heavy grazing at Balky Hill caused sufficient deterioration in the grasslands to cause lone females to seek out thickets. This is suggested by the fact that lone females at Frazer Creek did not undergo a similar clumping during the same period. If this interpretation is correct, then brood females may have some behavioral pattern that keeps them from aggregating when they have very young chicks. This argument is strengthened by the fact that both classes of females tended to aggregate in July–August, when chicks were older, a period when maternal concern of brood females seems to weaken. It suggests that during the immediate posthatch period, and perhaps earlier, dispersion may be more related to intrinsic behavioral mechanisms than to extrinsic environmental factors.

An alternative explanation for differences in the patterns of dispersion between lone and brood females on the two areas in June is that the two groups of hens have different requirements for, or tolerances toward, some environmental factor or factors. This cannot be discounted with data at hand but seems less likely than the former explanation because of the relatively even dispersion of brood hens over the grasslands of both areas, even though the grasslands at Balky Hill were more heterogeneous than at Frazer Creek.

A second question that one might ask is, what was the proximate factor causing clumping? The strong tendency to clump in and around thickets suggests that some extrinsic factor was involved. At Balky Hill, this may have been an aversion to overgrazed grasslands, as suggested above. I suspect that the tendency of brood and lone females to aggregate in July–August is related in some way to drying out of grasslands on the higher ridges, for at both areas, birds tended to occur in or near the bottom of draws or gullies (figs. 2, 3). However, at Frazer Creek, this clumping was principally in grassland, suggesting that thickets were not the main attracting force. Examination of figures 2 and 3 indicates that the availability of free water was not a major influence in this regard. Thus, the tendency to aggregate in and around thickets at Balky Hill may be an avoidance reaction to a deterioration in the heavily grazed

grasslands, with the reason for clumping at Frazer Creek less clear. At both areas, it may have been triggered extrinsically, perhaps by the short spell of hot, dry weather in early July.

In closing, I would note that because of the nature of the data used in this paper, all comparisons were between aggregated and dispersed distributions only. However, on the basis of general experience with Blue Grouse in both coastal and interior areas, I suspect that if one could determine time-specific locations of all brood females when chicks are young that one would find them distributed in a uniform or near uniform manner, which suggests some type of interaction. I base this suggestion on the observation that females with young chicks are rarely found together, or even in close proximity to one another, an observation in agreement with that of Bendell and Elliott (1967). If true, then spacing behavior of females is a potential mechanism for intrinsic limitation of numbers of females in a promiscuous species such as Blue Grouse.

SUMMARY

Blue Grouse were studied on a heavily grazed and an ungrazed area in the Methow Valley, Washington. During June, the first month after peak hatch, brood females were dispersed widely at both areas. Lone females were dispersed widely on the ungrazed area but aggregated, in or near thickets, on the grazed area. In July–August, both classes of females were more aggregated. The dispersed pattern of distribution of brood hens in June may not be related to extrinsic differences in the two environments and offers a possible explanation for behavioral limitation of numbers of females in a promiscuous species such as Blue Grouse.

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NOTCHED TOE PADS IN CLIMBING OSCINES

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The unusual structural and behavioral features of birds that typically climb on tree trunks or rock walls have attracted much attention (cf. Richardson, *Univ. Calif. Publ. Zool.*, 46:317-368, 1942; Bock and Miller, *Amer. Mus. Novitates*, 1931:1-45, 1959). However, previous authors have not mentioned the small notches in the pads on the toes of certain climbing species. I here summarize observations on the occurrence of these notches and offer functional and evolutionary interpretations.

OBSERVATIONS

Using a hand lens or binocular dissecting microscope, I inspected series of study skins at the Field Museum (Chicago), Yale Peabody Museum of Natural History, University of Arizona, and University of Connecticut.

In most of the more than 400 oscine species that I have examined, the distal most pads on the ventral surface of the toes typically lack indentations when viewed from the lateral or medial side. Climbing species illustrating this most common condition of oscines are *Sitta carolinensis* (toe IV shown in fig. 1A), *Hypositta corallirostris*, and *Rhabdornis mystacalis*. In contrast, certain other climbers have distinct indentations in the distal pad of all four toes: *Certhia familiaris* (toe III illustrated in fig. 1B), *C. himalayana*, *C. discolor*, *Tichodroma muraria*. Generally less conspicuous notches occur on all four toes in *Salpomis spilonota*, *Climacteris leucophaea*, *C. erythroptis*, *C. melanura*, and *Catherpes mexicanus*. Still other climbers have a notch only in the hindtoe, e.g., *Daphoenositta miranda*, *Neositta chrysoptera*, *N. pileata*, *N. leucocephala*, *N. leucoptera*, and *Mniotilta varia* (toe I shown in fig. 1C).

Although I examined mainly oscines, I also noted notches in some of the Dendrocolaptidae; in *Xiphorhynchus flavigaster*, for example, notches are most conspicuously apparent on the three forward toes. A number of common species of North American woodpeckers (Picidae) lack notches, but those species examined represent only a small part of the entire family.

Notches often vary individually in shape and sometimes even in occurrence. For example, in a series of 40 study skins of Black-and-white Warblers (*Mniotilta varia*) examined with a binocular dissecting microscope, four individuals exhibited no detectable notch on one hind toe, and another individual showed no clear indication of notching on either hind toe; all other specimens possessed notches as shown in figure 1C. Whether such individual variations arise

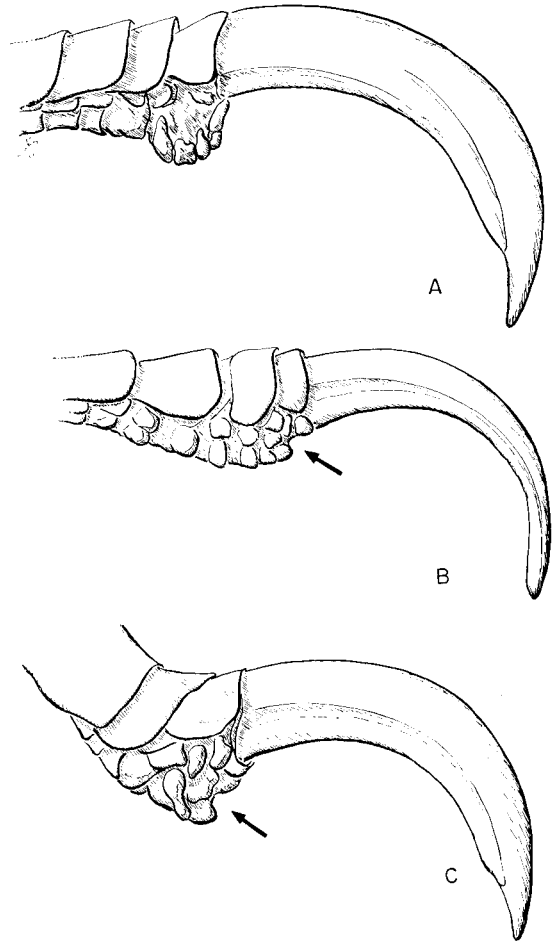


FIGURE 1. Distal toe pads of (A) *Sitta carolinensis*, (B) *Certhia familiaris*, and (C) *Mniotilta varia*. Only the latter two are notched.

during normal development and wear, or through changes during preservation of specimens, remains to be determined in studies of living birds.

The distinction between a roughened pad surface and a notch is sometimes arbitrary where notches are relatively small (e.g., in *Climacteris*). Notches are particularly striking in comparisons of notched species with unnotched ones of the same family as in the Troglodytidae and Parulidae.

DISCUSSION

The taxonomic distribution of notches strongly suggests that they function in climbing. Notches may aid in clinging to vertical surfaces, but studies on living birds are needed to establish the functional