SPECIES ABUNDANCE AND HABITAT RELATIONS OF AN INSULAR MONTANE AVIFAUNA

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The impoverishment of avifaunas inhabiting oceanic islands has been noted for many decades, but it was not until the formulation of the equilibrium theory of MacArthur and Wilson (1963, 1967) that reasons for the observed impoverishment could satisfactorily be postulated and, more importantly, tested. Recently, equilibrium theory has been tested using data from continental island systems, including the insular alpine avifaunas of the Andes (Vuilleumier 1970) and the insular montane avifaunas of the Great Basin (Johnson 1975, Behle 1977). These data have shown that, in addition to the "classical" determinants of insular species number (namely, island area and width of barrier), habitat diversity is also an important determinant of bird species number in systems of inland habitat islands.

Several studies of insular oceanic avifaunas have revealed that species impoverishment is intimately associated with community structure, evidenced in part by density compensation (Grant 1966a, MacArthur et al. 1972), abundance compensation (Crowell 1962), niche shifts (Diamond 1970a), and even competitive exclusion (MacArthur et al. 1972). Although a few investigators have provided an indication that this may be true of insular montane avifaunas as well (Miller 1955, Johnson 1965, 1975), others have noted no obvious differences in community structure between mainland and insular montane avifaunas (Hubbard 1965, Tatschl 1967, Wauer 1971). However, studies dealing specifically with the species abundance and habitat relationships of insular montane avifaunas in the northern Great Plains region are lacking.

I investigated sample abundances, habitat use, and altitudinal range of summer birds of the Sweetgrass Hills, an isolated mountain range in the northern Great Plains of Montana. The avifauna of this area has not previously been described, although the hills occupy a key position as the northernmost of the high intrusive mountain ranges of the area, and contain a surprising variety of montane habitats. Coues (1878) reported several species of birds he observed in the foothills and plains surrounding the Sweetgrass Hills during the U.S. Boundary Commission expedition of 1874, but he did not visit the higher elevations, and noted "no avian specialties" in the area.

STUDY AREA AND METHODS

The Great Plains region of north-central Montana and adjacent Canada (Fig. 1) is largely characterized by monotonous expanses of semi-arid steppe and dry cropland. Several isolated mountain ranges rise as "islands" above the prairie "sea" in this region, forming a fringing archipelago of montane habitat off the Cordilleran "mainland." These montane islands (Fig. 1) support coniferous forests and would appear to provide suitable habitat for breeding bird communities similar to those of the Rocky Mountains. Coniferous forests of river breaks are not uplifted and, hence, not truly montane.

I studied the Sweetgrass Hills, which are a group of three intrusive buttes approximately 140 km E of the Rocky Mountains. West Butte attains an elevation of 2,130 m, which is over 1,000 m above that of the surrounding plains. East Butte, while not quite as high, has a larger uplifted area. Gold Butte, a minor uplifted area between East and West buttes, is much smaller and will not be discussed further.

Vegetation and physiography of the Sweetgrass Hills study area have been described by Thompson and Kuijt (1976), who recognized 18 major communities—5 characteristic of the plains surrounding the buttes, 12 restricted to the montane regions, and 1 (riparian cottonwood forest) which occurs widely in the plains but also extends into the montane region. These community types, which are representative of major avian habitats in the study area, are grouped in Table 1, along with their approximate altitudinal range and dominant plant species.

Vegetation analysis and casual bird observations began on East Butte in the summer of 1972. Intensive field investigation of the montane avifaunas of West and East buttes began on 12 June 1973 and continued through 24 August 1973, with parts of 45 days spent in the study area. Data were recorded for all birds observed in the montane community types during 29 counts (51.0 h in West Butte and 63.5 h in East Butte). These data included species, number of individuals, time, location, elevation and habitat. The total number of birds of each species observed provides a measure of observed or "sample" abundance (see Preston 1948:245). Counts were made during all times of day; of the 114.5 total hours, 34% were spent between 04:00 and 09:00, 27% between 09:00 and 12:00, 18% between 12:00 and 15:00, and 13% after 18:00 (all DST). A typical count consisted of a 3–6 h, early morning or late evening walk from a base camp at the lower edge of the montane region to one of the peaks and a return to camp by a different route. Only birds seen clearly enough to identify were tallied during these counts; birds heard but not seen, as well as birds observed outside the counting periods, were noted but were not included in the sample abundance totals. I chose this method because of the difficulties in assigning numbers to calls while walk-
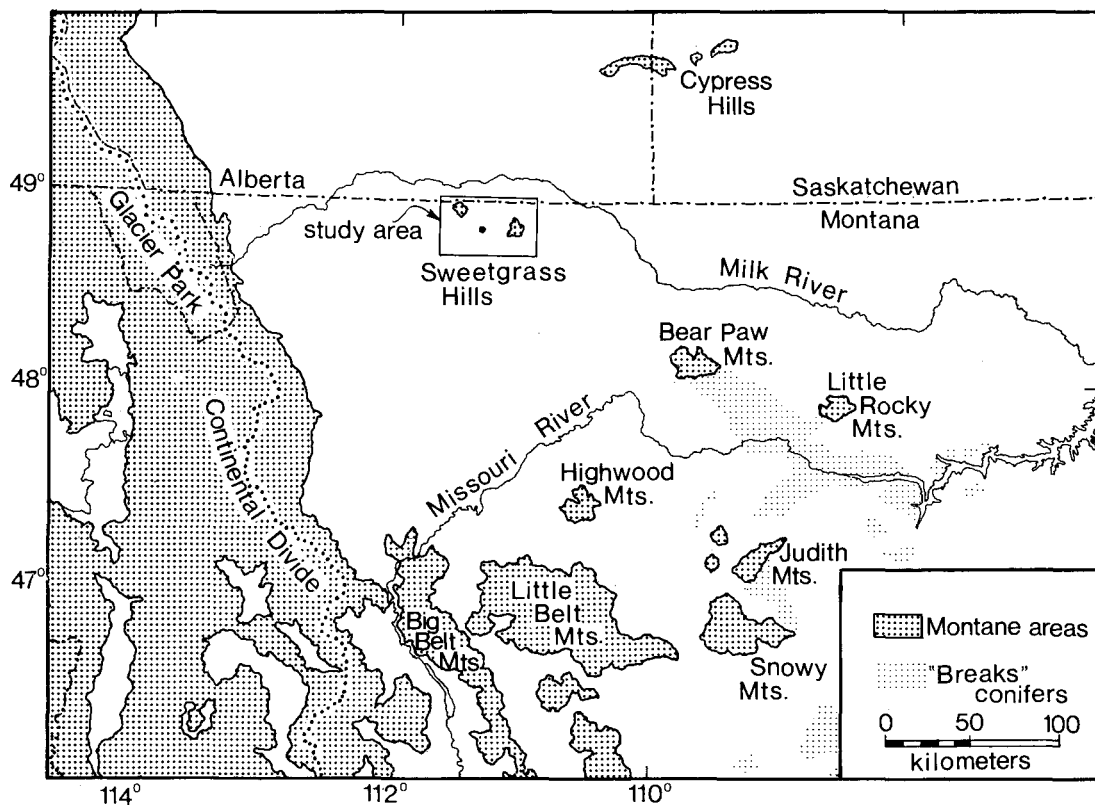
FIGURE 1. Location of the Sweetgrass Hills study area and other montane islands of the northern Great Plains.

ing a continuous and meandering transect. Where exact counts could not be made, the lowest estimate of numbers of individuals was recorded. Approximately one-third of my field time was spent on these counts; remaining field time was devoted to other work.

Additional visits to the Sweetgrass Hills were made during the summers of 1974 and 1975, mainly

TABLE 1. Major avian habitats of the Sweetgrass Hills study area.

Habitat	Altitudinal range (m)	Area (km²)	Dominant vegetation
Plains habitats	below 1,500	1,808	
Steppe (ST)[a]	below 1,500	1,788	*Agropyron* spp., *Stipa* spp., *Triticum* spp.
Riparian shrubbery (RS)	below 1,500	8	*Amelanchier alnifolia*, *Crataegus douglasii*, *Salix* spp.
Potholes and reservoirs (PR)	below 1,450	9	*Carex* spp., *Juncus* spp., *Scirpus* spp., *Typha latifolia*
Riparian woodland (RW)	below 1,550	3	*Populus trichocarpa, P. deltoides*
Montane habitats	1,420–summits	82	
Montane grassland (MG)[b]	1,500–summits	50	*Festuca idahoensis, F. scabrella, Potentilla fruticosa*
Rubble slopes (RB)	1,420–summits	7	
Aspen (AS)[c]	1,420–1,800	5	*Populus tremuloides*
Douglas fir forest (DF)	1,420–1,600	6	*Pseudotsuga menziesii*
Lodgepole pine forest (LP)	1,500–summits	7	*Pinus contorta*
Spruce-lodgepole forest (SL)[d]	1,600–summits	4	*Pinus contorta, Picea glauca* × *engelmannii, Abies lasiocarpa*
Mountain ravines (MR)	1,500–2,000	1	
Subalpine forest (SF)	2,000–summits	2	*Abies lasiocarpa, Pinus contorta, Pinus albicaulis*

[a] Includes agricultural land, foothills prairie, and coulee scrub types of Thompson and Kuijt (1976).
[b] Includes their montane grassland and subalpine grassland types.
[c] Includes their aspen groveland and aspen woodland types.
[d] Present on East Butte only; includes their spruce-lodgepole and temperate subalpine fir forest types.

to sites not investigated in 1973. I found no new montane species, although the observed range of habitats or elevations used was expanded in several cases. Several days were spent in each of the other montane islands shown in Figure 1, but I did not try to completely inventory their avifaunas.

Bird species were assigned to guilds (Root 1967, Willson 1974, Johnson 1975) based on major food source (seeds and vegetation, invertebrates, vertebrates, nectar, omnivorous), foraging stratum (bark, ground, low canopy, mid-to-high canopy, air, water), and method of foraging (bark and bole drilling, bark and bole gleaning, ground and brush foraging, timber foliage foraging, sallying, raptorial, dabbling, diving, water and mud probing, swooping).

RESULTS AND ANALYSIS

THE SWEETGRASS HILLS AVIFAUNA

I encountered 100 species of breeding birds in the study area. Their sample abundances, distribution among the habitat categories (Table 1), altitudinal range, and evidence of breeding, are presented in the Appendix. I considered 18 of these species to be "montane," that is, species which, in this part of their range, prefer montane coniferous forests or related montane habitats during the breeding season. This does not include those species that are obligatory alpine or nocturnal forms (e.g., *Strix* spp. and *Leucosticte* spp.). Montane species do not normally breed in the arid steppe, agricultural land, coulees, riparian cottonwood forests, forests of river breaks, or farm groves found in the prairie between the montane islands. Not all of the species which breed in montane habitats are montane by this definition.

In addition to the breeding species, 8 species believed to be late-summer visitors or migrants were observed in the study area. These are the Great Blue Heron (*Ardea herodias*), Prairie Falcon (*Falco mexicanus*), Lesser Yellowlegs (*Tringa flavipes*), Franklin's Gull (*Larus pipixcan*), Common Tern (*Sterna hirundo*), Rufous Hummingbird (*Selasphorus rufus*), Northern Waterthrush (*Seiurus noveboracensis*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). The Northern Waterthrush was reported from this area by Coues (1878). Other birds observed during this study which were previously reported by Coues (1878) are indicated in the Appendix. Species reported by Coues but not encountered in the present study are the Mountain Plover (*Charadrius montanus*), Solitary Sandpiper (*Tringa solitaria*), Burrowing Owl (*Athene cunicularia*), and Say's Phoebe (*Sayornis saya*). All specimens taken during this study have been deposited at the Charles C. Conner Museum, Washington State University, Pullman.

THE SPECIES-ABUNDANCE RELATION AND SAMPLING ADEQUACY

In determining species number, presence is more easily proven than absence. The reliability of each report of the absence of a particular species from a given area depends on the adequacy of sampling of that area. In their studies of avifaunal diversity, Vuilleumier (1970) and Johnson (1975) compared the total numbers of breeding bird species known from various islands. These totals included certain cases where only one or two years' field work had been conducted and where certain breeding species may have been overlooked. They also included cases where many years of observation have been combined, and where the cumulative species total is probably greater than the number of birds breeding during a given year, due to year-to-year changes in avifaunal composition. In these cases, the multi-year "universe" being sampled may be quite different from a single year's assemblage of breeding birds. If meaningful comparisons of species number among islands are to be made, estimates should ideally be based upon comparable amounts of field effort per unit area, or else incorporate a measure of the degree of sampling adequacy or intensity.

Examination of the species-abundance relation provides such an indication of sampling adequacy—one that allows a more precise estimate of species number. Preston (1948, 1962) suggested plotting sample abundance data using categories of the number of observations per species (octaves of 0–1, 1–2, 2–4, 4–8, 8–16, etc., observations per species) on the abscissa and the number of species falling into each category on the ordinate. The resultant plots describe a lognormal distribution of the form

$$S_r = S_o e^{-(aR)^2}$$

where S_r is the number of species in a category R octaves from the mode, S_o is the number of species in the modal octave, and a is a constant. The sample abundance data obtained in this study (see Appendix) yield an excellent fit ($r^2 = 0.99$), where $S_o = 5.45$ and $a = 0.24$. The "species curve" for these data is shown in Figure 2, and a second curve, representing the more diverse riparian avifauna of the Bear Paw Mountains (based on Walcheck 1969) is plotted for comparison. Although the sample abundances obtained in this and Walcheck's (1969) studies do not represent absolute abundances or even true relative abundances, they are entirely suitable
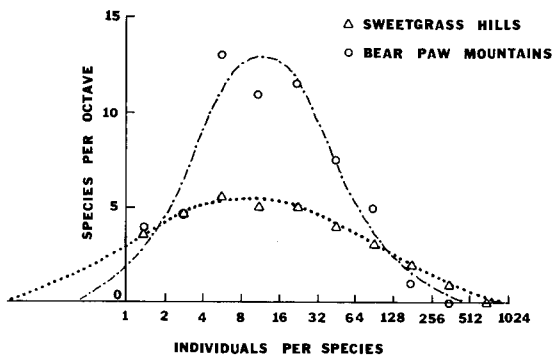
FIGURE 2. Species curves for the montane avifauna of the Sweetgrass Hills and the riparian avifauna of Beaver Creek in the Bear Paw Mountains (based on Walcheck 1969).
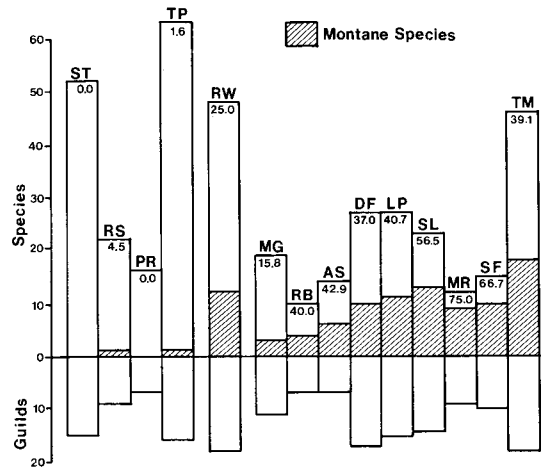

FIGURE 3. Observed distribution of bird species and breeding-season guilds among habitats. Abbreviations are as listed in Table 1 with two additions: TP = totals for all plains habitats; TM = totals for all montane habitats. Numbers within bars indicate percent contribution of montane species to total species number for each habitat.

for this type of analysis (Preston 1948:245).

The area to the right of the ordinate in Figure 2 represents the total number of bird species seen during counts (i.e., 36 breeding species), while the area to the left of the ordinate represents rare or inconspicuous species missed in sampling. The area under the entire species curve represents the theoretical total number of species S_t present in the universe being sampled, $S_t = S_o \sqrt{\pi}/a$ (Preston 1948, 1962). Using the values for S_o and a mentioned above, S_t for the universe from which samples were drawn (i.e., diurnal or crepuscular birds inhabiting montane habitats of the Sweetgrass Hills during the summer of 1973) equals 40, which is fewer than the 46 species actually observed. This analysis suggests that all breeding bird species present in the Sweetgrass Hills in 1973 were observed at least once, and that sampling of the breeding montane avifauna was complete.

HABITAT RELATIONS

The observed distribution of breeding bird species and guilds among the major avian habitats of the Sweetgrass Hills study area is shown in Figure 3, along with data for all plains and all montane habitats collectively. Habitat use by individual species is given in the Appendix.

Although I spent little time and effort investigating plains habitats, I found more breeding species (63) there than in the much more intensively studied and structurally diverse montane or riparian woodland areas. Steppe, the most extensive individual habitat, supported the most species (52, including waterfowl and shorebirds). Riparian woodland, though comprising less than 1% of the whole study area, supported nearly as many

species (48). This reflects both the greater structural diversity and the influence of adjacent prairie and montane habitats on the riparian woodland communities. The montane habitats together supported 46 species; of the individual montane habitats, the predominant coniferous forests (Douglas fir, lodgepole pine, and spruce-lodgepole forests) supported the greatest number of species.

As expected, the lowest proportion of montane species (0–4.5% of total species) was found in plains communities, where I saw only one montane bird (a Pine Siskin). Riparian woodland and montane area each supported 25.0% and 39.1% montane species, respectively. The spruce-lodgepole forest (found only on East Butte) supported the largest number of montane species (13) of all habitats. However, the greatest proportion of montane species was found in mountain ravine (75.0%) and subalpine forest (66.7%) communities, which were also the most cool and moist of the habitats studied.

The number of breeding-season guilds represented in each of the habitats is also shown in Figure 3. Note that the habitats are much less variable in terms of guild number than species number. Although plains habitats supported more species than montane habitats, they supported slightly fewer guilds (16 versus 18). Thus, the absence from montane habitats of certain guilds well-represented in the prairie habitats (e.g., diving, water and mud probing) is more than offset by the additions of guilds corresponding to the ad-

TABLE 2.   Breeding montane birds of Glacier National Park and several island mountain ranges of the northern Great Plains.[a]

Species	1	2	3	4	5	6	7	8	9	10	11
					Montane island number						
Accipiter gentilis[b]	0	0	0								0
Dendragapus obscurus[bc]	0	0	0	0	0	0	0				
Canachites canadensis[bc]	0										
Bonasa umbellus[bc]	0		0	0			0				0[d]
Stellula calliope	0	0									
Picoides arcticus[bc]	0										
Picoides tridactylus[bc]	0										
Empidonax hammondii		0									
Empidonax oberholseri	0		0	x	x	x	0	x	x	x	0
Empidonax difficilus	0	0		0	0	x		x	x		
Nuttallornis borealis	0	0		0							
Perisoreus canadensis[bc]	0	0	0	0							
Cyanocitta stelleri[bc]	0		0								
Nucifraga columbiana[bc]	0	0	0	x	0	x	x	x	x	x	
Parus gambeli[bc]	0	0	0	x	x	x	0	x	x	x	
Sitta carolinensis[bc]	0	0	0				0				
Sitta canadensis[b]	0	0	0	x	x	x	0	x	x	x	x
Certhia familiaris[b]	0					x					
Cinclus mexicanus[bc]	0	0		x							
Catharus guttata	0	0	0	0	0		x	x	x	x	
Catharus ustulata	0	0	0	0	0	x	x	x	x	x	0
Myadestes townsendi[b]	0	0	0	0	0	x		x	x	x	0
Regulus satrapa[b]	0							x	x		
Regulus calendula	0	0	0	x	x	x	0	x	x	x	0
Vireo solitarius	0						0				
Vermivora celata	0			0	0			x		x	0
Dendroica coronata	0	0	0	x	x	x	0	x	x	x	0
Oporornis tolmiei	0	0	0	0	0	0	0	x	x	x	0
Piranga ludoviciana	0	0	0	0	x	x	0	x	x	x	0
Hesperiphona vespertina	0	0			0						
Carpodacus cassinii[b]	0		0	0		x					
Pinicola enucleator[b]	0		0					x	x	x	
Spinus pinus[b]	0	0	0	x	x	x	0	x	x	x	x
Loxia curvirostra[b]	0	0	0	0	x	x	0	x	x	x	x
Loxia leucoptera[b]	0		0								0
Junco hyemalis[b]	0	0	0	x	x	x	0	x	x	x	x
Zonotrichia leucophrys	0	0	0	0	0	0	0				0
Melospiza lincolnii	0	0									
Total breeding montane species	37	25	24	23	19	18	18	18	17	16	15

[a] Letters in each column indicate probable breeding records for each montane island.   Records indicated by an x were made or confirmed by the author as part of this study.   Saunders (1921), Davis (1961; personal communication), Mussehl et al. (1971), Skaar (1975; pers. comm.), and R. Eng (pers. comm.) provided sources of many records throughout the region.   Sources of additional records (indicated by 0 in the table) are as follows: (1) Little Belt Mts.—Williams (1882), Bendire (1895), Hoffmann (1960), Johnson (1966).   (2) Pryor Mts.—DeLap and Thompson (1962).   (3) Big Snowy Mts.— Silloway (1903).   (4) Highwood Mts.—DeLap and Feist (1963).   (5) Little Rocky Mts.—DeLap (1961).   (6) Bear Paw Mts.—Walcheck (1969).   (7) Judith Mts. (8) Sweetgrass Hills. (9) East Butte.   (10) West Butte.   (11) Cypress Hills.— Godfrey (1950), Halladay (1965), Jones (1972), J. Salt (pers. comm.).   All species listed breed in Glacier Park (Parratt 1964), a representative sample area of the Rocky Mountain Cordillera.   Additional montane species found in Glacier Park which do not occur in any of the montane islands are *Histrionicus histrionicus*[b], *Cypseloides niger*, *Selasphorus rufus*, *Dryocopus pileatus*[bc], *Sphyrapicus thyroideus*, *Parus hudsonicus*[bc], *Troglodytes troglodytes*[b], *Ixoreus naevius*[b], *Dendroica townsendi*, and *Wilsonia pusilla*.
[b] Winters in Montana (may be weakly migratory).
[c] Resident or sedentary.
[d] Introduced (not included in species totals).

ditional tree layer (e.g., bark and bole gleaning, timber foliage foraging).   The influence of a tree layer in increasing the number of guilds has been noted by Willson (1974) and Johnson (1975).   Riparian woodland, with its well-developed shrub layer and high degree of horizontal patchiness, supported the greatest number of guilds (18) of any habitat, as many, in fact, as all montane habitats combined.   Of the montane habitats, the three major types of coniferous forest again supported the most guilds.

MONTANE SPECIES NUMBER

The number of breeding montane bird species (18) found in the Sweetgrass Hills in itself conveys little information.   However, when examined in the context of the montane archipelago of the northern Great Plains, it allows quantitative examination of factors affecting species number.

TABLE 3. Independent and dependent variables for the sample areas discussed in the text.[a]

Sample areas	Dependent variables					Independent variables										
	T	M	W	R	G	BE	ME	RE	TA	FA	TD	DB	DL	DM	CT	HD
Rocky Mountain Cordillera Glacier National Park	48	20	28	13	14	1,555	3,185	1,630	3,974	3,886	6,478	1	1	1	13	20
Montane islands																
(1) Little Belt Mts.	37	14	23	11	13	1,676	2,801	1,125	3,756	3,368	4,226	20	1	1	7	14
(2) Pryor Mts.	25	12	13	6	12	1,524	2,705	1,181	1,171	627	1,383	43	43	12	5	11
(3) Big Snowy Mts.	24	7	17	7	10	1,646	2,661	1,015	819	583	831	118	16	13.5	7	14
(4) Highwood Mts.	23	11	12	6	10	1,524	2,318	794	259	194	206	88	22	22	7	13
(5) Little Rocky Mts.	19	10	9	3	9	1,189	1,710	521	225	104	117	242	158	68	5	10
(6) Bear Paw Mts.	18	8	10	3	9	1,372	2,108	736	492	132	362	191	118	68	7	13
(7) Judith Mts.	18	9	9	5	7	1,372	1,862	490	329	207	161	153	60	13.5	6	11
(8) Sweetgrass Hills	18	9	9	2	8	1,420	2,130	710	82	20	58	126	126	120	6	11
(9) East Butte	17	8	9	2	7	1,460	2,121	661	46	12	30	143	143	23	6	11
(10) West Butte	16	8	8	2	7	1,420	2,130	710	36	8	26	126	126	23	5	10
(11) Cypress Hills	15	8	7	0	10	1,189	1,463	274	1,036	440	284	238	238	100	2	9

[a] Abbreviations defined in the text.

TABLE 4. Correlation coefficients (r) among dependent and independent variables.[a]

	BE	ME	RE	TA	FA	TD	CT	HD	DB	DL	DM
T	.62*	.86**	.89**	.93**	.95**	.98**	.82**	.90**	−.80**	−.72**	−.55
M	.39	.71**	.79**	.85**	.88**	.92**	.75**	.78**	−.72**	−.57	−.45
W	.71**	.89**	.90**	.92**	.94**	.95**	.81**	.91**	−.79**	−.76**	−.59*
R	.74**	.88**	.88**	.85**	.88**	.89**	.80**	.87**	−.83**	−.88**	−.70*
G	.48	.72**	.77**	.88**	.84**	.85**	.51	.69*	−.65*	−.55	−.36

[a] With $n = 12$, a significant r at $P < 0.05$ (*) is 0.58 and for $P < 0.01$ (**) is 0.71. Abbreviations of variables as described in the text.

Breeding records of montane bird species are presented in Table 2. Records are also given for the Pryor Mountains, a major montane island approximately 160 km SSE of the Snowy Mountains outside the area shown in Figure 1, and for Glacier Park (footnote), a representative sample of the Rocky Mountain Cordillera.

Data on the avifaunas and several physical parameters of each sample area are summarized in Table 3. The five dependent variables (pertaining to breeding montane birds) listed for each sample area are: total number of species (T); number of species which are long-distance migrants (M); number of species which are weakly migratory but which winter in Montana (W); number of sedentary (resident) species (R); and number of guilds represented by all breeding montane species (G). The 11 independent variables are as follows: "base" elevation (BE), or elevation at which the lowest montane coniferous forest zone begins; maximum elevation (ME); relief (RE), or the difference between BE and ME; total area above base elevation (TA); forested area above base elevation (FA); topographic diversity index (TD), which is equal to RE × TA × 10⁻³; shortest distance to the Cordillera assuming the Little Belt Mountains are, first, part of the island system (DB) or, second, part of the Cordillera (DL); distance to the nearest montane area (DM); number of coniferous tree species exclusive of *Juniperus* spp. (CT); and habitat diversity score (HD) as defined by Johnson (1975). Relations among dependent and independent variables were revealed by Pearson product-moment correlations (Table 4) and will be discussed below.

Island area. All dependent variables are significantly and positively correlated with both total area and forested area, as predicted by island equilibrium theory (MacArthur and Wilson 1967). This reflects the effects of island area on colonization rate (target size effects), on extinction rate (through total population size), on distribution of montane

bird species having a large minimum area or large territory size, and on habitat diversity.

Width of barrier. Except for the number of long-distance migrants and the number of guilds, all dependent variables are significantly and negatively correlated with distance from the Cordilleran mainland, whether or not the Little Belt Mountains are considered to be part of the massif. Distance effects for long-distance migrants are significant only if the Little Belt Mountains are considered to be a montane island rather than an extension of the Cordillera, indicating that this range is treated as a "sub-continent" rather than an island by these species. Distance to nearest montane neighbor is significantly and negatively correlated only with numbers of wintering and sedentary species. This is to be expected, for these are the species for which stepping-stone effects on colonization are most important. Long-distance migrants, which may cross hundreds of kilometers of inhospitable habitat with relative ease, can presumably colonize an isolated montane island as easily as one near a source area. Note that correlations of number of guilds with the three measures of barrier width are only marginally significant or not significant. This lends support to Johnson's (1975) findings that most montane islands support a "standard" set of montane species representing a wide variety of guilds. Should a sedentary species be absent from an isolated island, its guild may well be represented there by a standard migratory species.

Effects of barrier width on habitat diversity (Johnson 1975) are probably minor since the insular montane forests of the northern Great Plains are relics of periglacial forests (Thompson and Kuijt 1976), rather than the result of long-distance dispersal; the Sweetgrass Hills support nearly as many species of coniferous trees as the much larger Little Belt Mountains (Table 3).

Habitat effects. The remaining independent variables—base elevation, maximum elevation, relief, topographic diversity, number of conif-

erous tree species, and habitat diversity score—all provide rough measures of the diversity of breeding habitats available to a colonizing bird species on a given island. With three exceptions, the dependent variables are significantly and positively correlated with these independent variables. Species number of all four avian groups is correlated with the number of coniferous tree species, but the number of guilds is not. This suggests that the addition of a coniferous forest layer is sufficient to increase to near maximum the number of guilds represented in a montane community. Adding more species of conifers seems to result in expansion but not addition of guilds. The correlations of base elevations with number of migratory species and number of guilds are not significant; this is not surprising as the fact that species numbers of wintering, resident, and total montane bird species are significantly correlated with base elevation. The relation between base elevation and species number is not intuitively obvious. However, base elevation and maximum elevation were found to be highly correlated ($r = 0.88$, $P < .01$), indicating a Massenerhebung effect as described by Terborgh and Weske (1975)—that is, an upward shift in vegetation zonation as mountain mass increases. This is particularly evident in the Sweetgrass Hills, where the subalpine forest zone occurs well below 2,000 m. For each dependent variable, the highest correlation coefficients are those associated with the topographic diversity index. This indicates that, in this montane archipelago, topographic diversity—which reflects such parameters as number of canyons, number of plant species, interception of precipitation, steepness of slopes, etc.—is a better measure of habitat diversity than is the habitat rating system of Johnson (1975).

DISCUSSION

The preceding analysis has shown that species number of the Sweetgrass Hills montane avifauna is determined at least in part by habitat diversity, island area, and—in the case of non-migratory or weakly migratory species—distance from source fauna. However, the absence of certain species cannot readily be explained by these determinants of species number. For example, the absence of the Evening Grosbeak (*Hesperiphona vespertina*) or the White-crowned Sparrow (*Zonotrichia leucophrys*) is not due to lack of suitable habitat or inability to colonize.

My data on the species abundance and habitat relations of the montane avifauna allow me to evaluate possible relations between avifaunal diversity and community structure, specifically, niche shifts, density and abundance compensation, and competitive exclusion. A commonly described response of birds to the release from competition on species-poor oceanic islands is the expansion of variety of habitats used, altitudinal range, and/or foraging behavior (Crowell 1962, Sheppard et al. 1968, Diamond 1969, 1970a, 1971). This niche expansion or "ecological extension" has also been noted in insular montane avifaunas, including those of the Sierra del Carmen of Mexico (Miller 1955), the Spring and Sheep ranges of Nevada (Johnson 1965), and various high mountain ranges of New Guinea (Diamond 1970b). There is little indication that characteristic grassland birds have expanded into species-poor montane habitats of the Sweetgrass Hills. The only such species I found in montane grassland were the Western Meadowlark, Savannah Sparrow, and Vesper Sparrow. These species, although abundant in the plains, were scarce in the mountains and I did not see them in nongrassland montane habitats. However, I noted apparent habitat shifts for two non-montane species, the Mourning Dove and the Common Flicker, both of which were found to be abundant at all elevations and in a wide variety of habitats in both buttes (Appendix). Hoffman (1960) did not find Mourning Doves in the forests of the Little Belt Mountains, but I found them in nearly all forest habitats of the Sweetgrass Hills. The Common Flicker was the only species of woodpecker in montane communities; it foraged in conifers. Surprisingly, the Hairy Woodpecker, normally a common and conspicuous member of montane forest communities in Montana, was never seen outside the riparian woodlands. An altitudinal shift was noted for the Ovenbird, which was seen in lodgepole pine forests above 1,700 m.

Overall densities of all birds on oceanic islands may be greater than (Crowell 1962, Grant 1966a, MacArthur et al. 1972), similar to (MacArthur et al. 1972), or less than (Diamond 1970b) densities of birds on comparable areas of mainland, depending upon individual circumstances. However, on montane islands, avifaunal breeding density appears to be generally lower than in comparable habitat on the species-rich montane mainland (Diamond 1970b, Johnson 1975). This occurs in spite of increased abundances of certain species which have expanded their

niche to include habitats not normally occupied in mainland situations.

In the Sweetgrass Hills, five species (Clark's Nutcracker, Pine Siskin, Dark-eyed Junco, Red Crossbill, and Chipping Sparrow) accounted for over two-thirds of all observations made during counts (Appendix). Although I did not estimate their breeding density, these species appeared to be more abundant than in comparable areas of the Rocky Mountain Cordillera which I have visited. This indicates a possible response to lack of competition from characteristic montane species which are absent from the Sweetgrass Hills.

Despite the apparently high densities of these common species, my impression of the overall montane avifauna was of low individual densities of birds as well as species impoverishment. I made only 1,520 sightings of individual birds during the 114.5 h of counts.

The uneven distribution of individuals among species has several implications regarding the species-abundance relation discussed earlier. In the Sweetgrass Hills, there is a relatively high proportion of very common species to moderately common species as reflected in the relatively shallow shape of the species curve (Fig. 2). One would expect sample abundance data from the diverse Cordilleran avifauna to show a more equitable distribution of individuals among species, and hence a higher species curve than that obtained for impoverished insular montane avifaunas.

Several studies (Grant 1966b, 1969, 1970, Lack 1969, Crowell 1973) have indicated that islands are more frequently occupied by ecologically dissimilar species of animals than ecologically similar ones. Johnson (1975), in his study of montane islands of the Great Basin, found that the "standard" boreal or montane species (those which occur together on nearly all montane islands) represented a wide variety of dissimilar foraging niches or "guilds." Likewise, a group of ecologically dissimilar species is found on nearly every montane island of the northern Great Plains that has been studied, including the Sweetgrass Hills (Table 2). This group includes the Dusky Flycatcher, Clark's Nutcracker, Mountain Chickadee, Ruby-crowned Kinglet, Red-breasted Nuthatch, Swainson's Thrush, Townsend's Solitaire, Yellow-rumped Warbler, Western Tanager, Pine Siskin, Red Crossbill, and Dark-eyed Junco. Thus, the basic foraging niches are filled by a relatively small group of montane generalists on nearly all islands, regardless of island size. Restricted boreal or montane species are those which occur on relatively few montane islands. They are typically ecological specialists and are often congeneric with a standard species of the same guild or at least closely duplicate the foraging niche of a standard montane species.

Are restricted species excluded from all but the largest and most diverse islands due to competition from the more vigorous standard species of corresponding guilds? Many of the standard species may have expanded their niche to overlap largely with that of the restricted specialists. In other words, is avifaunal impoverishment a consequence as well as a cause of niche expansion in insular ecosystems?

The phenomenon of competitive exclusion among insular avifaunas has been discussed by MacArthur et al. (1972), who found that the establishment of a particular species on an island may forestall subsequent colonization by a congener or other ecologically similar species. Indeed, a "checkerboard" pattern of distribution of wrens on similar islands in the Panama area was observed, where each island contained only one of three possible species. The established species apparently made it "impossibly difficult" for an additional species also to colonize the island. On montane islands, where the extent and variety of resources are reduced largely by the same factors that reduce bird species number, the intensity of competition for a mutually shared resource should be especially keen among ecologically similar species. A given species may be excluded from an island of suitable habitat not only through competition with a single species sharing the same guild, but also by "diffuse competition from a mutually adjusted community of many species, each 'member of which overlaps the potential colonist's niche only partially" (MacArthur et al. 1972:340).

It is difficult, however, to imagine exactly how competitive exclusion would operate in a community of birds which are largely migratory, such as the Sweetgrass Hills avifauna. Much of the theoretical work of MacArthur and others was based on resident avifaunas, which have had more time to deplete resources or to become "mutually adjusted" than migrants which arrive within a few days or weeks of one another. Indeed, I found no clear evidence of such exclusion in this study, which deals with highly migratory species.

While avifaunal diversity and community structure are intimately related in montane island systems, the absence of several bird species from the Sweetgrass Hills is still unexplained. These absences may reflect the random element in insular colonizations and extinctions. Many species which migrate to the montane islands in spring may find suitable habitat there, but may not remain due to strong philopatry to a distant nesting site. Likewise, the very small breeding populations inhabiting such islands are highly susceptible to "random" extinction, which would result in "unexplained" absences from apparently suitable habitat. The dramatic year-to-year changes in avifaunal composition of montane islands (Johnson 1974) reflect such randomness or "ecologic noise" which tends to obscure more easily defined relationships.

SUMMARY

The summer birds of the Sweetgrass Hills, an isolated mountain range in the northern Great Plains region of Montana, were investigated. Of the 100 breeding species reported, 18 are restricted to montane habitats during the breeding season. Data are presented on local distribution, sample abundances, distribution among major habitats, summer altitudinal range, and evidence of breeding for each species observed. Sample abundance data were used to construct a species curve with which to test thoroughness of avifaunal sampling. While montane habitats supported fewer breeding bird species than the more extensive steppe habitats, they provided a slightly greater representation of breeding-season guilds. The number of breeding montane species inhabiting montane islands was found to be significantly correlated with island area, forested area, distance from mainland, and several measures of habitat diversity. Only species numbers of sedentary or weakly migratory montane species were correlated with barrier width. The relations between species number and community structure is discussed; while no evidence of competitive exclusion was noted in this largely migratory avifauna, evidence of niche expansion and abundance compensation was found, and may be reflected in differences in the species-abundance relation between mainland and insular avifaunas. Philopatry and chance may be the best explanation for the absence of species not clearly related to lack of suitable habitat or inability to colonize.

ACKNOWLEDGMENTS

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APPENDIX.   Breeding birds observed in the Sweetgrass Hills and vicinity.

Species	Distribution and sample abundance[a]			Communities where found[b]												Summer altitudinal range (m)[c]	Evidence of breeding[d]
				Plains						Montane							
	West Butte	East Butte	Total	ST	RS	PR	RW	MG	RB	AS	DF	LP	SL	MR	SF		
Mallard (*Anas platyrhynchos*)	x	0	x	ST	—	—	—	—	—	—	DF	—	—	—	—	1,000–1,400	NE
Gadwall (*A. strepera*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,200	RH
Pintail (*A. acuta*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,200	RH
Blue-winged Teal (*A. discors*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,400	RH
Cinnamon Teal (*A. cyanoptera*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,300	RH
American Wigeon (*A. americana*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,300	RH
Northern Shoveler (*A. clypeata*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,300	RH
Cooper's Hawk (*Accipiter cooperii*)[f]	0	x	x	—	—	—	—	MG	—	—	—	LP	SL	—	—	1,500–1,600	RH
Red-tailed Hawk (*Buteo jamaicensis*)	0	x	x	—	—	—	RW	MG	—	—	DF	—	SL	—	—	1,300–1,600	RH
Swainson's Hawk (*B. swainsoni*)	0	0	0	ST	—	—	—	—	—	—	—	—	—	—	—	1,200–1,300	NE
Ferruginous Hawk (*B. regalis*)[f]	0	0	0	ST	—	—	—	—	—	—	—	—	—	—	—	1,000–1,300	TO
Golden Eagle (*Aquila chrysaetos*)[e,f]	10	9	19	ST	—	—	—	MG	RB	—	DF	LP	SL	MR	SF	1,200–2,200	RH
Marsh Hawk (*Circus cyaneus*)[e]	3	x	3	ST	—	—	—	MG	—	—	—	LP	SL	—	—	1,100–1,800	RH
Merlin (*Falco columbarius*)	7	x	7	ST	—	—	RW	MG	—	—	DF	LP	SL	—	—	1,200–1,700	TO
American Kestrel (*F. sparverius*)	x	4	4	ST	—	—	RW	MG	—	—	DF	—	SL	—	—	1,000–1,800	RH
Sharp-tailed Grouse (*Pedioecetes phasianellus*)[e]	0	0	0	ST	RS	—	RW	—	—	—	—	—	—	—	—	1,200–1,400	PJ
Ring-necked Pheasant (*Phasianus colchicus*)	0	0	0	ST	—	—	RW	—	—	—	—	—	—	—	—	1,100–1,400	RH
Gray Partridge (*Perdix perdix*)	0	0	0	ST	—	—	—	—	—	—	—	—	—	—	—	1,100–1,400	RH
American Coot (*Fulica americana*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,300	RH
Killdeer (*Charadrius vociferus*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,400	TO
Common Snipe (*Capella gallinago*)	0	0	0	ST	RS	—	—	—	—	—	—	—	—	—	—	1,200–1,400	TO
Long-billed Curlew (*Numenius americanus*)	0	0	0	ST	—	—	—	—	—	—	—	—	—	—	—	1,100–1,200	RH
Upland Sandpiper (*Bartramia longicauda*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,400	PJ
Spotted Sandpiper (*Actitis macularia*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,200–1,400	RH
Willet (*Catoptrophorus semipalmatus*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,400	PJ
Marbled Godwit (*Limosa fedoa*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,200	RH
American Avocet (*Recurvirostra americana*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,300	PJ
Wilson's Phalarope (*Steganopus tricolor*)	0	0	0	ST	—	PR	—	—	—	—	—	—	—	—	—	1,100–1,300	RH
Mourning Dove (*Zenaida macroura*)	17	23	40	ST	—	—	—	MG	RB	—	DF	LP	SL	MR	SF	1,100–2,200	NY
Black-billed Cuckoo (*Coccyzus erythropthalmus*)[g]	0	0	0	—	RS	—	—	—	—	—	—	—	—	—	—	1,300–1,400	EF
Great Horned Owl (*Bubo virginianus*)[f]	0	0	0	ST	—	—	—	—	—	AS	DF	—	—	—	—	1,000–1,500	PJ
Long-eared Owl (*Asio otus*)	1	0	1	—	—	—	RW	—	—	AS	—	—	—	—	—	1,300–1,500	RH
Short-eared Owl (*A. flammeus*)	0	0	0	ST	—	—	RW	—	—	AS	DF	—	—	—	—	1,000–1,300	RH
Poor-will (*Phalaenoptilus nuttallii*)	x	0	x	—	—	—	—	MG	—	—	DF	LP	—	—	—	1,400–1,500	RH
Common Nighthawk (*Chordeiles minor*)	x	0	x	ST	RS	PR	RW	—	—	—	—	—	—	—	—	1,200–1,700	RH
Belted Kingfisher (*Megaceryle alcyon*)	0	0	0	—	—	—	RW	—	RB	—	—	—	—	—	—	1,200–1,500	RH
Common Flicker (*Colaptes auratus*)[g]	13	21	34	—	—	—	RW	MG	RB	AS	DF	LP	SL	MR	SF	1,400–2,200	PJ
Yellow-bellied Sapsucker (*Sphyrapicus varius*)[g]	2	x	2	—	—	—	RW	—	—	AS	DF	—	—	—	—	1,400–1,600	PJ
Hairy Woodpecker (*Picoides villosus*)	0	0	0	—	—	—	RW	—	—	—	—	—	—	—	—	1,300–1,400	RH

APPENDIX. (continued).

Species	West Butte	East Butte	Total	ST	RS	PR	RW	MG	RB	AS	DF	LP	SL	MR	SF	Summer altitudinal range (m)[c]	Evidence of breeding[d]
					Plains							Montane					
Downy Woodpecker (*P. pubescens*)[g]	0	0	0	—	—	—	RW	—	—	—	—	—	—	—	—	1,400–1,500	RH
Eastern Kingbird (*Tyrannus tyrannus*)[g]	0	0	0	ST	RS	—	RW	—	—	—	—	—	—	—	—	1,100–1,400	TO
Western Kingbird (*T. verticalis*)	0	0	0	ST	—	—	—	—	—	—	—	—	—	—	—	1,100–1,200	TO
Least Flycatcher (*Empidonax minimus*)[g]	0	0	0	—	—	—	RW	—	—	—	—	—	—	—	—	1,300–1,400	TO
*Dusky Flycatcher (*E. oberholseri*)[g]	5	4	9	—	—	—	RW	—	—	—	DF	LP	SL	MR	SF	1,400–2,000	NE
*Western Flycatcher (*E. difficilis*)[g]	0	7	7	—	—	—	RW	—	—	—	—	—	—	MR	—	1,400–1,700	PJ
Western Wood Pewee (*Contopus sordidulus*)[g]	0	0	0	—	—	—	RW	—	—	—	—	—	—	—	—	1,300–1,500	ET
Horned Lark (*Eremophila alpestris*)[c]	0	0	0	ST	—	—	—	—	—	—	—	—	—	—	—	1,000–1,300	TO
Violet-green Swallow (*Tachycineta thalassina*)	0	0	0	—	—	—	RW	—	—	—	—	—	—	—	—	1,300–1,400	RH
Rough-winged Swallow (*Stelgidopteryx ruficollis*)	0	0	0	ST	RS	—	—	—	—	—	—	—	—	—	—	1,100–1,300	AN
Barn Swallow (*Hirundo rustica*)[g]	0	0	0	ST	—	—	RW	MG	—	—	—	—	—	—	—	1,100–1,400	AN
Black-billed Magpie (*Pica pica*)[c]	3	17	20	—	RS	—	RW	—	—	—	DF	LP	SL	—	—	1,100–1,800	PJ
Common Crow (*Corvus brachyrhynchos*)	25	4	29	ST	—	—	RW	MG	—	—	DF	LP	SL	MR	SF	1,100–1,800	RH
*Clark's Nutcracker (*Nucifraga columbiana*)[g]	47	62	109	—	—	—	RW	MG	RB	—	DF	LP	SL	MR	—	1,400–2,200	RH
Black-capped Chickadee (*Parus atricapillus*)	14	x	14	—	—	—	RW	—	—	AS	DF	LP	SL	—	—	1,300–1,500	RH
*Mountain Chickadee (*P. gambeli*)[g]	20	27	47	—	—	—	—	—	—	AS	DF	LP	SL	—	SF	1,400–2,100	ET
*Red-breasted Nuthatch (*Sitta canadensis*)[g]	11	4	15	—	—	—	RW	—	—	—	DF	LP	SL	—	—	1,400–2,100	ET
House Wren (*Troglodytes aedon*)[g]	17	4	21	—	—	—	—	—	—	AS	DF	—	—	—	—	1,200–1,700	PJ
Rock Wren (*Salpinctes obsoletus*)[g]	x	1	1	—	—	—	RW	—	RB	—	—	—	SL	—	—	1,400–2,200	ET
Catbird (*Dumetella carolinensis*)	0	1	0	—	RS	—	RW	—	—	—	—	—	—	—	—	1,300–1,500	RH
American Robin (*Turdus migratorius*)	27	33	60	ST	RS	—	RW	MG	RB	AS	DF	LP	—	—	—	1,100–2,000	NE
*Hermit Thrush (*Catharus guttatus*)	2	x	2	—	—	—	RW	—	—	—	—	LP	SL	—	SF	1,600–2,100	RH
*Swainson's Thrush (*C. ustulatus*)	x	x	x	—	—	—	RW	—	—	—	—	LP	SL	—	—	1,400–1,700	RH
Veery (*C. fuscescens*)[g]	0	0	0	—	—	—	RW	—	—	—	—	—	—	—	—	1,300–1,500	ET
Mountain Bluebird (*Sialia currucoides*)	9	11	20	—	—	—	—	MG	—	—	—	LP	—	—	SF	1,800–2,200	PJ
*Townsend's Solitaire (*Myadestes townsendi*)	x	1	1	—	—	—	—	—	RB	—	—	—	SL	MR	SF	1,600–1,800	PJ
*Golden-crowned Kinglet (*Regulus satrapa*)[g]	0	6	6	—	—	—	—	—	—	—	—	—	SL	MR	—	1,600–1,900	TO
*Ruby-crowned Kinglet (*R. calendula*)	x	x	x	—	—	—	RW	—	—	—	—	LP	—	—	SF	1,500–2,100	RH
Sprague's Pipit (*Anthus spragueii*)	0	x	0	ST	—	—	RW	—	—	—	—	—	—	—	—	1,200–1,300	RH
Cedar Waxwing (*Bombycilla cedrorum*)[g]	4	1	5	—	—	—	RW	—	—	—	DF	LP	—	—	—	1,400–1,600	EF
Starling (*Sturnus vulgaris*)	0	0	0	ST	—	—	RW	—	—	—	—	—	—	—	—	1,100–1,200	RH
Warbling Vireo (*Vireo gilvus*)[g]	3	x	3	—	—	—	RW	—	—	AS	—	—	—	—	—	1,400–1,500	ET
*Orange-crowned Warbler (*Vermivora celata*)[g]	x	0	x	—	—	—	RW	—	—	AS	—	—	—	—	—	1,400–1,500	TO
Yellow Warbler (*Dendroica petechia*)	0	0	0	—	RS	—	RW	—	—	—	—	—	—	—	—	1,100–1,500	TO
*Yellow-rumped Warbler (*D. coronata*)[g]	36	38	74	—	—	—	RW	—	—	AS	DF	LP	SL	MR	SF	1,400–2,200	PJ
Ovenbird (*Seiurus aurocapillus*)	1	x	1	—	—	—	RW	—	—	AS	DF	LP	—	—	—	1,400–1,800	TO
*MacGillivray's Warbler (*Oporornis tolmiei*)[g]	x	5	5	—	—	—	RW	—	—	—	—	—	—	MR	—	1,400–1,800	EF
Common Yellowthroat (*Geothlypis trichas*)[g]	0	0	0	—	RS	—	RW	—	—	—	—	—	—	—	—	1,200–1,500	RH
Yellow-breasted Chat (*Icteria virens*)[g]	0	0	0	—	RS	—	—	—	—	—	—	—	—	—	—	1,300–1,400	TO

APPENDIX. (continued).

Species	Distribution and sample abundance[a]			Communities where found[b]												Summer altitudinal range (m)[c]	Evidence of breeding[d]
	West Butte	East Butte	Total	Plains				Montane									
				ST	RS	PR	RW	MG	RB	AS	DF	LP	SL	MR	SF		
House Sparrow (*Passer domesticus*)	0	0	0	ST	RS	–	RW	–	–	–	–	–	–	–	–	1,000–1,400	RH
Bobolink (*Dolichonyx oryzivorus*)	0	0	0	ST	–	–	–	–	–	–	–	–	–	–	–	1,100–1,300	RH
Western Meadowlark (*Sturnella neglecta*)	1	11	12	ST	–	–	–	MG	–	–	–	–	–	–	–	1,000–2,000	TO
Redwinged Blackbird (*Agelaius phoeniceus*)	0	0	0	ST	RS	PR	–	–	–	–	–	–	–	–	–	1,100–1,300	NY
Brewer's Blackbird (*Euphagus cyanocephalus*)	0	0	0	ST	–	–	–	–	–	–	–	–	–	–	–	1,100–1,400	RH
Brown-headed Cowbird (*Molothrus ater*)	0	0	0	ST	–	–	RW	–	–	–	–	–	–	–	–	1,100–1,400	RH
*Western Tanager (*Piranga ludoviciana*)g	6	6	12	–	–	–	RW	–	–	AS	DF	LP	–	–	–	1,400–1,700	ET
Lazuli Bunting (*Passerina amoena*)g	x	x	x	ST	RS	–	RW	–	–	–	DF	–	–	–	–	1,200–1,500	TO
*Pine Grosbeak (*Pinicola enucleator*)g	x	1	1	–	–	–	–	–	–	–	DF	–	SL	–	–	1,400–2,100	EF
*Pine Siskin (*Carduelis pinus*)g	93	137	230	–	RS	–	RW	MG	RB	AS	DF	LP	SL	MR	SF	1,100–2,200	NY
American Goldfinch (*C. tristis*)	0	0	0	ST	RS	–	RW	–	–	–	–	–	–	–	–	1,100–1,400	RH
*Red Crossbill (*Loxia curvirostra*)g	180	241	421	–	–	–	RW	MG	RB	AS	DF	LP	SL	MR	SF	1,400–2,200	EF
*Rufous-sided Towhee (*Pipilo erythrophthalmus*)	0	0	0	–	RS	–	RW	–	–	–	–	–	–	–	–	1,300–1,500	PJ
Lark Bunting (*Calamospiza melanocorys*)	0	0	0	ST	–	–	–	–	–	–	–	–	–	–	–	1,100–1,300	RH
Savannah Sparrow (*Passerculus sandwichensis*)g	x	0	x	ST	–	–	–	MG	–	–	–	–	–	–	–	1,100–1,400	EF
Vesper Sparrow (*Pooecetes gramineus*)	2	1	3	ST	–	–	–	MG	–	–	–	–	–	–	–	1,200–2,000	TO
Lark Sparrow (*Chondestes grammacus*)	0	0	0	–	RS	–	–	–	–	–	–	–	–	–	–	1,100–1,200	RH
*Dark-eyed Junco (*Junco hyemalis*)g	88	101	189	–	–	–	RW	–	–	–	DF	LP	SL	–	SF	1,400–2,200	EF
Chipping Sparrow (*Spizella passerina*)g	56	36	92	–	RS	–	RW	MG	–	–	DF	LP	SL	–	SF	1,100–2,200	PJ
Clay-colored Sparrow (*S. pallida*)	0	0	0	ST	RS	–	–	–	RB	–	–	–	–	–	–	1,100–1,500	RH
Song Sparrow (*Melospiza melodia*)g	0	0	0	–	RS	–	RW	–	–	–	–	–	–	–	–	1,100–1,400	ET
Chestnut-collared Longspur (*Calcarius ornatus*)	0	0	0	ST	–	–	–	–	–	–	–	–	–	–	–	1,100–1,200	RH

[a] Numbers indicate how many individuals were seen during counts; an "x" indicates birds observed at some time in montane habitats but not seen during counts. Birds observed only in the plains habitats between the buttes or in riparian woodland are indicated by zeros in all three columns.

[b] Based on all observations, including birds heard but not seen. Occurrence in each of 12 habitats is indicated by listing the abbreviation of each habitat in which an observation was made: ST = steppe, RS = riparian shrubbery; PR = potholes and reservoirs; RW = riparian woodland; MG = montane grassland; RB = rubble slopes; AS = aspen; DF = Douglas fir forest; LP = lodgepole pine forest; SL = spruce-lodgepole forest; MR = mountain ravines; SF = subalpine forest.

[c] Rounded to 100-m intervals (e.g., a species observed only at 1471 m and 2019 m is given an altitudinal range of 1400–2100 m).

[d] Evidence of breeding is presented using a modification of Binford's (1973) categories. Abbreviations are arranged in order of decreasing conclusiveness (only the highest-ranking evidence encountered is indicated for each breeding species): PJ = prejuvenal observed; NY = nest with young observed; NE = nest with eggs observed; AN = active nest observed, condition unknown; EF = enlarged follicles or oviduct in specimen; TO = territoriality observed; ET = enlarged testes in specimen; RH = range, habitat, dates.

[e] Reported by Coues (1878).

[f] Partial specimen(s) taken.

[g] Entire specimen(s) taken.

* Montane species (as defined in the text).