increased in intensity. Courtship at this time frequently was characterized by aggression among males, courtship flights, jump flights, and copulatory behavior. In addition, males performed a greater diversity of displays, and females displayed most often by inciting. Reproductive behavior continued at this high level until most females had paired. At this time, frequency of courtship usually declined but intensity of display remained unchanged. Late in the pairing process, attempts by single males to disrupt established pair bonds were never successful.

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Expectable decline of forest bird populations in severe and mild winters.—In an earlier paper (Graber and Graber, Wilson Bull. 91:88–103, 1979) we described the change of bird numbers in three habitats in southern Illinois between early winter (26 December–7 January) and late winter (3–18 February) during 1976–77, an especially cold winter with heavy snow. On average, bird populations that season declined about 58% in mature bottomland forest, and 66% in mature upland forest, but increased slightly (9%) in urban residential habitat. We attributed the change to mortality and local movements of birds. Those observations posed two other questions of interest to us: (1) How would populations vary in a mild winter? and (2) Is there a predictable rate of change during the winter season?—important questions for those who census birds.

Methods.—To find the answers we censused, using the same methods on some of the same areas, early (26 December–11 January) and late (25 January–15 February) winter in 1977–78 (another severe winter) and 1979–80 (a mild winter). The relative severity of those winters is indicated in Table 1. Our attempts to acquire data early and late in the winters of 1978–79 and 1981–82 were frustrated by floods and ice storms. Within the seasonal limits posed by the study, we censused every day that weather permitted. The periods of censusing were chosen to avoid early and late migration. We varied coverage of habitats in the different years to consider different problems concerned with the census. In 1977–78, to consider population variability, we censused seven bottomland forest areas (Nos. 1, 2, 6, 8, 10, and two forests at No. 11 in Fig. 1 of Graber and Graber [1979]). The variability shown (Table 2) includes variation from the census method and from the habitats as well as the populations. For that reason and because of the small number of areas that could be censused in the time available, the standard errors are large. Differences between early winter and late winter populations (all native species) in the seven bottomland forest areas were significant ($t = 2.72$, df $= 12$, $P < 0.02$).

Because it is important to know whether decline in numbers of birds represents mortality or movement to other habitats, we censused representative areas of the principal arboreal habitats in southern and central Illinois. In the mild winter of 1979–80 (Table 3), in addition to mature bottomland (No. 10 in Fig. 1 of Graber and Graber [1979]) and mature upland forest (Warbluff Forest, 10 km N, Golconda, Pope County), we censused upland forest-edge

TABLE 1

CELSIUS DEGREE DAYS (DD) BELOW FREEZING AND AVERAGE SNOW DEPTH NEAR STUDY AREAS CENSUSED FOR BIRDS IN WINTER (26 DEC.–12 FEB.)

	Decatur			Dixon Springs		
Season	DD	Days with snow cover	Avg. snow depth (cm)	DD	Days with snow cover	Avg. snow depth (cm)
1976–77	−437.5	41	23.4	−226.7	33	8.0
1977–78	−373.9	32	8.3	−232.5	32	13.6
1979–80	−146.9	14	2.4	−7.2	14	2.5

and shrub habitat, and 40-year-old loblolly pine (*Pinus taeda*) plantation habitat, both in the Warbluff area. In east-central Illinois we censused mature bottomland forest, mature upland forest, and forest-edge and shrub habitat, all in Allerton Park, Piatt County. The southern Illinois forests were described in the earlier paper. In central Illinois tree genera of the upland forest, listed in order of importance, were *Quercus*, *Carya*, *Ulmus*, *Acer*, and *Fraxinus* (comprising 85% of the Importance, Y). The bottomland forest consisted of *Acer*, *Celtis*, *Platanus*, *Fraxinus*, *Carya*, *Quercus*, and *Ulmus* (85% of Y). Each tract was censused twice in early winter and twice in late winter. As expected, variability was high, but differences between the early censuses in all tracts were not significant (t = 0.02, df = 12, $P > 0.90$), nor were those between the late censuses (t = 0.14, df = 12, $P > 0.80$). On that basis, the early pairs were combined and the late pairs, combined in Table 3. In all habitats, central and south, bird populations declined between the early and late winter counts (Table 3). Because censuses in the different areas were necessarily made on different dates, the periods between early and late censuses varied somewhat from habitat to habitat, and year-to-year. Therefore, in the text we have usually referred to population changes as average percentage change per day. Because we censused more areas of bottomland forest than of other habitats, the following discussion primarily concerns bottomland.

To save space, only the most common native species are listed in Tables 2 and 3, but the densities for all native species combined (excluding Cedar Waxwing [*Bombycilla cedrorum*]) are provided. The waxwing was excluded as the only native species present in early winter that always disappeared by late winter. Its inclusion would have accentuated the difference between early and late winter densities. The Eurasian Starling exhibited somewhat the same pattern. It disappeared from natural habitats between early and late winter (as in 1976–77) but increased greatly in urban habitat by late winter (Table 2).

Results and discusssion.—A pattern of population change observed in both the severe winters of 1976–77 and 1977–78 was that the steepness of the decline was related to the size of the early winter populations (Fig. 1). There were significant correlations between the early winter population and the population loss per day during the severe winters (1976–77, r = 0.83, F = 6.58, df = 3, 5, $P < 0.05$; 1977–78, r = 0.79, F = 8.52, df = 5, 7, $P < 0.01$). The slopes of the regression lines were not significantly different in the 2 years. The decline of populations in bottomland forests during both severe winters can be expressed by the equation: $P_d = D_i$ (0.00267), in which P_d is the average percent loss in population per day during the period covered by the censuses, and D_i is the initial population density (birds/40.5 ha). The equation may not apply to upland forests, which start (and end) the winter with generally lower populations, but we have insufficient censuses of upland areas or other habitats to test the equation. The end-of-winter densities in bottomland tend to converge at

TABLE 2

CHANGES IN NUMBERS OF WINTER BIRDS PER 40.5 HA IN ARBOREAL HABITATS IN SOUTHERN ILLINOIS DURING A SEVERE WINTER (1977–78)

Species	Bottomland forest			Upland forest			Urban residential		
	Early $\bar{x} \pm SE$	Late $\bar{x} \pm SE$	% Change	Early $\bar{x}$	Late $\bar{x}$	% Change	Early $\bar{x}$	Late $\bar{x}$	% Change
Yellow-shafted Flicker (*Colaptes auratus auratus*)	5.2 ± 1.38	0.8 ± 0.56	−86	2.5	1.3	−48	0	3.0	+
Red-bellied Woodpecker (*Melanerpes carolinus*)	7.1 ± 2.33	2.7 ± 1.08	−62	8.9	5.3	−40	6.1	6.9	+10
Red-headed Woodpecker (*M. erthyrocephalus*)	78.6 ± 12.33	74.6 ± 15.12	−3	24.9	7.9	−68	0	0	—
Downy Woodpecker (*Picoides pubescens*)	15.1 ± 4.00	11.7 ± 3.61	−22	3.8	6.0	+58	2.6	1.0	−61
Blue Jay (*Cyanocitta cristata*)	16.7 ± 6.34	7.9 ± 2.02	−53	13.4	13.9	+4	14.8	21.8	+47
Carolina Chickadee (*Parus carolinensis*)	10.6 ± 4.30	14.1 ± 5.14	+33	4.5	9.9	+120	0.9	4.0	+344
Tufted Titmouse (*P. b. bicolor*)	23.8 ± 4.22	11.7 ± 3.16	−51	8.9	4.0	−55	0	0	—
White-breasted Nuthatch (*Sitta carolinensis*)	3.9 ± 1.97	2.4 ± 1.14	−38	5.1	4.6	−10	0	0	—
Brown Creeper (*Certhia familiaris*)	1.6 ± 0.66	6.2 ± 1.86	+287	0.6	0.7	±	0	0	—
Golden-crowned Kinglet (*Regulus satrapa*)	0.6 ± 0.64	0.3 ± 0.30	−50	0	0.7	+	0	0	—
Ruby-crowned Kinglet (*R. calendula*)	1.0 ± 0.71	0	−100	0	0	—	0	0	—
Yellow-rumped Warbler (*Dendroica c. coronata*)	0	0	—	1.3	0.7	−46	0	0	—

TABLE 2
CONTINUED

Species	Bottomland forest			Upland forest			Urban residential		
	Early $\bar{x} \pm$ SE	Late $\bar{x} \pm$ SE	% Change	Early $\bar{x}$	Late $\bar{x}$	% Change	Early $\bar{x}$	Late $\bar{x}$	% Change
Northern Cardinal (*Cardinalis cardinalis*)	10.6 ± 4.23	4.8 ± 1.25	−55	0.6	2.0	+133	41.1	59.5	+45
Dark-eyed Junco (*Junco hyemalis*)	10.6 ± 6.80	2.1 ± 1.07	−80	7.6	0	−100	19.2	60.5	+215
All native birds	319.5 ± 54.07	170.0 ± 18.10	−47	91.1	59.6	−35	106.0	153.6	+44
Rock Dove (*Columba livia*)	—	—	—	—	—	—	54.2	23.8	−56
Eurasian Starling (*Sturnus vulgaris*)	—	—	—	—	—	—	466.5	825.6	+77
House Sparrow (*Passer domesticus*)	—	—	—	—	—	—	518.0	501.5	−3
No. ha censused	125.7	118.1	—	63.5	61.1	—	46.3	40.8	—

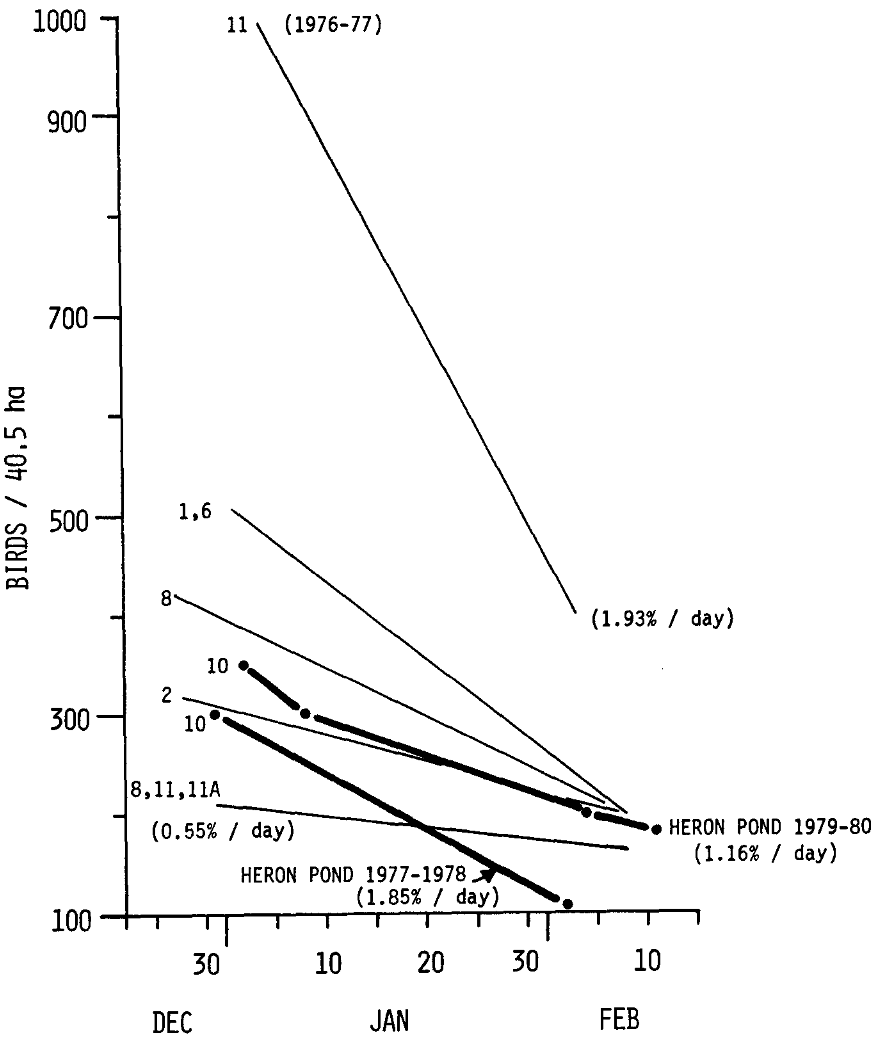

FIG. 1. Population densities of forest birds in early and late winter in seven bottomland forest areas in southern Illinois. Numerals indicate localities (see Wilson Bull. 91:89, 1979, for identifications). Nos. 11 and 11A are two forests in the same general area. Data refer to the severe winter of 1977–78 except where otherwise indicated.

a population level of about 150–200 birds/40.5 ha (Fig. 1), presumably the ultimate carrying capacity of the particular forest for the season.

The severity of the winter undoubtedly influences the rate of decline; 1976–77 and 1977–78 were about comparable in measurable factors of severity (Table 1), and rates of decline were similar in the two. In the mild winter of 1979–80 we censused only one bottomland forest (Heron Pond Nature Preserve) in which bird populations had a rate of decline during the winter of 1.16%/day, vs 1.85%/day in the severe winter (Fig. 1), even though the initial density was higher in the mild winter. Thus, we would not expect the equation for rate of decline to fit in a mild winter. Data for Wood Pigeon (*Columba palumba*) and Coal Tit (*Parus ater*) populations in England showed the same pattern of steep decline in severe winters, and less steep decline in mild winters (Lack, Population Studies of Birds, Clarendon Press, Oxford, England, 1966:88, 183) that we have seen in Illinois. It was not possible to determine precise rates of change for the England data, as the specific starting and ending dates of the studies were not stated.

The precision with which the initial population seems to predict rate of decline is somewhat surprising, as food resources (and other factors) could be expected to be an important factor bearing on population change during the winter. However, the direct influence of the food resources could be concealed if the initial population itself reflects the available food.

Though the slope of decline was less in a mild winter, it was still substantial (Table 3, Fig. 1). What caused the decline? A significant feature of the over-winter change in bird populations was its consistent trend in all forest habitats and nearly all forest species in both central and southern Illinois (Tables 2, 3). Major potential means by which winter population in an area may change significantly—local movement, migration, and mortality—may all be involved in the decline we observed. The only habitat that has consistently shown population increase by later winter was urban residential, a habitat, which though now rapidly expanding, accounts for only about 13% of arboreal habitat area in southern Illinois (Graber and Graber, Ill. Nat. Hist. Surv. Biol. Notes 97:6, 1976). Urban residential habitat would account for no more than 15% of the birds lost from natural habitats, based on data in Tables 2 and 3.

Little appears to be known about winter migration. Of the forest species we observed, only the Black-capped Chickadee is known to undertake (irregularly) winter migrations (DeSante, Am. Birds 30:679, 1976). In both severe and mild winters only two "species"—chickadees (at least Black-capped) and Brown Creeper—increased during the winter in natural habitats. Reference in Tables 2 and 3 to Carolina Chickadees (only) in extreme southern Illinois is based on the fact that we have rarely identified black-caps that far south in the state. It is possible that some of the chickadees we counted were actually black-caps, and that the observed increase in chickadees represented immigration. Winter migration of Brown Creepers has not been substantiated so far as we know, but our data indicate that such migrations occur.

Of the factors that could explain the observed general decline of birds during winter, we consider mortality to be most important. The observed rate was not necessarily above expected mortality. Annual mortality rates for adult song birds have been estimated from banding studies of different species and in different years to be 37–67% or 0.10–0.18%/day (Farner, Wilson Bull. 57:63, 1945; Hickey, U.S. Fish and Wildl. Serv. Spec. Sci. Rept. 15, 1952; Nice, Studies in the Life History of the Song Sparrow, Vol. 1, Dover Publications, New York, New York, 1964). Overwinter mortality of banded adult Song Sparrows was 14.26% (Nice 1964), and of adult Black-capped Chickadees, 10% or less to 20% in different years (Wallace, Bird-Banding 12:62–63, 1941). The high extremes in these banding studies approach or exceed the observed declines for a number of species on our study areas (Table 3). The winter declines we observed refer to a particular segment of any such populations (e.g., those that winter in the mid-temperate latitudes). Perhaps more importantly, the observed decline starts with the population of birds at a relatively high point in its annual cycle. Thus, the effect of a 1% per day average mortality could still leave the population at the end

TABLE 3

EARLY AND LATE WINTER BIRD POPULATIONS (NUMBERS PER 40.5 HA) IN ARBOREAL HABITATS OF CENTRAL (C) AND SOUTHERN (S) ILLINOIS DURING A MILD WINTER (1979–80)

Species	Region	Bottomland forest		Upland forest		Upland forest edge and shrub		Pines		% Change in $\bar{x}$
	C	27, 30[a] Dec	25, 29 Jan	28, 31 Dec	26, 31 Jan	26, 29 Dec	28 Jan, 1 Feb			
	S	2, 8 Jan	4, 11 Feb	5, 9 Jan	7, 10 Feb	1, 6 Jan	3, 9 Feb	4, 7 Jan	8, 12 Feb	
Yellow-shafted Flicker	C	8.3	9.4	2.2	0	9.8	5.5	—	—	−26.6
	S	3.7	1.9	6.5	2.8	5.3	1.0	1.2	1.2	−58.7
Red-bellied Woodpecker	C	17.7	13.5	6.6	1.0	8.7	3.3	—	—	−46.1
	S	8.3	6.6	5.6	5.6	5.3	1.0	4.7	1.2	−39.7
Red-headed Woodpecker	C	66.6	49.9	17.7	6.8	0	0	—	—	−32.7
	S	112.7	95.0	0	0.9	0	0	0	0	−14.9
Downy Woodpecker	C	18.7	13.5	6.6	5.2	10.9	9.9	—	—	−21.0
	S	23.1	8.5	1.9	4.6	1.0	2.1	1.2	4.7	−26.8
Blue Jay	C	11.4	10.4	14.4	1.0	18.5	8.8	—	—	−54.4
	S	44.3	16.9	13.1	7.4	13.7	17.6	4.7	14.2	−26.0
Black-capped Chickadee (*Parus atricapillus*)	C	26.0	26.0	5.5	9.4	13.1	23.0	—	—	+30.9
Carolina Chickadee	S	18.5	9.4	3.7	0	0	0	7.1	1.2	−63.8
Tufted Titmouse	C	29.1	21.8	13.3	3.1	7.6	0	—	—	−50.2
	S	35.1	11.3	0	0.9	0	0	8.3	3.6	−63.6
White-breasted Nuthatch	C	7.3	19.7	15.5	3.1	2.2	1.1	—	—	−4.4
	S	13.9	3.8	1.9	0	1.0	0	3.5	0	−81.3

TABLE 3
Continued

Species	Region	Bottomland forest		Upland forest		Upland forest edge and shrub		Pines		% Change in $\bar{x}$
	C	27, 30[a] Dec	25, 29 Jan	28, 31 Dec	26, 31 Jan	26, 29 Dec	28 Jan, 1 Feb			
	S	2, 8 Jan	4, 11 Feb	5, 9 Jan	7, 10 Feb	1, 6 Jan	3, 9 Feb	4, 7 Jan	8, 12 Feb	
Brown Creeper	C	12.5	10.4	5.5	2.1	2.2	2.2	—	—	−27.2
	S	1.8	0.9	0	2.8	0	0	9.4	3.6	−34.8
Golden-crowned Kinglet	C	0	0	0	0	0	0	—	—	—
	S	0	0	0.9	2.8	0	0	29.5	10.7	−55.6
Ruby-crowned Kinglet	C	0	0	0	0	0	0	—	—	—
	S	0.9	0	0	0	0	0	10.6	1.2	−89.6
Yellow-rumped Warbler	C	3.1	2.1	0	0	0	0	—	—	−32.3
	S	21.3	11.3	0.9	1.9	1.0	0	5.9	1.2	−50.5
Northern Cardinal	C	39.5	30.1	10.0	1.0	44.7	2.2	—	—	−64.6
	S	7.4	2.8	0	0	7.4	9.3	5.9	1.2	−35.7
Dark-eyed Junco	C	83.3	42.6	0	0	34.9	61.3	—	—	−12.1
	S	12.0	1.9	0	0.9	73.8	22.7	0	11.8	−56.5
Total density of all native species	C	381.0[b]	291.2	104.2	41.8	226.9[b]	137.0	—	—	−34.0
	S	327.1	192.0	40.1	38.1	245.8	150.7	138.0	126.8	−32.4
Ha censused	C	38.9	38.9	36.5	38.7	37.1	36.9	—	—	—
	S	43.8	43.0	43.3	43.6	38.4	39.2	34.3	34.1	—

[a] Dates of censuses.
[b] Excludes Cedar Waxwings.

of winter above that in the preceding spring, depending upon over-all productivity, mortality in other habitats and wintering areas, and other factors.

It is impossible for a single team of observers to adequately census all habitats in a region within the time limitations required, but studies that do not cover all of the habitats used by the winter species are likely to be misleading on questions of population change during the season. Habitat availability must also be considered in such studies, but data on availability of even gross (vs micro) habitat types are generally lacking. Two patterns that seem clear from this and our previous (1979) study is that notable declines occur over winter in natural habitats in mild as well as in severe winters, and that the steepness of the decline is related especially to the size of the starting population.

The observation that bird populations declined through the winter in both mild and severe winters is important to those who census winter birds. The seasonal limits designated for Audubon winter bird studies is 20 December–10 February (Robbins, Studies in Avian Biology 6:52–57, 1981). The results would differ according to the pattern of censusing in that period—early censuses indicating high populations, later censuses lower populations. Fortunately the dates of censuses are usually presented, but the rules of censusing may need to be more precisely delineated, as Robbins (1981) has suggested.

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Comparative preening behavior of wild-caught Canada Geese and Mallards.—Comfort movements have been described for many birds (c.f., Goodwin, Br. Birds 60:363–364, 1967; Weisbrod, Living Bird 10:271–284, 1971; Ainley, Behaviour 50:16–51, 1974; Potter and Hauser, Auk 91:537–563, 1974). Preening, perhaps the most conspicuous of all comfort movements, functions in cleaning, arranging, aligning, and oiling the feathers.

Preening is usually observed in bouts lasting from a few minutes (Coutlee, Wilson Bull. 75:342–357, 1963) to over 2 h (Schreiber, Ornithol. Monogr. No. 22, 1977). McKinney (Behaviour 25:120–220, 1965) divided preening bouts in waterfowl into two main components, oiling and nibbling. Oiling is characterized by contact with the uropygial gland and the subsequent bill movements which spread oil to the feathers. Nibbling consists of rapid movement of the mandibles in a "chewing" motion.

In this note I report on preening behavior in Canada Geese (*Branta canadensis*) and Mallards (*Anas platyrhynchos*) during summer and consider: (1) if there are any general behavioral patterns in a preening session; and (2) possible interspecific differences.

Methods.—This study was conducted at the W.K. Kellogg Bird Sanctuary of Michigan State University. Three-h observation periods were made during daylight hours at randomly chosen times. Observer disturbance was reduced by observing the geese from a distance of 35 m and the Mallards from a blind located 10 m from their pen. To further reduce bias, no data were recorded for the first 30–60 min of each observation period. Usually, only one or two preening sessions were recorded during the 2-h data collection period.

All geese were wing pinioned and housed in six similar outdoor pens (45 × 60 m). Three male and three female geese in each pen were identified by color-coded neck collars. Five male and four female wild-caught mallards were housed in a 8 × 15 m pen located on a small pond.