

FACTORS AFFECTING THE DISTRIBUTION OF MALLARDS WINTERING IN THE MISSISSIPPI ALLUVIAL VALLEY

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ABSTRACT.—The Mississippi Alluvial Valley (MAV) is the principal wintering area for Mallards (*Anas platyrhynchos*) in the Mississippi Flyway. Here, we consider it a distinct habitat (*sensu* Fretwell 1972), i.e. fitness is relatively homogeneous among ducks within the MAV but different from that of ducks in other such habitats. We analyzed recovery distributions of Mallards banded pre-season (July–September 1950–1980) to test hypotheses concerning the effects of winter temperatures, precipitation, and population levels on Mallard winter distribution. When two groups of years that comprised extremes of warm and cold winter weather were compared, recovery distributions of all four age and sex classes (adult males and females, young males and females) differed significantly; recoveries were located farther south in cold years. Recovery distributions also differed between wet and dry years in the MAV for all groups except adult males, higher proportions of recoveries of adult females and of young males and females occurring in the MAV during wet winters. Although differences in continental Mallard population size were associated with differences in recovery distributions only of adult males and young females, the proportion of young males and of all young Mallards recovered in the MAV increased during years of low populations. We conclude that temperature, water conditions, and population size affect the habitat suitability of Mallard wintering areas and that Mallards exhibit considerable flexibility in winter distribution associated with these factors. Received 25 October 1982, accepted 30 March 1983.

MIGRATORY birds travel substantial distances each year and must select appropriate summer, migration, and winter habitats. If the relative suitability, defined in terms of expected fitness (see Fretwell 1972), of potential summer or winter residences varies annually, and if such variation can be perceived by birds, then we might expect corresponding variation in choices of seasonal residences. A number of possible benefits associated with returning to the same areas each year, however, can also be imagined (e.g. "familiarity" with the distribution of food resources, nest or roost sites, predators, etc.). We would expect the degree of variation in choice of seasonal residence to be largely determined by the magnitude and variation of these sorts of relative "costs" and "benefits."

Mallards (*Anas platyrhynchos*) are widely distributed in the Holarctic and have been studied extensively in both North America and Europe. A number of workers have suggested that Mallards generally return in subsequent winters to the area in which they spend their initial winter (Munro 1943, Cartwright and Law 1952, Boyd and Ogilvie 1961, Crissey 1965, Gollop

unpubl. data), whereas others believe that Mallards may winter in different areas depending on such factors as winter weather conditions and food availability (Pulliainen 1963, Lensink 1964, Bellrose and Crompton 1970, Nilsson 1973). Nichols and Hines (in prep.) recently completed an extensive analysis of winter band-recovery records for North American Mallards and concluded that birds from specific breeding areas do exhibit some temporal variation in wintering-ground location. They further concluded that young (first year) birds appeared less likely to return to specific wintering areas in subsequent years than did adults.

The Mississippi Alluvial Valley (MAV; see Fig. 1) is an extremely important wintering area for North American Mallards (see Bellrose 1976) and exhibits considerable year-to-year variation in the number of birds present. Bellrose and Crompton (1970: 222) suggested that Mallards in the Mississippi migration corridor (see Bellrose 1968) exhibit "flexible homing to specific localities" and that this flexibility is keyed to such environmental variables as ice, snow cover, and water availability. Despite these

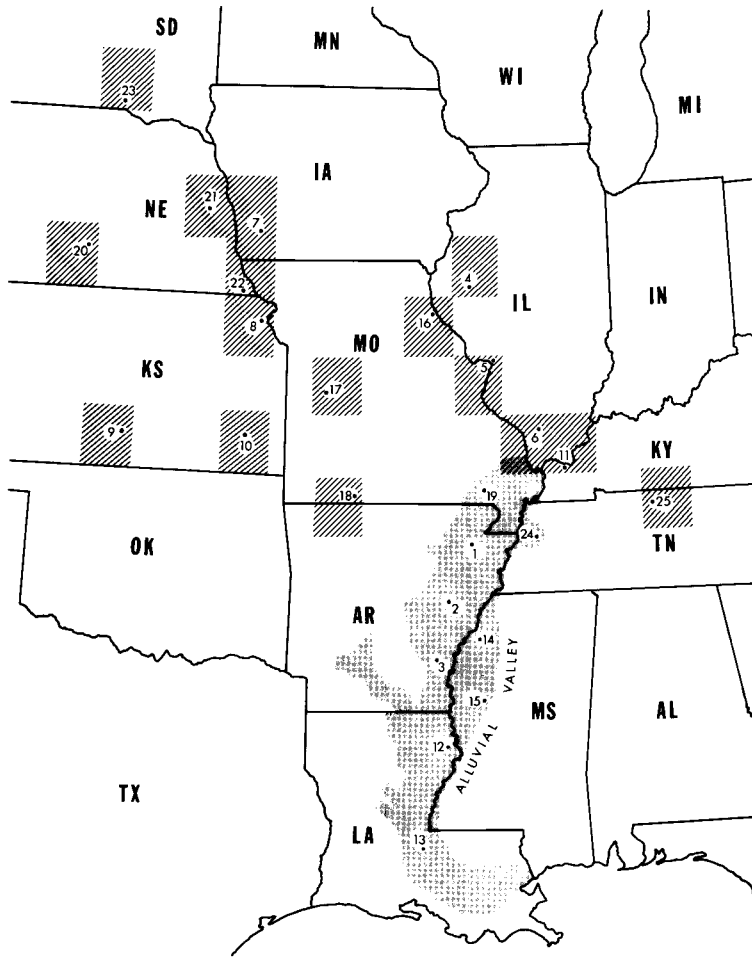


Fig. 1. Location of the Mississippi Alluvial Valley and distribution of the sites that provided climatic data (see Appendix 1 and text).

suggestions of an association between winter distribution and environmental variables, however, we are aware of no actual tests of this general hypothesis. In this paper we test hypotheses about the relationships between winter distribution patterns of Mallards associated with the MAV and (1) winter temperatures, (2) winter precipitation, and (3) wintering Mallard population densities.

METHODS

DATA SOURCES

Band recoveries.—Mallard winter band recoveries were obtained from the computer retrieval files of the U.S. Fish and Wildlife Service Bird Banding Laboratory (BBL), Laurel, Maryland. We used only direct

recoveries (occurring the first winter after banding) of normal, wild birds banded during the pre-season period (July–September), 1950–1980, and shot or found dead during December–February. Each banded bird was aged as either young (calendar year of hatching) or adult (older than 1 yr). All tests of band-recovery distributions involved recoveries resulting from bandings in specific pre-season banding “reference areas” that contributed large numbers of birds to the MAV. All minor reference areas within the following major reference areas (see Anderson and Henny 1972 for reference-area delineation) were selected for our tests: Southwestern Saskatchewan (04), Southeastern Saskatchewan (05), Southwestern Manitoba (06), Northern Saskatchewan–Northern Manitoba–Western Ontario (07; data from bandings in this reference area were insufficient, however, for use in any tests), Missouri River Basin (13), and Great Lakes (14). In all tests using band-recovery distributions,

we required 10 winter band recoveries for a specific banding area and age-sex class for each of the two compared sets of years as a minimum sample size.

As with any sampling methodology, there are potential problems associated with the use of band-recovery data to draw inferences about distribution patterns of birds (see Hickey 1951, Crissey 1955). One such problem is temporal and geographic variation in "band reporting rate" (probability that a band will be reported to the BBL, given that a banded bird has been shot or found dead). Henny and Burnham (1976) studied this problem with Mallards by using "reward bands" and detected regional geographic variation (between Atlantic Flyway + eastern Canada vs. Central + Mississippi flyways vs. Pacific Flyway + western Canada), temporal variation (between 1948–1950 and 1972–1973), and variation associated with distance between banding and recovery sites. Geographic variation should be unimportant in our study, because the majority of recoveries came from the same region (Central + Mississippi flyways), and virtually all of them occurred more than 80 km from the banding sites, the distance beyond which further reporting rate variation was thought to be insignificant (Henny and Burnham 1976). If geographic variation is unimportant, then temporal variation will likewise be unimportant, as our tests can only be affected by interactions between these two sources of variation.

The application of banding data to problems of distribution can also be hampered by variation in hunting-season dates and timing of migration. This sort of problem should have been minimized in our work, as we only used recoveries occurring from December–February and thus presumably were dealing with wintering birds or at least birds that had completed the largest portions of their migrations (Bellrose 1976). We note that the majority of our recoveries came from December and January and that possible late-season habitat shifts in February would not have been reflected well by our samples.

The biggest potential problem in our study involved the possibility of year-to-year changes in the geographic pattern of recovery probabilities. For example, we addressed the question of whether or not winter temperature influences the probability of a Mallard wintering in the MAV (as opposed to wintering elsewhere) by asking whether or not band-recovery distributions differed between years of warm and cold winters. If our tests indicated that the proportions of band recoveries occurring in the MAV were higher during cold winters, then we would conclude that Mallards responded to the low temperatures by moving into the MAV. This conclusion would not be warranted, however, if, for some reason, recovery probabilities happened to be higher in the MAV during cold winters and lower during warm winters. Within a given year, there may be some geographic variation in the probability of a bird being recovered (Anderson 1975; e.g. hunter effort and ac-

tivity may vary geographically). Such geographic variation in recovery probability may also change from year to year (e.g. hunting-season closing dates vary somewhat) and may result in temporal variation of recovery probability within areas. Even if such variation were relatively large, our null hypotheses should still be reasonable, and we would be misled only in unusual circumstances, such as the hypothetical warm vs. cold winter situation described above (i.e. even if recovery probabilities in and out of the MAV vary from year to year, it would still be unlikely for high MAV recovery-probability years to coincide with cold winters and vice versa). In any case, we examined available hunting-season data (mainly season dates and bag limits; see Martin and Carney 1977) for the selected years of extreme environmental variation and do not believe that any misleading coincidences occurred.

Winter surveys.—We also analyzed winter population data from the January waterfowl survey conducted by cooperating states, the U.S. Fish and Wildlife Service, and the Canadian Wildlife Service (e.g. Novara et al. 1981). This survey includes counts of ducks in major wintering areas of the United States. Little is known about the accuracy and sampling variation associated with this survey. Because we have more confidence in the spring breeding-ground surveys, which involve aerial counts over a series of transects and include corresponding ground counts for an estimation of the proportion of ducks seen from the air (see Martin et al. 1979: 193), we used these data (available for 1960–1981) to evaluate the reliability of the winter counts. Specifically, we used Spearman rank correlation analysis (Snedecor and Cochran 1967: 193) to test for an association between winter Mallard counts and spring breeding-population-size estimates for the same calendar year. The Spearman correlation coefficient ($r_s = 0.50$, $df = 20$, $P < 0.05$) indicated a significant positive correlation between the two sets of values; consequently, we decided to use the winter-count data in some of our analyses.

Temperature and precipitation.—Weather data were obtained from NOAA (1950–1981). We selected 9 reporting stations distributed throughout the MAV and 16 stations in other areas known [based on the band-recovery distribution maps of Anderson and Henny (1972) and Nichols and Hines (in prep.)] to be potential alternate wintering areas for MAV Mallards (Fig. 1, Appendix 1). For sites outside the MAV, we selected only stations to the north of 36°N latitude. Temperature data from more southerly stations were similar to those of the MAV, and we thus did not expect Mallards to differentiate between these two general areas on the basis of temperature. For stations outside the MAV, we recorded (1) mean monthly temperatures for December–January and (2) cumulative days per month with a minimum daily temperature of less than 0°C, December–January. For

the MAV stations we recorded cumulative monthly precipitation for November–January.

STATISTICAL TESTS

Most of our tests involved comparisons of band-recovery distributions between groups of winters characterized by opposite extremes of an environmental variable of interest (e.g. warm vs. cold winters). We asked two kinds of questions and thus used two kinds of tests for these comparisons. First, we asked if the bivariate distributions of winter band recoveries (each characterized by latitude and longitude measured to the nearest 10' coordinates) differed between the two sets of years. We used the nonparametric test of Mardia (1967, 1972: 197) to test this hypothesis. "Ties" between observations from the two samples were encountered infrequently and were handled in the manner suggested by Robson (1968). These tests provided test statistics for each age-sex class of Mallards by reference area. Because the test statistics approximately follow a Chi-square distribution, summary test statistics (over reference areas or age-sex classes) were obtained by summing test statistics and their associated degrees of freedom.

The second kind of question asked was whether or not the proportion of recoveries occurring in the MAV differed in a predicted direction between winters characterized by environmental extremes. We used one-tailed z -tests for proportions (Snedecor and Cochran 1967: 220) to address these questions. Such tests were conditional on the numbers of recoveries occurring from specific banded samples during the winters of interest (these numbers are random variables). Because the z_i (the z statistic for reference area i) are distributed approximately as Normal (0,1) under the null hypothesis, summary statistics were computed as $Z = \sum_{i=1}^n z_i / \sqrt{n}$, where n is the number of individual test statistics contributing to the summary statistic and Z is also distributed as Normal (0,1).

We acknowledge that the extreme-year tests described above may not be "optimal" ways of investigating relationships between Mallard winter distributions and environmental variables. One undesirable characteristic of such tests is that the use of only two groups (e.g.

warm and cold winters) ignores much of the year-to-year variation in the environmental variables and, presumably, in Mallard distribution patterns. For example, if we had good samples of winter band recoveries for every year for which measurements of the environmental variable of interest were available, we could perhaps use correlation analysis to test for association between these measurements and a statistic (e.g. mean latitude of recovery) characterizing Mallard distribution. Sufficient data for this type of analysis were not available. Another undesirable characteristic is the "single factor" nature of these tests. A single analysis including all the environmental variables of interest (such as multiple regression) would be desirable, but the lack of annual values of some statistic characterizing Mallard distribution prevents this type of multifactor analysis.

HYPOTHESES AND PREDICTIONS

Conceptual framework.—In their discussions of habitat selection, Fretwell and Lucas (1970) and Fretwell (1972) defined the realized suitability, S_i , of habitat i as the average expected "success rate" (where success rate indexes relative fitness) of individuals in that habitat. They then expressed S_i in terms of a "basic suitability," B_i , and a habitat-specific function of density, $f_i(d_i)$, where d_i is the density of conspecifics in habitat i (equation 2 of Fretwell and Lucas 1970). Here, we modify this basic model to allow both realized and basic suitability to vary with time as follows:

$$S_{ij} = B_{ij} - f_j(d_i) \quad (1)$$

where j indexes year. The function $f_j(d_i)$ always increases with density, so S_{ij} approaches the maximum possible value of B_{ij} when density approaches 0 and then decreases as density increases. We believe that the MAV is generally a habitat with high B_{ij} (define $i = m$ to denote the MAV). We further hypothesize that $B_{m,j} = g_m(P_{m,j})$, where $g_m(P_{m,j})$ is a function that increases with increases in MAV winter precipitation, $P_{m,j}$. Finally, we hypothesize that B_{ij} for certain northern wintering habitats is a function of winter temperatures in such areas ($B_{ij} = h_j(C_{ij})$), where C_{ij} denotes temperature in habitat i , year j), and that B_{ij} for these areas decreases with decreasing temperatures. If suitability of these northern areas does decrease with

decreasing temperature, then the *relative* suitability of wintering areas farther south (e.g. the MAV) should be high in years of low temperature.

If Mallards can assess habitat suitability, then we can test these general hypotheses about S_{ij} and B_{ij} by contrasting Mallard distribution patterns (which should reflect S_{ij}) for years of differing temperature, precipitation, and Mallard population size. For each of these variables, we first tested a general hypothesis about variation in winter distribution patterns (reflecting S_{ij}) and then tested more specific hypotheses about the proportion of birds from particular breeding areas that wintered in the MAV (reflecting $S_{m,j}$).

Winter temperature.—Low winter temperatures increase energy requirements for the maintenance of homeothermy and at the same time reduce food availability by freezing wetland feeding sites. Waterfowl mortality certainly occurs during prolonged periods of severe winter weather (e.g. Harrison and Hudson 1964), and North (1979) and North and Morgan (1979) have presented convincing evidence of the dependence of Grey Heron (*Ardea cinerea*) survival rates on winter temperatures. If winter temperatures influence Mallard fitness, then we would predict more southerly wintering locations during "cold" than "warm" winters. Although the MAV spans a range of latitudes, it is farther south than a number of alternative Central and Mississippi Flyway Mallard wintering areas. We were thus interested in determining whether or not Mallards exhibited a greater tendency to winter in the MAV during cold years.

Although February can be considered part of the winter period, we believe that wintering-ground locations are determined before then, and thus we used temperature data from December and January for our tests. Annual summary statistics computed for stations outside the MAV were: (1) mean December–January temperature and (2) total number of days with minimum temperatures less than 0°C during both months. We computed mean temperatures as (1) the unweighted arithmetic mean of the stations and (2) a weighted arithmetic mean in which station statistics were weighted using long-term (1950–1980) winter-survey estimates of the proportions of Central and Mississippi Flyway Mallards wintering in the represented states (this gave higher "weights" to stations in

states in which larger numbers of Mallards generally wintered). There was little difference between the results of these two methods, so we used the unweighted arithmetic means for simplicity (Appendix 2). Years with mean December–January temperatures greater than 0°C were designated as "warm," and years with means less than -2.8°C were categorized as "cold" (Appendix 2). With respect to the other temperature criterion, we selected years with fewer than 26 days of subfreezing temperatures in December and January as "warm" and years with more than 28 days as "cold" (Appendix 2). Certainly, the two temperature criteria are not independent (we found a highly significant inverse correlation between them, as expected), and thus neither are the tests based on them. It was not clear to us which variable should be more important, so we used both.

We conducted three separate sets of tests to explore the relationship between winter temperature and Mallard distribution. First, we used Mardia's (1967) test to determine whether or not winter band-recovery distributions differed between warm and cold winters, as defined by the two temperature criteria. Second, we tested the general hypothesis that the proportion of Mallards wintering in southern areas varied inversely with temperature. Using winter-survey data, we computed the proportion of the total Mississippi and Central Flyway Mallards wintering in the following states: New Mexico, Texas, Oklahoma, Arkansas, Louisiana, Tennessee, Mississippi, and Alabama. We used Spearman rank correlation analysis to test for an association between this proportion and the temperature variables of Appendix 2. Finally, we used z statistics to test the hypothesis that the proportion of winter band recoveries occurring in the MAV was greater during cold than warm winters.

Winter precipitation.—The extent of shallow surface water during the winter influences day-to-day Mallard distribution patterns at the local level (Reinecke unpubl. data) and is thought to be important to wintering populations throughout the MAV. Heitmeyer and Fredrickson (1981) presented evidence that winter precipitation in the MAV influences subsequent Mallard reproduction, thus providing a possible link with fitness. We wanted to test the prediction that Mallards exhibit a greater tendency to winter in the MAV during years when wetland conditions are favorable.

After calculating the cumulative precipitation for November, December, and January by station, we computed a 31-yr (1950–1980) average for each location. We then calculated annual deviations from the 31-yr averages. Finally, we computed the average deviation over all stations (Appendix 2) and used these annual deviation statistics as indicators of winter water conditions in the MAV. Extreme "wet" winters were defined as those with mean deviations greater than 10 cm, and "dry" winters were those with mean deviations less than -10 cm (Appendix 2).

We used two sets of tests to investigate the relationship between wintering Mallard distributions and MAV water conditions. With the same banding reference areas as before, we used Mardia's (1967) test to examine the hypothesis that winter band-recovery distributions differed between winters in which the MAV was characterized as "wet" or "dry." We then calculated z statistics to test the hypothesis that the proportions of winter band recoveries occurring in the MAV were greater during wet than dry years.

Winter population size.—Fretwell and Lucas (1970) and Fretwell (1972) discussed the influence of population density on habitat suitability and incorporated density into their models of suitability (see equation 1). They also suggested that the best habitat among a number of alternatives (the habitat with the highest "basic suitability") should be selected by animals until the population density reaches the point at which the actual or realized suitability of this habitat equals the basic suitability of the next best habitat. At this point, animals should be equally likely to select either of the two habitats. Continuation of this process results in the "ideal free distribution" of Fretwell and Lucas (1970) and Fretwell (1972). One prediction of this model is that the proportion of the total population inhabiting the best habitat (with the highest basic suitability) should be inversely related to total population size. Because the MAV represents generally good habitat (i.e. with high basic suitability), we would predict larger proportions of Mallards wintering in the MAV during years of low continental population size than in years of high population size.

We therefore used January continental survey data to test these hypotheses about changes in winter distribution patterns. Years with fewer than 6 million Mallards were defined as

"low" population-size years, and years with more than 8 million were labeled "high" (Appendix 2). With the same banding data as before, we used Mardia's (1967) test to examine the hypothesis of no difference in band-recovery distribution patterns between years characterized by high and low population size. We then used z statistics to test the hypothesis that the proportions of winter band recoveries occurring in the MAV were greater during low than high population years.

RESULTS

Winter temperatures.—Our tests rejected the null hypothesis of no difference in winter band-recovery distribution patterns between years of warm and cold winters for some of the individual reference areas and not for others ($P < 0.10$ for 16 of the 54 individual test statistics). Three of the four composite test statistics for each of the temperature criteria, however, indicated rejection of the null hypothesis ($P < 0.05$), as did composite test statistics computed over all age-sex classes (Table 1). We expected the mean latitudes of the band-recovery distributions to be smaller in cold winters than in warm ones. Using the mean December-January temperature criterion to select extremes, we found the mean latitude to be less for cold winters than for warm winters in 20 of the 25 individual reference areas tested (binomial probability of getting a result this extreme if there was really no tendency to winter farther south in cold winters is $P_b < 0.01$). Using the number of December-January days with temperatures less than 0°C criterion, we found the mean latitude to be less for cold winters than for warm winters in 23 of 29 data sets tested ($P_b < 0.01$). We conclude that band-recovery distributions did differ between warm and cold winters and that distributions were generally centered farther south in cold years.

Correlation analyses using the proportion of Mississippi and Central Flyway Mallards counted in southern states supported the results of the band-recovery distribution tests. The correlation between this proportion and mean December-January temperature for northern reporting stations was significant ($r_s = -0.42$, 29 df, $P < 0.05$). The correlation between the proportion of Mallards wintering in the south and mean December-January days with temperatures less than 0°C was in the expected di-

TABLE 1. Results of testing the null hypothesis of equivalent winter band-recovery distributions of Mallards banded pre-season and recovered during warm and cold winters.^a

Sex and age	Total recoveries	Mean December-January temperature criterion ^b					Mean December-January days < 0°C criterion ^b					
		Mean latitude ^c		Chi-square ^d	df ^e	P	Total recoveries	Mean latitude ^c		Chi-square ^d	df ^e	P
		Warm	Cold					Warm	Cold			
Adult												
Male	914	35.2	34.8	15.97	12	0.19	845	35.7	35.0	72.96	16	0.00
Female	197	35.3	33.9	20.20	8	0.01	303	35.0	34.5	15.82	12	0.20
Young												
Male	693	35.7	35.1	27.76	16	0.03	890	35.8	35.1	47.74	16	0.00
Female	546	35.1	34.5	26.29	14	0.02	688	35.1	34.6	23.67	14	0.05
Totals	2,350	35.3	34.6	90.22	50	0.00	2,726	35.4	34.8	160.19	58	0.00

^a Temperature data represent northern Central and Mississippi Flyway Mallard wintering areas.

^b Extreme years chosen using the two temperature criteria are presented in Appendix 2.

^c Expressed as degrees N latitude.

^d Test of Mardia (1967) was used with data from each reference area and a summary statistic computed over all areas.

^e The number of reference-area statistics contributing to each composite statistic is equal to $df/2$.

rection but not significant ($r_s = -0.15$, 29 df, $P > 0.10$).

The one-tailed z tests provided little evidence for rejecting the hypothesis of no difference in the proportion of winter recoveries occurring in the MAV during cold vs. warm winters (Table 2). When we selected extreme years, using the mean temperature criterion, only 2 of the 25 individual reference-area test statistics were significant ($P < 0.10$) and none of the 4 composite statistics was. A composite statistic computed over all age-sex classes was likewise nonsignificant ($P > 0.10$, Table 2). When the days with temperatures less than 0°C criterion was used, 3 of 29 individual test statistics were significant ($P < 0.10$) and none of the composite statistics was (Table 2). A composite statistic computed over all age-sex classes was also nonsignificant ($P > 0.10$). We conclude that there is no tendency for winter recoveries to occur in greater proportions in the MAV during cold winters.

Winter precipitation.—The null hypothesis of equivalent recovery distributions during wet and dry winters was rejected ($P < 0.10$) for 11 of the 24 individual reference-area data sets as well as for all 4 combined data sets (Table 3). The composite test statistic over all ages and sexes was also significant ($P < 0.01$). We conclude that winter Mallard recovery distribu-

tions did differ between these sets of wet and dry years.

The hypothesis that greater proportions of winter recoveries occurred in the MAV during wet winters was supported by significant ($P < 0.10$) one-tailed z statistics in 5 of the 24 individual data sets and 3 of the 4 composite statistics (Table 4). The Z statistic for adult males was the only one that was not significant. The composite statistic computed over all age and sex classes, however, was significant ($P < 0.01$). Finally, we note that in 18 of the 24 individual data sets ($P_b = 0.01$), the proportion of winter recoveries in the MAV was greater in the wet winter years than in the dry winter years.

Winter population size.—Tests for differences in winter recovery distribution between years of high and low population size were not as conclusive as the tests for differences between years of temperature and precipitation extremes. Four of the 12 individual test statistics for adult males and young females were significant ($P < 0.10$), as were the composite statistics for these age-sex classes (Table 5). No individual or composite statistics were significant for young males or adult females, however. The composite test statistic for all age-sex classes combined was significant ($P < 0.05$), but the major contribution to this statistic clearly came from only two age-sex classes. We con-

TABLE 2. Proportions of December–February band recoveries of Mallards banded preseason and recovered in the MAV during warm and cold winters.^a

Sex and age	Mean December–January temperature criterion ^b						Mean December–January days < 0°C criterion ^b					
	Refer-ence areas	Total recov-eries	Mean proportion in ^c		Z ^d	P ^e	Refer-ence areas	Total recov-eries	Mean proportion in ^c		Z ^d	P ^e
			Warm	Cold					Warm	Cold		
Adult												
Male	6	924	0.50	0.42	0.86	0.81	8	854	0.39	0.43	-0.90	0.18
Female	4	198	0.50	0.53	-0.16	0.44	6	310	0.41	0.41	-0.19	0.42
Young												
Male	8	701	0.45	0.49	-0.28	0.39	8	898	0.48	0.40	2.30	0.99
Female	7	551	0.43	0.41	0.69	0.75	7	698	0.41	0.42	0.44	0.67
Totals	25	2,374	0.47	0.46	0.57	0.72	29	2,760	0.42	0.42	0.87	0.81

^a Temperature data represent northern Central and Mississippi Flyway Mallard wintering areas.

^b Extreme years chosen using the two temperature criteria are presented in Appendix 2.

^c The arithmetic mean proportion of band recoveries occurring in the MAV, computed over all reference areas.

^d See Snedecor and Cochran (1967: 220). A composite Z was computed over all reference areas. Negative Z indicates a greater proportion of recoveries in the MAV during cold winters.

^e Probabilities correspond to a one-tailed test.

clude that there is evidence of a difference in recovery distribution patterns between years of high and low winter population size, although the evidence is strongest for adult males and young females.

When we compared the proportions of Mallard recoveries occurring in the MAV during winters of high and low population size, we again obtained results that varied among age-sex classes (Table 6). There was evidence that recoveries of young male ($P = 0.04$) and young female ($P = 0.13$) Mallards occurred with great

er probability in the MAV during years of low population size. Adult Mallards did not exhibit this tendency and in fact appeared to have lower recovery proportions in the MAV during years of low population size. The composite test statistic over all age-sex classes was nonsignificant ($P > 0.10$), but a composite statistic for young Mallards of both sexes was significant ($Z = -2.11, P < 0.05$).

Supplemental tests.—As explained in the

TABLE 3. Results of testing the null hypothesis of equivalent winter band-recovery distributions of Mallards banded preseason and recovered during dry and wet winters.^a

Sex and age	Total recoveries	Chi-square ^b	df ^c	P
Adult				
Male	670	40.41	12	0.00
Female	257	21.21	10	0.02
Young				
Male	715	23.44	14	0.05
Female	576	21.58	12	0.04
Totals	2,218	106.64	48	0.00

^a Dry and wet winters were chosen using winter precipitation data for the MAV (Appendix 2).

^b Test of Mardia (1967) was used with data from each reference area and a summary statistic computed over all areas.

^c The number of reference-area statistics contributing to each composite statistic is equal to $df/2$.

TABLE 4. Proportions of December–February band recoveries of Mallards banded preseason and recovered in the MAV during dry and wet winters.^a

Sex and age	Refer-ence areas	Total recov-eries	Mean proportion in ^b		Z ^c	P ^d
			Dry	Wet		
Adult						
Male	6	677	0.39	0.42	-0.19	0.42
Female	5	261	0.35	0.41	-1.29	0.10
Young						
Male	7	720	0.40	0.50	-2.45	0.01
Female	6	579	0.38	0.49	-2.34	0.01
Totals	24	2,237	0.38	0.46	-3.18	0.01

^a Dry and wet winters were chosen using winter precipitation data for the MAV (Appendix 2).

^b The arithmetic mean proportion of band recoveries occurring in the MAV, computed over all reference areas.

^c See Snedecor and Cochran (1967: 220). A composite Z was computed over all reference areas. Negative Z indicates a greater proportion of recoveries in the MAV during wet winters.

^d Probabilities correspond to a one-tailed test.

TABLE 5. Results of testing the null hypothesis of equivalent winter band-recovery distributions of Mallards banded pre-season and recovered during winters of high and low population size.^a

Sex and age	Total recoveries	Chi-square ^b	df ^c	P
Adult				
Male	578	27.83	16	0.03
Female	166	6.43	6	0.38
Young				
Male	608	10.15	12	0.60
Female	263	14.99	8	0.06
Totals	1,615	59.40	42	0.04

^a Winter population-size data were obtained from the winter waterfowl survey (Appendix 2).

^b Test of Mardia (1967) was used with data from each reference area and a summary statistic computed over all areas.

^c The number of reference-area statistics contributing to each composite statistic is equal to $df/2$.

Methods section, we were forced by data requirements to use a single-factor approach in which we selected years that were extreme with respect to single variables and ignored other variables in the selection process. Although we believe that this approach was necessary, we conducted two additional sets of tests to provide a partial check on this analysis.

We essentially repeated the tests of Tables 4 and 6, this time attempting to "control" for the other potentially important variable (precipitation or population size, whichever was not the variable of interest) by selecting years that were extreme *only* with respect to the variable of interest. In our wet-dry comparisons, for example, we omitted years that also had extreme high or low population sizes. Thus, the extreme year comparisons were repeated without the following years: 1955, 1957, 1958, 1961, 1973 (see Appendix 2). We realized that this reduction in tested years would greatly reduce the sample size and, hence, the power of both groups of tests. We were interested, however, in determining whether or not the results were at least consistent with those of Tables 4 and 6.

Only two wet years remained for the wet-dry comparison, and sample sizes, expressed both in numbers of recoveries and reference areas, were reduced. The composite test statistic over all age-sex classes was not significant ($Z = -0.42, P = 0.34$) but was of the same sign as that in Table 4. Of the 21 individual reference areas, 13 ($P_b = 0.19$) showed greater proportions of winter recoveries in the MAV dur-

TABLE 6. Proportions of December-February band recoveries of Mallards banded pre-season and recovered in the MAV during winters of high and low population size.^a

Sex and age	Refer-ence areas	Total recoveries	Mean proportion in ^b		Z ^c	P ^d
			High	Low		
Adult						
Male	8	582	0.40	0.34	1.51	0.93
Female	4	204	0.45	0.32	2.04	0.98
Young						
Male	6	614	0.36	0.48	-1.81	0.04
Female	4	270	0.36	0.44	-1.12	0.13
Totals	22	1,670	0.39	0.40	0.36	0.64

^a Winter population-size data were obtained from the winter waterfowl survey (Appendix 2).

^b The arithmetic mean proportion of band recoveries occurring in the MAV, computed over all reference areas.

^c See Snedecor and Cochran (1967: 220). A composite Z was computed over all reference areas. Negative Z indicates a greater proportion of recoveries in the MAV during years of low population size.

^d Probabilities correspond to a one-tailed test.

ing wet years. Thus, the results supported those of Table 4 but were not as conclusive. We attribute this to the reduction in power resulting from our reduced sample sizes, but we cannot entirely rule out other possibilities.

The comparison of years of high and low population size also produced results similar to those of Table 6. The composite statistics for young males ($Z = -1.03, P = 0.15$) and young females ($Z = -1.20, P = 0.11$) approached significance, and the composite statistic for all young birds (sexes combined) was significant ($Z = -1.58, P < 0.10$). As in Table 6, the composite adult statistics were not significant, and neither was the composite statistic for all age-sex classes combined ($Z = -0.50, P > 0.10$).

DISCUSSION

Previous analyses of band recoveries have presented static patterns of winter, migration, and breeding distribution. Here, we have provided evidence that three factors—winter temperature, precipitation, and population size—can influence Mallard winter band-recovery distributions. These effects are not surprising, because all three factors are thought to affect Mallard fitness.

First, we showed that Mallards from selected breeding reference areas wintered farther south during years characterized by low tempera-

tures in northern wintering areas, thus corroborating hypotheses advanced by Lensink (1964) and Bellrose and Crompton (1970). The results indicated a general southward movement in response to low temperature but did not support the hypothesis that more Mallards wintered in the MAV during years of extreme cold. In terms of the model presented earlier, we conclude that the suitability of at least some wintering habitats is affected by temperatures in northern wintering areas.

Although our analyses did detect variation associated with winter temperature, there is evidence that the "averaging" necessitated by our extreme years comparisons continues to mask some of the variability in winter distribution. For example, if Mallards adjust their wintering sites according to the magnitude of body-heat loss in relation to ambient temperature (a linear relationship, e.g. Kendeigh et al. 1977), then we would expect a gradual shift in distribution to the south matching winter isotherms or degree days of cooling. This would be consistent with our results and our method of expressing cold as mean December–January temperature. Other data, however, suggest that a "threshold" temperature effect has occurred on at least two recent occasions.

When we reviewed the January Mallard survey data from the winters of 1950–1951 (January 1951) to the present, we noted that, in general, the annual count for Arkansas was 2–3 times larger than that for Louisiana. During two of these years (January 1977 and 1979), however, the difference was reversed, with 3–5 times more birds counted in Louisiana than Arkansas. Appendix 2 indicates that these were the two coldest winters during the last 31 yr as measured by our temperature criteria. This suggests a "threshold" response to temperature acting via ice cover on wetlands, rather than a gradual shift in response to increased heat loss, and is more consistent with measuring winter cold as cumulative December–January days with temperatures less than °C.

The second part of our analysis showed that (1) winter precipitation influences Mallard winter distribution, (2) the proportion of recoveries occurring in the MAV increases during wet years in the MAV, and (3) the response among young birds is particularly strong (Table 4). These results are consistent with intuitive ideas about the effect of precipitation on wetland habitat conditions, with Fretwell's

model of habitat suitability, and with recent evidence that flooded bottomland winter habitat may influence Mallard fitness via effects on subsequent reproduction (Heitmeyer and Fredrickson 1981). Heitmeyer and Fredrickson (1981) also considered winter precipitation to be the best available measure of the number and quality of seasonally flooded, bottomland, hardwood habitats. The strength of the response by young Mallards to wet conditions in the MAV suggests that they may be more flexible in selecting winter habitat than are adults, a result consistent with other work on Mallards (Nichols and Hines in prep.) and with suggestions about other species (Gauthreaux 1978).

The last part of our analysis provided evidence that young Mallards winter in the MAV with greater probability during years of low than high population size. If the MAV, in general, constitutes preferred winter habitat, and if habitat suitability is influenced by the density of conspecifics, then the findings are again consistent with one of the models of Fretwell and Lucas (1970) and Fretwell (1972). There was evidence, however, that adult birds wintered in the MAV in greater proportions when population size was high. We speculate that the age-specific response to population size results from differences in competitive ability. As a normally preferred habitat becomes less suitable because of increasing density of conspecifics, individuals with the lowest competitive ability should be the most responsive. Presumably, young Mallards do not compete equally with adults.

In sum, the evidence presented here strengthens Bellrose and Crompton's (1970) concept of "flexible homing to specific localities" by Mallards as a response to winter temperature, precipitation, and population size. Finally, we note that results of the precipitation analysis also support decisions made in recent years to increase wetland preservation efforts in the MAV (Ladd 1978) to offset the massive flood control and drainage efforts that, to date, have cleared more than 80% of the bottomland forests and wetlands within the MAV (Forsythe and Gard 1980).

It is difficult to draw inferences about the generality of such year-to-year variation in the habitat selection of avian migrants. Variation among years in precipitation and temperature is associated with breeding-site selection in some wetland species (Smith 1970, Ogden et al.

1980), and a number of arid-land Australian birds respond dramatically to precipitation (e.g. Keast 1959). Although many species are thought to return to the same wintering grounds each year (see Gauthreaux 1978: 37), certain boreal species exhibit eruptive movements during fall and winter, presumably in response to food supplies (Lack 1954: 227, Bock and Lepthien 1976). We are not aware of other work showing variation among years in wintering-ground locations associated with climatic variables. Mean temperature and precipitation conditions over years, however, are associated with winter habitat suitability in some species (Ketterson and Nolan 1976, 1979; Geldenhuys 1981), and extreme climatic conditions within years can also cause local movements during winter (e.g. Bennett and Bolen 1978, Sayler and Afton 1981).

The age-specific responses of Mallards to precipitation and density are consistent with a growing body of literature on the age- and sex-specificity of winter distributions (Ketterson and Nolan 1976, 1979; Ralph 1977; Gauthreaux 1978; Nichols and Haramis 1980; Myers 1981; Sayler and Afton 1981; Dolbeer 1982). The consistency of these relationships suggests that it may be appropriate to incorporate age- and sex-specificity in future applications of habitat distribution models. Fretwell and Lucas (1970) extended their basic model to include territorial behavior by defining apparent habitat suitability, T_i , as $T_i = S[1 - t(d_i)]$, where $t(d_i)$ is an increasing function of density and $0 \leq t(d_i) \leq 1$. Fretwell (1972) later suggested that this model could adequately represent dominance behavior as well. One hypothesis for the age-specificity of Mallard wintering patterns might involve behavioral dominance of adults over young. In this case, we could define age-specific t -functions and densities. If y and a denote young and adults, respectively, then adult dominance suggests that $t_a(d_{i,a}^*, d_{i,y}^*) < t_y(d_{i,a}^*, d_{i,y}^*)$, where $d_{i,a}^*$ and $d_{i,y}^*$ denote fixed densities of adult and young birds, and

$$\frac{\partial t_y}{\partial d_{i,a}} > \frac{\partial t_a}{\partial d_{i,a}}, \quad \frac{\partial t_y}{\partial d_{i,y}} > \frac{\partial t_a}{\partial d_{i,y}}.$$

These inequalities express the hypotheses that specified densities of birds affect habitat suitability to a greater extent for young birds than adults and that both adults and young are affected to a greater extent by adult densities than by densities of young birds.

Other interpretations of the observed age-specificity might involve differences between the ages in resource-acquiring ability or in physiological tolerance of climatic stress (see related discussions in Ketterson and Nolan 1976, Ketterson and King 1977, Nichols and Haramis 1980, Sayler and Afton 1981). The first hypothesis could be modeled via age-specific f -functions (equation 1) and densities. In fact, substitution of f for t in the above inequalities would be consistent with the hypothesis that adults are better at exploiting resources used by both age classes than are young. The second hypothesis could be modeled via age-specific g -functions, h -functions, and B_{ij} . Although our analysis was not directed at hypotheses of age- or sex-specificity, the above framework may prove useful in further investigations of this sort.

Last, we note three other factors that may be important to future models of winter habitat selection. First, it has been claimed that "the advantage of being able to return to a familiar wintering ground is obvious" (Ralph and Mewaldt 1975: 704), and it may be that familiarity is an important determinant of habitat suitability. Second, we might consider a "cost of migration" (e.g. Ketterson and Nolan 1976), with survival probabilities inversely related to migration distances, like the "search cost," incorporated explicitly into the optimal emigration threshold models of Parker and Stuart (1976). Finally, as Fretwell and Lucas (1970: 34) pointed out, animals must rely on environmental cues in order to assess habitats, and such cues may not be perfectly correlated with suitability. Not only is knowledge of the suitability of the habitat in which a bird is located imperfect, but the suitability of distant habitats is certainly not known. These sources of uncertainty can be dealt with using stochastic models, such as those studied by Williams and Nichols (in press; see Janetos 1980 for a special case), and it will be interesting to learn how implications of these models differ from those of their deterministic counterparts.

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APPENDIX 1. Sources of climatic data.

State and climatic division	Reporting station (alternate) ^a	Map symbol ^b	Temperature ^c	Precipitation ^c
Arkansas				
Northeast	Jonesboro (Paragould)	1		XX
East central	Brinkley (Marianna)	2		XX
Southeast	Dumas (Portland)	3		XX
Illinois				
West	Rushville (Quincy FAA AP)	4	XX	
West southwest	Alton Dam (Jerseyville)	5	XX	
Southwest	Carbondale Sewage Plant (Du Quoin)	6	XX	
Iowa				
Southwest	Red Oak (Glenwood)	7	XX	
Kansas				
Northeast	Atchison (Troy)	8	XX	
South central	Kingman (Pratt)	9	XX	
Southeast	Chanute FAA AP	10	XX	
Kentucky				
Western	Paducah Sewage Plant (Paducah FAA AP)	11	XX	
Louisiana				
Northeast	Tallulah (Winnsboro)	12		XX
Central	Melville (Grand Coteau)	13		XX
Mississippi				
Upper delta	Clarksdale	14		XX
Lower delta	Belzoni (Moorhead)	15		XX
Missouri				
Northeast prairie	Hannibal Waterworks	16	XX	
West central plains	Clinton (Appleton City)	17	XX	
West Ozarks	Ozark Beach (Seligman)	18	XX	
Bootheel	Poplar Bluff (Wappapello Dam)	19		XX
Nebraska				
Central	Kearney (Ravenna)	20	XX	
East central	Fremont (Blair)	21	XX	
Southeast	Falls City	22	XX	
South Dakota				
Southeast	Pickstown	23	XX	
Tennessee				
Western	Dyersburg FAA AP (Covington)	24		XX
Middle	Springfield Experiment Station	25	XX	

^a Alternative locations provided temperature and precipitation data when primary stations had missing values.

^b See Fig. 1.

^c NOAA (1950-1981).

APPENDIX 2. Summary of winter-temperature, precipitation, and Mallard population-size data.

Year ^a	Temperature ^b		Cumulative precipitation (cm) ^c		Winter population count (thousands) ^d
	Mean °C	Days < 0°C	Mean	Mean deviation ^c	
1950	-1.4	28.3 (C)	38.40	4.27	6,146.7
1951	-0.3	24.6 (W)	39.75	5.61	4,604.0 (L)
1952	0.7 (W)	26.5	30.66	-3.51	7,003.9
1953	-0.2	26.5	33.53	-0.61	7,511.0
1954	0.4 (W)	27.0	23.80	-10.34 (D)	7,380.6
1955	-2.0	28.6 (C)	22.00	-12.14 (D)	9,211.2 (H)
1956	-0.7	26.1	37.77	3.61	9,505.7 (H)
1957	1.3 (W)	24.9 (W)	49.25	15.09 (W)	10,630.9 (H)
1958	-2.7	28.6 (C)	23.98	-10.16 (D)	9,427.4 (H)
1959	0.9 (W)	23.9 (W)	29.79	-4.34	7,366.8
1960	-1.6	28.9 (C)	27.28	-6.86	7,275.8
1961	-3.3 (C)	27.6	56.77	22.61 (W)	5,629.3 (L)
1962	-3.6 (C)	27.5	17.09	-17.07 (D)	7,267.7
1963	-2.1	28.4 (C)	27.43	-6.71	8,707.5 (H)
1964	-0.9	26.1	31.98	-2.16	6,568.8
1965	-0.1	25.0 (W)	24.77	-9.40	7,707.4
1966	-0.1	26.7	23.34	-10.80 (D)	7,783.9
1967	-0.8	25.3 (W)	38.30	4.14	6,652.8
1968	-2.5	27.4	42.75	8.61	5,408.5 (L)
1969	-2.9 (C)	28.9 (C)	33.38	-0.79	8,889.6 (H)
1970	-0.9	27.4	24.61	-9.53	8,630.1 (H)
1971	-0.1	24.1 (W)	37.77	3.63	8,973.3 (H)
1972	-2.1	26.8	53.95	19.79 (W)	7,219.6
1973	-1.8	25.9 (W)	61.65	27.51 (W)	5,294.3 (L)
1974	0.1 (W)	27.1	36.07	1.93	6,220.7
1975	-0.5	27.8	29.62	-4.55	7,614.1
1976	-5.2 (C)	30.6 (C)	22.63	-11.51 (D)	6,978.2
1977	-4.6 (C)	27.8	38.35	4.22	6,522.7
1978	-5.2 (C)	29.5 (C)	48.11	13.97 (W)	6,128.7
1979	0.3 (W)	26.9	34.29	0.15	5,841.3 (L)
1980	-0.1	27.3	19.51	-14.66 (D)	6,727.8

^a Corresponds to November and December of calendar year *t* and January of year *t* + 1 (i.e. data for 1970 correspond to the winter of 1970-1971).

^b Statistics are December-January means for the following reporting stations: 4-11, 16-18, 20-23, 25 (see Fig. 1, Appendix 1). Extreme warm and cold winters are denoted (W) and (C), respectively.

^c November-January data for MAV reporting stations: 1-3, 12-15, 19, 24 (see Fig. 1, Appendix 1). Mean deviation represents the mean, over all stations, of the difference between the cumulative precipitation for year *t* and the 31-yr average for each station. Extreme wet and dry winters are denoted (W) and (D), respectively.

^d Mallard population data are from the annual winter (January) waterfowl survey (e.g. Novara et al. 1981; data from Migratory Bird Management Office files). Extreme high and low Mallard population sizes are denoted (H) and (L), respectively.