

PARTIAL MIGRATION AND DIFFERENTIAL WINTER DISTRIBUTION OF HOUSE FINCHES IN THE EASTERN UNITED STATES¹

JAMES R. BELTHOFF AND SIDNEY A. GAUTHREUX, JR.
Department of Biological Sciences, Clemson University, Clemson, SC 29634

Abstract. Three hypotheses that attempt to explain latitudinal sex ratio variation on wintering grounds are: 1) the behavioral dominance hypothesis, 2) the arrival time/sexual selection hypothesis, and 3) the body size/physiological hypothesis. Testing these hypotheses is difficult because many predictions are not mutually exclusive. By examining migratory behavior and winter distributions of House Finches (*Carpodacus mexicanus*), a species in which females dominate males despite their smaller size, we controlled for confounding effects of body size on behavioral dominance. We examined U.S. Fish and Wildlife Service records of House Finches banded throughout the eastern United States following their introduction in 1940. These data suggest the evolution of partial migration among the introduced population of finches, with a trend in recent years (1975-1989) for females to migrate farther than males. The proportion of males on wintering grounds varied significantly and consistently with latitude in the East. Sex ratios north of 38°N latitude were male-biased, while those south of this were female-biased. Similar patterns were not apparent among western House Finches during winter or in the eastern population during the breeding season. Of the three hypotheses, only the body size hypothesis correctly predicts the pattern observed among wintering finches. Therefore, different energetic constraints facing male and female House Finches, perhaps related to body size, may be influencing migratory behavior and winter distributions.

Key words: *Latitudinal sex ratio variation; differential migration; House Finch; Carpodacus mexicanus; winter distribution.*

INTRODUCTION

In recent years biologists have questioned why some individuals of a species undertake long migrations while others do not migrate (partial migration), and why some individuals migrate much greater distances (differential migration) than others (Gauthreaux 1978, 1982; Myers 1981; Ketterson and Nolan 1983; Berthold 1984). Such migratory behaviors are thought to give rise to marked segregation of sex and age classes on the wintering grounds. Geographic differences in winter distribution among age and sex classes in migrants is said to be nearly ubiquitous (Kerlinger and Lein 1986; but see Perdeck and Clason 1983; Diefenbach et al. 1988, 1990).

At least three hypotheses attempt to explain patterns of latitudinal variation in winter sex ratio among birds (reviewed by Gauthreaux 1982, Ketterson and Nolan 1983, Berthold 1984). The body-size or physiological hypothesis predicts

that individuals of the larger sex winter farther north (i.e., in harsher climates) because of their ability to fast for longer time periods and their greater tolerance of cold temperatures (Ketterson and Nolan 1976, 1979; Ketterson and King 1977). The behavioral dominance hypothesis (Lack 1944; Kalela 1954; Balph 1975; Gauthreaux 1978, 1982) predicts that intersexual competition forces members of the subordinate sex to migrate farther, resulting in members of the dominant sex (i.e., the sex that wins encounters with and obtains priority of access to resources) wintering north of the subordinate sex. Finally, the arrival-time hypothesis (King et al. 1965 and references therein, Myers 1981) suggests that intrasexual selection drives individuals of the sex that establishes breeding territories to winter closer to the breeding range. Such individuals may benefit by early arrival on breeding grounds, shorter migration distances, and initial choice of breeding areas. Each hypothesis assumes some cost to migrating longer distances.

Testing these hypotheses has proven difficult because many predictions are not mutually exclusive (Myers 1981, Ketterson and Nolan 1983,

¹ Received 24 August 1990. Final acceptance 23 January 1991.

Kerlinger and Lein 1986). Among passerine birds, for example, males are generally larger, and they also exhibit dominance over females. Thus, both the body size and behavioral dominance hypotheses predict males wintering north of females. Among *Carpodacus* finches, however, dominance patterns are reversed so that females dominate males (Thompson 1960a; Samson 1977; Brown and Brown 1988; Belthoff and Gauthreaux, unpublished data). Study of winter distributions of these finches offers a critical test of (at least) the behavioral dominance hypothesis. This hypothesis predicts that among North American *Carpodacus* finches, males winter south of females. This is the reverse of typical passerine patterns. In contrast to many species in this genus, young male House Finches (*C. mexicanus*) develop red plumage in their first autumn (Michener and Michener 1931, Yunick 1987, Hill 1990). Therefore, sex classes are easily distinguishable, making House Finches ideal for examining hypotheses for the evolution of latitudinal sex ratio variation.

House Finches are seed-eating, gregarious birds that breed in semi-colonial assemblages during summer, particularly in areas inhabited by humans (Thompson 1960a, 1960b). In winter, flocks of finches generally wander between food sources. Throughout western North America, House Finches are resident from southern British Columbia south to the Mexican border. Individuals of this species were introduced into the New York City area from ancestral southern California populations ca. 1940 (Elliot and Arbib 1953, Munding 1975, Aldrich and Weske 1978) and since have spread north to southern Ontario, west to Illinois, and south to Alabama. In contrast to western populations where individuals show little or no latitudinal migration (Bergtold 1913, Thompson 1960b), House Finches in the East migrate frequently (Stewart 1989, 1990; Belthoff et al. 1990). In South Carolina, for example, large influxes of migrant finches appear during autumn and winter, while some locally breeding individuals remain throughout the year (Belthoff et al. 1990).

Our objective in the present study was to describe the migratory behavior and wintering distribution of male and female House Finches in the eastern United States. Using this information, we evaluated competing hypotheses for the evolution of latitudinal sex ratio variation in House Finches.

MATERIALS AND METHODS

We obtained banding summary data and recovery records for eastern House Finches from U.S. Fish and Wildlife Service's (USFWS) Bird Banding Laboratory (Laurel, MD). From a total of 2,307 recoveries (either recaptured by banders or found dead), we determined recovery distances for all *direct* recoveries, which we defined as those where one migratory season occurred between banding and recovery. To determine *direct* recoveries, we used birds originally banded during winter (November through February) and recaptured the following spring or summer on their breeding grounds (15 April through August), and birds originally banded during the breeding season and recaptured the following winter. *Indirect* recoveries involved birds captured in alternate seasons but separated by greater than one migratory season. We assumed that birds captured during the breeding season were on or near their breeding grounds and that birds captured during the winter season were on their wintering grounds. We compared the mean number of 10' blocks traversed by males and females using the Mann-Whitney *U*-test (Zar 1984). The frequency with which males and females leave the breeding grounds to winter was compared using a 2×2 contingency table and Chi-square test (Zar 1984). Distance moved between banding and recovery, measured in number of 10' blocks (six 10' blocks per degree of latitude) is given as mean \pm one standard error throughout the paper. All tests were two-tailed with rejection levels set at $\alpha = 0.05$.

To determine the timing of House Finch migratory movements we reviewed *direct* recoveries for which the time interval between banding and recapture was short. To determine the estimated arrival dates of migrant finches in South Carolina during autumn, we also recorded House Finch sightings along weekly census routes during 1980–1988. Our census route, approximately 20 km in length, encompasses mainly rural and agricultural areas of Anderson County, SC. Annual census efforts typically began in late summer–early autumn and continued through the beginning of winter. Because there is little or no breeding by House Finches along this route (pers. observ.), individuals represent migrants from the north and perhaps some individuals that have moved from local breeding grounds.

To determine if male and female House Finch-

es were differentially distributed during winter in the East (USFWS Regions 100–299), we calculated the total number of males and females banded by latitude (we included latitudes where >300 finches were banded). We excluded birds of unknown sex. The percentage of individuals in the banding data sexed as unknowns was low, averaging 5.2%, ranging from 1.2% at 43°N to 9.8% at 40°N latitude. We then evaluated the null hypothesis that proportions of males and females are the same among banded individuals at each degree of latitude using the log-likelihood ratio for contingency tables and associated *G*-statistic (Zar 1984). We make two assumptions with this approach. First, that males and females had an equal probability of being captured by banders in the field. Even if a sex bias in capture probability were present, however, we believe it unlikely that this bias would differ with latitude. Our analysis, therefore, should have detected any latitudinal variation in sex ratio that may have been present. Our second assumption is that banders showed no bias in applying bands to birds once captured; that is, regardless of the sex ratio of captured birds, banders were as likely to band males as they were to band females. Our analysis also used data pooled over many years (~30). If in some years one sex class moves and in others they do not, then, when such years are combined, this tends to minimize latitudinal segregation of the sexes. Therefore, our analysis is conservative because it reduces the probability of detecting significant patterns. During the period between 1 October and 31 December, finches with fully pneumatized skulls, both adults and young of the year, are assigned to the unknown (U) age class by banders. This precludes accurate information on age biased migration or patterns of winter distribution. We therefore pooled all age classes for analysis of winter distribution patterns.

We analyzed winter sex ratios throughout western North America (USFWS Regions 300–645) similarly. For western House Finches, only 30°N and 43°N latitude included fewer than 500 finches banded. To confirm that any pattern exhibited by eastern finches during winter did not also occur during the breeding season, we calculated sex ratios of adult (second year or older) House Finches between May and August for the years 1955–1989. Because they have only recently colonized southern latitudes for breed-

ing, latitudes south of 38°N each represent fewer than 150 finches.

To determine relative body sizes of male and female House Finches, we sampled 192 males and 292 females on our study area, located near Clemson, Pickens County, South Carolina (between January–February and October–December 1989). To obtain an index of body size, JRB measured the relaxed wing chord length, tarsus length, bill length (exposed culmen), medial rectrix length (all to the nearest 0.5 mm), and body mass (to the nearest 0.5 g with a spring-loaded Pesola scale) for each finch captured. We compared the effect of sex on these five measures using multivariate analysis of variance (MANOVA). If significant effects existed, we estimated means (least squares means) and compared these means using *t*-tests.

RESULTS

TIMING OF MIGRATION

There are few records that indicate the precise timing of autumn migration. Available recoveries suggest that House Finches are moving generally during October and perhaps very early November. For example, male #880-85561 was banded in New Jersey (40°10'N latitude) on 3 October 1976 and later recovered 20' south in Pennsylvania (39°50'N) on 5 November. Two additional recoveries demonstrate slightly longer autumn movements but provide less precise information on their timing. Male #2051-47722, banded in New York (43°10'N) on 11 September 1986, moved south in New York one degree of latitude (42°10'N) by 27 December. Female #2020-06903, banded in Michigan (42°20'N) on 9 October 1985, was recovered in Indiana (40°30'N) on 17 December, almost two degrees of latitude south.

Examining initial sighting records also provides an indication of the timing of autumn movements for birds wintering in South Carolina. Initial arrival dates for House Finches wintering along our weekly census route indicate that many migrants have arrived on their wintering grounds by November of each year (Table 1).

Northward migratory movements from wintering areas occur during March and early April. The following records illustrate the movement: 1) an AHY male (#570-49720) banded 5 April 1980 in Virginia (37°50'N) was recovered 10 days

TABLE 1. Timing of initial House Finch sightings in areas throughout Anderson County, South Carolina (1980–1988) during weekly censusing.

Year	Arrival date	Location
1980	2 November	Little Beaver Dam
1981	15 November	Little Beaver Dam
1982	14 November	Townville
1983	27 November	Big Beaver Dam
1984	11 November	Little Beaver Dam
1985	27 October	Little Beaver Dam
1986	12 November	Townville
1987	8 November	Little Beaver Dam
1988	13 November	Little Beaver Dam

later (14 April) in New Jersey (39°30'N), representing a movement of almost 2° of latitude, 2) a female (#770-37722) banded 19 March 1981 in Virginia (37°30'N) migrated to New York (40°40'N) by 14 April, and 3) another female (#2000-72546), banded on 8 March 1985 in Maryland (38°50'N), moved to New York (40°40'N) by 14 April.

DISTANCE OF MIGRATION

Between 1952–1988, there were 333 direct recoveries of House Finches on breeding grounds and wintering areas. Overall, the mean number of 10' blocks traversed between breeding grounds and wintering areas (i.e., change in latitude) was 5.9 ± 0.41 . Females ($n = 153$) moved an average of 6.0 ± 0.60 10' blocks (maximum = 37), while males ($n = 180$) averaged 5.6 ± 0.56 (maximum = 41) (Fig. 1). The difference between the sexes was not significant (normal approximation to Mann-Whitney U -test, $U = 14,940$, $Z = 1.347$, $P > 0.177$). Males remained at the same 10' of latitude for breeding and wintering (i.e., showed no migration) in 27.8% of recoveries, and 20.9% of recovered females did not migrate from breeding areas. We failed to reject the null hypothesis that males and females did not differ in the tendency to stay in the breeding area ($\chi^2 = 1.181$, $df = 1$, $0.10 < P < 0.25$). If foreign recoveries (i.e., those north or south of the 10' block of banding) represent random wandering rather than directional migration, one might expect about the same number of recoveries north and south of the breeding location to occur during winter. Only 16 recoveries (4.8%; Fig. 1) occurred north of the breeding location. The remaining recoveries are south of the breeding location and would

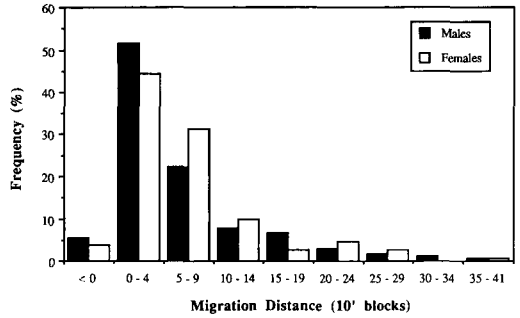


FIGURE 1. Frequency histogram of House Finch direct recovery distances from USFWS data. Sample sizes: Females $n = 153$; males $n = 180$.

suggest directional migration by House Finches (75.2% and 66.7% for females and males, respectively, excluding birds recovered at the same latitude). When we excluded residents and northward migrants (i.e., those with zeros of negative value for migration distance) and pooled data by five-year periods, median migration distance for males and females increased with time. Median migration distances were either equivalent or slightly greater for females until 1964, but the number of direct recoveries was generally small (Fig. 2). Males moved slightly farther than females from 1965–1974. After this time, however, the median distance moved by females was greater than for males in each of the remaining time periods.

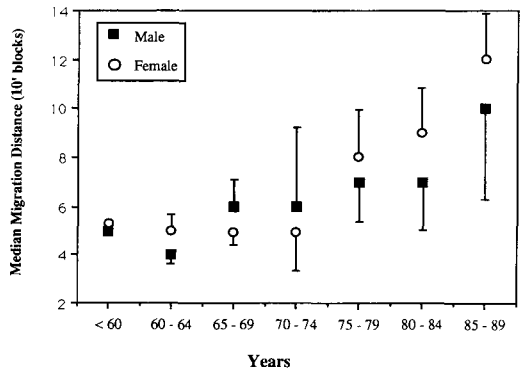


FIGURE 2. Median (± 1 SE) migration distance (i.e., direct recoveries) of male and female House Finches by half decade. Residents and northward migrants have been excluded. Sample sizes are 1, 6, 36, 13, 23, 32, and 9 for males and 1, 7, 39, 9, 19, 31, and 9 for females, respectively. Note: median migration distance for males and females is similar in the first time period (<60).

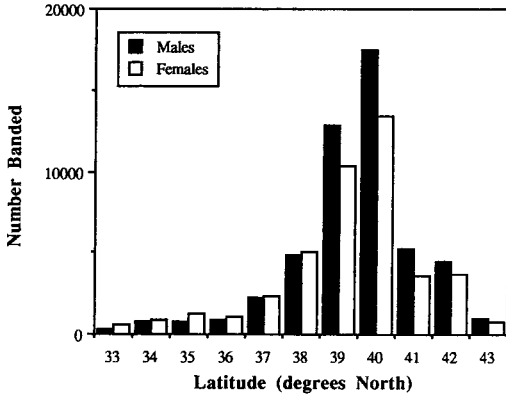


FIGURE 3. Number of male and female House Finches banded during winter (November–February) by latitude in the eastern United States (USFWS Regions 100–299) between 1955–1987.

Indirect recoveries ($n = 266$) included 169 males and 97 females. The mean number of 10' blocks between breeding grounds and wintering areas was 4.6 ± 0.50 . There was no significant difference between males and females (4.5 ± 0.51 and 4.9 ± 1.05 10' blocks, respectively; Mann-Whitney U -test, $U = 8,550.5$, $Z = 0.599$, $P > 0.50$). As with direct recoveries, we observed no significant difference between the sexes in the tendency to remain on breeding grounds (males = 35.1%; females = 32.6%).

LATITUDINAL SEX RATIO VARIATION

During November–February (1955–1987), 50,743 male and 42,912 female House Finches were banded on their wintering grounds in the eastern U.S. These finches were banded between

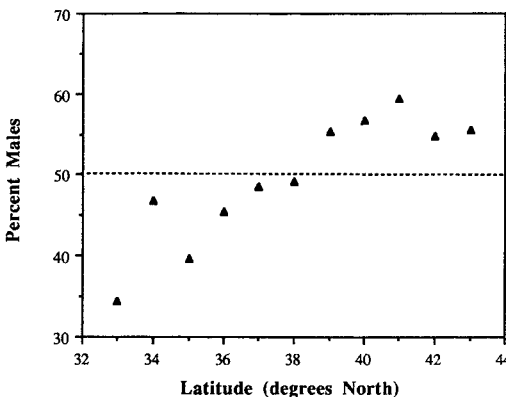


FIGURE 4. Percentage of male House Finches banded on wintering grounds by latitude in the eastern United States. Sample sizes are represented in Figure 3.

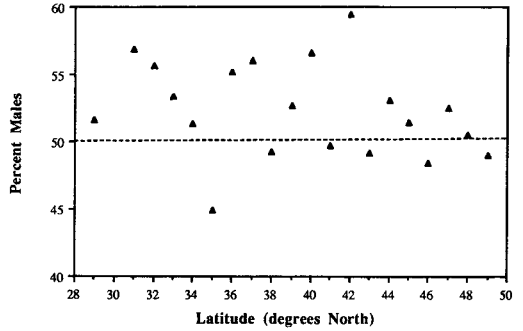


FIGURE 5. Percentage of male House Finches banded on wintering grounds (November–February) in western North America (USFWS Regions 300–644) between 1955–1988. Finches of known sex banded by latitude (29° thru 49°) are 684, 141, 1117, 6252, 1929, 5997, 2185, 732, 6918, 3497, 3879, 4329, 2929, 1981, 319, 2630, 4692, 750, 1177, 1117, and 488, respectively.

33°N and 43°N latitudes (Fig. 3), with the greatest number of finches banded at 39°N and 40°N latitude. The proportion of males (i.e., sex ratio) varied significantly with latitude ($G = 164,353$, $df = 10$, $P < 0.001$; Fig. 4). There was also a significant positive correlation between latitude and proportion of males (Spearman's rank correlation; $r_s = 0.873$, $P < 0.002$). The proportion of males was greatest at northern latitudes (those $> 38^\circ\text{N}$), while females outnumbered males at all latitudes south of 39°N. These data indicate differential winter distribution between the sexes, with female House Finches wintering south of males. We did not observe similar sex ratio

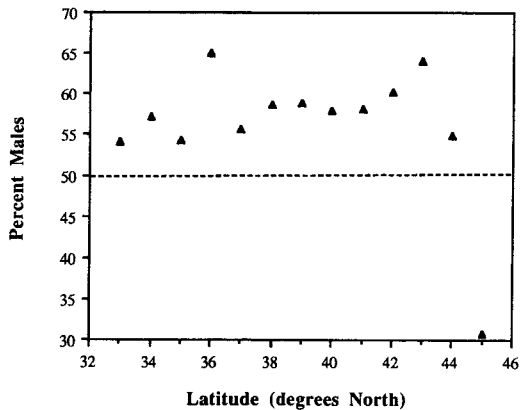


FIGURE 6. Percentage of male House Finches (adults only) banded on breeding ranges in the eastern U.S. during summer (May–August) from 1955–1989. Finches of known sex banded by latitude (33° thru 45°) are 59, 14, 127, 40, 140, 1227, 3908, 14171, 6507, 6065, 2474, 62, and 78, respectively.

TABLE 2. Mean body size measures (least squares means \pm SE) for male ($n = 192$) and female ($n = 292$) House Finches during autumn and winter in Pickens Co., South Carolina.

Character	Males		Females		P-value ¹
	$\bar{x} \pm$ SE	Range	$\bar{x} \pm$ SE	Range	
Wing length (mm)	78.3 \pm 0.12	74–82	76.0 \pm 0.10	72–81	<0.0001
Tarsus (mm)	20.2 \pm 0.04	18–21	20.1 \pm 0.03	18–22	>0.077
Bill (mm)	9.9 \pm 0.03	9–11	9.8 \pm 0.02	9–11	>0.358
Tail (mm)	58.0 \pm 0.14	51–62	56.7 \pm 0.11	50–62	<0.0001
Mass (g)	21.0 \pm 0.09	17–24	20.7 \pm 0.08	17–25	<0.015

¹ Significance levels determined using pairwise t-tests. See text for results of MANOVA.

variation in either the western North American population of House Finches during winter (Fig. 5) or during the breeding season in the East (Fig. 6).

HOUSE FINCH MORPHOMETRICS

Mean body size of male and female House Finches differed significantly (MANOVA, Wilk's Lambda = 0.69812, $F_{5,478} = 41.34$, $P < 0.001$). Males had significantly greater mean wing lengths, tail lengths and mass than females (Table 2). Mean bill length did not differ significantly between the sexes ($P > 0.358$). Males also had slightly longer tarsi, but the difference only approached significance ($P > 0.077$; Table 2). Aldrich (1982) also found that male House Finches had significantly longer wings and tails than females. Thus, because of significantly greater wing length, tail length, and mass, male House Finches can be considered to have larger body size than females.

DISCUSSION

Since being introduced into the eastern United States, House Finch populations have experienced rapid evolutionary changes, presumably from the selective forces of different climatic and environmental conditions, from founder effects, or both. The new population has developed shorter wings, tails, tarsi, and toes, and longer bills than ancestral California populations (Aldrich and Weske 1978, Aldrich 1982). It appears that newly encountered selective pressures have promoted the evolution of migratory behavior among eastern House Finches as well, and this behavior may be related to climatic factors (e.g., lower ambient temperatures, greater humidity, more prolonged winter). House Finches are ideally adapted to warm, arid environments (Salt 1952), and this seems to have prevented members of this species from exploiting cooler, more humid areas in the past. Dawson et al. (1983) showed that members of the introduced eastern

population exhibit less cold tolerance than populations in Colorado, but greater tolerance than California populations, and speculated that eastern populations are in the midst of evolving increased cold tolerance. Sprenkle and Blem (1984) believe that without access to artificial food sources (i.e., feeders). House Finches in the newly colonized part of the range have difficulty surviving harsh mid-winter conditions. They suggest that decreasing numbers of House Finches visiting feeders in Virginia during individual winters reflect large die-offs. Although winter mortality probably accounts for a part of this decrease, an increased tendency to migrate during this time may also account for some decreases in numbers of finches.

Although many House Finches migrate from breeding grounds during autumn, some individuals remain throughout the winter. Thus, House Finches in the eastern U.S. are best described as partial migrants (Lack 1944, Gauthreaux 1982). We could not reject the null hypothesis that females and males migrate similar distances. However, the ability of our statistical test to reject a false null hypothesis (i.e., power) in this case was undoubtedly low. We calculated the power for a comparable t-test to be near 0.14 (Cohen 1988). Power curves for Mann-Whitney U -tests were not available, but this suggests an extremely low probability of rejection even if the null hypothesis were false. Despite our failure to reject this null hypothesis, three additional factors suggest that the winter sex ratio variation we observed may have been influenced by differential migration. First, over the past one and one-half decades, before which no pattern was apparent, females migrated longer distances than males. Such data suggest that the winter pattern we observed may become increasingly apparent in future years. Next, clinal variation in winter sex ratio was not present among western House Finches for the same years it occurred in the East. Therefore,

latitudinal migration, which reportedly is rare in western House Finches, may be driving winter segregation patterns. Finally, because sex ratios in the East were male biased during the breeding season at all latitudes except 45°N (the northernmost sample), clinal sex ratio variation was absent in summer. Thus, female-biased sex ratios at southern latitudes during winter imply that females moved south more often or farther than males, or males suffered greater mortality than females at southern, but not northern latitudes. We believe the latter is unlikely and that the migratory pattern exhibited by House Finches is similar to that of many other migrants (both partial migrants and those showing differential migration), where females migrate longer distances to winter south of males (e.g., Nice 1933, Lack 1944, Bellrose et al. 1961, Ketterson and Nolan 1976, Nichols and Haramis 1980, Dolbeer 1982, Mearns 1982, Morton 1984, Village 1985, Prescott and Middleton 1990).

The banding data reflect a clear, significant pattern of clinal latitudinal sex ratio variation among wintering House Finches in the eastern U.S., with males wintering north of females. Both the arrival time and behavioral dominance hypotheses are rejected as explanations for distribution patterns of sexes on the wintering grounds. The arrival time or sexual selection hypothesis implies that a species' social system is an important predictor of winter sexual segregation and requires knowledge of schedules of arrival on the breeding grounds for members of each sex. Arrival schedules are not available for male and female House Finches, and it would be difficult to gather such data because of overlap between residents and migrants. Thus, we cannot evaluate this hypothesis directly with the available data. However, Myers (1981) suggests that selective pressures on the sex that establishes territories should lead both to individuals of that sex leaving sooner and wintering farther north. If so, winter sexual segregation should be widespread among migrant species in which one sex defends a breeding territory (Myers 1981). The mating system of House Finches and other *Carpodacus* finches is characterized by males that do not defend breeding territories, and they may or may not defend the immediate area surrounding the nest site (Thompson 1960a, 1960b; Samson 1976). Instead, females choose the nesting site (territory) and may take over the duties of its defense entirely (Thompson 1960a, 1960b; Samson 1976). Thus, if the immediate area surround-

ing a nest site is considered the territory, this hypothesis predicts that females (because they are the sex that predominantly competes for nest sites) should both winter farther north and arrive on breeding grounds earlier than males (see also Prescott and Middleton (1990) for predictions pertaining to American Goldfinches, *Carduelis tristis*). Assuming there is no advantage to males of early arrival, supported by their lack of territorial defense, the observed pattern of winter distributions is not consistent with predictions of the arrival time hypothesis.

Because members of the dominant sex obtain priority of access to critical winter resources, the behavioral dominance hypothesis predicts that subordinate members of the population are forced to migrate, or extend their migration in search of available resources (Gauthreaux 1978). Because dominant females winter south of subordinate males, we reject the behavioral dominance hypothesis as an explanation of latitudinal variation in sex ratio among House Finches in the eastern U.S.

Why might it be that females leave and males stay despite the fact that females dominate males? The answer to this may be related to physiological constraints and the thermoregulatory consequences of body size. House Finches are sexually dimorphic with respect to body size, i.e., male House Finches are, on average, larger than females (Aldrich and Weske 1978, Aldrich 1982, this study). The fact that males winter farther north than females is consistent with the body size hypothesis and suggests that differential winter locations may be related to bioenergetic constraints (Ketterson and Nolan 1976). The proposed mechanism for differential movements is that smaller females cannot endure cold temperatures and fasting to the extent that larger males can (a consequence of the "fasting-endurance hypothesis"; Calder 1974), thus, females are forced to move south in search of milder climates and available resources (Ketterson and Nolan 1983). We do not know if the slight but significant differences in body size between male and female House Finches could influence their thermal biology, but evidence that smaller females may not be able to survive periods of harsh weather as well as males is available for several species of birds (e.g., Mourning Doves, *Zenaidura macroura*, Ivacic and Labisky 1973; White-crowned Sparrows, *Zonotrichia leucophrys*, Ketterson and King 1977; Canvasbacks, *Aythya valisineria*, Nichols and Haramis 1980; but see Stuebe

and Ketterson 1982). Dolbeer (1982) also supported the physiological hypothesis after demonstrating that increased sexual dimorphism among blackbird species was correlated with increased sexual segregation on wintering grounds.

Predictions of the body size hypothesis are plausible only if individuals encounter cold temperatures or run the risk of prolonged fasting (Ketterson and King 1977, Myers 1981). Cold temperatures and fasting ability are certainly important considerations for House Finches in the eastern U.S. Inclement weather is common, and snow cover may limit the availability of resources. In fact, mortality of House Finches during severe winter weather has been reported as far south as Virginia and North Carolina (Sprenkle and Blem 1985, Stewart 1988). Thus, selective pressures associated with cold temperatures, limited fasting abilities and other physiological constraints could force female House Finches to leave nesting grounds more often and migrate farther than males, even though females dominate males.

Our approach to evaluating these competing hypotheses is straightforward, but we echo the sentiment among biologists that one or more of the proposed mechanisms may be operating at any given time to produce patterns of sexual segregation on wintering areas (Myers 1981, Ketterson and Nolan 1983, Kerlinger and Lein 1986). Our study is uniquely important because we control for confounding effects of body size on behavioral dominance. By examining a species in which females dominate males despite their smaller size, we conducted a critical test of the behavioral dominance and body size hypotheses. We conclude that behavioral dominance is not responsible for patterns of partial migration and does not explain latitudinal variation in winter sex ratios among House Finches in the eastern U.S. Different physiological constraints facing males and females, perhaps related to body size, remain a tenable explanation for winter segregation of sexes.

ACKNOWLEDGMENTS

We thank the many banders who contributed data to the USFWS Bird Banding Laboratory; without their efforts this report could not have been compiled. J. Tautin, D. Bystrak, and K. Klimkiewicz at the Bird Banding Laboratory were extremely helpful in providing banding data and other information for which we are grateful. J. Buckalew, E. Cox, M. Doscher, A. Fletcher, R. McKinney, and F. Scott kindly allowed us to report their unpublished House Finch banding data.

Our research has been funded by Sigma Xi, The Scientific Research Society; the Eastern Bird Banding Association; and a Paul A. Stewart Award from The Wilson Ornithological Society. We thank members of the behavioral ecology research group at Clemson University and C. Belsler, D. Droge, P. Gowaty, S. Haig, J. Plissner, D. Tonkyn and S. Wagner for constructive comments on earlier versions of the manuscript. We also thank E. Ketterson and R. Mulvihill for thoughtful and constructive reviews of the submitted version.

LITERATURE CITED

- ALDRICH, J. W. 1982. Rapid evolution in the House Finch (*Carpodacus mexicanus*). *J. Yamashina Inst. Ornith.* 14:179-186.
- ALDRICH, J. W., AND J. S. WESKE. 1978. Origin and evolution of the eastern House Finch population. *Auk* 95:528-536.
- BALPH, M. H. 1975. Wing length, hood coloration, and sex ratio in Dark-eyed Juncos wintering in northern Utah. *Bird Banding* 46:126-130.
- BELLROSE, F. C., T. G. SCOTT, A. S. HAWKINS, AND J. B. LOW. 1961. Sex ratios and age ratios in North American ducks. III. *Nat. Hist. Surv. Bull.* 27:391-474.
- BELTHOFF, J. R., S. A. GAUTHREUX, JR., AND B. HILTON, JR. 1990. Breeding ranges of *Carpodacus* finches wintering in South Carolina. *Chat* 54:60-61.
- BERGTOLD, W. H. 1913. A study of the House Finch (*Carpodacus mexicanus frontalis*). *Auk* 30:40-73.
- BERTHOLD, P. 1984. The control of partial migration in birds: a review. *Ring* 10:253-265.
- BROWN, M. B., AND C. M. BROWN. 1988. Access to winter food resources by bright- versus dull-colored House Finches. *Condor* 90:729-731.
- CALDER, W. A. 1974. Consequences of body size for avian energetics, p. 86-144. *In* R. A. Paynter [ed.], *Avian energetics*. Nuttall Ornithological Club Publ. 15. Cambridge, MA.
- COHEN, J. 1988. *Statistical power analysis for the behavioral sciences*. 2nd edition. Lawrence Erlbaum Associates, Hillsdale, NJ.
- DAWSON, W. R., R. L. MARSH, W. A. BUTTEMER, AND C. CAREY. 1983. Seasonal and geographic variation of cold resistance in House Finches (*Carpodacus mexicanus*). *Physiol. Zool.* 56:353-369.
- DIEFENBACH, D. R., E. L. DERLETH, W. M. VANDER HAEGEN, J. D. NICHOLS, AND J. E. HINES. 1990. American Woodcock winter distribution and fidelity to wintering areas. *Auk* 107:745-749.
- DIEFENBACH, D. R., J. D. NICHOLS, AND J. E. HINES. 1988. Distribution patterns during winter and fidelity to wintering areas of American Black Ducks. *Can. J. Zool.* 66:1506-1513.
- DOLBEER, R. A. 1982. Migration patterns for age and sex classes of blackbirds and starlings. *J. Field Ornithol.* 53:28-46.
- ELLIOT, J. J., AND R. S. ARBIB, JR. 1953. Origin and status of the House Finch in the eastern United States. *Auk* 70:31-37.
- GAUTHREUX, S. A., JR. 1978. The ecological significance of behavioral dominance, p. 17-54. *In* P.P.G. Bateson and P. H. Klopfer [eds.], *Perspectives in ethology*, Vol. 3. Plenum Press, New York.

- GAUTHREAU, S. A., JR. 1982. The ecology and evolution of avian migration systems, p. 93-167. In D. S. Farner and J. R. King [eds.], *Avian biology*, Vol. 6. Academic Press, New York and London.
- HILL, G. E. 1990. Female House Finches prefer colourful males: sexual selection for a condition-dependent trait. *Anim. Behav.* 40:563-572.
- IVACIC, D. L., AND R. F. LABISKY. 1973. Metabolic responses of Mourning Doves to short-term food and temperature stresses in winter. *Wilson Bull.* 85:182-196.
- KALELA, O. 1954. Populationsökologische Gresschichtspunkte zur Entstehung des Vogelzuges. *Ann. Zool. Fenn.* 16:1-30.
- KERLINGER, P., AND M. R. LEIN. 1986. Differences in winter range among age-sex classes of Snowy Owls *Nyctea scandiaca* in North America. *Ornis Scand.* 17:1-7.
- KETTERSON, E. D., AND J. R. KING. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Phys. Zool.* 50:115-129.
- KETTERSON, E. D., AND V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology* 57:679-693.
- KETTERSON, E. D., AND V. NOLAN, JR. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (*Junco hyemalis*). *Auk* 99:243-259.
- KETTERSON, E. D., AND V. NOLAN, JR. 1983. The evolution of differential bird migration, p. 357-402. In R. F. Johnston [ed.], *Current ornithology*, Vol. 1. Plenum Press, New York.
- KING, J. R., D. S. FARNER, AND L. R. MEWALDT. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrow of the race *gambelii*. *Condor* 67:489-504.
- LACK, D. 1944. The problem of partial migration. *Br. Birds.* 37:143-150.
- MEARNS, R. 1982. Winter occupation of breeding territories and winter diet of peregrines in south Scotland. *Ornis Scand.* 13:79-83.
- MICHENER, H., AND J. R. MICHENER. 1931. Variation in color of male House Finches. *Condor* 33:159-175.
- MORTON, M. L. 1984. Sex and age ratios in wintering White-crowned Sparrows. *Condor* 86:85-87.
- MUNDINGER, P. M. 1975. Song dialects and colonization of the House Finch *Carpodacus mexicanus* on the East Coast. *Condor* 77:407-422.
- MYERS, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* 59:1527-1534.
- NICE, M. M., 1933. Migratory behavior in Song Sparrows. *Condor* 35:219-224.
- NICHOLS, J. D., AND G. M. HARAMIS. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. *Condor* 82:406-416.
- PERDECK, A. C., AND C. CLASON. 1983. Sexual differences in migration and winter quarters of ducks in the Netherlands. *Wildfowl* 34:137-143.
- PRESCOTT, D. R. C., AND A. L. A. MIDDLETON. 1990. Age and sex differences in winter distribution of American Goldfinches in eastern North America. *Ornis Scand.* 21:99-104.
- SALT, G. W. 1952. The relation of metabolism to climate and distribution in three finches of the genus *Carpodacus*. *Ecol. Monogr.* 22:121-152.
- SAMSON, F. B. 1976. Territory, breeding density, and fall departure in Cassin's Finch. *Auk* 93:477-497.
- SAMSON, F. B. 1977. Social dominance in winter flocks of Cassin's Finch. *Auk* 89:57-66.
- SPRENKLE, J. M., AND C. R. BLEM. 1984. Metabolism and food selection of eastern House Finches. *Wilson Bull.* 96:184-195.
- STEWART, P. A. 1988. Observations on avian morbidity and mortality at a winter feeding station. *Chat* 52:6-7.
- STEWART, P. A. 1989. Nesting localities of House Finches wintering in North Carolina. *Chat* 53:90.
- STEWART, P. A. 1990. Movements of House Finches banded in New York and Pennsylvania. *N. Am. Bird Bander* 14:118-119.
- STUEBE, M. M., AND E. D. KETTERSON. 1982. A study of fasting in Tree Sparrows (*Spizella arborea*) and Dark-eyed Juncos (*Junco hyemalis*): ecological implications. *Auk* 99:299-308.
- THOMPSON, W. L. 1960a. Agonistic behavior in the House Finch. Part II: factors in aggressiveness and sociality. *Condor* 62:378-402.
- THOMPSON, W. L. 1960b. Agonistic behavior in the House Finch. Part I: annual cycle and display patterns. *Condor* 62:245-271.
- VILLAGE, A. 1985. Turnover, age and sex ratios of Kestrels (*Falco tinnunculus*) in south Scotland. *J. Zool.* 206:175-179.
- YUNICK, R. P. 1987. Age determination of male House Finches. *N. Am. Bird Bander* 12:8-11.
- ZAR, J. H. 1984. *Statistical analysis*. 2nd edition. Prentice-Hall, Englewood Cliffs, NJ.