

DIFFERENTIAL OVERNIGHT SURVIVAL BY BUMPUS' HOUSE SPARROWS: AN ALTERNATE INTERPRETATION¹

WILLIAM A. BUTTEMER

Department of Physiology, University of Tasmania, Hobart, Australia 7001

Abstract. Functional appraisal of the differential survival pattern reported by Bumpus (1899) for House Sparrows (*Passer domesticus*) prompted this study of morphometric and energy relations of birds collected at a winter roost in Ann Arbor. There was no relation between overall size (mass or Principal Component I score) and total body length of males, but PC-I scores and body mass were correlated significantly in Ann Arbor males and females. Female Ann Arbor sparrows had higher proportionate energy reserves than males and, overall, were predicted to have greater fasting endurance. When body masses of Bumpus' male and female birds were evaluated as a function of their PC-I scores (based on six skeletal measures), survivors of a given gender had the same slope but significantly lower elevation than non-survivors. The consistently higher body mass of non-survivors for a given PC-I score in Bumpus' sample suggests that these birds died of exposure soon after the storm's onset and, consequently, used far less of their energy stores than their surviving counterparts. If the birds classed as survivors by Bumpus were fully representative of House Sparrows enduring the storm of 1898, then larger males and intermediate-sized females were more likely to secure and remain at protected roost sites during the 1898 storm than their less fortunate roostmates. On the other hand, because Bumpus' sample was collected by hand and had a disproportionately low female composition, conclusions about gender differences in pattern of selection in Bumpus' birds must be questioned.

Key words: Hermon Bumpus, House Sparrow; *Passer domesticus*; differential survival; morphometrics; body lipids; fasting endurance.

INTRODUCTION

Nearly a century ago, Hermon Bumpus received 136 House Sparrows (*Passer domesticus*) that had been collected after a severe winter storm in Providence, Rhode Island (Bumpus 1899). Over half of these birds revived in his laboratory and Bumpus proceeded to evaluate physical characteristics that might distinguish these survivors from their dead counterparts. He concluded that the storm had taken a greater toll on individuals whose morphometrics deviated most from the "ideal type" (Bumpus 1899). Bumpus was unabashed in claiming this pattern of differential survival to be due to the agency of natural selection. The provocative nature of his interpretation, coupled with publication of the complete data set on which it is based, has prompted repeated analysis of Bumpus' study (e.g., Harris 1911, Calhoun 1947, Grant 1972, Johnston et al. 1972, Lande and Arnold 1983, Crespi and Bookstein 1989). Studies reappraising the Bumpus data generally agree that females suffered proportionately greater mortality than males and

that female survivorship reflects stabilizing or normalizing selection (Grant 1972, Johnston et al. 1972, Lande and Arnold 1983). Disagreement persists, however, in deciding whether male survivorship reflects directional selection and, if so, whether this selection favors larger (Johnston et al. 1972) versus smaller individuals (Lande and Arnold 1983, Clutton-Brock 1988).

Such contradictory conclusions from the same data set reflect differences in confidence that various authors place in Bumpus' morphometric measures. Those accepting at face value all nine of Bumpus' morphometric measures conclude that the winter storm selected against larger adult males, because male survivors had significantly less mass and shorter total length than did their dead counterparts. On the other hand, some contend that his measures involving plumage (alar extent and total length) and mass may be biased, albeit for different reasons, and should not be considered when comparing characteristics of survivors to non-survivors (Calhoun 1947, Grant 1972, Johnston et al. 1972, Crespi and Bookstein 1989). When analysis is restricted to each of the six skeletal measures, adult male survivors and non-survivors cannot be distinguished from one

¹ Received 14 April 1992. Accepted 17 July 1992.

another and, accordingly, directional selection is not indicated (Grant 1972). On the other hand, if these six measures are used for a principal components analysis, the PC-I scores indicate surviving males were significantly larger overall than were non-survivors (Johnston et al. 1972). Thus, the varied interpretations concerning the type and presence of selection acting upon Bumpus' male sparrows depend directly on which of the nine morphometric measures are used for inferring size.

Because Bumpus' collection of birds is lost, it is impossible to ascertain which of his reported measures portrays accurately the overall size of individual birds in his sample. Nevertheless, insight could be gained from evaluating freshly-captured House Sparrows using similar morphometric appraisal. Furthermore, if this analysis were performed on birds captured soon after entering their winter roosts and included quantification of each bird's energy reserves (body fat and crop contents), then gender and size-ordered differences in foraging success might also be revealed. If, for example, the pattern of survivorship noted by Bumpus reflects differential feeding ability by wintering House Sparrows as suggested by Grant (1972), then one would expect the energy stores of House Sparrows entering winter roosts to reflect these asymmetries. Consequently, if the analysis of Johnston et al. (1972) is correct, then I would expect the largest males and medium-sized females to have greater relative energy reserves than their roostmates. If this expected pattern is not shown by winter birds, then hypotheses other than differential foraging ability should be advanced and tested.

I report here morphometric and energetic relations for House Sparrows taken from a common winter roost. Based on these relations, the pattern of survival shown by the Bumpus sparrows is reconsidered and a non-terminal method to evaluate morphometric and energetic relations in free-living birds is suggested.

MATERIALS AND METHODS

House Sparrows were observed roosting nightly within ivy covering a wall of a building on the University of Michigan campus at Ann Arbor, Michigan. The weather during these observations was typical for this time of year with daily temperatures below freezing and persistent snowcover on the ground. On 12 February, a 4 by 15 m mist net was placed alongside the roost,

which was rushed simultaneously from both ends. The roost was charged once again and resulted in capture of 43 birds between 20:00 and 20:10 EST. Within 30 min of capture, the birds were killed by cervical dislocation, weighed to the nearest 0.01 g, placed in plastic bags, and frozen. After thawing, the following skeletal components were measured to the nearest 0.1 mm using dial calipers: skull, keel, humerus, femur, tibiotarsus, and tarsometatarsus lengths, and skull width. In addition, total length, from tip of bill to tip of longest rectrix, and wing chord were measured to the nearest 0.5 mm using a ruler. These morphological characters, with the exception of wing chord and tarsometatarsus lengths, correspond to those measured by Bumpus and were taken according to descriptions given by Bumpus (1899) and Johnston and Selander (1971).

After removing crop and stomach contents, carcasses were freeze-dried to determine their water-free masses. The neutral lipid content of each bird was determined using methods described by Carey et al. (1978). For estimating energy reserves, I assume that these lipids have an energy content of 39.3 kJ g⁻¹ (Schmidt-Nielsen 1990) and that all but 0.1 g of these reserves are available for thermogenic needs (Newton 1969). Seeds removed from the crop and proventriculus were also freeze-dried and were assumed to have a metabolizable energy equivalent to 16.1 kJ g⁻¹ dry mass (Kendeigh and West 1965, Brooks 1968). The seed-energy content for each bird was summed with that of its lipid reserves to determine the amount of energy stores that a bird had for fueling its metabolic needs while roosting. This raises an important consideration; the amount of stored energy a bird brings to roost has far less functional significance than the amount of energy storage it has relative to the amount of energy it must expend. If, for example, two birds entered roosts with the same amount of stored energy but the first bird had a much higher rate of energy expenditure, the second bird would be able to fast far longer than the first one and, thus, would have a higher probability of surviving brief periods of feeding restriction imposed by ice storms and blizzards. An improved understanding of the significance of variations in avian energy stores, consequently, would result from an evaluation of how such variations affect fasting endurance.

Before fasting endurance can be evaluated, however, a reasonable estimate of energy expen-

TABLE 1. Morphometric measurements, fat, and seed content of Ann Arbor House Sparrows.¹

Variable	Male values	Female values	<i>t</i> -value ²
Total length	158.6 ± 3.6	156.3 ± 3.4	2.19*
Skull length	31.87 ± 0.57	31.69 ± 0.62	1.01
Skull width	15.65 ± 0.28	15.34 ± 0.43	2.78**
Tarsometatarsus length	19.63 ± 0.65	19.60 ± 0.89	-1.37
Tibiotarsus length	28.97 ± 0.76	28.37 ± 1.03	2.17*
Femur length	17.71 ± 0.47	17.37 ± 0.65	1.96
Wing length	77.21 ± 1.59	73.79 ± 1.75	6.71***
Humerus length	18.91 ± 0.49	18.39 ± 0.59	3.16**
Keel length	21.87 ± 0.75	20.63 ± 1.03	4.31***
Fresh body mass (g)	29.41 ± 0.86	28.49 ± 1.72	2.19*
Lipid content as % fresh body mass	7.41 ± 0.66	8.17 ± 1.33	2.35*
Crop and proventriculus content (g dry mass)	0.26 ± 0.14	0.26 ± 0.23	-0.04

¹ All values are means ± 1 standard deviation and were measured from 22 male and 21 female sparrows collected at the same winter roost. All length and width values are in mm.

² Based on a two-tailed Student's *t* test with 41 degrees of freedom; *P* values less than 0.05 designated by *, those less than 0.01 by **, and those less than 0.001 by ***.

diture must be made. As in other endotherms, avian metabolic rates are very labile, even for animals at rest, and can vary as functions of temperature, time of day, and characteristics of a given population, among other factors (Hudson and Kimzey 1966). To simplify the comparison, I assume roost temperature remains at 0°C and use nocturnal metabolic rates measured by Hudson and Kimzey (1966) for House Sparrows from Ann Arbor to estimate roosting costs. Because metabolic rate also varies as a function of body mass, estimates of roosting energy expenditure were adjusted for differences in mass through,

$$\text{Fasting Energy Expenditure} \\ = (m_1/25.8 \text{ g})^{0.72} 3.5 \text{ kJ h}^{-1} \quad (1)$$

where, m_1 is the seed- and fat-free lean body mass of birds of the present study, 25.8 g is the average body mass of the Ann Arbor birds studied by Hudson and Kimzey (1966), 3.5 kJ h⁻¹ is the average rate of nocturnal energy expenditure of the latter birds at 0°C, and 0.72 is the mass exponent of avian metabolism as a function of body mass (Lasiewski and Dawson 1967).

The morphological data permitted mass-independent evaluation of overall size of each bird by subjecting these data to Principal Components Analysis (PCA). This technique transforms measures of many variables for a given individual into a few unmeasured factor scores. When morphological data are subjected to PCA, the first factor extracted (PC-I) is generally believed to best represent overall body size (Robins and Schnell 1971, Johnston et al. 1972, Bookstein

1989). Principal components analyses reported below are based on Pearson correlation matrices of six morphological variables; skull, keel, humerus, femur, and tibiotarsus lengths, and skull width. Correlation rather than covariance matrices were chosen for PCA because the former procedure weights all morphometric variables equally whereas covariance-based PCA is strongly weighted by variables with the most variance and, thus, gives disproportionate emphasis to long bone measurements (Freeman and Jackson 1990). Although logarithmic transformation of variables used for covariance-based PCA is presumed to equalize intertrait variance, this occurs only when all variances scale proportionally to the square of the trait means (Bryant 1986).

Unless stated otherwise, values are presented as means and standard deviations.

RESULTS AND DISCUSSION

MORPHOMETRIC COMPARISON OF ANN ARBOR HOUSE SPARROWS

Following their introduction to North America in the 19th century, House Sparrows have undergone rapid morphological change (Calhoun 1947), resulting in larger overall size, particularly in the more seasonal regions of the continent (Johnston and Selander 1971, Fleischer and Johnston 1984, Murphy 1985). Comparison of individual House Sparrows from a given region, however, reveals significant secondary sexual dimorphism with males having markedly larger pectoral and wing elements than females (John-

TABLE 2. First principal component factor score loadings for male and female Ann Arbor House Sparrows. All values were extracted from a Pearson correlation matrix of six bony measurements.¹

Variable	Male sparrows	Female sparrows
Skull length	0.17	0.78
Skull width	0.51	0.83
Humerus	0.95	0.89
Femur	0.87	0.89
Tibiotarsus	0.83	0.94
Keel	0.67	0.37

¹ Sample size is 21 female and 22 male sparrows.

ston and Selander 1971). With the exceptions of tibiotarsus length and body mass, all other body measurements of the Ann Arbor Sparrows (Table 1) share the pattern of sexual dimorphism noted by Johnston et al. (1972) for Bumpus' (1899) combined sample.

From PC analysis of the Ann Arbor males, all skeletal measures except skull length loaded significantly ($P < 0.02$ for skull width; $P < .001$ for others) and positively on the first component, which accounted for 51% of the variation (Table 2). The second component explained 20% of the variation for male sparrows and had significant and negative loadings from skull length and width. For females, PC-I accounted for 65% of the observed variation and had significant ($P < 0.001$) and positive loadings from all measures except keel length (Table 2). The latter variable was the only character in females to load significantly and positively on the second component which accounted for 18% of the variation.

In view of the general consensus that the PC-I score from a PC analysis is a valid descriptor of overall size, it is worthwhile to see how this variable and single morphometrics correlate with body mass, another measure of overall size. For males, fresh body mass (body mass at time of capture less crop and stomach contents) correlated best with PC-I score followed closely by humerus and keel lengths (Table 3). Similar correlative patterns were seen for male lean body masses but the correlation coefficients were generally higher than those for fresh body masses. Body masses of female sparrows were also most highly correlated with PC-I scores followed by humerus and tibiotarsus lengths (Table 3). There was little difference between female lean and fresh body masses in the order or extent of their correlation to the morphometric variables.

TABLE 3. Correlation coefficients between fresh body mass (body mass at time of capture less crop and stomach contents) or lean body mass (lipid-free body mass) and selected morphometric measurements for winter-captured male and female Ann Arbor House Sparrows.¹

Variable	Wing chord	Body length	Skull length	Skull width	Tarso-metatarsus	Tibio-tarsus	Humerus	Femur	Keel	PC-I score ²
Fresh body mass (males)	-0.24	0.08	0.02	0.23	0.06	0.46*	0.61**	0.54**	0.59**	0.63**
Lean body mass (males)	-0.34	-0.03	-0.02	0.25	0.09	0.53**	0.70**	0.61**	0.56**	0.69**
Fresh body mass (females)	0.20	0.65**	0.56**	0.70**	0.76**	0.80**	0.80**	0.78**	0.33	0.85**
Lean body mass (females)	0.20	0.59**	0.52*	0.68**	0.75**	0.78**	0.81**	0.77**	0.25	0.82**

¹ Correlation coefficients derive from measurement of 22 male and 21 female House Sparrows collected at the same winter roost. Significance is signified by * for $P < 0.05$ and ** for $P < 0.01$.
² PC-I scores were calculated separately for each gender from Pearson correlation matrices of skull, keel, humerus, femur, and tibiotarsus lengths and skull widths for 22 male and 21 female House Sparrows.

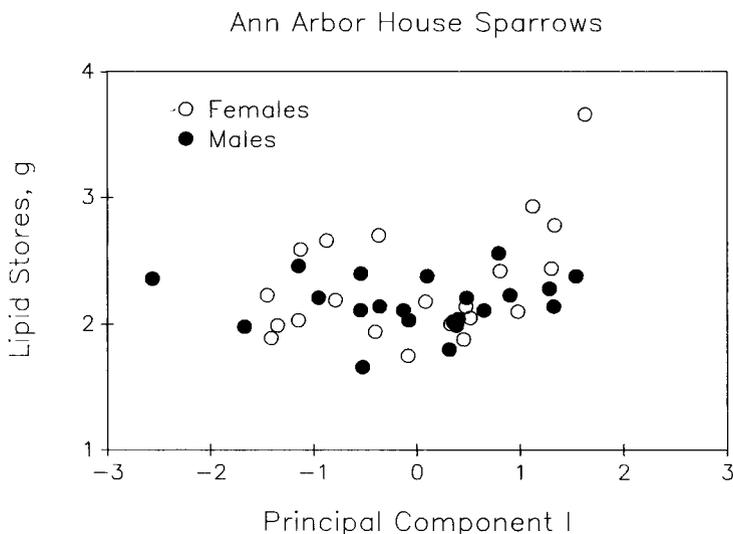


FIGURE 1. Amount of extractable neutral lipids in female (open circles) and male (filled circles) House Sparrows of the Ann Arbor sample as a function of their principal component I score which is based on six skeletal measures.

The two measures that included plumage, wing chord and body length were very poor descriptors of body mass in males, showing one of the lowest correlation coefficients of any morphometric measured (Table 3). For females, body length correlated significantly with body mass ($P < 0.01$ for both fresh and lean body masses) but wing chord did not ($P > 0.3$). Comparison of PC-I scores to wing chord and total body lengths revealed no significant correlations for males ($r = -0.02$ and 0.06 , respectively) or for females ($r = -0.01$ and 0.41 , respectively).

ENERGY STORAGE RELATIONS OF ANN ARBOR SPARROWS

On arriving at winter roosts, birds typically begin overnight fasts with their crops and stomachs replete with food and with body lipids at their highest daily level. Because the Ann Arbor sparrows were captured at least 3 hr after they last fed, their seed content was very small and averaged 0.26 ± 0.19 g dry mass for both genders (Table 1). Consequently, variation in body fat, not seed content, was mainly responsible for interindividual variation in amount of energy storage.

In the 21 females sampled, extractable lipids averaged 2.31 g (± 0.45 ; range = 1.75 to 3.66 g) and, for the 22 males, this value averaged 2.16 g (± 0.22 ; range = 1.66 to 2.56 g). Body lipids

correlated directly with total body and keel lengths in females ($P = 0.03$; $r = 0.478$ and $P = 0.05$; $r = 0.433$, respectively) and, although not significant, the same trend was shown by males ($P = 0.08$; $r = 0.381$ and $P = 0.11$; $r = 0.332$, respectively). From the multivariate analyses, PC-I scores correlated directly with lipid content in females ($P = 0.04$; $r = 0.447$) but showed no significant relation with male lipid values ($P > 0.50$; $r = 0.035$; Fig. 1).

Comparison of average values, however, obscures any size-ordered differences in fat content that might be present for each gender. From studies of overwinter survival in House Sparrows, Fleischer and Johnston (1984) found evidence of directional selection against large females. One explanation they offered for large females being disfavored was that these birds would suffer greater restriction on feeding because they are more likely to have agonistic interactions with aggressive male birds than their smaller counterparts. If such tendencies held for the Ann Arbor winter sparrows, then the largest females should have arrived at the roost with significantly less fuel. Contrary to this expectation, the larger Ann Arbor females showed no evidence of being energetically compromised. In fact, the three highest levels of fat noted in the entire Ann Arbor sample belonged to three females having ranks of 1, 2, and 4 in the female PC-I scores.

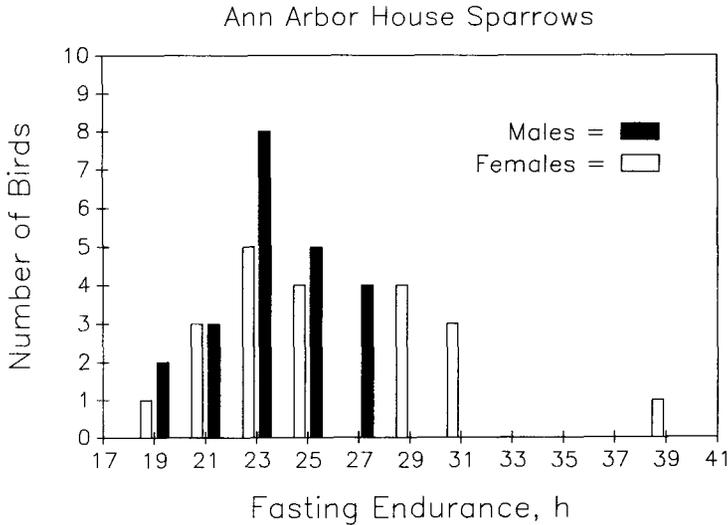


FIGURE 2. Frequency distribution of estimated fasting endurance for 22 male (filled bars) and 21 female (open bars) House Sparrows collected from the same winter roost in Ann Arbor.

Such gender differences in relations between PC-I score and fat content are at variance with assumptions that females in general, and large females in particular, are food-limited by male conspecifics. Such conclusions are premature, however, until differences in how this energy is allocated during roosting are also considered. That is, the amount of energy stores measured for each bird must be evaluated in relation to their expected rate of energy expenditure (Eq. 1). From these estimates of fasting endurance, not only are females well-prepared to endure overnight fasting, nearly half of them would outlast their male roostmates (Fig. 2). This suggests that female sparrows from the Ann Arbor sample are not being denied access to food by males.

BUMPUS' SPARROWS REVISITED

Gaining insight into factors underlying the pattern of survival noted by Bumpus (1899) from a small population of birds nearly a century and 1,000 km removed may be a dubious proposition. Nevertheless, some useful considerations derive from this effort. First, if we make the assumption that the energy relations of the Ann Arbor winter sample, which was captured at a time of complete snow cover, are shared by the Bumpus sparrows, then factors other than food acquisition must be considered as bases for the pattern of differential survival of the 1898 winter storm. One likely possibility is that variation in

the extent of thermal stress underlies the pattern of survivorship seen in the Bumpus sample.

For small birds, roost-site quality importantly affects their rate of nocturnal metabolism. Because of their small diameter, these animals are very susceptible to convective heat loss (Buttemer 1985, Walsberg 1986). Roost sites that are protected from wind, consequently, are very important in permitting these birds to husband their energy reserves through the protracted winter night. Therefore, the pattern of selection operating on the Bumpus sample might reflect differences in the extent to which survivors were protected from the storm which preceded their capture. Unfortunately, Bumpus (1899) does not provide sufficient detail about the storm or the conditions under which the birds were captured to evaluate whether survivorship was influenced more by overnight protection from the storm or by ability to find food following its passage.

I was unable to find much information concerning weather in Providence, Rhode Island at the time Bumpus received his sparrows, but, in nearby Boston, Massachusetts a winter blizzard arrived at 01:00 hr on 1 February 1898 and dropped over 30 cm of snow by 05:00 (New York Times; 2 February 1898). This snow was very wet and, coupled with a wind speed of 80 km/hr, prostrated all telephone and telegraph lines out of Boston and Providence. Such a storm would have damaged many trees and, thus, prob-

Bumpus House Sparrows – Females

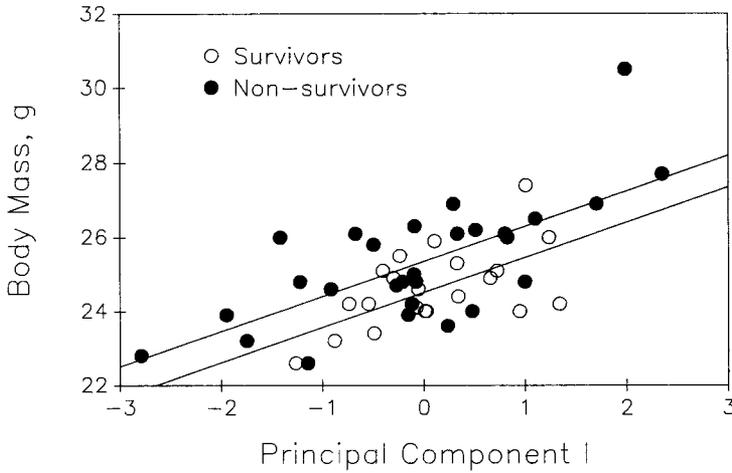


FIGURE 3. Relation between body mass and principal component I score based on six skeletal measures for individual female House Sparrows of the Bumpus sample which survived (open circles) or did not survive (closed circles) a severe winter storm. The upper and lower least-squares regression lines are for non-survivors and survivors, respectively.

ably dislodged birds from their roosts. Birds not finding shelter following such a disturbance would have been subjected to severe windchill and likely would have become hypothermic and eventually died. Extending this scenario to the Bumpus sparrow sample, if birds classed as non-survivors are largely those that died from exposure following roost dislodgement, one would expect their body masses to be higher than those of their surviving counterparts after differences in size are accounted for. This follows from the pattern of daily mass variation seen in most birds where body mass peaks before roost entry and reaches its daily nadir just before morning feeding (Evans 1969).

Comparison of body masses of the Bumpus sample as a function of PC-I scores from his six skeletal measurements supports this suggestion (Figs. 3, 4). In both male and female samples, the slope of the least-squares regression best describing body mass as a function of PC-I scores for survivors did not differ significantly from that describing the same relation for non-survivors (using ANOVA, for females: $P = 0.5$; $F = 0.047$; and for males, $P = 0.5$; $F = 0.054$). Importantly, the elevation of the regression for surviving males is significantly lower than that of dead counterparts ($P < 0.001$; $F = 21.62$; Fig. 4) and, similarly, that of surviving females is significantly

lower than that of non-surviving females ($P < 0.02$; $F = 7.43$; Fig. 3). Interestingly, the elevations differ to a similar extent in both genders, having a 0.9 g separation between the female regressions and a 1.2 g separation for males. This supports the notion that non-survivors died at a similar time following the storm's arrival and did so before they depleted their energy reserves. Although surviving birds could resume feeding at daylight, the extent of snowfall and the tremendous snowdrifts noted for this storm (New York Times; 2 February 1898) would have made foraging very difficult for these ground-feeding birds. Indirect evidence for this comes from the fact that all sparrows in the Bumpus sample were collected by hand, hence birds classed as survivors by Bumpus were too weak to fly.

DIRECTIONAL SELECTION IN BUMPUS' MALE SPARROWS

Those analyzing Bumpus' data agree that surviving birds were lighter in mass and surviving males were shorter in length than their non-surviving counterparts (Grant 1972, Johnston et al. 1972, Lande and Arnold 1981, Crespi and Bookstein 1989). This implies that survivors were smaller than non-survivors which is contrary to what is expected from empirical (Kendeigh 1945)

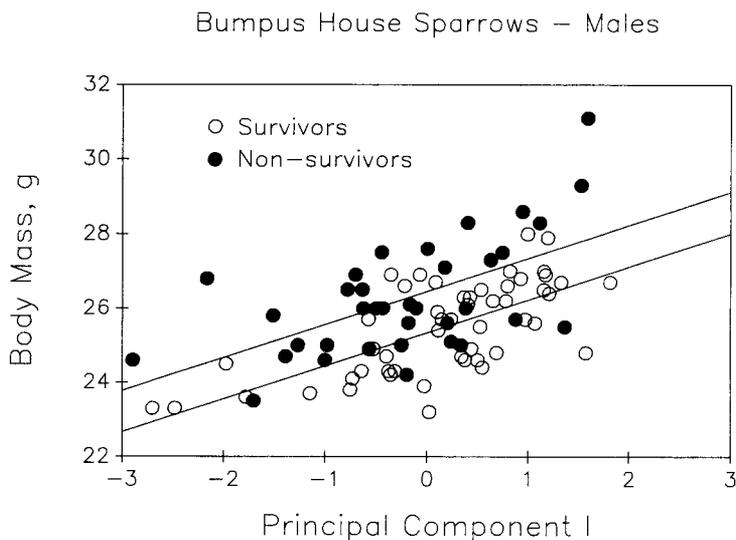


FIGURE 4. Relation between body mass and principal component I score based on six skeletal measures for individual male House Sparrows of the Bumpus sample which survived (open circles) or did not survive (closed circles) a severe winter storm. The upper and lower least-squares regression lines are for non-survivors and survivors, respectively.

or theoretical (Calder 1974) considerations of size effects on fasting endurance. Before concluding that Bumpus' sample proves selection against large males, however, it is important to consider arguments against inferring size from this measure of mass and body length.

Some have suggested that the body masses of Bumpus' sample are subject to bias as body mass will be affected by extent of energy depletion as well as overall size (Grant 1972, Johnston et al. 1972, Crespi and Bookstein 1989). Because those birds classed as survivors by Bumpus lived longer than the non-survivors, differences in mass may reflect disparate fasting periods and, consequently, differential depletion of body energy stores by the two groups. The latter explanation is consistent with the significantly greater overall size (based solely on PC analysis of skeletal measures) shown by the surviving males compared to their heavier, non-surviving, counterparts (Johnston et al. 1972). In addition, the common slope but significantly lower elevation of the regression describing body mass as a function of PC-I scores for surviving Bumpus males compared to non-surviving males (Fig. 4) accords fully with interpretations that differences in mass between survivors and non-survivors reflects mainly differences in extent of depletion of energy stores between these groups. The strong cor-

relation between PC-I scores and body mass for Ann Arbor males collected soon after entering their winter roosts (Table 3) lends credence to the latter interpretation.

The fact that surviving males were significantly shorter in total length, however, remains contrary to claims that male survivors were larger birds than non-survivors. Bumpus' measurements of alar and total length have been suggested to be systematically biased owing to differences in posture (Grant 1972), extent of rigor mortis (Crespi and Bookstein 1989) between survivors and non-survivors, and size-independent differences in feather wear (Calhoun 1947). Although Bumpus (1899) does not provide sufficient information to evaluate these claims, body measurements involving feather components (wing chord and total body length) bore no relation to PC-I scores or fresh body mass, both indicators of overall size, in the Ann Arbor sample of male House Sparrows (Table 3).

Taken together, the morphometric relations between PC-I and fresh body mass of the Ann Arbor male sparrows and the regression analysis of Bumpus' male sparrows (Fig. 4) strongly supports the conclusion of Johnston et al. (1972) that male birds classed as survivors by Bumpus were significantly larger than those males termed non-survivors.

CENTRIPETAL SELECTION IN BUMPUS' FEMALE SPARROWS

The proportionately higher female mortality noted for the Bumpus sample has been interpreted to result from restricted access to food owing to females being generally subordinate to male House Sparrows (Grant 1972). If this argument were valid, one would expect females, on average, to have lower energy stores relative to male birds upon entering the roost. Such was not the case for the Ann Arbor House Sparrows; in fact, females have proportionately greater lipid reserves than their male counterparts (Table 1). The female Bumpus' sparrows differ further from males in showing normalizing rather than directional selection, resulting in average-sized females being favored (Grant 1972, Johnston et al. 1972). Selection against small females during winter storms follows logically from the known direct relation between size and fasting endurance (Kendeigh 1945) but selection against large females is more difficult to explain. Grant (1972) suggested that, because mass-specific metabolism is inversely related to body mass, larger females may have been unable to mobilize their energy stores rapidly enough. This argument, even if it were physiologically valid, is contraindicated by the fact that the larger male birds, based on PC analysis of Bumpus' sample, were not similarly affected. Furthermore, direct evidence shows that avian mortality following severe cold stress is inversely related to size (Lustick and Adams 1977).

In summary, the energy relations of the Ann Arbor female sparrows cast doubt on food limitation being the proximate cause of stabilizing selection in Bumpus' female birds. Selection against small females is consistent with known advantages of large size during cold stress but selection against large size during winter storms is counterintuitive.

ALTERNATE INTERPRETATIONS OF DIFFERENTIAL SURVIVAL BY BUMPUS' SPARROWS

The simplest explanation for the cause of fatality in Bumpus' nonsurvivors is that these birds were unable to cope with the cold stress attending the severe winter storm. The fact that these birds had higher average body masses than survivors of the same size (based on PC-I score of skeletal elements; Figs. 3, 4) suggests that these birds died from hypothermia and not energy depletion.

Consequently, the pattern of selection shown by Bumpus' sample of House Sparrows is more likely due to differences in extent of exposure to the winter storm than by differences in feeding before its arrival. Such selection could result if there were size- and gender-ordered tendencies for dominance and that dominant birds were more likely to occupy better roost sites at the onset of the storm or, if forced from their roost by the storm, were better able to wrest alternate sites from their submissive counterparts. There are observations of subordinate birds being displaced from roost sites during inclement weather. For example, in rooks (*Corvus frugilegus*), dominant males select roost sites high in trees less prone to predation (Swingland 1977). However, these sites are more susceptible to radiant and convective heat losses and, when weather conditions worsen, these males move to more energetically-favorable sites, displacing subordinate birds (Swingland 1977).

If such behavior occurs in wintering House Sparrows and results in dominant birds selecting better roost sites, then selection against subordinate birds is expected. To account for the pattern of selection shown by Bumpus (1899), however, would require that dominance hierarchies have different size-orderings for each gender; i.e., large males, but not large females, on average, would be dominant, whereas, small females and small males, on average, would be subordinate. It seems logical that large males would dominate smaller birds, but implausible that the largest female House Sparrows would be less dominant than medium-sized ones.

Is there a simpler explanation for the differential pattern of survival shown by Bumpus' females? The entire Bumpus sample consisted of 136 birds, 87 males and 49 females, which were brought to his lab following a severe storm of snow, rain, and sleet (Bumpus 1899). Of these birds, 59 of the males and 21 of the females revived but the remainder did not. There are two aspects of his sample which are at variance with my Ann Arbor sample. First, the higher proportionate fatality suffered by females compared to males in Bumpus' sample is hard to reconcile with the higher proportionate energy reserves (Table 1) and generally greater predicted fasting endurance (Fig. 2) shown by Ann Arbor females compared to males. Second, the non-equal gender representation in Bumpus' sample (36% female) compared to mine taken from a

common roost (49% female) suggests strongly that his sample may be biased and thus not representative of the female population in Providence at the time. The issue of Bumpus' data having systematic bias has been raised by Lande and Arnold (1983) who noted that the manner by which Bumpus' birds were collected excluded any which had not fallen to the ground. Those birds least compromised energetically by the storm, consequently, are unlikely to be found in his sample. If the energy relations of the Ann Arbor winter sparrows reflect those of Bumpus' sparrows before the storm, it is very likely that females, particularly those with higher PC-I scores, were underrepresented in his sample. If this were so, the main cause of differential survival by Bumpus' House Sparrows would remain differential exposure to severe cold stress, but whether the pattern of selection shown by his collection operated on the population as a whole depends importantly on the extent to which survivors captured by hand represent those able to fly.

CONCLUDING COMMENTS AND SUGGESTIONS FOR FUTURE STUDIES

While competition for food during protracted periods of food scarcity is known to produce asymmetries in avian survivor types (Boag and Grant 1981, Price et al. 1984, Johnston and Fleischer 1981) episodic events, such as severe winter storms, may also impose differential selection. The pattern of survivorship shown by Bumpus' sample of House Sparrows following such an event is often cited as an example of size- and gender-ordered natural selection operating on a free-living population. As stated above, however, Bumpus' sample may not represent truly most birds surviving the storm.

The issue of whether Bumpus' data accurately reflects the selective forces of a severe winter storm on an avian population may never be resolved. What can be learned, instead, is recognition of what is needed to assure proper sampling of future storm-induced mortality in avian populations. Of critical importance is knowledge of size distribution among members within a population based on samples taken before or soon after a storm's occurrence. Birds should be collected near roosting or feeding areas using mist nets to avoid sampling bias. These data are essential to provide valid size comparators for in-

ference of differential selection from measurements of dead birds.

In situations where differential selection is suspected, insight into the factors underlying this pattern could be gained using methods employed in the present study. For example, asymmetries in feeding ability could be inferred from morphometric relations of estimated fasting endurance for male and female birds collected soon after roosting. Similar analyses performed on birds collected at the same roosts just before dawn could be compared to these roost-entry relations to evaluate patterns of overnight energy expenditure among size-classes. By repeating such sampling over a range of climatic conditions, insight into the physiological bases of differential selection would be gained.

It is possible, but less accurate, to estimate energy and size relations of birds without killing them. Fat content can be evaluated indirectly through measurements of total body water using tritium or deuterium (Johnson and Farrell 1988), bio-impedance analysis (Lukaski 1987), or through total body electrical conductivity (Walsberg 1988, Castro et al. 1990, Scott et al. 1991). Measurements of size should be based on external measures which are temporally invariant (e.g., tarsus length) and which are known to correlate highly with PC-I scores derived from skeletal elements. Selecting appropriate external metrics requires prior analysis of skeletal and external morphometric relations (Freeman and Jackson 1990) for each species under study.

ACKNOWLEDGMENTS

Marshall Yacoe helped capture the sparrows and Lee Astheimer assisted with the morphometric evaluations. Space and facilities for analyzing body composition were provided by Coby Schal and Don Caccamise at Rutgers University. I thank Lee Astheimer, Ray Huey, and Sievert Rohwer for thoughtful discussions on an earlier version of this manuscript and Tom Scanlon for bringing the Bumpus study to my attention.

LITERATURE CITED

- BOAG, P. T., AND P. R. GRANT. 1981. Intense natural selection in a population of Darwin's Finches (*Geospizinae*) in the Galápagos. *Science* 214:82-85.
- BOOKSTEIN, F. L. 1989. "Size and shape": a comment on semantics. *Syst. Zool.*
- BROOKS, W. S. 1968. Comparative adaptations of the Alaskan redpolls to the arctic environment. *Wilson Bull.* 80:253-280.
- BRYANT, E. H. 1986. On use of logarithms to accommodate scale. *Syst. Zool.* 35:552-559.

- BUMPUS, H. C. 1899. The elimination of the unfit as illustrated by the introduced House Sparrow, *Passer domesticus*. Biol. Lectures, Marine Biol. Lab., Woods Hole:209-226.
- BUTTEMER, W. A. 1985. Energy relations of winter roost-site utilization by American Goldfinches (*Carduelis tristis*). *Oecologia* 68:126-132.
- CALDER, W. A. 1974. Consequences of body size for avian energetics, p. 86-151. In R. A. Paynter [ed.], Avian energetics, No. 15. Publ. Nuttall Ornithological Club. Cambridge, MA.
- CALHOUN, J. B. 1947. The role of temperature and natural selection in relation to the variations in the size of the English Sparrow in the United States. *Am. Nat.* 81:203-228.
- CAREY, C., W. R. DAWSON, L. C. MAXWELL, AND J. A. FAULKNER. 1978. Seasonal acclimatization to temperature in Cardueline finches. II. Changes in body composition and mass in relation to season and acute cold stress. *J. Comp. Physiol.* 125:101-113.
- CASTRO, G., B. A. WUNDER, AND F. L. KNOPF. 1990. Total body electrical conductivity (TOBEC) to estimate total body fat of free-living birds. *Condor* 92:496-499.
- CLUTTON-BROCK, T. H. 1988. Reproductive success, p. 472-520. In T. H. Clutton-Brock [ed.], Reproductive success: studies of individual variation in contrasting breeding systems. Univ. of Chicago Press, Chicago.
- CRESPI, B. J., AND F. L. BOOKSTEIN. 1989. A path-analytic model for the measurement of selection on morphology. *Evolution* 43:18-28.
- EVANS, P. R. 1969. Winter fat deposition and overnight survival of Yellow Buntings (*Emberiza citrinella* L.). *J. Anim. Ecol.* 38:415-423.
- FLEISCHER, R. C., AND R. F. JOHNSTON. 1984. The relationships between winter climate and selection on body size of House Sparrows. *Can. J. Zool.* 62:405-410.
- FREEMAN, S., AND W. M. JACKSON. 1990. Univariate metrics are not adequate to measure avian body size. *Auk* 107:69-74.
- GRANT, P. R. 1972. Centripetal selection and the House Sparrow. *Syst. Zool.* 21:23-30.
- HARRIS, J. A. 1911. A neglected paper on natural selection in the English Sparrow. *Am. Nat.* 45:314-318.
- HUDSON, J. W., AND S. L. KIMZEY. 1966. Temperature regulation in populations of the House Sparrow, *Passer domesticus*. *Comp. Biochem. Physiol.* 17:203-217.
- JOHNSON, R. J., AND D. J. FARRELL. 1988. The prediction of body composition in poultry by estimation in vivo of total body water with tritiated water and deuterium oxide. *Br. J. Nutr.* 59:109-124.
- JOHNSON, R. F., AND R. C. FLEISCHER. 1981. Over-winter mortality and sexual size dimorphism in the House Sparrow. *Auk* 98:503-511.
- JOHNSON, R. F., D. M. NILES, AND S. A. ROHWER. 1972. Hermon Bumpus and natural selection in the House Sparrow, *Passer domesticus*. *Evolution* 26:20-31.
- JOHNSON, R. F., AND R. K. SELANDER. 1971. Evolution in the House Sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1-28.
- KENDEIGH, S. C. 1945. Resistance to hunger in birds. *J. Wildl. Manag.* 9:217-226.
- KENDEIGH, S. C., AND G. C. WEST. 1965. Caloric values of plant seeds eaten by birds. *Ecology* 46:553-555.
- LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210-1226.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- LUKASKI, H. C. 1987. Methods for the assessment of human body composition: traditional and new. *Am. J. Clin. Nutr.* 46:537-556.
- LUSTICK, S., AND J. ADAMS. 1977. Seasonal variation in the effects of wetting on the energetics and survival of starlings (*Sturnus vulgaris*). *Comp. Biochem. Physiol.* 56A:173-177.
- MURPHY, E. C. 1985. Bergmann's rule, seasonality, and geographic variation in body size of House Sparrows. *Evolution* 39:1327-1334.
- NEWTON, I. 1969. Winter fattening in the bullfinch. *Physiol. Zool.* 42:96-107.
- PRICE, T. D., P. R. GRANT, H. L. GIBBS, AND P. T. BOAG. 1984. Recurrent patterns of natural selection in a population of Darwin's Finches. *Nature* 309:787-789.
- ROBINS, J. D., AND G. D. SCHNELL. 1971. Skeletal analysis of the *Ammodramus-Ammonspiza* complex: a numerical taxonomic study. *Auk* 88:567-590.
- SCHMIDT-NIELSEN, K. 1990. Animal physiology: adaptation and environment, 4th ed. Cambridge Univ. Press, Cambridge, England.
- SCOTT, I., M. GRANT, AND P. R. EVANS. 1991. Estimation of fat-free mass of live birds: use of total body electrical conductivity (TOBEC) measurements in studies of single species in the field. *Funct. Ecol.* 5:314-320.
- SWINGLAND, I. R. 1977. The social and spatial organization of winter communal roosting in rooks (*Corvus frugilegus*). *J. Zool.* 182:509-528.
- WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *Auk* 103:1-7.
- WALSBERG, G. E. 1988. Evaluation of a non-destructive method for determining fat stores in small birds and mammals. *Physiol. Zool.* 61:153-159.