

# GEOGRAPHIC VARIATION IN WING-LOADING OF THE HOUSE SPARROW

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Intraspecific variation in size of widely distributed birds often agrees with modern interpretation of Bergmann's Rule; that is, size is correlated with a combination of climatic variables that includes temperature and/or moisture (James 1968, 1970, Power 1969). Northern races of birds are frequently larger (Mayr 1963:320), but the adaptive significance of increased size has been widely debated (Scholander 1955, Mayr 1956, Salt 1963, Kendeigh 1969, McNab 1971). In general, the word size in ornithological literature refers to wing length, which is often an accurate indicator of body size (James 1970). Wing length varies independently of, or inversely with, body weight in some species (Snow 1958, Hamilton 1961, Rand 1961). Selection for larger body mass without a concomitant increase in wing length could result in conflict between opposing selective forces, particularly in species that depend on flight for foraging or escape from predators. Large birds with relatively small wings will obviously have greater wing-loads and may approach an upper limit at which flying becomes energetically expensive or restricts the ability of the bird to escape predation. In this paper I describe geographic trends in wing-loading in North American populations of the House Sparrow, *Passer domesticus*, and assess the importance of upper limits of wing-loading using data on the flying ability of experimentally loaded birds.

## METHODS

Sparrows used in this experiment were captured during winter (November–February) at 11 sites representing a wide latitudinal range (Table 1). Although House Sparrows at northern sites have fewer hours of daylight during the winter for collecting food, they store greater amounts of fat which is necessary for overnight survival (Blem 1973a). Collections were made in late afternoon or early evening and are therefore comparable and representative of birds prepared for surviving a midwinter's night fast.

Chords of both wings of each bird were measured to the nearest 0.1 mm using vernier calipers. Wings were cut off as close to the body as possible and pinned out so that the anterior and proximal edges of the wing were straight and perpendicular to one another. Major wing feathers were positioned in what seemed to be a natural manner and the wing allowed to dry. No shrinkage of the wing occurred with drying. A precise outline was produced by spraying a light layer of paint around the edge of the wing. The area of the resulting silhouette was then determined to the nearest 0.1 cm<sup>2</sup> with a compensating polar planimeter. Subsequent carcass analysis (Blem 1973a) made measurement of wing areas of all birds impossible, so the relationship between wing chord and wing area was determined from measurements of Ohio and Virginia sparrows. The least squares relationship between the average of the chords of both wings and total wing surface

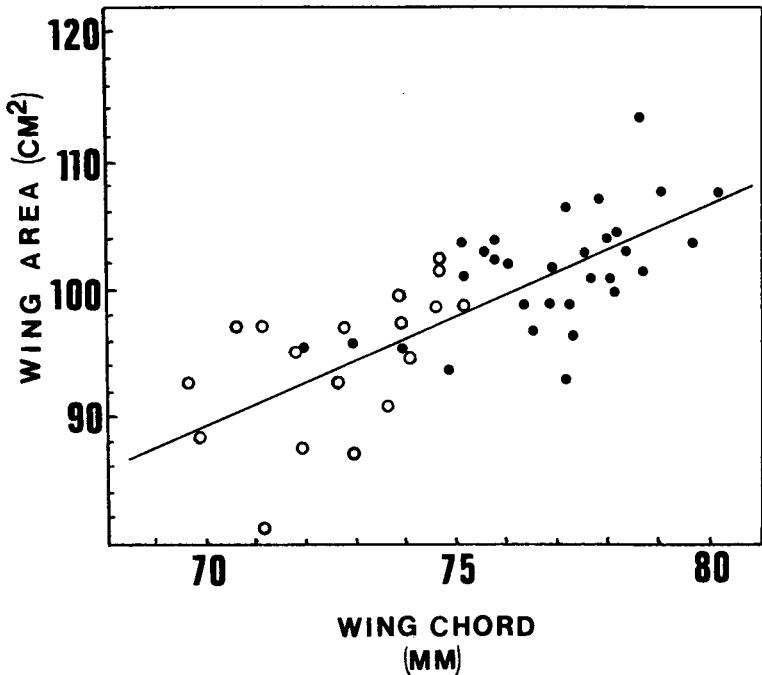


FIG. 1. Relationship between wing area and wing chord in male (●) and female (○) House Sparrows. Wing area ( $\text{cm}^2$ ) =  $1.66$  wing chord (mm)  $-25.86 \pm 4.07$ .

is significantly linear and was used to predict wing area in the remainder of the samples (Fig. 1). There is no difference between equations for Ohio and Virginia birds, or between sexes, therefore all data were pooled.

Laboratory tests of the flying ability of artificially weighted sparrows were performed in order to determine the effects of extreme wing-loading and the lower limit at which weight hinders a House Sparrow's flight. Male sparrows freshly caught at Richmond, Virginia were fitted with a harness attached around the neck and body. The harness did not visibly interfere with the flight of any of the sparrows tested. Lead weights were attached to the harness near the keel of the sternum. The locations used were near sites of fat deposition (furcula, lower abdomen, ventral feather tracts) and the center of gravity of the bird. Tests were carried out in a 30 m hallway with 3 m ceilings. Flying ability was subjectively assessed on the basis of altitude of flight, flying time, ability to sustain flight without tiring, and avoidance of capture. Wing-loading was determined after each test from the total weight of bird, harness, and lead weights, and the wing area predicted from the chords of the wings.

#### RESULTS

Male House Sparrows had significantly different body weight, wing chord, and wing area than females (Table 1). There was a small, but statistically

TABLE I  
MID-WINTER BODY WEIGHT, WING CHORD AND AREA, AND WING-LOAD IN HOUSE SPARROWS

Location (°N. Latitude)	MALES					FEMALES				
	N*	Weight (g)	Wing chord (mm)	Wing area (cm <sup>2</sup> )	Wing- load (g/cm <sup>2</sup> )	N	Weight (g)	Wing chord (mm)	Wing area (cm <sup>2</sup> )	Wing- load (g/cm <sup>2</sup> )
Churchill, Manitoba (59)	7	33.5** ±0.5	76.7 ±0.7	101.2 ±1.2	0.332 ±0.003	5	32.7 ±1.0	74.0 ±0.4	96.7 ±0.7	0.339 ±0.012
Saskatoon, Saskatchewan (52)	6	34.6 ±0.8	78.6 ±0.9	104.3 ±1.5	0.332 ±0.011	6	32.8 ±0.4	75.5 ±0.5	93.2 ±0.9	0.331 ±0.005
St. James, Minnesota (44)	7	32.4 ±0.6	76.9 ±0.6	101.5 ±1.0	0.319 ±0.007	6	31.9 ±0.5	74.5 ±0.7	97.5 ±1.1	0.327 ±0.004
Dunkirk, Ohio (41)	11	29.4 ±0.5	77.8 ±0.5	102.6 ±1.4	0.290 ±0.006	4	28.2 ±0.6	72.9 ±0.6	93.9 ±1.4	0.301 ±0.008
Monticello, Illinois (40)	12	31.3 ±0.5	78.3 ±0.4	103.8 ±0.7	0.302 ±0.005	13	30.7 ±0.4	75.6 ±0.3	93.4 ±0.5	0.309 ±0.004
Columbus, Ohio (40)	6	30.0 ±1.1	77.8 ±0.4	103.7 ±2.2	0.290 ±0.014	4	27.8 ±1.3	72.2 ±0.5	90.5 ±3.7	0.308 ±0.010
Plainview, Texas (34)	6	29.2 ±0.4	77.1 ±0.8	101.8 ±1.3	0.287 ±0.006	6	28.3 ±0.5	74.3 ±0.7	97.2 ±1.2	0.292 ±0.005
Richmond, Virginia (37.5)	15	28.4 ±0.4	75.9 ±0.4	99.9 ±1.0	0.285 ±0.006	10	28.3 ±0.7	72.9 ±0.7	96.2 ±1.7	0.291 ±0.006
Tucson, Arizona (32)	5	26.6 ±0.8	76.8 ±1.0	101.3 ±1.7	0.262 ±0.007	8	27.2 ±0.6	74.7 ±0.6	97.8 ±1.0	0.278 ±0.005
Riverside, California (34)	5	28.1 ±0.6	76.4 ±1.2	100.7 ±2.0	0.280 ±0.010	8	27.1 ±0.4	73.2 ±0.4	95.0 ±0.8	0.285 ±0.003
Vero Beach, Florida (28)	6	27.7 ±0.4	77.0 ±0.5	101.6 ±0.9	0.272 ±0.003	6	26.5 ±0.8	75.3 ±0.7	98.8 ±1.1	0.269 ±0.009

\* Sample size.

\*\* Mean ± 1 S.E.

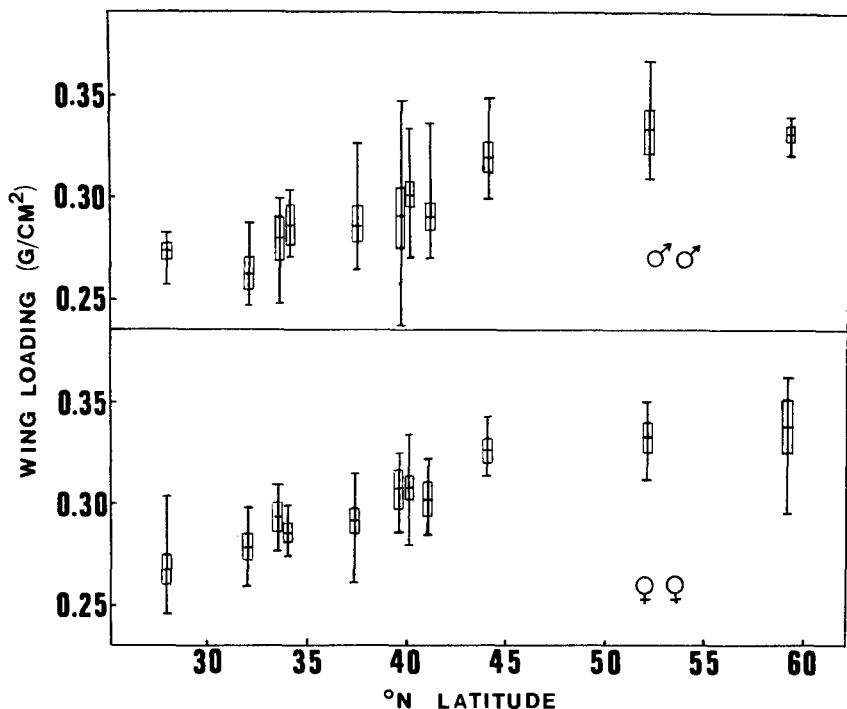


FIG. 2. Wing-loading in House Sparrows in relation to ° N latitude. The vertical line is the range, central horizontal line the mean, and the rectangle represents  $\pm 1$  S.E.

significant sexual difference in wing-loading and females had a greater wing-load at 9 of the 11 localities examined. Body weight varies geographically in both sexes and has been discussed elsewhere (Johnston and Selander 1964, Blem 1973a). I found no consistent geographic variation in wing chord or wing area in either sex. Wing-loading increases northward in both sexes, but seems to plateau at the 3 northernmost sites (Fig. 2). Analysis of variance indicates a significant latitudinal effect upon wing-loading in both sexes. The largest sparrow collected during this study, a 37.9 g male from Saskatchewan, also had the greatest wing-load ( $0.37 \text{ g/cm}^2$ ). Three other sparrows from northern localities were loaded more than  $0.35 \text{ g/cm}^2$ . In tests of artificially weighted birds (Table 2), difficulties in flying were first evident in a wing-loading range of  $0.33$  to  $0.35 \text{ g/cm}^2$ . This range is beyond the normal levels of free-living Richmond sparrows, but not that of northern birds. Severe difficulties were usually observed whenever wing-loading exceeded  $0.36 \text{ g/cm}^2$ . Although sparrows were loaded up to  $0.41 \text{ g/cm}^2$ , no bird failed to take off and all were able to fly at least one length of the test area.

TABLE 2  
FLYING ABILITY OF ARTIFICIALLY WEIGHTED MALE HOUSE SPARROWS

Flying ability	Number of birds	Range of wing-loading (g/cm <sup>2</sup> )
Natural flight	8	0.26-0.33
Rate of climb visibly impaired, less able to avoid recapture	6	0.33-0.35
Low flight, never able to fly more than 2 lengths of test area before recapture	7	0.36-0.39
Barely able to take off, flight less than 1 m in altitude	5	0.37-0.41

#### DISCUSSION

Concomitant geographic variation in body weight and wing length can occur several ways. For example, in some species of tits (*Parus*), body weight and wing length increase simultaneously and are correlated with mean temperature of the coldest month (Snow 1954). In the Cardinal (*Cardinalis cardinalis*) there is a trend for increased wing length in the southwestern U.S. and Mexico, while body weight increases northward (Hamilton 1958). Johnston and Selander (1964, 1972, 1973) demonstrated that body weight in House Sparrows varies geographically in accordance with Bergmann's Rule and that wing length clinally increases with latitude and altitude.

If increased body weight is not accompanied by a proportional increase in wing area, it is possible that wing-loading may come into selective conflict with other benefits of increased size, particularly late in each cycle of daily activity when fattening and contents of the digestive tract are at a maximum. Calhoun (1947) demonstrated that average wing length in some U.S. populations of the House Sparrow had increased more than 1 mm between the time of introduction and 1930. This suggests there is selection for increased wing length, although the corresponding changes in body weight are not available.

Wing-loading is not extreme within the area in which the House Sparrow has been long established, but is a potential problem at extreme northern sites (Fig. 2). Blem (1973a) analyzed carcasses of House Sparrows from a wide latitudinal range and found a northward increase in body weight of 6 g. The additional weight consisted of water (48%), fat (31%), lean dry weight (17%), and feathers (4%). Avian races in northern or elevated parts of a species range need to accumulate greater energy reserves for overnight survival because of longer winter nights and/or lower ambient temperatures. Greater fat deposits and increased weight of gut contents would result in

heavier wing-loads. Selection might favor increased wing length and/or area to offset such loads and may likewise favor increased mass of breast muscle. House Sparrows at the northern edge of the range are loaded to an extent determined to affect flying ability in laboratory tests. Partial protection from the cold and a nearby food source may allow them to exist here when they might not otherwise. At northern collecting sites, sparrows make extensive use of grain elevators or other protective man-made structures.

There is considerable controversy about the adaptive value of size variation in terms of energetics, but it is possible that some of the wing and body size increases in cooler climates are responses to the necessity for carrying about greater amounts of food in the digestive tract and supporting larger amounts of depot fat. Mathematically eliminating the fat needed to survive cold winter nights reduces wing-loading at northern sites to levels near that of more southerly locations. In addition, increased lean dry weight at northern locales is probably partly composed of increased mass of breast muscle, another adaptation that may be related to carrying greater loads.

Mayr (1956) suggests "multiple solutions for biological needs are the general rule in evolution." Likewise, size gradients may be solutions to multiple needs. Increased size in birds may simultaneously provide better insulation with no relative increase in plumage (Blem 1973b), a relatively greater mechanism for heat production (Blem 1973a), and a solution for increased wing-loading at northern sites.

#### SUMMARY

Wing-loading of House Sparrows in midwinter increases northward and is greater in females than males. Experimental tests of wing-loading in male House Sparrows indicates that sparrows at northernmost localities may be excessively weighted by increased amounts of fat and water needed to survive long, cold winter nights. Survival may result from their close association with man.

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