

BODY WEIGHTS OF BIRDS: A REVIEW

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Although body weights are relevant to many branches of avian biology, they have not been recently reviewed. I here survey sources and uses for weight data, with reference to such variables as time of day, season, year, sex, migration, geography, climate, buoyancy, food size, and habitat. In addition, I consider uses of weights as standards for body size, in systematics, in assessing the physiological condition of individuals, and in analyses of ecological communities. Excellent previous reviews of this subject by Nice (1938), Baldwin and Kendeigh (1938), Amadon (1943), Fisher (1955), Blake (1956), and Perrins (*in* Thomson 1964) do not cover many recent discoveries and interpretations.

OBTAINING WEIGHTS

Pettingill (1970:446), Bub (1967:61-63), and Giles (1963:4-5) outlined weighing techniques in which beam balances or small spring scales are used (Berger 1968), with live birds usually being confined in tubes or chambers for weighing. Records of age, sex, fat levels, time, locality, and other variables are useful in analyzing weights. Baldwin and Kendeigh (1938), Owen (1962), and others have properly emphasized the need for large samples of weights in comparing similar populations. For some studies weights need to be taken as uniformly as possible, e.g., sampling diurnally feeding species early in the morning to minimize variation from daily weight cycles (Kontogiannis 1967). Breeding birds are best compared at known stages, because some species (e.g., certain penguins) vary greatly in weight through the breeding cycle, and females of many species vary considerably during the period of egg laying.

After being banded, many, but not all, migratory birds lose weight for a day or two (Leberman and Stern 1977). This phenomenon can, of course, be detected only in recaptured individuals who are ordinarily a minority (commonly less than 20%) of the migrants initially captured. The cause of weight declines in many recaptured migrants is not well understood, and the reasons for the individual variations are unknown. Possible causes of the weight decreases include (1) illness or other abnormalities, (2) recovery time for migrants that have completed

particularly stressful flights, (3) failure to locate food in an unsuitable or unfamiliar area, (4) failure to obtain enough food due to social subordination (Rappole and Warner 1976), (5) reduction in weight that is adaptive for prolonged stopovers, (6) loss of opportunity to feed through time spent in nets or being processed by banders, and (7) handling shock (Mueller and Berger 1966, Leberman and Stern 1977). Determining the relative contribution of these factors in any particular case can be difficult. Further attention should also be given to the possible occurrence of weight decreases due to handling of nonmigratory birds (Rogers and Odum 1966). To avoid possible effects of handling, wild birds might in some cases be weighed without capture by use of weighing perches (Moore 1953, Ellis and Varney 1974) and uniquely marked with dye applied by remote control.

Ornithologists have assumed that a freshly killed bird weighs the same as a live one, but this may not be valid. Von Bröckel (1973) weighed 237 Garden Warblers (*Sylvia borin*) alive and 80 others within 15 min after death and found that the dead birds averaged more than 1 g (5.5%) lighter. Possible differences in weight between life and death need more study. Under ordinary laboratory conditions dead birds gradually lose weight over a period of hours by desiccation. However, dead birds that are weighed, then frozen in sealed plastic bags, kept in humid conditions, and later thawed and reweighed, lose relatively little weight (2% or less) over a period of weeks (Grant 1965, Holmes 1976).

Researchers sometimes cannot directly obtain weight data and therefore turn to the literature. Although weights have been published for thousands of species, they are often difficult to find. Examples of publications listing many North American weights are Irving (1960), Hartman (1961), and Clench and Leberman (1978), but others are too numerous to mention. Brief summaries of weights should ideally include the sources of data, the mean, standard deviation, range, and sample size for ten or preferably more adults of each sex in specified conditions, e.g., early in the day at a particular stage in the breeding season. Samples from representative geographic localities are also desirable.

However, few published data meet these standards. Frequently samples are small, and weights have been obtained at varied, unspecified times of day and at different times of year. Data from different investigators are often not comparable, for some specify age, sex, fat, migration status, and other variables, whereas others do not. Moreover, sources sometimes partially repeat data, e.g., one reference including weights from another but not clearly stating the nature of the duplication. Users of published weights should be cautious, for pooling heterogeneous data from the literature can be misleading. Alternatively, one might use only certain kinds of published data and omit others, but to do this uniformly is often difficult. Explicit details should be given if weights and other measurements are taken from different published sources (Blake 1956).

Adequate samples of weights are unavailable for many common species. For example, I know of no published mean weights for series of males and females for wild or captive adult Ostriches (*Struthio camelus*), which are of special interest as the heaviest living birds. During the past 40 years weighing has become common in banding and collecting, and thousands of weights remain unpublished and dispersed in the files of banders and on specimen labels. Regrettably, most museum specimens collected before 1940 lack data on weights, but collections at the Museum of Vertebrate Zoology, University of California, Berkeley, and the Museum of Zoology, University of Michigan, Ann Arbor, contain many North American specimens with field weights.

VARIATION WITHIN SPECIES

Daily. The weight of many birds fluctuates during a day with daily increases of 5 to 10% (exceptionally 15%) over minimal weight occurring in many small land birds of both temperate and tropical regions (Baldwin and Kendeigh 1938, Snow and Snow 1963, Ward 1969, King 1972, Blem 1976). Weight is usually greatest in late afternoon and least after a night of fasting. This daily cycle in weight is due to variation in gut contents, fat deposits, size of various organs, glycogen stores, and other factors (King 1972, Blem 1976). In winter many small birds must feed daily to survive the following night (King 1972, Blem 1976) though larger birds can live longer without food (Kendeigh 1945). In summer at high latitudes in continuous daylight, birds can feed at any time and

daily cycles in weight are less pronounced (Irving 1960). Much remains to be learned about effects of temperature and photoperiod in influencing daily weight cycles and about geographic and taxonomic differences in these cycles.

Seasonal and migratory. Weights are often high during winter in north temperate areas and during dry seasons in tropical regions (King 1972). A greater weight in winter of many small, north temperate species reduces the chance of starving to death in severe weather (Blem 1973, Calder 1974). In some species, individuals are heavier during colder parts of the winter (Baldwin and Kendeigh 1938, King 1972). In contrast, Wood Pigeons (*Columba palumbus*) in Scandinavia weigh less in winter (Ljunggren 1968). Individual ducks near the northern limits of their winter range decrease in weight through the winter while using fat reserves accumulated in fall (Ryan 1972). Limited evidence suggests that in uniform tropical conditions resident species do not vary seasonally in weight (Ward 1969), although such fluctuations do occur in tropical areas with dry seasons (McNeil 1971). At least some species of birds taken from the field and kept under constant laboratory conditions continue to exhibit seasonal fluctuations in weight for a year or longer, indicating the presence of endogenous circannual rhythms that influence weight even in the absence of immediate environmental stimuli (King 1968, Gwinner 1977). Under field conditions the timing of the endogenous rhythms is entrained by photoperiods to the natural cycles. The neuroendocrinological bases for long-term endogenous cycles in weight remain poorly understood, but for the White-throated Sparrow (*Zonotrichia albicollis*) experiments indicate that changes in the timing of release of corticosterone and prolactin control seasonal variations in fat stores (Meier and Burns 1976).

In many species reproduction, including egg production, incubation, and parental care of young, makes major energy demands sometimes resulting in loss of weight; Ricklefs (1974) cited examples for grouse and finches. For the female Snow Goose (*Chen caerulescens*), accumulation of nutrient reserves, reflected in body weight prior to breeding, is an important factor in determining clutch size and even survival of the bird through the breeding season (Ankney and MacInnes 1978). Marked shifts in the weight of females are in some cases associated with the stage of egg production (Calder and Rowe 1977). In certain penguins, fat reserves increase

before incubation, and weight then declines as the fat is consumed. As would be expected, birds that incubate continually for days or weeks show major decreases in weight as in Emperor Penguin (*Aptenodytes forsteri*), which loses up to 40% of body weight (Le Maho 1977). In contrast to such extremes are birds that carry only small reserves of fat during much of the breeding season such as passerines in deciduous forests of New Hampshire during years of relatively abundant insect food (Holmes 1976); in this case it would be interesting to know the levels of fat reserves in summers when food is less readily available.

Changes in weight during molt differ markedly among taxa. Species in which molt interferes with feeding can lose considerable weight (e.g., penguins; Williams et al. 1977). The extreme contrast is provided by species that become heavier during molt [e.g., Bullfinches (*Pyrrhula pyrrhula*); Newton 1966].

Migrants exhibit some of the greatest weight fluctuations. Although some begin migrating with little or no extra fat reserves (Odum et al. 1961, D. W. Johnston 1966, Berthold 1975), long-distance migrants typically accumulate large fat deposits just prior to long flights over unfavorable habitats, e.g., oceans or deserts for landbirds. In some species at least, circannual rhythms strongly influence the timing of weight increase for migration (Gwinner 1977). The extent of weight gain before migration appears to be related to the distance to be flown (Odum et al. 1961, Berthold 1975) and tends to be greatest for those parts of the migration that are fastest and most precise temporally. For long migratory flights by small birds, weight can increase from 50% to 100% above non-migratory values. Although fat as a major energy source accounts for most of the weight changes during migration, weights of fat-free components also change (e.g., see Rogers and Odum 1966, Fry et al. 1970, Berthold 1975). In addition, fat-free weights can differ between spring and fall (King 1963). During prolonged migratory flight over inhospitable environments, birds may become emaciated, sometimes weighing less than ordinary fat-free levels due to decrease in both fat and other components (Rogers and Odum 1966, Pennycuik 1975). Weight increases before migration are often proportionately greater for birds flying into relatively severe climates, e.g., in north temperate birds flying north in spring as opposed to south in fall (King 1963, Berthold 1975).

Age. In many species, immature birds remain lighter than adults after the end of parental care. Mueller et al. (1976) suggested that such lower weight and a lower wing loading of immature Goshawks (*Accipiter gentilis*) may reduce energy expenditure and thus lessen the need for prey when foraging behavior has not yet matured. In contrast are species whose young outweigh adults for a brief time after fledging, e.g., some seabirds in which a high weight at fledging may provide extra energy reserves to sustain the young while they learn how to forage (Lack 1968).

Year-to-year variations. Birds often vary in weight from year to year depending on climate and food availability (Cooch et al. 1960, Redfield 1973, Decoux 1976). Such variations have apparently not yet been reported for small birds (less than 25 g) but can be expected to occur.

Sexual dimorphism. In most avian species males are larger (Amadon 1959) as indicated by linear measurements and frequently confirmed by weights. In many species the sexual differences are slight, however, and females during egg formation often outweigh the males (Amadon 1959). Females are consistently heavier in tinamous, the parasitic Black-headed Duck (*Heteronetta atricapilla*), some ratites, certain hawks and owls, button quail, a number of Charadriiformes, some hummingbirds, and a few dicæids (Amadon 1959, Weller 1967, Snyder and Wiley 1976). The adaptive significance of sexual size dimorphism doubtless varies among taxa and remains poorly understood and controversial with authors differing on the possible roles of sexual differences in aggressiveness, parental care, energetics, and foraging (Weller 1967, Selander 1972, Hespenheide 1973, Downhower 1976, Snyder and Wiley 1976, Amadon 1977). An analysis by R. F. Johnston et al. (1972) revealed that sexual dimorphism in weight of House Sparrows (*Passer domesticus*) involves not only sexual selection but also sexual differences in response to selection by climatic variables as indicated by a severe winter storm that favored males of larger size but females of intermediate size.

Geographic variation. Weights of a species often vary geographically. The Canada Goose (*Branta canadensis*) is a well-known, dramatic example in which birds of the largest subspecies are, within a sex, two to three times heavier than those of the smallest subspecies (Palmer 1976), if indeed such extremes do still belong to a single species. In

another example, the Ipswich Sparrow (*Passerculus sandwichensis princeps*), which breeds predominantly on Sable Island off Nova Scotia, averages slightly more than 25.5 g yet interbreeds to a limited extent on the mainland with a Savannah Sparrow population (*P. s. savanna*) averaging less than 20 g (Stobo and McLaren 1975).

The intraspecific tendency for landbirds to weigh more in the cooler and drier parts of their range (Rand 1961a, Tomlinson 1975), termed Bergmann's Rule, has been studied mainly with wing lengths (James 1970), but weights vary similarly in many cases (Rand 1961a). Indeed, longer wing lengths may in some cases be closely associated with greater weights for reasons of aerodynamic efficiency (Blem 1975). The trend to greater weight in cooler and drier climates occurs not only over latitude and longitude but also with altitude (Moreau 1944, Nottebohm 1975, Köster 1976). The adaptive significance of geographic gradients in weight has been and continues to be highly controversial. Although larger birds have relatively less surface area and hence relative advantages in heat retention, this feature alone does not account for larger body sizes in cooler climates (McNab 1971, Calder 1974). One apparent major advantage of larger size in cooler climates is a lessened likelihood of starving to death in severe weather due to greater efficiency in use of stored energy reserves (Calder 1974, Ketterson and Nolan 1976). Furthermore, larger individuals may carry proportionately greater fat reserves (Blem 1973) and possibly derive benefits of added insulation from their large fat stores (Blem 1974). By contrast, in hot climates the relatively greater surface area of small birds should be advantageous in facilitating cooling (James 1970). However, McNab (1971) has emphasized geographic variations in food size and competitors as determinants of latitudinal gradients in weights. Although he mentioned also a tendency for insular populations to be larger than mainland representatives of a species, there are many contrary cases (Grant 1968), and the determinants of body weight in insular populations are not well understood.

Numerous exceptions to Bergmann's Rule warrant special attention (Rand 1961a, Niles 1973). In parts of the western continental U.S., mountainous topography favors great variation in climate over relatively short distances. Not surprisingly, many species there do not follow Bergmann's Rule (Rand 1961a, Salt 1963). For 53 such species Salt (1963) found that breeding weights tend to

be least in the center of the geographic range and to rise peripherally. He considered the region of lowest weight to be that of maximal adaptation of a species and also that occupied the longest. Correspondingly, the higher peripheral weights indicated both lesser adaptation and more recent occupation. I suggest that the species studied by Salt (1963) be reexamined to look for adaptations to local climates (cf. James 1970) which are presumably more severe in peripheral areas and thus favor greater energy stores in those areas. In addition, independent evidence should be sought for the historic directions of range occupation. The migratory status of most temperate and arctic species greatly complicates the analysis of geographic variations in weight by requiring consideration of seasonal differences.

Johnston and Selander (see R. F. Johnston 1972) found that largely nonmigratory populations of House Sparrows in North America and Europe generally follow Bergmann's Rule except in far northern North America, where winter day length may limit feeding time and hence body weight (Johnston 1972). The geographic size variation in North American populations arose within a century after the species was introduced from Europe. Johnston and Selander attributed this variation in part to regional genetic differences produced by natural selection, but obtaining direct evidence for a genetic basis for the phenotypic variation has been difficult (Johnston 1975). In contrast, Köster (1976) interpreted altitudinal weight differences of apparently recent origin in South America Smooth-billed Anis (*Crotophaga ani*) and Tropical Kingbirds (*Tyrannus melancholicus*) as probably not inherited. Laboratory experiments on captive nidifugous birds from different geographic areas reared under various climatic conditions might provide additional evidence on possible genetic bases for geographic variation in weights. For example, Bobwhites (*Colinus virginianus*) tend to be heavier in more northern localities (Ripley 1960), and the effect of genotype as opposed to climate on weight might be tested by rearing northern birds under southern conditions and vice versa.

EVOLUTION OF TAXONOMIC DIFFERENCES IN WEIGHTS

Independent gains and decreases of weight have occurred repeatedly during evolution as shown by marked weight differences between species within and among many families and

orders (Clark 1973). Among species with similar body shapes the relatively smaller surface area of larger birds reduces buoyancy for flight (Storer 1955). Accordingly, soaring and gliding species tend to have large surface areas for flight relative to their weights (Hartman 1961). Among diving birds, greater density (weight/volume) can counter buoyant tendencies and thus reduce the energy cost in diving (Storer 1960, Simpson 1976:45). For example, the Green-winged Teal (*Anas crecca carolinensis*), a dabbling duck, and the Bufflehead (*Bucephala albeola*), a diver, have similar body lengths, but the male Bufflehead regularly outweighs the male teal by 1.2 times or more (data from Palmer 1976). Ideally volumetric data should be used in such comparisons, but they are unavailable. Reduced buoyancy facilitates diving but hinders flight; the least buoyant birds are flightless divers such as penguins (Simpson 1976).

Biotic factors including size of food and its distribution greatly influence the evolution of taxonomic differences in weight. Larger species have advantages over smaller ones in usually eating not only larger food items but also a wider range of sizes of food (Wilson 1975). Although within a species social dominance is often not directly associated with weight (Swingland 1975), heavier species usually dominate lighter ones (Morse 1974) and thus are likely to win in direct competition for food or space. Smaller species have advantages in being able to use food items, nest sites, and perches too small for heavy birds, and small birds can also use denser vegetation for foraging and protection. Differences in weight among closely related, syntopic species help to reduce the likelihood of interspecific competition (Hespenheide 1973).

The lightest of birds are certain hummingbirds, a few of which weigh only about 2 g (Hartman 1961). Lasiewski (1963) reported that the Cuban Bee Hummingbird (*Calypte helenae*) weighs as little as 1.7 g, perhaps the smallest of all birds. Both miniaturization and energetics appear to limit minimal weights for birds (Kendeigh 1972, Greenewalt 1975). The heaviest of living flying birds reach 12 kg and include Mute Swans (*Cygnus olor*), condors (*Vultur*), and bustards (*Ardeotis*), although the Pleistocene fossil vulture *Teratornis merriami* and the Miocene seabird *Osteodontornis* were larger. The largest extant flightless birds are Ostriches, adult males of which often exceed 100 kg and sometimes more than 140 kg in captivity.

Rahn et al. (1975) calculated from egg volumes that the largest of the fossil elephant-birds (Aepyornithidae) might have weighed 1000 kg, a value twice that estimated by Amadon (1947) on the basis of body lengths. However, there is no clear evidence as to which estimate is more accurate, and weight estimates for fossils that are unlike modern genera are generally difficult to test. Factors limiting maximal size for both flying and flightless birds have not yet been critically analyzed. Biotic environmental factors in evolution have presumably generally restrained weights below the maxima that might be attainable if only physical factors were limiting.

USES OF WEIGHTS

Standards for body size. A standard for body size is frequently useful in comparing either individuals or species, and numerous references discuss this subject for birds (Amadon 1943, Calder 1974). Body size has usually been measured with weights or linear dimensions, either of which can be useful depending on the circumstances.

Weight summarizes the total biomass of an individual and is probably the most convenient standard for energetic comparisons. Furthermore, in comparing properties of distantly related taxa, e.g., woodpeckers and nuthatches, weight may be a better standard of body size than any linear measurement. Weights are handicapped, however, because of variation within individuals and within species. For determining the larger of two populations with very similar mean weights, it is sometimes more practical to use numerous linear measurements (e.g., of long bones) instead of weights.

If density is uniform, weight is proportional to volume which in turn is proportional to the cube of a linear dimension. Hence, for comparing linear dimensions the cube root of weight can be an advantageous standard in providing a clearer indication of proportions and in reducing variation in weights to a level more like that of linear measurements (Amadon 1943).

When weights are unavailable or inadequate, linear measures such as wing length must represent body size. Although wing length often correlates with weight within a species (Rand 1961a, b; but see Owen 1962), exceptions are frequent. For example, Grant (1965) found wing length to be a poor index of body weight in intraspecific comparisons between birds of the Tres Marias Islands and

mainland Mexico. Linear measures along the vertebral column have often been used to represent body size. However, these measurements can also mislead due to differences in column length relative to weight, as in the two closely related species of murrelets (*Uria*; Spring 1971). In other cases, addition of measurements of numerous bones has yielded a so-called skeletal sum, or multiplication of three skeletal measurements has formed an artificial "cubic" measurement (see R uger 1972 for references). Such computed indices should be compared with actual weights, or their cube roots, to be confident that the indices do indeed represent overall size (R uger 1972). Where many linear measurements are obtainable, as on skeletons, principal components analysis yields an abstract index of size and hence weight, though also influenced by shape (R. F. Johnston 1972, Niles 1973).

A major analytic method both within and among species is the allometric description of aspects of structure, physiology, and behavior with body weight as the standard for comparison (Calder 1974). Examples of features thus described include basal metabolism, dimensions related to flight, respiration, circulation, and temperature (Calder 1974, Greenewalt 1975). Ecological properties such as home range size (Calder 1974) and behavioral features such as characteristics of vocalizations (Bergmann 1976) can also be stated allometrically, although the scatter sometimes exceeds that for physiological properties (Calder 1974). Allometric equations are basically descriptive but within empirical limits may predict properties of species not studied directly. However, caution is advisable in extrapolating beyond empirical limits or in assuming causation on the basis of correlation. For example, both feather number and egg weight can be significantly correlated with body weight and with each other, but this does not indicate that egg weight determines feather number or vice versa.

Systematics. Differences in weights can sometimes serve along with other features to separate taxa (Amadon 1943, Moreau 1944). For example, Ripley (1960) used weights in distinguishing subspecies of the Bobwhite. Fisher (1952) presented data showing that Antarctic Fulmars (*Fulmarus glacialis*) on the average outweigh Northern Fulmars (*F. glacialis glacialis*), although this difference has apparently not been used in their systematics. Many higher categories are also separable by weights, e.g., titmice (Paridae)

and corvids (Corvidae), but I know of no case in which weights were explicitly used as a taxonomic character among the higher categories. Similar adult weights of different species might conceivably be a shared, derived character indicating evolutionary affinities, but weights themselves are simple characters and readily subject to convergence.

Assessing physiological condition. Weight changes often reflect critical events, as in sick individuals undergoing marked declines. Weights may indicate levels of metabolic reserves of breeding individuals (Korschgen 1977). Calder and Rowe (1977), for example, found indications that changes in weight of a female Brown Kiwi (*Apteryx australis*) were closely associated with stages of egg production.

Weights have also been used to calculate potential flight ranges of certain migrant species in which wing length correlates strongly with fat-free body weight. Measurements of wing length and total body weight then enable estimation of fat reserves and hence of potential flight range (Odum et al. 1961, McNeil and Cadieux 1972). However, wing lengths and fat-free weights are poorly correlated in other species so that the method is not always applicable (Moreau and Dolf 1970, Berthold 1975).

Community analysis. Weights have been used in analyses of the factors that influence differences in species diversity between communities (e.g., Karr 1968, 1971, 1976, Pearson 1975, Faaborg 1977). Weights and census data have often been combined to calculate the total weight (biomass) of a particular species or group of species in an area. For example, Willson (1974) found that total biomass of birds in Illinois grassland, shrub, and forest communities was not correlated with productivity of the vegetation or of the invertebrates in those communities. In another case, Salt (1957) assessed the relative efficiency of temperate zone communities on the basis of their proportion of large birds. As larger birds have a greater efficiency per gram (Calder 1974), a given amount of food can sustain a larger biomass of heavier birds than of lighter ones. In late successional stages of Wyoming coniferous forests, Salt found relatively more large birds and hence by his criterion a greater efficiency for the avifauna as a whole compared with earlier successional stages. Moreover, he suggested that birds might regularly serve as indices of metabolism and efficiency for entire biotic communities, a possibility that merits further study.

Many ornithologists have used body weights to estimate energy consumption by avian communities over periods of time. The calculations require census data on number of individuals per species, their body weights, allometric equations relating weight to basal metabolism, and estimates of other energy costs to assess total energy requirements (see, for example, Wiens and Innis 1974, Wiens and Scott 1975, Holmes and Sturges 1975). Although several assumptions must be made, the results lead to predictions that are potentially independently verifiable, e.g., through study of the feeding rates of individual birds.

SOME TOPICS FOR FUTURE STUDIES

My review of this subject disclosed many unsolved problems, several of which have already been mentioned. Weights have been most extensively reported for European and North American birds and additional data are especially needed for other avifaunas. For all regions, knowledge of geographic variation in weights is deficient due to lack of data, particularly for breeding and wintering populations. Relatively extensive data are available for a few species, such as the House Sparrow, but even for these species large populations remain relatively unstudied, e.g., the House Sparrow populations of the southern hemisphere. Amadon (1943) provided the most recent general discussion for birds on the relative variability of weights both within and among species, and the subsequently published data, widely scattered through the literature, have not been comprehensively analyzed.

Much research is needed on the determinants of weight of different species in relation to their food and habitat requirements. Rensch (1960) reviewed several papers reporting better learning abilities for birds from heavier populations or species (see also Stichmann 1962); such a tendency if widespread is of general interest in the evolution of body weights. The buoyancy differences among diving birds have not been extensively studied. Weights should be investigated as indicators of nutrient reserves and of energy requirements for individuals and populations. Moreover, weights should continue to be of major importance in studies of community organization.

SUMMARY

This survey covers procedures and problems in obtaining body weights in the field and

from the literature. Possible effects of handling live birds and of postmortem changes are briefly considered. Weight variation within species is discussed in relation to time of day, season, migration, year, age, sex, geography, and other factors. Evolutionary specializations include increased buoyancy in gliding and soaring species and reduced buoyancy in divers. Body weight is closely related evolutionarily to the foods consumed and to the structure of habitats. Weights are useful as standards for body size, in systematics, for assessing the physiological condition of birds, and in ecological community analysis.

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LITERATURE CITED

- AMADON, D. 1943. Bird weights as an aid in taxonomy. *Wilson Bull.* 55:164-177.
- AMADON, D. 1947. An estimated weight of the largest known bird. *Condor* 49:159-164.
- AMADON, D. 1959. The significance of sexual differences in size among birds. *Proc. Am. Philos. Soc.* 103:531-536.
- AMADON, D. 1977. Further comments on sexual size dimorphism in birds. *Wilson Bull.* 89:619-620.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-471.
- BALDWIN, S. P., AND S. C. KENDEICH. 1938. Variations in the weight of birds. *Auk* 55:416-467.
- BERGER, E. J., JR. 1968. Accuracy of Pesola spring scales and Harvard trip balances. *EBBA News* 31:107-108.
- BERGMANN, H.-H. 1976. Konstitutionsbedingte Merkmale in Gesängen und Rufen europäischer Grasmücken (Gattung *Sylvia*). *Z. Tierpsychol.* 42:315-329.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology, p. 77-128. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 5. Academic Press, New York.
- BLAKE, C. H. 1956. Weight changes in birds. *Bird-Banding* 27:16-22.
- BLEM, C. R. 1973. Geographic variation in the bioenergetics of the House Sparrow. *Ornithol. Monogr.* 14:96-121.
- BLEM, C. R. 1974. Geographic variation of thermal conductance in the House Sparrow *Passer domesticus*. *Comp. Biochem. Physiol.* 47A:101-108.
- BLEM, C. R. 1975. Geographic variation in wing-loading of the House Sparrow. *Wilson Bull.* 87:543-549.

- BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. *Am. Zool.* 16:671-684.
- BUB, H. 1967. Vogelfang und Vogelberingung. Teil 1. Ziemsens, Wittenberg Lutherstadt.
- CALDER, W. A., III. 1974. Consequences of body size for avian energetics, p. 86-144. *In* R. A. Paynter, Jr. [ed.], *Avian energetics*. Publ. Nuttall Ornithol. Club No. 15.
- CALDER, W. A., III, AND B. ROWE. 1977. Body mass changes and energetics of the Kiwi's egg cycle. *Notornis* 24:129-135.
- CLARK, G. A., JR. 1973. Convergence and parallelism in the evolution of birds. *Biologist* 55:112-118.
- CLENCH, M. H., AND R. C. LEBERMAN. 1978. Weights of 151 species of Pennsylvania birds analyzed by month, age, and sex. *Bull. Carnegie Mus. Nat. Hist.* 5.
- COOCH, F. G., G. M. STIRRETT, AND G. F. BOYER. 1960. Autumn weights of Blue Geese (*Chen caerulescens*). *Auk* 77:460-465.
- DECOUX, J. P. 1976. Regime, comportement alimentaire et regulation ecologique du metabolisme chez *Colinus striatus*. *Terre et Vie* 30:395-420.
- DOWNHOWER, J. F. 1976. Darwin's Finches and the evolution of sexual dimorphism in body size. *Nature* 263:558-563.
- ELLIS, D., AND J. VARNEY. 1974. Using telemetry to study the Golden Eagle. *Int. Foundation Telemetry J.* 1:14-18.
- FAABORG, J. 1977. Metabolic rates, resources, and the occurrence of nonpasserines in terrestrial avian communities. *Am. Nat.* 111:903-916.
- FISHER, H. I. 1955. Avian anatomy, 1925-1950, and some suggested problems, p. 57-104. *In* A. Wolfson [ed.], *Recent studies in avian biology*. Univ. of Illinois Press, Urbana.
- FISHER, J. 1952. *The fulmar*. Collins, London.
- FRY, C. H., J. S. ASH, AND I. J. FERGUSON-LEES. 1970. Spring weights of some Palaearctic migrants at Lake Chad. *Ibis* 112:58-82.
- GILES, R. H., JR. 1963. Instrumentation in wildlife investigations, p. 1-21. *In* H. S. Mosby [ed.], *Wildlife investigational techniques*. Second ed. Edwards, Ann Arbor, Michigan.
- GRANT, P. R. 1965. A systematic study of the terrestrial birds of the Tres Marias Islands, Mexico. *Postilla* 90:1-106.
- GRANT, P. R. 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.* 17:319-333.
- GREENEWALT, C. H. 1975. The flight of birds. *Trans. Am. Philos. Soc. N. S.* 65(4):1-67.
- GWINNER, E. 1977. Circannual rhythms in bird migration. *Annu. Rev. Ecol. Syst.* 8:381-405.
- HARTMAN, F. 1961. Locomotor mechanisms of birds. *Smithson. Misc. Collect.* 143:1-91.
- HESPENHEIDE, H. A. 1973. Ecological inferences from morphological data. *Annu. Rev. Ecol. Syst.* 4:213-229.
- HOLMES, R. T. 1976. Body composition, lipid reserves and caloric densities of summer birds in a northern deciduous forest. *Am. Midl. Nat.* 96:281-290.
- HOLMES, R. T., AND F. W. STURGES. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. *J. Anim. Ecol.* 44:175-200.
- IRVING, L. 1960. Birds of Anaktuvuk Pass, Kobuk, and Old Crow. *U.S. Natl. Mus. Bull.* 217.
- JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365-390.
- JOHNSTON, D. W. 1966. A review of the vernal fat deposition picture in overland migrant birds. *Bird-Banding* 37:172-183.
- JOHNSTON, R. F. 1972. Ecological differentiation in North American birds, p. 101-126. *In* R. T. Allen and F. C. James [eds.], *A symposium on ecosystematics*. Univ. Arkansas Mus. Occas. Pap. No. 4.
- JOHNSTON, R. F. 1975. Studies in phenetic and genetic covariation, p. 333-353. *In* G. Estabrook [ed.], *Proceedings of the 8th Int. Conf. of Numerical Taxonomy*. Freeman, San Francisco.
- JOHNSTON, 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.
- KARR, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. *Condor* 70:348-357.
- KARR, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* 41:207-233.
- KARR, J. R. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *Am. Nat.* 110:973-994.
- KENDEIGH, S. C. 1945. Resistance to hunger in birds. *J. Wildl. Manage.* 9:217-226.
- KENDEIGH, S. C. 1972. Energy control of size limits in birds. *Am. Nat.* 106:79-88.
- 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.
- KING, J. R. 1963. Autumnal migratory-fat deposition in the White-crowned Sparrow. *Proc. XIII Int. Ornithol. Congr. (1962)*:940-949.
- KING, J. R. 1968. Cycles of fat deposition and molt in White-crowned Sparrows in constant environmental conditions. *Comp. Biochem. Physiol.* 24:827-837.
- KING, J. R. 1972. Adaptive periodic fat storage by birds. *Proc. XV Int. Ornithol. Congr. (1970)*:200-217.
- KONTOGIANNIS, J. E. 1967. Day and night changes in body weight of the White-throated Sparrow, *Zonotrichia albicollis*. *Auk* 84:390-395.
- KORSCHGEN, C. E. 1977. Breeding stress of female eiders in Maine. *J. Wildl. Manage.* 41:360-373.
- KÖSTER, F. 1976. Über die Höhenanpassung von *Crotophaga ani* und *Tyrannus melancholicus* in den Anden Kolumbiens. *J. Ornithol.* 117:75-99.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LASIEWSKI, R. C. 1963. The energetic cost of small size in hummingbirds. *Proc. XIII Int. Ornithol. Congr. (1962)*:1095-1103.
- LEBERMAN, R. C., AND M. A. STERN. 1977. Handling-induced shock in migrant songbirds. *North Am. Bird-bander* 2:50-54.
- LE MAHO, Y. 1977. The Emperor Penguin: a strategy to live and breed in the cold. *Am. Sci.* 65:680-693.
- LJUNGGREN, L. 1968. Seasonal studies of Wood Pigeon populations. *Viltrevy* 5:435-504.
- MENAB, B. K. 1971. On the ecological significance of Bergmann's Rule. *Ecology* 52:845-854.
- MCNEIL, R. 1971. Lean-season fat in a South American population of Black-necked Stilts. *Condor* 73:472-475.
- MCNEIL, R., AND F. CADIEUX. 1972. Numerical

- formulae to estimate flight range of some North American shorebirds from fresh weight and wing length. *Bird-Banding* 42:107-113.
- MEIER, A. H., AND J. T. BURNS. 1976. Circadian hormone rhythms in lipid regulation. *Am. Zool.* 16:649-659.
- MOORE, N. C. 1953. A balance for weighing tits without capture. *Br. Birds* 46:103-105.
- MOREAU, R. E. 1944. Some weights of African and of wintering Palearctic birds. *Ibis* 86:16-30.
- MOREAU, R. E., AND R. M. DOLF. 1970. Fat, water, weights and wing-lengths of autumn migrants in transit on the northwest coast of Egypt. *Ibis* 112:209-228.
- MORSE, D. H. 1974. Niche breadth as a function of social dominance. *Am. Nat.* 108:818-830.
- MUELLER, H. C., AND D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. *Bird-Banding* 37:83-112.
- MUELLER, H. C., D. D. BERGER, AND G. ALLEZ. 1976. Age and sex variation in the size of Goshawks. *Bird-Banding* 47:310-318.
- NEWTON, I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108:41-67.
- NICE, M. M. 1938. The biological significance of bird weights. *Bird-Banding* 9:1-11.
- NILES, D. M. 1973. Adaptive variation in body size and skeletal proportions of Horned Larks of the southwestern United States. *Evolution* 27:405-426.
- NOTTEBOHM, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *Am. Nat.* 109:605-624.
- ODUM, E. P., C. E. CONNELL, AND H. L. STODDARD. 1961. Flight energy and estimated flight ranges of some migratory birds. *Auk* 78:515-527.
- OWEN, D. F. 1962. Wing length, body weight, and geography. *Wilson Bull.* 74:185.
- PALMER, R. S. [ED.] 1976. Handbook of North American birds. Vols. 2 and 3. Yale Univ. Press, New Haven.
- PEARSON, D. L. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. *Condor* 77:453-466.
- PENNYCUICK, C. J. 1975. Mechanics of flight, p. 1-75. In D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 5. Academic Press, New York.
- PETTINGILL, O. S., JR. 1970. Ornithology in laboratory and field. Fourth ed. Burgess, Minneapolis, Minn.
- RAHN, H., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.
- RAND, A. L. 1961a. Some size gradients in North American birds. *Wilson Bull.* 73:46-56.
- RAND, A. L. 1961b. Wing length as an indicator of weight: a contribution. *Bird-Banding* 32:71-79.
- RAPOLE, J. H., AND D. W. WARNER. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stop-over site. *Oecologia* 26:193-212.
- REDFIELD, J. A. 1973. Variations in weight of Blue Grouse (*Dendragapus obscurus*). *Condor* 75:312-321.
- RENSCH, B. 1960. Evolution above the species level. Columbia Univ. Press, New York.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152-292. In R. A. Paynter, Jr. [ed.], *Avian energetics*. Publ. Nuttall Ornithol. Club No. 15.
- RIPLEY, T. H. 1960. Weights of Massachusetts quail and comparisons with other geographic samples for taxonomic significance. *Auk* 77:445-447.
- ROGERS, D. T., JR., AND E. P. ODUM. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. *Wilson Bull.* 78:415-433.
- RÜGER, A. 1972. Funktionell-anatomische Untersuchungen an Spechten. *Z. wiss. Zool.* 184:63-163.
- RYAN, R. A. 1972. Body weight and weight changes of wintering diving ducks. *J. Wildl. Manage.* 36:759-765.
- SALT, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. *Condor* 59:373-393.
- SALT, G. W. 1963. Avian body weight, adaptation, and evolution in western North America. *Proc. XIII Int. Ornithol. Congr.* (1962):905-917.
- SELANDER, R. K. 1972. Sexual selection and dimorphism in birds, p. 180-230. In B. Campbell [ed.], *Sexual dimorphism and the descent of man*. Aldine, Chicago.
- SIMPSON, G. G. 1976. Penguins. Past and present, here and there. Yale Univ. Press, New Haven.
- SNOW, D. W., AND B. K. SNOW. 1963. Weights and wing-lengths of some Trinidad birds. *Zoologica* 48:1-12.
- SNYDER, N. F. R., AND J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol. Monogr.* 20.
- SPRING, L. 1971. A comparison of functional and morphological adaptations in the Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*). *Condor* 73:1-27.
- STICHMANN, W. 1962. Transpositionsversuche mit Haushuhnrasen stark verschiedener Körpergröße. *Z. Tierpsychol.* 19:290-320.
- STOBO, W. T., AND I. A. MCLAREN. 1975. The Ipswich Sparrow. Nova Scotian Institute of Science, Halifax.
- STORER, R. W. 1955. Weight, wing area, and skeletal proportions in three accipiters. *Proc. XI Int. Ornithol. Congr.* (1954):287-290.
- STORER, R. W. 1960. Evolution in the diving birds. *Proc. XII Int. Ornithol. Congr.* (1958):694-707.
- SWINGLAND, I. R. 1975. The influence of weather and individual interactions on the food intake of captive Rooks (*Corvus frugilegus*). *Physiol. Zool.* 48:295-302.
- THOMSON, A. L. [ED.] 1964. A new dictionary of birds. McGraw-Hill, New York.
- TOMLINSON, R. E. 1975. Weights and wing lengths of wild Sonoran Masked Bobwhites during fall and winter. *Wilson Bull.* 87:180-186.
- VON BRÖCKEL, K. 1973. Vergleichende Messungen an lebenden und frischtoten Gartengräsmücken (*Sylvia borin*). *J. Ornithol.* 114:114-122.
- WARD, P. 1969. Seasonal and diurnal changes in the fat content of an equatorial bird. *Physiol. Zool.* 42:85-89.
- WELLER, M. W. 1967. Notes on plumages and weights of the Black-headed Duck, *Heteronetta atricapilla*. *Condor* 69:133-145.
- WIENS, J. A., AND G. S. INNIS. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. *Ecology* 55:730-746.
- WIENS, J. A., AND J. M. SCOTT. 1975. Model estimation of energy flow in Oregon coastal seabird populations. *Condor* 77:439-452.
- WILLIAMS, A. J., W. R. SIEGFRIED, A. E. BURGER,

AND A. BERRUTI. 1977. Body composition and energy metabolism of molting eudyptid penguins. *Comp. Biochem. Physiol.* 56A:27-30.

WILLSON, M. F. 1974. Avian community organization and habitat structure. *Ecology* 55:1017-1029.

WILSON, D. S. 1975. The adequacy of body size as a niche difference. *Am. Nat.* 109:769-784.

Hundreds of additional references are included in a

more extensive bibliography and supplements that have been filed in the Josselyn Van Tyne Memorial Library, Museum of Zoology, University of Michigan, Ann Arbor, and the library of the Division of Birds, National Museum of Natural History, Washington, D.C.

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RECENT PUBLICATIONS

Ravens, Crows, Magpies, and Jays.—Tony Angell. 1978. University of Washington Press, Seattle. 112 p. \$14.95. Corvids have long been among the most intriguing of birds to mankind, and they have been credited with various admirable or sinister qualities. Angell here pays tribute to them with an easily readable text and many striking line drawings. He first gives a one-page description of each of the North American species and then discusses certain aspects of the family as a whole: roles of corvids in art and mythology, social behavior, feeding habits, and communication. Text and illustrations both reflect the author's appreciation for the birds. Speaking of the drawings in the Foreword, J. Fenwick Lansdowne says that "These are not intended to be portraits but rather are expressions of the birds' personalities. . . ." One of the most attractive bird books to have appeared in years. Bibliography.

The Gannet.—Bryan Nelson. 1978. Buteo Books, Vermillion, South Dakota. 336 p. \$25.00. Following hard on his encyclopedic *The Sulidae* (noticed in *Condor* 80:456), Nelson has written a new book that is chiefly about the best-known member of the family. This work is not an extract from the first; it is freshly written and is aimed at a more general audience. Five chapters cover the bird itself, numbers and distribution, breeding behavior and ecology, and habits at sea. Other chapters compare the sulids (with scant attention to other pelecaniformes) and relate the history of gannets and mankind. Many tables of data, maps, photographs, and a full bibliography. Illustrated with fine drawings by John Busby. Although this book is no substitute for its predecessor, it will amply serve ornithologists and birders who do not want such extensive coverage of sulids or cannot afford it.

The Art of Natural History/Animal Illustrators and Their Work.—S. Peter Dance. 1978. The Overlook Press, Woodstock, New York. 224 p. \$60.00. This sumptuous, oversize volume presents a selective history of zoological illustration, with emphasis on work that was duplicated by various means. Except for the era before printing, the author does not attempt to consider one-of-a-kind works of art. He restricts his coverage almost entirely to the work of western European and American artists, from 15th century woodcuts to 19th century colored lithographs. The major part of the book is a chronological account, the remainder being devoted to four special studies which did not fit into that framework. The volume is lavishly illustrated with reproductions of the artwork; the color plates are exceptionally fine. As Dance remarks, if this "somewhat personal interpretation of zoological art antagonizes some readers, they will surely find solace in looking at the illustrations, which are, after all, what this book is really about."

The Illustrated Bird.—Edited by Maggie Oster and designed by Sonja Douglas. 1978. Dolphin Books/Doubleday & Co., Inc., Garden City, New York. 80 p. Paper cover. \$6.95. This is a picture book about the portrayal of birds in art—as symbolic, decorative, or inspirational figures. In contrast to the preceding book, it is not concerned with illustrations of books about birds. Many of the examples are unfamiliar and they represent a wide variety of media, nationalities, periods, and artists. Reproduction of the color plates is generally excellent. The text is subordinate to the illustrations and is a mixture of snippets about natural history, mythology, and birds in human affairs, treated in a superficial manner. Essentially a coffee table book, this work may have value to scholars who will follow up the material themselves.