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Establishing body-size indicators in a study of female spruce grouse *Dendragapus canadensis*

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(With 2 figures in the text)

Seven measurements were taken from 72 adult and yearling spruce grouse *Dendragapus canadensis* hens collected over a 10-year period from north-eastern Ontario, Canada. A principal components analysis (PCA) indicated keel ridge length, keel total length, and femur length, these being the most representative measurements of general body size. Skeletal mass, caecal length, wing length, and foot length had lower character loadings on the first principal component axis (PC1), suggesting they are unreliable measurements of body size. Measurements taken from bones (i.e. keel, femur) were more representative of general body size than external morphometric measurements (e.g. wing and foot length) which ornithologists traditionally use to estimate body size. Pre-laying adults were the smallest individuals and pre-laying yearlings the largest in the population studied. A discriminant functions analysis (DFA) of the seven measurements, with separated body mass as an eighth variable, demonstrated distinct separation between pre-laying and post-laying groups of birds on the basis of separated body mass. Keel ridge length was further implicated as an effective variable in the discrimination of birds from different laying groups.

Introduction

Researchers have long explored the relationship between body size and a number of biological parameters (Peters, 1983; Schmidt-Nielsen, 1984). However, body size is difficult to define and, for that reason, body mass is often the simplest measurement of size. Body size is a primary determinant of mass, with bigger birds on average being heavier than smaller ones. Body mass is related to survival in wild turkeys *Meleagris gallopavo* (Porter, Nelson & Mattson, 1983) and to reproductive success in red grouse *Lagopus lagopus scoticus* (Jenkins, Watson & Miller, 1963) and in captive ruffed grouse *Bonasa umbellus* (Beckerton & Middleton, 1982, 1983). Mass has traditionally been employed in taxonomic studies (Amadon, 1943), but in females the seasonal variability associated with reproductive condition makes mass entirely unsatisfactory as a body-size indicator.

To investigate the relationship between body size and life-history traits or physiological characteristics, ornithologists therefore commonly use a linear dimension as an estimate of relative body size. This dimension should remain constant throughout the year (Moser & Rusch, 1988) and decrease the amount of measured variation within a sample of birds studied (Bailey, 1979). The most effective size indicator is that best correlated with all other morphological dimensions on the examined specimen.

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Ornithologists have measured wing length (Ringelman & Szymczak, 1985; Hepp, Kennamer & Harvey, 1990), but feather wear and variable annual fluctuations in feather growth make it unreliable. Rising & Somers (1989) encourage researchers to avoid measurements that are affected by variables inherently independent of body size (e.g. wear, moult), suggesting leg lengths, in particular, as being much more representative of overall body size. Foot or tarsus length has been employed specifically in galliform research (Naylor & Bendell, 1989; Robb, Martin & Hannon, 1992).

In waterfowl species, correlation with skeletal dimensions commonly provides the strictest indication of body size. Skeletal mass was predicted by body length and wing length in the American wigeon *Anas americana* and serves as an excellent body size indicator (Wishart, 1979). In Canada geese *Branta canadensis*, skeletal volume, measured by water displacement of excised bones, was accurately predicted by correlation with body length and mid-wing length (Moser & Rusch, 1988).

On single bones, the length of the external ridge of the keel is the most commonly used dimension for size estimation (Owen & Cook, 1977; Wishart, 1979; Hannon & Roland, 1984; Johnson *et al*., 1985; Burgess, 1987; Lozano, 1994).

Norman & Kirkpatrick (1984) used caecal length to estimate body size in ruffed grouse but found marked fluctuations in its value on a seasonal basis. Variations in the dimensions and masses of soft tissues occur with dietary changes between winter and summer (Pendergast & Boag, 1973; Fenna & Boag, 1974).

In this paper, I test the suitability of seven morphometric measurements, regularly used in avian research, to estimate body size of spruce grouse hens. I investigate whether adult and yearling hens can be effectively separated on the basis of body size. The effects of seasonality on body-size estimation are also examined in a comparison of pre-laying and post-laying hens. Variation in the size of hens may be indicative of differences in 'structural size' (Campbell & Dobson, 1992). Alternatively, hens may be of similar structural size but disparities in body mass may be apparent. This 'physiological' aspect of size relates to the allocation of resources to various body tissues which is directly measured in condition indices (Reynolds, 1993).

Methods

Study area

Spruce grouse hens were collected over a 10-year period (1982–1992) from forests in north-eastern Ontario about 150 km north of Sudbury, near Gogama (approximately 47 °N, 83 °W). A detailed description of the understorey and overstorey vegetation in the study area is provided by Naylor & Bendell (1989).

Groupings of hens for analysis

The majority of birds were shot either during the course of a removal and replacement study (Burgess, 1987) or as part of ongoing research (J. F. Bendell, pers. comm.). Some were accidentally killed during noosing (Zwickel & Bendell, 1967) and others were victims of lynx *Felis lynx*, black bear *Ursus americanus*, or goshawk *Accipiter gentilis* predation.

Individual birds were classified as adults or yearlings using the method of Szuba, Bendell & Naylor (1987). They were then categorized at the simplest level into being either from the pre-laying or the post-laying period. Laying dates were known for the majority of hens (Szuba, 1989; Bendell, unpubl. data) which were

TABLE I

Reproductive periods of spruce grouse hens. Adapted from Szuba (1989)

Age	Period	
	Pre-laying	Post-laying
Adults	10 March–15 May (11)	29 May–18 July (14)
Yearlings	1 March–18 May (31)	28 May–18 August (16)

Note: sample sizes appear in parentheses

assigned confidently to a group according to their time of death (Table I) within particular years. The reproductive status of all hens was known from the size and mass of the oviduct which were always recorded during the necropsy, providing information about oogenetic events.

Field measurements

Wing length was defined as the distance from the condyles of the humerus to the distal end of the second phalanx on a straightened and flattened wing and was measured to the nearest 0.5 mm. With the leg bent, foot length was measured to the nearest 1 mm from the back of the joint between the tarsometatarsus and the tibiotarsus to the end of the middle toe. Body mass of each hen was measured to the nearest 5 g using a Pesola spring balance.

Necropsy procedure

Carcasses of birds were placed in sealed plastic bags immediately after recovery. They were either necropsied fresh or after freezing. The caeca were dissected, emptied by flushing through with distilled water and measured to the nearest 0.5 mm. The separated body mass variable was calculated by subtracting the combined masses of crop contents and egg load (i.e. mass of developing eggs in the oviduct) from body mass.

The wings were removed by cutting through the ligaments and disarticulating the humerus from the radius and ulna. The lower legs (i.e. fibula, tibiotarsus, tarsometatarsus, and the phalanges), the pygidium, and the skin were removed. Following a lateral cut through the parietal and frontal bones of the cranium, the brain of each specimen was excised.

All remaining soft tissues were processed according to routine necropsy protocol (Schemnitz, 1980). The remaining partial skeleton was scraped clean to remove any residual soft tissues before air drying for at least 10 months.

Preparation of skeletons

Skeletons were cleaned by a colony of buffalo beetles *Dermestes vulpinus* at the Royal Ontario Museum, Toronto. Cleaning took an average of 17 days after which the remains of the cranium and mandible were disarticulated from the first vertebra and discarded to standardize the skeletal mass measurement across all specimens. Skeletons were weighed on an electronic balance (Sartorius 2002 MP1) to the nearest 10 mg.

Femur and keel measurements were taken using dial callipers (Westward Precision Plastic Measuring Instruments) to an accuracy of 0.01 mm. The femur length measurement was the distance from the tip of the external condyle to the tip of the greater trochanter above the femoral head. Two keel measurements were obtained. The keel ridge length measurement extended posteriorly from the tip of the sternal crest to its proximal end. Keel total length was measured from the mesial caudal process to the cranial process of the manubrium.

Statistical analysis

Investigation of the appropriate morphometric dimension(s) which best indicated body size was carried out by principal components analysis (PCA), procedure PRINCOMP (SAS Institute Inc., 1988). In combination with the PCA that best summarized total variation in the entire sample of spruce grouse hens, a canonical discriminant functions analysis (DFA) was performed, procedure CANDISC (SAS Institute Inc., 1988), which best summarized the between-age and -laying group variation. The PCA and DFA quantified the power of potential body-size indicators to differentiate between the comparative groups and to explain the variance in all morphometric measurements.

Results

The means, ranges, and coefficients of variation were obtained for each of the proposed body-size indicators (Table II), as well as for separated body mass. The two mass variables (separated body mass and skeletal mass) have the highest coefficients of variation, with the former also having the highest variance of all the variables. Separated body mass varied quite markedly in the sample of birds, and it was therefore omitted from the PCA; its inclusion might have severely disrupted the loadings of the variables on the first principal component (PC1).

A PCA was carried out on morphometric measurements taken from adults and yearlings in both laying periods. Principal components were extracted from a matrix of correlations among the seven variables considered (Table III), yielding three eigenvectors with eigenvalues greater than one. The first four eigenvectors explained 81.3% of the total variation in the original matrix, with the first eigenvector alone explaining 37.5% of the total. Associated character loadings were positive (Table IV), this unipolar axis indicating that the PC1 scores were largely a measure of body size. Relatively high degrees of correlation between PC1 and the measured variables, and an eigenvalue of 2.63, indicated that individual birds with a high value on this axis had large femora and keels.

Figure 1 shows PC1 and PC2 represented graphically. There is as much variation in body size in adult birds as there is in yearlings. Pre-laying adults are perhaps the smallest individuals and pre-laying yearlings the largest.

TABLE II

Means, ranges (minimum to maximum), and coefficients of variation (CV) of eight body-size measurements for 43 spruce grouse hens (adults and yearlings)

Variable[a]	Mean	Range	CV
Caecal length	334.0	270.0–420.0	11.44
Wing length	101.0	83.0–136.5	8.34
Foot length	55	77–90	3.69
Femur length	55.09	48.81–57.35	2.69
Keel ridge length	75.07	65.62–80.42	4.01
Keel total length	89.58	84.20–93.93	2.58
Skeletal mass	8.80	6.37–14.95	18.96
Separated body mass	460	340–540	10.60

[a]Measurements are in millimetres except for mass variables (in g)

TABLE III

Correlations among the seven measurements of size for the 43 spruce grouse hens

Size measurement	Caecal length	Wing length	Foot length	Femur length	Keel ridge	Keel total length	Skeletal mass length
Caecal length	1.00	0.17	0.19	0.11	0.12	0.17	0.17
Wing length		1.00	0.38*	0.31*	0.20	0.24	0.02
Foot length			1.00	0.44†	0.14	0.28	0.11
Femur length				1.00	0.40†	0.52‡	0.17
Keel ridge length					1.00	0.78§	0.10
Keel total length						1.00	0.16
Skeletal mass							1.00

$*P \leqslant 0.05$; $^{\dagger}P \leqslant 0.01$; $^{\ddagger}P \leqslant 0.001$; $^{\S}P \leqslant 0.0001$

PC2 is a balanced axis with keel dimensions loading negatively and the remaining characters loading positively (Table IV). While PC2, with an eigenvalue of 1.17, provided very little insight into the variation in femur length and skeletal mass, it indicated that individuals with a high value on this axis had a relatively short keel ridge length and relatively long feet and wings. PC2 is a measurement of body shape and, from graphical interpretation, there appears to be much more variation in adult body shape than there is in yearlings.

PC3 had an eigenvalue of 1.04 and high degrees of correlation with some variables, but its significance in this kind of morphometric study is hard to rationalize without further analysis.

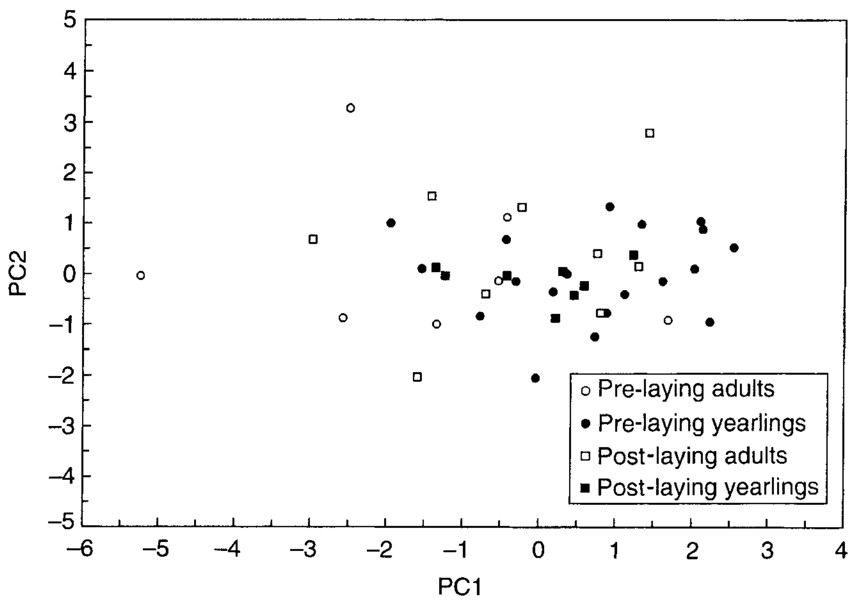

FIG. 1. Plot of first (PC1) and second (PC2) principal components from a principal components analysis of seven morphometric measurements from 43 spruce grouse hens.

TABLE IV

Character loadings on principal component axes (PC1, PC2, and PC3) for a principal components analysis based on a correlation matrix for seven morphometric measurements taken from spruce grouse hens

	Principal component		
Variable	PC1	PC2	PC3
Caecal length	0.21	0.35	0.49
Wing length	0.33	0.43	−0.34
Foot length	0.36	0.51	−0.20
Femur length	0.47	0.04	−0.12
Keel ridge length	0.45	−0.52	−0.01
Keel total length	0.51	−0.39	0.00
Skeletal mass	0.18	0.09	0.77
Eigenvalue	2.63	1.17	1.04
% Variance explained	37.5	16.7	14.9

Separation of laying and age groups using body-size indicator(s)

The PCA reduced the seven-dimensional variable space to a four-dimensional one with a loss of 18.7% of the original variance. The three potential body-size indicators (keel ridge length, keel total length, and femur length) were well correlated with PC1. How efficiently will they allow differentiation between adult and yearling birds in both laying groups?

A DFA was carried out on the seven morphometric measurements employed in the PCA, and separated body mass was included as an additional test variable. Univariate statistics provided significant differences for six of the eight characters, the largest F for this group of variables being 18.69 (*d.f.* 3, 39) for separated body mass and the lowest being 3.64 for the keel total length. A

TABLE V

Standardized character loadings on discriminant axes (CAN1 and CAN2) for a discriminant functions analysis for eight morphometric measurements taken from spruce grouse hens

	Canonical variable	
Variable	CAN1	CAN2
Caecal length	0.36	1.04
Wing length	−0.49	−0.29
Foot length	−0.06	−0.09
Femur length	−0.18	1.04
Keel ridge length	−0.64	0.73
Keel total length	0.20	−0.27
Skeletal mass	0.43	−0.09
Separated body mass	1.14	−0.32
Eigenvalue	2.50	1.54
% Variance explained	58.4	36.1

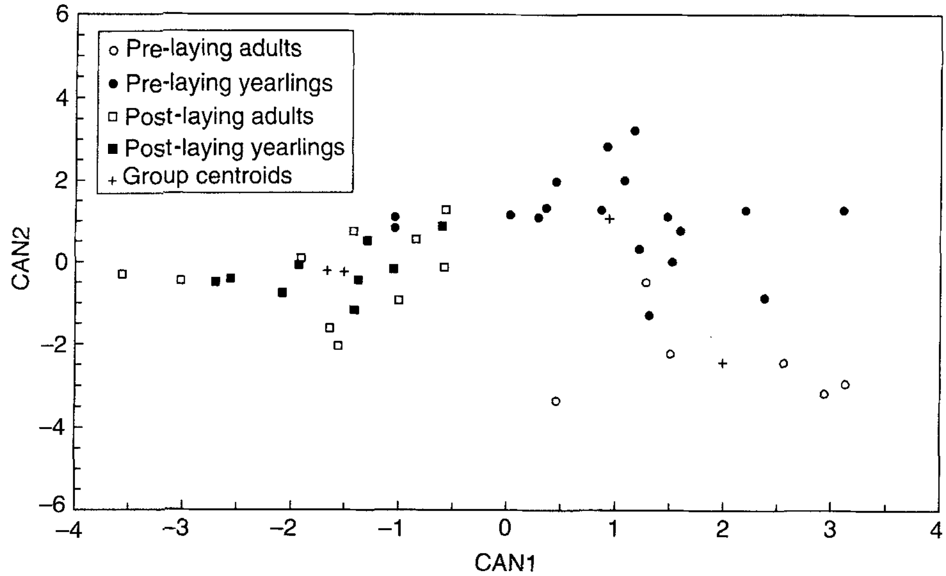

FIG. 2. Plot of first (CAN1) and second (CAN2) discriminant axes from a discriminant functions analysis of eight morphometric measurements from 43 spruce grouse hens.

MANOVA provided strong evidence of multivariate differences between group centroids (Wilk's $\lambda = 0.0909$, F Approx. = 5.00, *d.f.* 24, 93.41, $P \leqslant 0.0001$).

The first two canonical variables provided significant discrimination between age and laying groups of birds ($P \leqslant 0.0001$ for CAN1; $P \leqslant 0.0002$ for CAN2). They explained virtually all of the inter-group variance (Table V). The third axis was unstable and its discriminatory power was not significant with respect to group separation ($P \leqslant 0.28$).

The first discriminant axis (CAN1) separated the pre-laying birds (adults and yearlings) from the post-laying individuals (Fig. 2). Standardized character loadings (Table V) suggested that birds with higher CAN1 scores (pre-laying adults and yearlings) tended to have greater separated body masses but shorter keel ridge lengths and wing lengths than birds with lower CAN1 scores (post-laying adults and yearlings). The second discriminant axis (CAN2) provided poor resolution between the age and laying groups of hens. Individuals with higher CAN2 scores tend to have longer caeca and femora than those with lower scores.

Discussion

The results from the PCA and their implications for a body-size indicator in spruce grouse were consistent with findings of other galliform studies (Modafferi, 1975; Brittas & Marcström, 1982; Hannon & Roland, 1984; Burgess, 1987). Skeletal mass was a poor indicator with the lowest character loading on PC1. So too was caecal length reflecting its marked variation in length with the onset of the spring dietary changes (Pendergast & Boag, 1973; Fenna & Boag, 1974). Breitenbach, Nagra & Meyer (1963) found that the lower the quality of food, the greater the length of small and large intestines (including the caeca) in ring-necked pheasants *Phasianus colchicus*. Necropsy records of spruce grouse hens in this study indicated that a dietary shift occurred from the pre-laying to the post-laying period (Reynolds, 1993). Nine of 10 pre-laying adults and 20 of 24 pre-laying yearlings had gizzards containing over 80% jack pine *Pinus banksiana* needles. In contrast, only five of 14 post-laying adults and five of 16 post-laying yearlings showed any evidence of conifer browsing.

Wing length was poorly associated with PC1 with a character loading of 0.33, reinforcing the warnings of Rising & Somers (1989) to avoid wing length measurements as size indicators because of unpredictable feather wear and differential post-moult growth from one individual to another. In a practical sense, wing length is difficult to measure accurately in the field as the wing naturally curves and the distal end of the second phalanx is difficult to locate. Similarly, for the foot length measurement, locating the tibiotarsus-tarsometatarsus joint is difficult on live birds, highlighted in the poor association of foot length with PC1 (character loading of 0.36).

Femur length, keel ridge length and keel total length were the three dimensions best correlated with PC1, and are the most reliable measurements of body size in the overall sample of spruce grouse hens.

In discrimination of birds from different age and laying groups, the results from the PCA suggested that pre-laying adults were among the smallest of all birds in the sample population and pre-laying yearlings were among the largest. Although not a considered variable in the PCA, the separated body mass measurement, with a loading on CAN1 of 1.14, was implicated in the DFA to be of much value in separating the laying and age groups of hens. Keel ridge length also had a high character loading (−0.64) and therefore it is not only a valuable size indicator for entire sample assessment, but also for inter-group differentiation. A character loading of −0.49 may indicate wing length could be of some discriminatory value but it is an unreliable indicator in most birds, as discussed above. Leverton (1989) found significant differences in wing length between adult and yearling blackbirds *Turdus merula* that could not be attributed to body-size differences alone.

These age-related differences are opposed to those reported in other Galliformes. In blue grouse *Dendragapus obscurus*, yearlings were smaller than adults in spring (Redfield, 1973) and the same was found in spruce grouse by Szuba & Bendell (1984) and Naylor & Bendell (1989). In these studies, however, body mass was used which is a crude size indicator compared to the PCA-derived measurements used in this study.

Although this investigation was carried out on dead birds, it is hoped that the conclusions and recommendations are just as applicable to live spruce grouse. Freeman & Jackson (1990) discuss the usefulness of an external morphological element in the assessment of body-size of birds in the field but urge the researcher to consider external metrics of many different body components before proposing a single measurement. Their advice is heeded in this study. Femur length may be difficult to measure with location of the proximal end of the bone being problematic in live specimens. In a practical sense, ridge length would be the easiest of the two keel dimensions to record through the overlying breast muscle. This measurement may be the most precise of all morphometric measurements that could be used to assess the body-size of a bird in the field.

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