

BODY LENGTH AND WING LENGTH PROVIDE UNIVARIATE ESTIMATES OF OVERALL BODY SIZE IN THE MERLIN¹

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Abstract. I analyzed the variation in body size among Merlins using nine morphological characters. Repeatabilities did not differ between bone and feather characters. There was a large individual variation in tail length particularly in males. In females, foot span and length of the middle toe varied slightly more than tail length did. The difference in character values between males and females, i.e., reversed sexual dimorphism in size, varied from 5 to 10%, females being larger than males. The correlation analyses indicated that there were stronger correlations within than between bone and feather characters, respectively. Similarly, the multivariate analysis showed higher scores on PCI for feather than for bone characters except for tail length. The highest scores were obtained for body length and wing length. Each one of these characters seems to provide a fairly good estimate of overall body size.

Key words: *Merlin; raptors; reversed sexual size dimorphism; RSD; body size; body length; wing length; PCA.*

INTRODUCTION

Body size influences many aspects of an individual's biology such as behavior, ecology and physiology (Peters 1986, Reiss 1989). There are several difficulties in obtaining adequate measures of body size, however. Overall body size is sometimes estimated from univariate measures assuming allometric growth, although some of these measures may be less useful. For instance, body mass fluctuates seasonally or even hourly depending on variables such as time since feeding and activity. In birds, there is also a sexually dependent variability in body mass because body mass varies more in females than in males during the breeding season particularly among raptors (e.g. Newton 1986). Moreover, analyses based on characters that consist of feathers could be unsatisfactory because of seasonal and age-related variability in feather growth, respectively (Newton 1986). It should be noted, however, that the apparent overall body size of birds is to a large extent determined by feathers.

An alternative approach has been to use multivariate measures such as principal component analysis, PCA (Rising and Somers 1989, Freeman and Jackson 1990, Seutin et al. 1993). How-

ever, the methods used in PCA as well as the interpretation of principal components are still debated (Bookstein 1989, Rising and Somers 1989, Somers 1989, Sundberg 1989). Bookstein (1989) concluded that the first principal component, PCI, is an allometric size variable, and that the shape dimension, including the remaining principal components, lacks all information regarding allometry. Moreover, Bookstein (1989) proposed that in PCA overall body size is equal to the score on PCI.

In many bird studies, univariate, morphological measures have often been used to represent overall body size without previous examination of the relationship between this measure and a measure of overall body size e.g. PCA. In this study, I analyzed sex-dependent variation in morphological characters in the Merlin *Falco columbarius*, using both univariate and multivariate measurements. Moreover, I examined if any univariate measures could be used as an approximation of overall body size using PCI.

The Merlin is a typical bird of prey with sex-role partitioning of breeding duties and reversed sexual size dimorphism i.e. the female is larger than the male. Egg laying, incubation, brooding, and feeding the young are done by the female while the male spends much time flying (Newton 1979, 1986, Wiklund 1990a). He provides the family with food and defends the nest, particularly before the eggs hatch (Newton 1979, Wik-

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lund 1990b). At the end of the nestling period, the female may also hunt for the young.

In birds of prey, the most dimorphic species are found among those that feed on the fastest and most agile prey (Newton 1979). Since Merlins hunt small passerines which have high aerial agility (Newton 1979, Wiklund 1986), a correspondingly high aerial agility is required by the Merlins. Theoretical arguments suggest that small birds perform better than large ones in five out of six aspects of flight (Andersson and Norberg 1981). These achievements are related to wing loading, which depends on certain morphological features such as body mass, wing area and aspects ratios of the wings (Andersson and Norberg 1981). It is therefore inevitable that morphological structures associated with flight performance also affect survival of birds (see Norberg 1994, Hedenström 1995).

MATERIALS AND METHODS

STUDY AREA AND HANDLING OF THE BIRDS

Data were collected among Merlins breeding in Padjelanta and Stora Sjöfallet National Parks, N Sweden (67° N, 17° E) during 1984–1994. Each year, I attempted to trap all breeding birds, using a decoy and mist nets near the nest. Laying was used as a definition of a breeding attempt. Each of the trapped birds was equipped with a unique combination of color bands and a Swedish standard aluminum band. The ages of adult birds which had not been banded as nestlings were determined in the hand. Each bird was then classed into one of three age categories. Females: 1 year old—the back and most upper tail coverts were brown, 2 years old—tail coverts consisted of a few brown and many gray feathers, and 2+ years old—tail coverts were gray. Males: 1 year old—moulting to adult plumage, 2 years old—one or more juvenile coverts on the dorsal side of the wing, and 3+ years old—full adult plumage. Further details of the study area and handling of birds are given by Wiklund (1986, 1990a, 1990b, 1995) and Wiklund and Larsson (1994).

MEASURING AND ANALYSING MORPHOLOGICAL CHARACTERS IN MALES AND FEMALES

Assisted by a co-worker who held the bird, I made all measurements on the birds included in this study. I measured four different parts of the

right leg of each bird: *tarsometatarsus* from the joint with the middle toe to that with fibulatiotarsus, *tibiotarsus* from the joint with femur to the joint with tarsometatarsus, the length of the *middle toe* from the joint with tarsometatarsus (the joint became visible when the toe was bent slightly downward) to the posterior end of the middle toe not including the claw (the toe was bent downward and gently stretched and measured on the dorsal side), and *foot span*, i.e. the distance on the ventral side between the tip of the hind toe and the tip of the middle toe not including claws (the toes were gently stretched out so that the longitudinal axis of tarsometatarsus was normal to the longitudinal axis of the toes). All measurements were made to the nearest 0.1 mm using calipers. Moreover, I measured four different characters that included measurements of feathers; *hand-wing* (right hand-wing stretched and flattened), the length of the right *wing* (stretched and flattened) from the body to the tip of the longest primary (the starting point of the ruler was the chest flank at the joint between the wing and the body), and *tail* from the pygostyl to the tip of the central feathers. Wing and tail measurements were made on the ventral side of the body parts and to the nearest 1 mm. *Body length* was measured to the nearest 1 mm from the tip of the central tail feathers to the crown of the bird lying relaxed on the ruler. (The longitudinal axis of the bird's head was normal to the longitudinal axis of the body. A bird was considered relaxed when the neck was relaxed, which could be accomplished by letting the bird grapple a stick with the feet). *Body mass* was measured to the nearest 1 g using a Pesola spring balance. In this report, tarsometarsus, tibiotarsus, foot span and middle toe are alternatively called bone characters while hand-wing, wing, tail and body are referred to as feather characters.

All measurements were made on live birds. The sample consists of 116 males and 96 females which were mist-netted and measured, at most, once per year up until 1994. Birds that were molting the longest primaries and/or the central tail feathers were excluded from the sample. Moreover, one-year-old birds were excluded from the analysis because they may have shorter feathers than older birds (Newton 1986, Warkentin et al. 1992). One effect of this treatment was that fewer females than males were included in the sample because more females than males bred in their first year (Wiklund 1995 and unpubl.

data). For birds that had been captured and measured more than once, I used the most recent measurements.

Repeatabilities were estimated following Lessells and Boag (1987), and included only birds whose characters had been measured more than once. I calculated the variance among and within individuals running an ANOVA in GLM (SAS 1988). As the design was unbalanced, I corrected for the variability in n , before estimating repeatabilities (Lessells and Boag 1987).

For the multivariate analysis, I used PCA which summarizes covarying patterns of variation in morphometric data. The products are independent composite variables of which PCI is interpreted as an allometric size variable, given that the character variables are positively correlated (Chatfield and Collins 1980, Bookstein 1989). If variables are not correlated, the PCA simply finds components which are close to the original variables and arranges them in decreasing order of variance (Chatfield and Collins 1980). By using different transformations of the data prior to PCA, slightly different versions of size and shape axes may be produced (Pimentel 1979, Rising and Somers 1989). Rising and Somers (1989) pointed out that analyses using the variance-covariance matrix are influenced by the variation of each character relative to the variation of all other characters. Thus, if characters differ much in size, the correlation matrix should be used in the analysis because all variables are then scaled to have unit variance and in some sense equal importance (Chatfield and Collins 1980, SAS 1988). Therefore, I used the correlation matrix to estimate the principal components.

Since the sample consists of birds measured during the breeding season, there was a tendency for body mass to decrease later in the season particularly in females. A large intra-individual variation in body mass of females is common among breeding raptors (Newton 1979, 1986). Since characters with the highest variance will have the greatest influence on PCI (Rising and Somers 1989), the results of the PCA would have been biased due to the reproductive condition of the bird if body mass had been included in the analysis. Therefore, I excluded body mass from the PCA.

I used the Princomp procedure in SAS (1988) to estimate principal components, which allows partialling out of unnecessary variables. Other statistical tests also follow SAS (1988).

RESULTS

REPEATABILITY OF MEASUREMENTS

Repeatability of measurements varied between characters both in males and females (Table 1). In both sexes, repeatabilities were comparatively high for tarsometatarsus, wing and, particularly in females, body length (Table 1). In contrast, there were low repeatabilities for tail length and possibly middle toe in females (Table 1). However, there may be an effect of sample size on the repeatabilities for tibiotarsus, foot span and middle toe (Table 1).

To study if repeatabilities differed between bone characters and feather characters, I used data from males and females and combined the repeatability values for each type of character. There was no significant difference in repeatabilities between bone and feather characters (Mann-Whitney U -test, $U = 21$, ns). Similarly, a comparison between bone less foot characters and feather characters less tail length did not indicate a difference in repeatabilities (Mann-Whitney U -test, $U = 3$). Hence, it is premature to conclude that the measurement error is larger in feather than bone characters, although there was a lower reproducibility of size in certain characters such as tail length.

INDIVIDUAL VARIATION IN CHARACTER SIZE

Table 1 shows the character values obtained for males and females. All characters were significantly larger in females than in males (for all characters, non-parametric ANOVA, $P < 0.001$). Using average values for the characters (Table 1), reversed sexual size dimorphism (male character size/female character size) varied from 0.95 (tarsometatarsus) to 0.90 (hand-wing and wing length).

Average body mass of males was 167 g ($n = 115$), while average body mass of females measured after 10th July, the mid-nestling period and onwards, was 225 g ($n = 25$). I scaled body mass to a linear measure by using the cube root of body mass and then compared body size of males and females. There was a difference of 10% between the two sexes.

The coefficients of variation were comparatively low particularly for body length but also for wing, hand-wing and tibiotarsus (Table 1). In contrast, there were larger individual variations

TABLE 1. Size of various morphological characters (mm) in male and female Merlins. Coefficients of variation, CV, repeatability of measurements, r , and F ratios, Fr, in the repeatability analysis. Within parentheses are sample sizes, and degrees of freedom (numerator, denominator) in the repeatability analysis. * = $P < 0.01$ from the repeatability analysis indicates significantly higher variation in character size among than within individuals.

Character	Mean \pm SD (n)	Range	CV	$r \pm$ SE	Fr (df)
Males					
Tarsometatarsus	36.7 \pm 0.86 (99)	34.4–38.8	2.3	0.77 \pm 0.02	7.93* (18, 21)
Tibiotarsus	56.6 \pm 1.22 (66)	53.8–59.6	2.1	0.88 \pm 0.03	8.17* (7, 8)
Foot span	49.0 \pm 1.29 (62)	45.4–51.5	2.6	0.62 \pm 0.07	2.51 (7, 8)
Middle toe	30.2 \pm 0.83 (76)	28.2–32.3	2.8	0.68 \pm 0.03	5.59* (11, 12)
Hand-wing	200.8 \pm 4.16 (105)	191.0–221.0	2.1	0.65 \pm 0.02	4.97* (23, 27)
Wing length	265.8 \pm 5.47 (101)	248.0–276.0	2.1	0.80 \pm 0.02	9.19* (18, 21)
Tail length	122.7 \pm 5.06 (90)	115.0–139.0	4.1	0.50 \pm 0.04	3.16* (16, 19)
Body length	267.7 \pm 5.14 (90)	257.0–278.0	1.9	0.61 \pm 0.04	4.38* (14, 17)
Females					
Tarsometatarsus	38.5 \pm 0.96 (85)	36.6–40.8	2.5	0.90 \pm 0.01	21.00* (14, 20)
Tibiotarsus	61.5 \pm 1.25 (46)	59.7–65.3	2.0	0.83 \pm 0.04	7.81* (6, 8)
Foot span	53.7 \pm 1.78 (47)	50.4–59.7	3.3	0.74 \pm 0.04	6.94* (6, 8)
Middle toe	32.7 \pm 1.07 (55)	30.7–35.3	3.3	0.58 \pm 0.06	4.21* (7, 11)
Hand-wing	221.8 \pm 4.33 (86)	212.0–236.0	1.9	0.70 \pm 0.03	5.75* (17, 23)
Wing length	294.7 \pm 6.50 (86)	276.0–310.0	2.2	0.78 \pm 0.02	9.00* (14, 18)
Tail length	135.2 \pm 4.23 (69)	125.0–148.0	3.1	0.57 \pm 0.05	3.90* (10, 13)
Body length	294.8 \pm 4.85 (70)	282.0–308.0	1.6	0.80 \pm 0.02	9.73* (10, 13)

in tail length, particularly among males, and in foot span and middle toe length among females (Table 1). Moreover, it appeared that there was a slightly larger range in the coefficients of variation among males than among females (males: 2.2 and females: 1.7, Table 1).

CORRELATED CHARACTERS

In males, body length was positively correlated with all other characters except tibiotarsus. Similarly, body length of females was correlated with other characters except tibiotarsus and also tarsometatarsus (Table 2).

There were strong positive correlations be-

tween feather characters in both sexes (Table 2). Among bone characters, middle toe length was correlated with other bone characters in both males and females, except that middle toe length was not correlated with tibiotarsus in females (Table 2). Moreover, there were correlations between characters that were not part of each other, also within each group of character e.g. tarsometatarsus and middle toe length as well as body length and wing length (Table 2). The correlation coefficients for tibiotarsus were consistently low in both females and males with only one exception, tibiotarsus-tarsometatarsus in males (Table 2).

TABLE 2. Pearson product-moment correlations among characters in male and female Merlins. Male figures above and female figures below the diagonal. Tmt = tarsometatarsus, Ti = tibiotarsus, Foot = foot span, Toe = middle toe length, Hand = hand-wing, Wing = wing length, Tail = tail length, Body = body length.

	Tmt	Ti	Foot	Toe	Hand	Wing	Tail	Body
Tmt		0.62***	0.22	0.31**	0.25*	0.43***	0.20	0.21*
Ti	0.25		0.22	0.31*	0.07	0.15	0.01	0.07
Foot	0.44**	0.23		0.64***	0.02	0.37**	0.00	0.32*
Toe	0.36**	0.04	0.68***		0.10	0.09	-0.01	0.28*
Hand	0.09	0.12	0.17	0.18		0.44***	0.58***	0.45***
Wing	0.34**	0.17	0.35**	0.23	0.56***		0.29**	0.39***
Tail	0.14	0.01	0.21	0.26	0.43***	0.15		0.27**
Body	0.21	0.16	0.58***	0.31*	0.33***	0.59***	0.31**	

*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$.

TABLE 3. Principal component scores of male and female Merlins. Scores of principal components I and II are shown for each character included in the principal component analysis. Eigenvalues and cumulative increase in the variance explained by the two first principal components. The estimates are based on 7 morphological characters measured on live males ($n = 59$) and females ($n = 40$). The correlation matrix was used in the analysis.

Character	Males		Females	
	PCI	PCII	PCI	PCII
Tarsometatarsus	0.30	-0.03	0.30	0.34
Foot span	0.29	0.57	0.37	0.46
Middle toe	0.31	0.54	0.31	0.55
Hand-wing	0.42	-0.44	0.39	-0.44
Wing length	0.46	-0.05	0.44	-0.27
Tail length	0.32	-0.43	0.33	-0.28
Body length	0.50	0.04	0.46	-0.13
Eigenvalue	2.96	1.58	3.43	1.36
Cumulative	0.41	0.64	0.49	0.68

MULTIVARIATE ANALYSIS

In males as well as females, the highest score on PCI was recorded for body length (Table 3). The scores on PCI were higher for feather characters than bone characters except for tail length in females. In both sexes, tail length was an exception as the PCI-loadings of this character were similar to those of bone characters, not feather characters (Table 3). The variation in size explained by PCI was 41% in males and 49% in females (Table 3). As tibiotarsus was not correlated with other characters, it was a character that did not add significant information in the PCA (Chatfield and Collins 1980). It was therefore partialled out in the PCA.

The high scores on PCI for body length suggested that this character contributed most to the size-vector. It was not meaningful to run correlation analyses between PCI and characters included in the PCA because data are not independent. However, bivariate plots of raw-data and PCI give an idea about the differences in spread of data between the characters contributing most to PCI. Figures 1 and 2 show a smaller spread in data for body length than wing length and hand-wing length.

Except for tarsometatarsus and body length in males, one noticeable difference between bone and feather characters was that the PCII-loadings of the former were positive while those of the latter were negative (Table 3). By adding the sec-

ond principal component, the degree of explanation of variation in size and shape increased by about 23% in males and 19% in females. The eigenvalues of the third principal components were 0.78 for males and 0.79 for females. Moreover, the total variance in size and shape that was explained increased little, about 12% in both males and females, by adding the third principal components.

DISCUSSION

There was a certain variation in the repeatability values of different characters. Repeatabilities were similar to those found in other studies of wild birds, however (Boag 1983). It appeared that repeatability values for characters mainly consisting of feathers were similar to those obtained for characters including mainly bones, although repeatabilities for bone less foot characters were high. Moreover, most differences in repeatability values between the sexes were fairly small, and there was no consistent trend in the direction of these differences. Thus, accuracy of the measurements was not related to the bird's sex.

BODY SIZE OF MALES AND FEMALES

Character values of females were larger than those of males. The difference in character values between the sexes varied from 5 to 10% depending on the character, including body mass. However, character values varied much between individuals, and there was an overlap between the sexes in all character values except body length and tibiotarsus.

Tail length is variable in falcons (Palokangas et al. 1992, Warkentin et al. 1992, this study). Palokangas et al. (1992) proposed that female Kestrels, *Falco tinnunculus*, choose long-tailed males. Another study of the same species did not confirm that result, however (Palokangas et al. 1994). My study indicated a slightly higher individual variation in tail length in males than in females. However, this difference in variability in tail length between the sexes seems to be too small to conclude that tail length in males is a sexually selected trait. Moreover, there is an indication of positive assortment in tail length among Merlins (Warkentin et al. 1992). Hence, an alternative explanation for the high variability in tail length is that growth of the tail is limited by food stress. The tail is moulted during the breeding season (Wiklund unpubl. data). It is therefore possible that a longer tail is grown

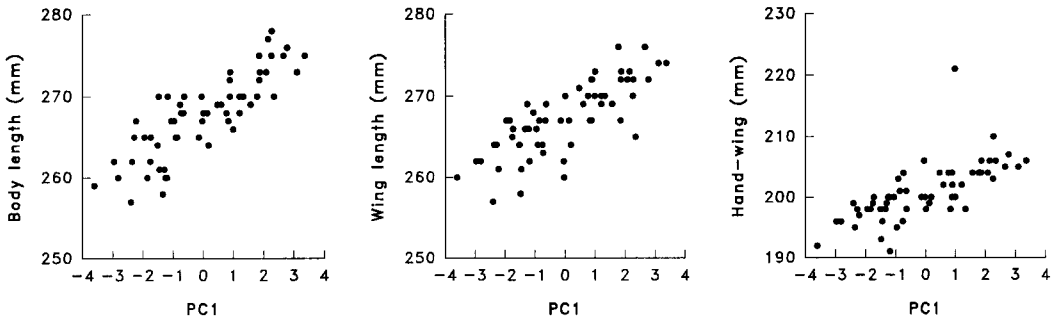


FIGURE 1. Bivariate plots of overall body size as indicated by PCI versus body length, and wing length, and hand-wing length for 59 Merlin males.

among birds that breed in areas or in years with abundant food than among birds breeding where/when food is sparse. Another indication that food stress may influence growth of the tail is that stress bars are common on tail feathers (Wiklund unpubl. data).

A comparison of the coefficients of variation between the sexes indicated that each character, except for tail length, foot span and middle toe length, varied as much in females as in males. There was a larger individual variation in foot span and middle toe length in females than in males. Moreover, foot span and middle toe length differed by 8% while tarsometatarsus differed by 5% between the sexes. In raptors, size and form of the feet are related to prey choice because they are important for catching and killing prey (Brown 1976). For instance, female *Microhierax* Falconets hunt birds as well as insects and have large feet compared with insectivorous Kestrels, *Falco* spp. (Kemp and Crowe 1994). In the case of the Merlin, foraging by males and females differs in

that females sometimes hunt larger prey than the male (e.g., Newton 1979, Wiklund 1986). Therefore, females with large feet may be more successful in hunting birds above the size of pipits, *Anthus* spp., than other females.

CORRELATED CHARACTERS

Wyllie and Newton (1994) reported strong correlations between hand-wing and other characters in a large sample of female Sparrowhawks, *Accipiter nisus*, and concluded that hand-wing was the character that best predicted overall body size. They did not measure body length and length of the wing, however. In my study, correlation coefficients indicate that both body length and wing length may better predict general body size than the hand-wing.

The highest correlation coefficients were obtained among feather characters other than tail length and bone characters other than tibiotarsus. These correlations also include characters that were not a structural part of another char-

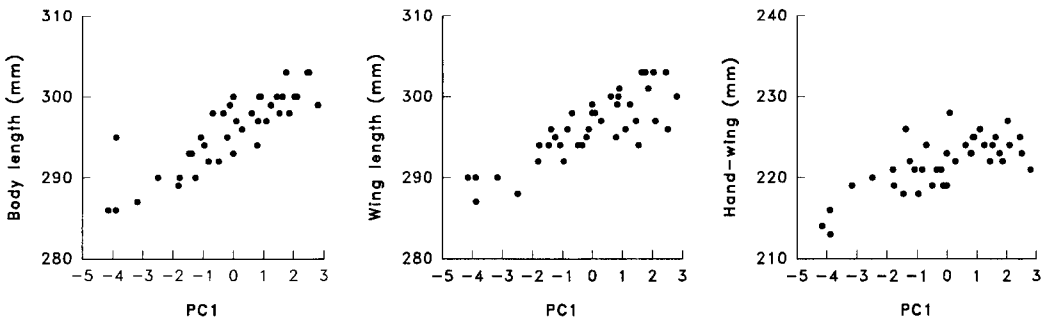


FIGURE 2. Bivariate plots of overall body size as indicated by PCI versus body length, and wing length, and hand-wing length for 40 Merlin females.

acter. In contrast, bone and feather characters were significantly correlated only in a few cases.

Many falcons including the Merlin are specialised foragers, capturing small birds in flight. This mode of hunting requires high maneuverability (Howland 1974). One determinant of flight performance is wing loading, which depends on size and shape of the wing and the tail as well as body mass (Pennycuik 1975, Andersson and Norberg 1981, Norberg 1994). Conceivably this foraging specialization is maintained by selection on characters associated with prey capture. In Merlins, however, there were only weak correlations between characters associated with catching/holding the prey and flight performance, respectively. The selection pressures may therefore differ between bone and feather characters. Strong phenotypic correlations are expected mainly among characters that are under similar selection pressure.

MULTIVARIATE OR UNIVARIATE MEASURES OF BODY SIZE?

In the principal component analysis, scores on PCI were similar both within and among each group of characters, although slightly higher for feather characters except tail length. Similar to the result of the correlation analysis, one of the shape variables, PCII (i.e. the first principal component of the residuals from the regression of PCI), indicated that bone and feather characters form two groups of characters. One possible explanation is that phenotypic correlations reflect underlying genetic correlations (Boag 1983, Freeman and Jackson 1990), and that one type of characters may be controlled by genes independent of those controlling the other type of characters.

The variance explained by the first eigenvalues (PCI) was 41% in males and 49% in females. Since the eigenvalues of PCII were above 1, two principal components were required to meet the Kaiser-Guttman criterion for the number of principal components that should be used to describe body size and shape (Jackson 1993). Moreover, some correlation coefficients were low indicating that some of the variation that remained to be explained could still be size (pointed out by J. D. Rising).

Scores on the first principal component were highest for body length, wing length and hand-wing. Moreover, bivariate plots of PCI and these characters showed a limited scatter in data par-

ticularly for body length. A PCA based on body length, wing length and hand-wing and using the co-variance matrix indicated that PCI explained some 60% of the variance in body size, in both males and females, and that overall body size could be described by PCI according to the Kaiser-Guttman criterion (Jackson 1993). Probably, this result depended on that the characters were strongly correlated because the degree of variance that is explained in principal component analysis is in part related to the correlation between characters (Chatfield and Collins 1980, Jackson 1993). Thus, body length and wing length are characters that may represent overall body size better than any other single character would do, perhaps also better than PCA including characters that are weakly correlated. This agrees with the observations made in female Sparrowhawks, that feather characters may better represent overall body size of raptors than bone characters do (Wyllie and Newton 1994).

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