MORPHOLOGICAL AND DIETARY CORRELATES OF CLUTCH SIZE IN NORTH AMERICAN WOODPECKERS

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ABSTRACT.—There are diverse relations among ecological, morphological, and life-history traits in North American woodpeckers (family Picidae).Within the family as a whole, clutch size does not correlate with body size. However, clutch size increases with body size within the genus *Melanerpes* and decreases with size in *Picoides*. In the family as a whole, species that specialize on wood-boring larvae have small clutches. Such species use pecking as a major foraging technique, and pecking is associated with a wide suite of morphological specializations, including relatively wide first ribs, long pygostyle disks, short tibia, wide crania, wide maxillae, long mandibular symphyses, less cranial kinesis, and greater culmen sexual dimorphism. Hence, these morphological characters also correlate with clutch size, in two cases (length of the mandibular symphysis and cranial kinesis) even after controlling for both body size and generic effects. The observed correlations between clutch size and morphology are probably the result of dietary influences. These correlations, however, may at least in part be due to morphological constraints. Morphological design may thus constrain life-history evolution at the intrafamilial and intrageneric levels as well as at higher taxonomic levels. *Received 8 September 1986, accepted 20 May 1987.*

NUMEROUS studies have pointed out strong classwide correlations between life-history traits (LHTs) and body size (e.g. mammals: Blueweiss et al. 1978, Western 1979, Tuomi 1980, Millar and Zammuto 1983, Stearns 1983; birds: Amadon 1943, Lack 1968, Rahn et al. 1975; reptiles: Stearns 1984). These studies suggest that phylogenetic constraints, as reflected by differences in body size, may be important in determining life-history variation. Further, covariation in LHTs may be an indirect consequence of selection on size alone rather than a direct adaptive shift to environmental conditions or ecological factors (Stearns 1983, 1984). These results also raise the possibility that analogous types of morphological constraints may be important in shaping LHTs at low taxonomic levels as well, such as on an intrafamilial or even intraspecific basis. The existence of such low-level interactions would indicate that correlations determined from broad-scale, classwide analyses may be incomplete or misleading, and thus would have important implications to the interpretation of interspecific variation in life history.

Nonetheless, there have been few studies of the ecological correlates of clutch size in closely related taxa, and virtually none of morphological correlates, with the exception of correlations with body size. I analyzed interspecific patterns of clutch-size variation in North American woodpeckers (family Picidae) with respect to dietary and morphological characters in this family. My goal was to identify the correlations among these three sets of traits and to discuss the possible causal relationships producing the observed patterns. Although comparative data on LHTs other than clutch size are not currently available for woodpeckers, the extensive background of ecomorphological studies on this taxon make it an excellent one for such an exploratory analysis.

MATERIALS AND METHODS

North American woodpeckers, excluding the virtually extinct Ivory-billed Woodpecker (*Campephilus principalis*), include 21 species in 5 genera. For all species except Acorn Woodpeckers (*Melanerpes formicivorus*), data on clutch size were taken from museum collections. Only data from complete clutches, as indicated by the incubation status listed by the original collector, were used. The locality for each clutch was recorded, and the latitude was determined to the nearest degree. Because two or more females may contribute to nests in the Acorn Woodpecker (Koenig and Pitelka 1979, Mumme et al. 1983), I used clutch sizes only from 90 nests of single females determined as part of an ongoing field study of this species at Hastings Reservation in Monterey Co., California (Koenig and Mumme 1987).

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TABLE 1. Mean clutch size of North American woodpeckers. Sample sizes are given in parentheses.

Species	Mean clutch size ± SD	Mean clutch size adjusted for latitude	Body mass[a]
Melanerpes lewis	5.88 ± 1.19 (51)	5.70	97.7 (7)
M. erythrocephalus	4.82 ± 0.80 (71)	4.74	66.8 (3)
M. formicivorus[b]	4.36 ± 1.03 (90)	4.46	79.8 (12)
M. uropygialis	3.75 ± 0.93 (69)	4.13	62.3 (18)
M. aurifrons	4.65 ± 0.80 (55)	5.39	79.8 (4)
M. carolinus	4.31 ± 0.76 (61)	4.63	69.1 (5)
Sphyrapicus varius	4.93 ± 1.02 (46)	4.33	47.2 (2)
S. nuchalis	4.76 ± 1.09 (17)	4.57	50.8 (6)
S. ruber	4.69 ± 0.72 (42)	4.48	52.2 (8)
S. thyroideus	5.67 ± 0.85 (49)	5.56	52.3 (10)
Picoides scalaris	3.81 ± 0.76 (58)	4.30	31.6 (16)
P. nuttallii	4.34 ± 0.77 (88)	4.46	36.0 (10)
P. pubescens	4.81 ± 0.78 (205)	4.63	26.7 (20)
P. villosus	3.93 ± 0.72 (159)	3.75	63.4 (27)
P. stricklandi	3.50 ± 0.84 (6)	3.87	42.7 (5)
P. borealis	3.68 ± 0.69 (25)	4.08	47.3 (20)
P. albolarvatus	4.35 ± 0.73 (98)	4.31	55.8 (12)
P. tridactylus	3.87 ± 0.64 (15)	2.83	55.3 (3)
P. arcticus	3.89 ± 0.85 (27)	3.21	70.8 (4)
Colaptes auratus	6.21 ± 1.56 (467)	6.19	146.4 (20)
Dryocopus pileatus	3.80 ± 0.77 (92)	3.74	265.3 (4)

[a] Females taken September–March; mass in grams.

[b] Clutches of single females only (see text).

Mean clutch size was determined for each species and then adjusted by an analysis of covariance controlling for the latitude at which each clutch was collected; only the adjusted values were used in subsequent analyses. This procedure corrects for the latitudinal gradient in clutch size within the family (Koenig 1986) and results in estimates of mean clutch size independent of latitudinal differences in range.

Morphological measurements generally were taken from previous authors, including Ridgway (1914, using mean values for the most widespread subspecies), Burt (1930), Spring (1965), and Kirby (1980, *in litt.*). Measurements used were of females when possible, because females are directly responsible for laying the clutches whose size was of interest. Measurements from males and females were highly correlated, however, for all characters for which I had data (correlations for femur length, pygostyle disk length, tibia length, culmen length, body mass, cranium width, and wing length all $r_s > 0.90$, $P < 0.001$). Thus, analyses using measurements from males would yield similar or identical results.

Body-mass data were taken from females collected during the nonbreeding season (September–March) and are from specimens in the Museum of Vertebrate Zoology. Only a single such specimen was found for the Red-cockaded Woodpecker (*Picoides borealis*), so I used body-mass data for this species from live birds caught between September and December in North Carolina (R. Repasky pers. comm.).

Dietary information is from Beal (1911); egg measurements are from Bent (1939). Relative egg mass was estimated by the "egg-value" (length × breadth^2/1,000; Amadon 1943). This value was then divided by female body mass to yield relative egg volume and, in a separate calculation, multiplied by mean clutch size and divided by female body mass to derive the relative clutch volume for each species. Such ratio measures can be misleading. As the primary focus of the analyses performed here is on clutch size variation, however, they are adequate to outline general patterns in these measures.

Taxa used follow the A.O.U. (1983, 1985). In all, data on 1,791 clutches were used in the analyses. I use nonparametric Spearman rank tests for pairwise correlations and, in lieu of a comparable nonparametric multivariate technique, multiple regressions and ANCOVA for examining interrelationships of three or more variables. P values ≤ 0.05 (two-tailed for Spearman rank tests) are considered significant.

Two potential shortcomings of these data should be noted. First, I have used data from a variety of sources. As a result, sample sizes vary and the data are undoubtedly of variable quality. I have preferred older sources to measurements of my own, however, because the data they contain invariably were gathered for reasons unrelated to the analyses performed here. Thus, the results are certainly unbiased. Second, although I have taken into account some of the geographic variation in clutch size by controlling for latitude, I have ignored intraspecific variation in morphology. Although such patterns are of considerable

TABLE 2. Spearman rank correlations of clutch size with body size and culmen dimorphism in North American woodpeckers.[a]

Variable	Clutch size adjusted for latitude	Relative egg volume	Relative clutch volume	Source
All species (n = 21 species; 17 for femur length)				
Female body mass	0.17	−0.83***	−0.60**	This study
Male femur length	0.16	−0.85***	−0.64**	Kirby *in litt.*
Female tarsus length	0.21	−0.77***	−0.51*	Ridgway 1914
Culmen dimorphism[b]	−0.51*	0.24	−0.47*	Ridgway 1914
Genus *Melanerpes* (n = 6 species)				
Female body mass	0.70	−1.00***	0.41	This study
Male femur length	0.77	−0.99***	0.43	This study
Female tarsus length	0.83*	−0.67	0.77	Ridgway 1914
Culmen dimorphism[b]	−0.49	0.32	−0.83*	Ridgway 1914
Genus *Picoides* (n = 9 species)				
Female body mass	−0.70*	−0.67*	−0.93***	This study
Male femur length	−0.84**	−0.65	−0.96***	This study
Female tarsus length	−0.57	−0.58	−0.87**	Ridgway 1914
Culmen dimorphism[b]	−0.13	0.13	−0.02	Ridgway 1914

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[b] Expressed as the ratio of mean male to female culmen length.

interest (e.g. James 1970), I have chosen to simplify the analyses by using mean morphological measurements from the most widespread subspecies when authors examined more than one race.

RESULTS

The body mass of extant North American woodpeckers spans an order of magnitude from the 26.7-g Downy Woodpecker (*Picoides pubescens*) to the 265.3-g Pileated Woodpecker (*Dryocopus pileatus*) (Table 1). Mean clutch sizes vary slightly less than twofold, from 3.50 in Strickland's Woodpecker (*P. stricklandi*) to 6.21 in the Northern Flicker (*Colaptes auratus*); differences in clutch size among species are significant (Kruskal-Wallis 1-way ANOVA; $\chi^2 = 765$, df = 20, $P < 0.001$). Controlling for latitude, mean clutch size ranges from 2.83 in the Three-toed Woodpecker (*P. tridactylus*) to 6.19 in the Northern Flicker.

Clutch size, body size, and culmen dimorphism.—In the family as a whole, clutch size is uncorrelated with female body mass, male femur length, or female tarsus length, three indices of body size (Table 2). Both relative egg and clutch volume, however, are inversely and significantly correlated with body size. Thus, as in several other avian taxa (Rahn et al. 1975), larger species of woodpeckers lay relatively small eggs and have small relative clutch volumes (Table 2).

A primary reason for the lack of any correlation between clutch size and body size in the family as a whole is that the two major genera *Melanerpes* and *Picoides* provide opposite clutch to body size relationships (Table 2). Within *Melanerpes*, clutch size increases with body size, significantly so using tarsus length, whereas within *Picoides* the reverse is true. Relative egg volume decreases with body size in both taxa, whereas relative clutch volume decreases with body size in *Picoides* but not in *Melanerpes*. Correlations with culmen dimorphism are not significant except for an inverse correlation with relative clutch volume in *Melanerpes*.

Clutch size and morphology independent of body size.—I performed two sets of analyses to assess the relationship of a series of seven morphological variables with clutch size while controlling for the effects of body size. First, I regressed clutch size on pairs of morphological characters. In each case the first character was the one whose influence on clutch size was directly of interest, while the second was femur length, a good index of overall body size in woodpeckers (Kirby 1980). The significance of each variable as a predictor of clutch size was calculated while controlling for the other; hence, the effect of each morphological character independent of body size was determined. This procedure avoids the difficulties that arise from the alternative of using ratios to standardize for

Table 3. Clutch size and morphology in North American woodpeckers.[a,b]

	First-rib width	Pygostyle-disk length	Tibia length	Cranium width	Maxilla width	Mandibular symphysis	Cranial kinesis
Multiple regression							
Variable[c]							
Standardized β	−1.05	−1.30	4.38	−1.39	−2.16	−1.11	0.92
F-value	26.2***	5.7*	7.4*	6.0*	23.1**	13.3**	19.5**
Femur length							
Standardized β	0.72	1.06	−4.39	1.17	1.91	0.71	0.43
F-value	12.4**	3.8	7.5*	4.2	18.2**	5.5*	4.5
Multiple R^2	0.65	0.42	0.48	0.43	0.74	0.63	0.74
Overall F-value	13.1***	2.9	3.7	3.0	11.6***	6.7*	9.9**
Analysis of covariance (F-values)							
Variable	0.3	0.2	3.6	1.3	5.1	11.9*	106.3**
Femur length	0.0	0.0	4.4	0.4	1.7	4.9	4.3
Genus	5.5*	3.3	6.1	4.2	7.3*	12.6*	284.2***
Overall F-value	4.1*	2.3	4.8	3.1	5.9	10.7*	219.5***
n species	17	11	11	11	11	11	10
Source	Kirby *in litt.*	Burt 1930	Burt 1930	Burt 1930	Burt 1930	Burt 1930	Spring 1965

[a] Regressions are of clutch size adjusted for latitude on each pair of variables. All variables except first-rib width and cranial kinesis are for females. Femur length is used to control for body size (see text). For individual variables, df = 1, $n - 3$ where n is the number of species; for the overall F-value, df = 2, $n - 3$. For the analyses of covariance, the influence of the variable is assessed controlling for femur length and generic effects (see text). For the variable and femur length, df = 1, $n - 1$; for generic effects, df = 4, $n - 1$; overall df = 6, $n - 1$.

[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[c] "Variable" refers to the variable listed at the top of the table.

body size (see Atchley 1978, Atchley and Anderson 1978, Blem 1984).

Second, I performed analyses of covariance using the morphological variable of interest and femur length as covariates and genus as a factor. The purpose of these analyses was to examine the relationships between each variable and clutch size independent of both body size and generic effects; thus, the factor was controlled before consideration of the covariates. These tests thus correct both for biased taxonomic representation within the family (see Clutton-Brock and Harvey 1984) and for differences in the relationships of variables between genera.

From the multiple regression, clutch size is significantly related to all seven characters tested, including first-rib width, pygostyle-disk length, tibia length, cranium width, maxilla width, length of the mandibular symphysis, and cranial kinesis (Table 3). Clutch size is also significantly related to femur length in four cases, despite the lack of significant correlations between clutch size and body size alone (Table 2). The overall F-values are significant for four of the seven regressions, with the proportion of variance in interspecific mean clutch size explained (multiple R^2) ranging from 42% to 74%.

The analyses of covariance (Table 3) offer additional support of real relationships between two of these morphological variables and clutch size. Length of the mandibular symphysis and cranial kinesis are both significantly related to clutch size, while femur length is not significant in any of the seven tests. Generic effects are significant in four of the analyses. These results suggest that the significant effect of femur length found in the regressions is due to intergeneric differences (see Table 2), and that at least some of the correlations between morphology and clutch size within the family are not based solely on either allometry or phylogenetic differences between taxa.

Correlation of clutch size and diet.—I correlated clutch size with five major components of the diet of woodpeckers as determined by Beal (1911). The results (Table 4) show a significant inverse correlation of clutch size with the percentage of animal matter in the diet; the apparent reason for this is the significant inverse correlation between clutch size with the percentage of the diet composed of beetles (Coleoptera). No significant correlations exist between clutch size and the percentage of the diet made up of fruit, mast, or ants (Formicidae), or between diet and relative egg or clutch volume. Within the genus *Picoides* there is also a significant inverse correlation between clutch size and Coleoptera in the diet; in addition, species that eat more beetles have relatively smaller eggs. None of the correlations with diet are significant within the genus *Melanerpes.*

In summary: (1) For all North American picids and within the genus *Picoides,* species that eat wood-boring coleopteran beetle larvae have smaller clutches. (2) Larger species of *Melanerpes* lay larger clutches, while larger species of *Picoides* lay smaller clutches. Within the family as a whole, there is no relationship between clutch size and body size (Table 2); significant effects of femur length when analyzed in multiple regressions disappear when genera are included in an ANCOVA and thus appear to be due to intergeneric effects (Table 3). (3) Species with large clutches tend to have less sexual dimorphism in culmen length, relatively narrow first ribs, short pygostyle disks, long tibia, narrow crania, narrow maxillae, short mandibular symphyses, and greater cranial kinesis after controlling for body size. Only the last two variables, however, are still related significantly to clutch size when further controlling for generic effects.

DISCUSSION

WHY THE CORRELATIONS BETWEEN CLUTCH SIZE AND MORPHOLOGY?

Although body size correlates with clutch size in *Melanerpes* and *Picoides,* the opposite directions within these two genera result in no overall body-size effect within the family as a whole. As in mammals (Western 1979, Stearns 1983), larger *Picoides* lay smaller clutches. In contrast, as in most poikilotherms (e.g. Roff 1981), the reverse appears true in *Melanerpes.* Overall, larger species lay smaller eggs and have smaller total clutch volumes relative to their body mass, similar to the pattern found in other homeotherms (Amadon 1943, Lack 1968, Rahn et al. 1975, Stearns 1983).

Stearns (1983, 1984), on the basis of similar types of correlations between body size and life-history traits in mammals and reptiles, suggested that selection for size alone may be responsible for many widespread patterns in life-history evolution. [Specific conclusions from the latter study must be taken with caution (Dunham and Miles 1985, Hedges 1985, Vitt and Seigel 1985), but Stearns's general conclusion that phylogenetic constraints cannot be ignored when considering the evolution of life-history traits holds (Dunham and Miles1985).] Size may have been similarly important in influencing clutch-size evolution within these two woodpecker genera as well.

TABLE 4. Spearman rank correlations of clutch size and diet in North American woodpeckers.[a]

Variable (*n* species)	Clutch size adjusted for latitude	Relative egg volume	Relative clutch volume
All species			
% animal (19)	−0.47*	0.32	−0.06
% Coleoptera (15)	−0.64**	0.29	−0.39
% Formicidae (16)	0.16	0.01	0.18
% fruit (16)	0.39	−0.38	0.07
% mast (16)	0.25	0.20	0.18
Genus *Melanerpes*			
% animal (6)	0.31	0.06	0.03
% Coleoptera (4)	0.40	0.80	0.40
Genus *Picoides*			
% animal (8)	−0.67	−0.10	−0.38
% Coleoptera (6)	−0.83*	−0.94**	−0.77

[a] Dietary data is from Beal (1911). * = $P < 0.05$, ** = $P < 0.01$.

I do not know the reasons for the opposite relationships between clutch size and body size in these two genera. Western and Ssemakula (1982) concluded that a large proportion of variance in life-history patterns both between mammals and birds and within orders of birds can be explained by differences in neural mass, metabolic rate, and body temperature. How any of these features vary within or between genera of woodpeckers is unknown. In any case, the opposing correlations between clutch size and body size found in the two largest genera examined here suggests that design constraints such as size may act in quite different ways within lower taxa, and thus that trends found at or above the familial level may be misleading.

Independent of body size, there is a diverse array of morphological characters correlating significantly with clutch size within the family.

Although the interpretation of these correlations is not immediately apparent, a relatively straightforward explanation exists for many of the trends in Table 3, stemming from the correlation between clutch size and the proportion of beetles in the diet (Table 4). This fraction of the diet primarily represents wood-boring larvae, which are obtained by "pecking" (strikes or blows made in limbs and trunks of trees with the bill). This behavior has long been known to be associated with numerous morphological specializations. Hence, the tendency for clutch size to decrease with increasing specialization on wood-boring larvae and increasing reliance on pecking may explain the following correlations:

First-rib width.—Shufeldt (1900) first pointed out that woodpeckers exhibit a pronounced broadening of the first thoracic rib, a phenomenon whose functional significance was examined comparatively by Kirby (1980). She concluded that species that excavate frequently while foraging have relatively wider ribs. The significance of this pattern is due to the greater musculature associated with the wider rib, stabilizing the base of the neck against bending, and thus allowing the generation of more forceful blows during foraging (Kirby 1980). Widening of the ribs thus enables woodpeckers to specialize on prey obtained by pecking. Such species have smaller clutch sizes, and thus the relative first-rib width correlates inversely with clutch size in the multiple regression analysis (Table 3).

Pygostyle-disk length.—The pygostyle disk serves as a major point of attachment for the tail musculature (Burt 1930). The tail in woodpeckers is used as a prop (Thomson 1964); hence, the pygostyle disk is relatively longer in species that forage by pecking for larvae (Burt 1930). Thus, the pygostyle-disk length correlates inversely with clutch size; that is, species that peck for food have relatively large pygostyle disks and small clutches.

Tibia length.—Spring (1965) discussed the skeletal modifications for climbing and pecking in woodpeckers and concluded that shortening of the distal leg bones is a modification for the delivery of harder blows. He suggested that this shortening might increase the effective power of the muscles inserting on them, thereby increasing the hardness of blows made by the bird as it pulls its body toward the tree. Shorter distal bones also might allow the bird to hold itself relatively farther from the trunk, thereby augmenting its capacity to generate blow momentum. Within the family as a whole, species with relatively shorter tibia are those that peck for food and have smaller clutch sizes.

Cranial measurements.—Burt (1930) discussed a series of cranial adaptations of woodpeckers, including the width of the cranium, width of the maxillae, and length of the mandibular symphysis. These morphological features all increase skull strength and thus the ability of the bird to inflict hard blows. In turn, pecking species have wider crania, wider maxillae, and longer mandibular symphyses. Within the family, all three of these characters correlate inversely with clutch size, the last significantly so even when controlling for generic effects (Table 3).

Cranial kinesis.—Cranial kinesis is the mechanism that permits the upper bill to move independently with respect to the brain case (Bock 1964, Spring 1965). Spring (1965) considered several functional hypotheses of differing degrees of cranial kinesis in woodpeckers. He concluded that this phenomenon acts as a buffering mechanism, and that to deliver more forceful blows during pecking, kinesis would decline as the bones and ligaments tending to restrict cranial movement were used to steady the bill at the moment of impact. Following this reasoning, the family-wide correlation between kinesis and clutch size follows from the tendency of species dependent on pecking to have reduced cranial kinesis.

Sexual dimorphism in culmen length.—Cabana et al. (1982) suggested, primarily on the basis of sexual-selection theory, that there should be a positive correlation between the degree of sexual dimorphism in body size and female reproductive effort. Their analyses showed a positive correlation between sexual dimorphism and clutch mass in 114 species of nonpasserines due mostly to increasing clutch size in species with relatively large males. The correlation of both clutch size and relative clutch volume with sexual dimorphism in bill length in North American woodpeckers found here (Table 2) is in the opposite direction, and thus does not support Cabana et al.'s (1982) thesis.

An alternative explanation for the pattern observed here stems from Selander's (1966) hypothesis of ecological release leading to divergence in foraging behavior and bill dimorphism under conditions of low competition. From this hypothesis the greater bill dimorphism in pecking species would be predicted if there are few competitors for wood-boring larvae. This lack of competition might then correlate with wood-boring larvae being a relatively stable resource, a situation correlating with high adult survivorship and small clutch size (Cody 1966, Stearns 1976).

There are no data to determine unambiguously if there is relatively little competition for wood-boring larvae. Nonmigratory species of woodpeckers eat significantly more Coleoptera than migratory species, however (Mann-Whitney *U*-test, $U = 9.5$, $n_1 = 7$, $n_2 = 8$, $P < 0.05$). At the very least this indicates that wood-boring larvae are more stable on an annual basis than other resources used by members of this family.

Besides a relative lack of competition leading to ecological release, an additional feature that might select for sexual dimorphism is if wood-boring larvae were relatively rare. A scarcity might increase sexual dimorphism in foraging behavior (Peters and Grubb 1983) and thus lead to morphological dimorphism. Additional life-history data are necessary to test this hypothesis critically.

INTERPRETATION OF THE INTERCORRELATIONS

A long history of ecomorphological studies in woodpeckers argues for the relationship between morphology and diet being adaptive. How, though, can we interpret the correlation between clutch size and diet?

One interpretation, discussed above for the relationship between diet and culmen dimorphism, is that wood-boring larvae may be more stable than other food resources or differ in availability in some other way so as to afford high adult survivorship and relatively low reproductive effort. Again, if wood-boring larvae were seasonally stable but relatively rare, this might further selection for reduced reproductive effort. By this line of reasoning, the variation in clutch size among species is due to the dietary differences among them, and the morphological correlates of clutch size are an indirect result of the mutual dependence of morphology and clutch size on diet.

An alternative interpretation is that the relationship between clutch size and diet may be, at least in part, a side effect of selection for the morphological specializations attendant to dietary shifts. Because of the presumably functional relationship between diet and morphology, to the extent that the latter constrains clutch size, a correlation between clutch size and diet would emerge even if no functional relationship exists between them.

Numerous workers have demonstrated that phylogenetic constraints, as reflected by differences in body size, are important in determining classwide variations in life-history variation (e.g. Western 1979; Stearns 1983, 1984). The correlations between clutch size and body size within the genera *Picoides* and *Melanerpes* found here suggest that size constraints may be important within these lower taxa as well, albeit in opposite directions. In addition, the correlations between clutch size and morphology independent of body size found within the family suggest the possibility that other types of morphological constraints may influence clutch size. Thus, clutch size within the family Picidae and within the genera *Picoides* and *Melanerpes* may at least in part be a secondary consequence of constraints imposed by size and by other morphological adaptations to particular foraging modes.

I am unable to propose any likely scenario as to the exact nature of the constraints that might be involved. Certainly, no obvious relationship exists between any of the skeletal features presented in Table 3 and organs involved directly with producing eggs. Nevertheless, virtually any morphological modification could constrain clutch size if associated muscle or skeletal development requires space or energy that might otherwise be devoted to egg production. Although such interactions are speculative, the same is true of the precise nature of the constraint on fecundity imposed by large body size (e.g. Blueweiss et al. 1978; Western 1979; Western and Ssemakula 1982; Stearns 1983, 1984; Calder 1984).

There is considerable interest in the interactions between ecology and morphology; indeed, it is this interface with which the field of ecomorphology is concerned. However, correlations between life-history phenomena and either morphology, with the exception of body size, or feeding ecology have been virtually ignored. My analyses suggest that these major phenotypic features may covary in a coherent fashion both within families and within genera. Similar analyses on taxa for which more complete demographic data are available, such as primates and rodents, are likely to be particularly illuminating. Examination of intraspecific correlations between morphology and life-history patterns would also be of considerable interest.

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LITERATURE CITED

AMADON, D. 1943. Bird weights and egg weights. Auk 60: 221-234.

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. Washington, D.C., Amer. Ornithol. Union.

———. 1985. Thirty-fifth supplement to the American Ornithologists' Union check-list of North American birds. Auk 102: 680-686.

ATCHLEY, W. R. 1978. Ratios, regression intercepts, and the scaling of data. Syst. Zool. 27: 78-83.

———, & D. R. ANDERSON. 1978. Ratios and the statistical analysis of biological data. Syst. Zool. 27: 71-78.

BEAL, F. E. L. 1911. Food of the woodpeckers of the United States. U.S. Dept. Agr., Biol. Surv. Bull. 37.

BENT, A. C. 1939. Life histories of North American woodpeckers. U.S. Natl. Mus. Bull. 174.

BLEM, C. R. 1984. Ratios in avian physiology. Auk 101: 153-155.

BLUEWEISS, L., H. FOX, V. KUDZMA, D. NAKASHIMA, R. PETERS, & S. SAMS. 1978. Relationships between body size and some life history parameters. Oecologia 37: 257-272.

BOCK, W. J. 1964. Kinetics of the avian skull. J. Morphol. 114: 1-42.

BURT, W. H. 1930. Adaptive modifications in the woodpeckers. Univ. California Publ. Zool. 32: 455-524.

CABANA, G., A. FREWIN, R. H. PETERS, & L. RANDALL. 1982. The effect of sexual size dimorphism on variations in reproductive effort of birds and mammals. Amer. Natur. 120: 17-25.

CALDER, W. A. 1984. Size, function, and life history. Cambridge, Massachusetts, Harvard Univ. Press.

CLUTTON-BROCK, T. H., & P. H. HARVEY. 1984. Comparative approaches to investigating adaptation. Pp. 7-29 *in* Behavioural ecology: an evolutionary approach, 2nd ed. (J. R. Krebs and N. B. Davies, Eds.). Sunderland, Massachusetts, Sinauer.

CODY, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.

DUNHAM, A. E., & D. B. MILES. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. Amer. Natur. 126: 231-257.

HEDGES, S. B. 1985. The influence of size and phylogeny on life history variation in reptiles: a response to Stearns. Amer. Natur. 126: 258-260.

JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365-390.

KIRBY, V. C. 1980. An adaptive modification in the ribs of woodpeckers and piculets (Picidae). Auk 97: 521-532.

KOENIG, W. D. 1986. Geographical ecology of clutch size variation in North American woodpeckers. Condor 88: 499-504.

———, & R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton, New Jersey, Princeton Univ. Press.

———, & F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterploys in the communally nesting Acorn Woodpecker. Science 206: 1103-1105.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

MILLAR, J. S., & R. M. ZAMMUTO. 1983. Life histories of mammals: an analysis of life tables. Ecology 64: 631-635.

MUMME, R. L., W. D. KOENIG, & F. A. PITELKA. 1983. Reproductive competition in the communal Acorn Woodpecker: sisters destroy each other's eggs. Nature 306: 583-584.

PETERS, W. D., & T. C. GRUBB, JR. 1983. An experimental analysis of sex-specific foraging in the Downy Woodpecker *Picoides pubescens*. Ecology 64: 1437-1443.

RAHN, H., C. V. PAGANELLI, & A. AR. 1975. Relation of avian egg weight to body weight. Auk 92: 750-767.

RIDGWAY, R. 1914. The birds of North and Middle America. VI. U.S. Natl. Mus. Bull. 50.

ROFF, D. 1981. On being the right size. Amer. Natur. 118: 405-422.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68: 113–151.

SHUFELDT, R. W. 1900. On the osteology of woodpeckers. Proc. Amer. Phil. Soc. 39: 578–622.

SPRING, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. Condor 67: 457–488.

STEARNS, S. C. 1976. Life history tactics: a review of the ideas. Q. Rev. Biol. 51: 3–47.

———. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. Oikos 41: 173–187.

———. 1984. The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. Amer. Natur. 123: 56–72.

THOMSON, A. J. 1964. A new dictionary of birds. London, Nelson.

TUOMI, J. 1980. Mammalian reproductive strategies: a generalized relation of litter size to body size. Oecologia 45: 39–44.

VITT, L. J., & R. A. SEIGEL. 1985. Life history traits of lizards and snakes. Amer. Natur. 125: 480–484.

WESTERN, D. 1979. Size, life history and ecology in mammals. African J. Ecol. 17: 185–204.

———, & J. SSEMAKULA. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. Oecologia 54: 281–290.