Body Condition in Eastern Kingbirds

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Murphy (1986) reported the effects of body size and body condition on the timing of breeding (ToB), on egg size, and on egg production in Eastern Kingbirds (*Tyrannus tyrannus*). Murphy did three things, in particular, that led us to conclude that most of his conclusions are unsupported or equivocal at best: (1) he used an inappropriate sample of birds, (2) he confused body size with body condition, and (3) he used questionable methods for assessing outlying data in bivariate correlations.

First, Murphy's data were from 23 females of which "18 were collected 0-2 days after laying the last egg, and 1 each 5, 8, 21, and 25 days after the laying of the final egg. One female was collected on the evening before she laid her first egg" (p. 466). These data were inappropriate to assess the importance of nutrient reserves to breeding kingbirds because, in addition to postlayers and one layer, it was necessary to have both prelayers and more layers. For example, Ankney and MacInnes (1978) found no differences in body weights or fat, protein, and calcium reserves among postlaying female Lesser Snow Geese (Chen c. caerulescens) that had just laid 2-6 eggs. If they had not collected a sample of prelaying females and had followed Murphy's approach, they would have concluded falsely that clutch size was unrelated to the size of nutrient reserves in that species. A comparison of the nutrient reserves of postlaying females that have laid different-size clutches can have several outcomes: (1) females that laid larger clutches have larger reserves, (2) females that laid larger clutches have smaller reserves, or (3) there are no differences in reserve size among females that laid clutches of different size. Without adequate data from prelaying and laying females, it is impossible to interpret any of the outcomes, because each has alternative explanations. For example, outcome 3 could result if females, on average, started laying with reserves of equal size but did not use reserves for egg formation (as happens in Brown-headed Cowbirds, Molothrus ater; Ankney and Scott 1980), or if females with larger prelaying reserves put more of their reserves into egg production than females with smaller prelaying reserves (as in Lesser Snow Geese; Ankney and MacInnes 1978).

Ironically, Murphy stated (p. 474) that he was unable to "assess directly whether females store and deplete resources during clutch production," yet he conducted his analyses anyway. We were particularly surprised at this because other studies, which Murphy

cited (e.g. Jones and Ward 1976, Hails and Turner 1985), included prelaying, laying, and postlaying females. Clearly, if levels of nutrient reserves are an important factor determining when kingbirds breed and how much nutrient is allocated to clutch formation, then it must be the size of those reserves accumulated before and possibly during egg formation that are important, not how much are present after egg laying. We submit that using only postlayers to investigate the influence of their "condition" on clutch formation is analogous to calculating how far a car has traveled with a knowledge of how much gas is present in the tank at the end of a trip, but with no knowledge of how much gas was in the tank at the start of the trip, nor of the rate of consumption during the trip.

The same problem applies to Murphy's analyses of the relation between the body condition of postlaying females and egg composition. For example, he found (his fig. 5b) a negative relation between an index of a female kingbird's calcium reserves and the shell weight of her eggs, i.e. females that had produced heavier shells had less body minerals. He also found a positive correlation between an index of a female's protein reserves and the weight of her egg (his fig. 3), i.e. females that had laid heavier eggs had larger protein reserves. Despite the opposite signs of the slopes, Murphy concluded that females in good condition lay high-quality eggs, and that egg weight "was more a matter of body condition than size" (p. 474). These conclusions may be correct, but they were derived illogically because body condition of postlaying females cannot affect the sizes of eggs that already have been laid.

Second, we question Murphy's use of total muscle weight (TMW) as a measure of body size (p. 468). Because nutrient reserves of passerines can be highly variable (both within and among days, e.g. Blem and Pagels 1984), nutrient reserves should be used as measures of size in intraspecific comparisons only with caution. Although scores from the first principal component (PC1) of a number of morphological measures may be correlated with muscle weight, each of the two variables contains different kinds of information. Depending on the morphological variables chosen, PC1 scores can be used to reflect body or structural size, but muscle weight contains information on both body size and the nutritional condition of the bird. Murphy used the proper approach to derive an index of structural size by using PC1, but when only a "marginally significant" relationship between ToB and PC1 was found (P = 0.06), Murphy altered his definition of size and equated it with TMW, which was "strongly correlated" (r = 0.58) with ToB (P = 0.01). The residuals of TMW from a regression on PC1 scores should

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be used to assess if that proportion of the variance in TMW unrelated to body size is related to ToB. Although smaller kingbirds may nest earlier than larger ones (P = 0.06 is certainly suggestive of that), Murphy's conclusions referring to "a direct energetic basis for differences in ToB" (p. 468) were premature.

Third, removing an outlying point in bivariate plots is invalid unless there is good reason to suspect that the observation came from a bird that was not part of the statistical population being studied, e.g. a nonbreeder instead of a breeder, a yearling instead of an adult, etc. Murphy argued that one female "laid unusually early" and used this as justification to ignore her, thereby resulting "in a highly significant relationship" (his fig. 2). Murphy stated further that the patterns in fig. 4 were obscured by one "nest in particular" that "eliminated several potentially significant relationships"; no reason was provided for discarding that observation. We note, however, that Murphy did not ignore the equally "unusual" female (in fig. 2) that nested late, at about the 66th day, with about 4.5 g of TMW. We suggest, from inspection of fig. 2, that had Murphy discarded the "unusually" late female instead of the unusually early one, his analysis would have shown a negative relation between TMW and ToB! Equally invalid reasoning could be used to justify ignoring the female in fig. 2 that produced 4 eggs but was "unusual" in that she had a much higher TMW than any other female that laid 4 eggs. Outliers are most influential when sample sizes are very small, and thus a posteriori decisions to remove them must be well justified. If such justification is not evident, then formal procedures for objectively detecting outliers should be used (e.g. Sokal and Rohlf 1981: 413, Owen and Chmielewski 1985). Regardless, robust inferences generally are precluded if small sample sizes are used for statistical analyses.

We do not believe that Murphy, given the timing of collections and the number of birds analyzed, could have tested his hypotheses about timing of breeding, clutch size, and egg composition of Eastern Kingbirds. We view those sections of the paper that deal with the relation between body size and ToB as exercises in data exploration—a procedure that is useful for formulating hypotheses. Murphy has shown that smaller female kingbirds may nest earlier than larger ones, but clearly other data are required to investigate why they do.

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Response to Alisauskas, Ankney, and Krementz

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Alisauskas et al. (1987) claimed that my recent analysis of body composition in Eastern Kingbirds (*Tyrannus tyrannus*; Murphy 1986a), and the relation of composition to reproduction, was flawed. Further, they charged that my conclusions concerning the relation between female body composition and egg composition were "derived illogically." I here provide body composition data for prelaying females, and defend my measures of size and conclusions concerning the determinants of egg composition. I also discuss my rationale for deleting points in particular analyses.

First, I collected and analyzed the body composition of 5 prelaying female kingbirds. I did not report the data (except for bone weights; see table 5) because

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