

cause the pectoral muscles were used for short-term (i.e. daily) storage of lipids used in egg formation. Large eggs also required more minerals for shell formation, and this was presumably the basis for the negative relation between egg size and body minerals. I fail to see why opposite signs in these slopes caused problems for Alisauskas et al.

Lastly, Alisauskas et al. objected strongly to my treatment of the egg composition/female body composition data because I chose to exclude one point from the analysis because it "eliminated several potentially significant relationships" (see fig. 4). My rationale for excluding this point was simple: given the virtual nonexistence of this type of data (but see Houston et al. 1983), I felt it would be reasonable to speculate as to the basis for differences in egg composition among females. I make no apologies for this. Healthy speculation, which I consider the egg composition/body composition data to be, is required for generating and testing new hypotheses.

The data on kingbirds provide one of the strongest supporting cases for Downhower's (1976) body-size/timing-of-breeding hypothesis. Relative to the other years of my study, timing of breeding was delayed in the year in which these data were collected (Murphy 1986b), and it is probable that one is most likely to detect body size-dependent breeding under such conditions. In years of more benign conditions body size may have little effect on breeding date. Nonetheless, intermittent selective events such as this can be ecologically and evolutionarily important (e.g. Johnston and Fleischer 1981). If Alisauskas et al. still object, it is their responsibility to provide a more co-

gent explanation for the observed direct relationship between body size and timing of breeding in kingbirds.

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### Female Choice in Middendorff's Grasshopper-Warbler?

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Recently, Nagata (1986) suggested that the polygyny-threshold (Verner 1964, Verner and Willson 1966, Orians 1969) and sexy-son (Weatherhead and Robertson 1977, 1979) hypotheses may be applicable models for female choice in monogamous species. He suggested also that female Middendorff's Grasshopper-Warblers (*Locustella ochotensis*) base their choice of mate on the quality of the male's territory rather than of the male.

The polygyny-threshold and sexy-son hypotheses were developed to explain why some males in polygynous species acquire more than one mate while others have only one. These hypotheses are useful as

tools to understanding female choice only in polygynous species, not in monogamous species. To imply that the polygyny-threshold hypothesis is synonymous with a hypothesis that holds that females base their choice of mate on the quality of his territory is misleading. Under this hypothesis, females are assumed to assess the quality of the breeding situation, which includes the quality of the male. To imply that the sexy-son hypothesis is synonymous with the hypothesis that females choose mates based on the quality of the male alone is also misleading. Again, under this hypothesis, females are assumed to base their choice of mate on the quality of the territory as well as the male. The two hypotheses differ in the way females should be compensated for choosing a polygynous situation over a monogamous one. The polygyny-threshold hypothesis suggests that females

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can be compensated for mating polygynously by being in such a superior breeding situation that they expect the same reproductive success as would be achieved in a poorer situation. The sexy-son hypothesis suggests that females choosing polygyny with attractive males will have attractive sons with large harems, and, thus, these females will leave more grandoffspring, rather than more of their own offspring. Clearly, these two hypotheses cannot be used to examine female choice in monogamous species.

Nagata did not properly determine whether females choose mates on the basis of male quality. He found no correlations between pairing date and male morphological characteristics, but he did not examine any male behavior. Females may have chosen mates on the basis of male courtship abilities (Weatherhead and Robertson 1977, Borgia et al. 1985).

Nagata did not show convincingly that females choose mates based on territory quality. He showed a significant correlation of pairing date with territory size and, to a lesser degree, with a food score, and concluded that this demonstrated female choice on the basis of territory quality. This conclusion may not be valid for several reasons. Food score was proportional directly to territory size, and when he held territory size constant the correlation between pairing date and food score was reduced. This suggests that food was not the main feature of territories upon which females made their choice. Territory size may be synonymous with territory quality if larger territories contain more food and the extra food increases reproductive success or nestling growth rates, or if larger territories contain more nest sites and males with large territories can attract more females. The former was not examined by Nagata, and the latter does not apply to a monogamous species. Therefore, there is no valid reason to conclude that female choice of large territories is adaptive in this species.

In addition, a correlation between arrival date and territory size need not indicate females prefer large territories. A correlation between arrival date and ter-

ritory size would be expected if females settled randomly. I showed recently that a neutral mate-choice hypothesis, in which females settle randomly and males compete for territories to gain access to females, applies to at least one population of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Lightbody and Weatherhead in press). This is a viable alternative explanation that Nagata failed to consider. Unless it can be shown clearly that choosing a large territory is adaptive, it is premature to conclude that female Middendorff's Grasshopper-Warblers choose mates on the basis of territory quality.

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#### Response to J. P. Lightbody

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Lightbody (1987) argued that the polygyny-threshold hypothesis (Verner 1964, Verner and Willson 1966, Orians 1969) and sexy-son hypothesis (Weatherhead and Robertson 1979) are useful to explain only why some males in polygynous species acquire more than one mate. Females will try to mate with fitter males

in monogamous species, however, if there are variations among territories or genetic qualities, and if those variations reflect upon the fitness of females. A threshold never need be exceeded. The polygyny-threshold hypothesis assumes that territory quality is the main cue of female mate choice, and for monogamous species or primary females predicts that the male with the best territory will be chosen. The sexy-son hypothesis extends the concept of the polygyny threshold to the quality of a female's offspring. The

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