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 territory 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

Hisashi Nagata[1]

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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sexy-son hypothesis assumes that a sexy character is highly heritable and implies that a female that chooses a male with such a character can gain compensation for the reduction of her children in future generations through the success of their sexy sons.

There are some differences between the two hypotheses in the definition of the fitness gain of the females. In the polygyny-threshold hypothesis fitness is defined as immediate reproductive success, while in the sexy-son hypothesis it is defined as the number of descendants, i.e. the ultimate contribution to the gene pool. Therefore, if females assess the territory quality and choose mates to maximize the current reproductive success, the polygyny-threshold hypothesis is applicable for female choice in monogamous species. If females assess male quality and choose mates to maximize the number of grandoffspring, then the sexy-son hypothesis is applicable in monogamous species.

As pointed out by Lightbody (1987), the correlation between pairing date and food score for Middendorff's Grasshopper-Warbler (*Locustella ochotensis*) was reduced when territory size was held constant (Nagata 1986), which indicated only that females did not use the density of available food to assess territory quality. Larger territories may contain more food, however, as preferable food resources are distributed randomly, and larger territories may contain more potential nest sites. Females that failed to breed renested at a distance from their first nests (Nagata unpubl. data). Large territories will provide alternative nest sites for females and allow the possibility of polygynous mating, if a polygyny threshold is exceeded. I observed only two cases of occasional polygyny over 6 yr of observation (Nagata in prep.). In those cases males with large territories acquired additional females. Therefore, I conclude that female grasshopper-warblers choose males with large territories.

The fact that I found no correlation between pairing date and morphological traits of males (Nagata 1986) indicated only that such characteristics did not reflect male fitness. To negate the possibility that females choose mates on the basis of male courtship ability requires examination of the correlation between male behaviors and pairing date.

Lightbody (1987) proposed that a neutral female-choice hypothesis was applicable to Middendorff's Grasshopper-Warbler. If females choose males randomly, polygyny is expected more frequently. Monogamy is the predominant mating system in this species, however. There was evidence that the location where females arrived first was distant from the territory where they settled and that some males led one female into their territory. These observations suggest that females choose their mates selectively rather than randomly. Moreover, arrival date did not correlate with territory size ($r = -0.38$, not significant; Nagata 1986). Therefore, the neutral mate-choice hypothesis cannot apply to the Middendorff's Grasshopper-Warbler.

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