emerged insects than do dippers (Ormerod and Tyler 1987). Because early dietary experience can affect later choice (e.g. Rabinowitch 1968), the dietary preferences of dipper nestlings fed by wagtails might be atypical.

We do not understand what benefit, if any, accrued to the wagtail from feeding the dipper nestlings. Dawkins (1976) suggested that birds adopting alien young might benefit in gaining experience as a parent. Although this explanation might account for inexperienced birds feeding heterospecific nestlings, it seems unsuitable for the behavior of this Gray Wagtail, given that he simultaneously fed his own brood, at least one of which fledged. Instead, the prolonged investment in the dipper nestlings was more probably a maladaptive response to the proximity of loudly begging chicks. Strong responsiveness to stimuli associated with dependent young may have advantages that compensate for the rare instances in which that responsiveness results in maladaptive behavior. It may be significant that wagtail nestlings are much quieter than dipper nestlings. The dippers' calls may have acted as a "super-normal" stimulus (Tinbergen 1948) to trigger feeding of the alien young as the male passed en route to his own nest with food. One prediction of this hypothesis is that noisy nestlings would be more likely to be fed by heterospecifics than quiet nestlings, especially if the young of the adopting species are quiet.

A significant aspect of our observations is that spontaneous interspecific feeding, once initiated, may be self-perpetuating. First, increased feeding by the heterospecific reduces the parents' contribution and, consequently, their activity near the nest. The interspecific aggression that might deter the adopting bird is therefore less likely to occur. Second, the sign stimuli that initially occasioned the interspecific feeding (e.g. begging calls, gaping mouths) may become associated with the sight of the alien nest and with approaches to it, thus increasing the probability that the adopting bird will return to the alien nest. A comprehensive understanding of the proximal mechanisms underlying interspecific feeding, and any ecological and evolutionary consequences, awaits additional data.

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Mate Attraction by Autumnal Song in the Northern Mockingbird (*Mimus polyglottos*)

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The Northern Mockingbird (*Mimus polyglottos*) is perennially territorial in the southeastern United States. Both mated and unmated males defend autumnal territories, and both sing throughout the months of September and October (Breitwisch et al. 1986, Logan 1987). In the spring, unmated males sing more than mated males (Breitwisch and Whitesides 1987), and mockingbird song appears to function in mate attraction. Merritt (1985) removed females from the territories of mated males in the spring; the song production of males whose females were removed was greater than that of mated males and approximated amounts of singing produced by unmated males. Autumnal song is produced from early September to November, and mockingbirds have been observed to form pairs in autumn (Logan unpubl.
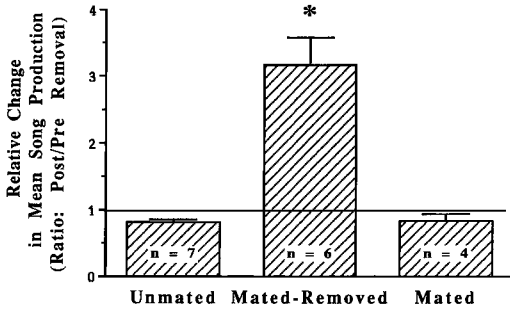
Fig. 1. Average ratio (±SE) of postremoval song production to preremoval song production in unmated males (Unmated), mated males whose females were removed (Mated-Removed), and mated males whose females were not removed (Mated). The horizontal line indicates a ratio of 1.0: no change in average song production before and after the time at which females were removed from the territories of mated males. * = Kruskal-Wallis, $P < 0.025$.

obs.). We used female removal to determine if autumnal song functions in mate attraction outside the breeding season. If this is the case (as it is in the breeding season), then unmated males should sing more than mated males, and female removal should increase the amount of song produced by males whose mates are removed (e.g. Cuthill and Hindmarsh 1985).

We studied free-living, color-banded mockingbirds that inhabited the residential campus of the University of North Carolina at Greensboro. Eight to ten 30-min baseline samples per bird were taken from 8 unmated and 10 mated males from 13 September through 29 October, 1987, and 7 September through 19 October, 1988. Because autumnal singing begins at different times for different males, sampling was begun only after the bird produced at least 1.5 min (mated) or 3 min (unmated) of song per 15 min. Weather permitting, preremoval sampling occurred twice per day for 5 consecutive days between 0700–1100 and 1400–1800. On day 6, or as soon after as possible (mean = 3.1 days), the females of mated pairs were captured in baited potter traps and removed. To equalize disruption from capture, both mated and unmated males were also captured and immediately returned into their territories. Postremoval sampling began for mated males the day following female removal. The sampling of unmated males resumed the day after capture. Postremoval sampling ended on 7 November 1987 and 29 October 1988 either when a bird added no more than 5% additional singing time to his running average for six consecutive samples or on the fifth day after female removal, whichever came first. Following sampling, females were returned to their home territories.

Throughout each sample we noted the occurrence of territorial fights, fights with other species, and ag-

gressive calls including the hew and chatburst (Logan et al. 1983). We measured song production by the number of 15-s time bins per sample in which song occurred. This measure reflects the amount of time spent singing, but not the quality of the song. Though qualitative aspects of song may affect mate attraction (Derrickson 1987, 1988), we assumed that males advertising for mates should sing more than mated males. On this view, the amount of song produced provides one—but not the only—index of song's use in mate attraction. We also monitored the number of 15-s time bins per sample in which the observer lost audio and visual contact with the focal male. If we lost contact with the bird for >10 min per sample, the sample was aborted and begun later; data from aborted samples were not included in the analyses. Unless otherwise indicated, statistical tests used the Wilcoxon matched-pairs signed-rank test (related samples) or the Mann-Whitney U-test (independent samples) (Siegel 1956). Values are reported as means (±SE).

The amount of song produced in preremoval samples indicated that mated males sang significantly less per 30 min than unmated males (mated = 14.0 ± 3.0 15-s bins with song; unmated = 31.7 ± 4.0; U [one-tailed] = 9, $P < 0.01$). Females were removed from 5 of the 10 mated pairs. One mated male lost his mate midway through behavioral sampling. After the female left, his average song production per sample increased from 20.8 to 52.7 bins with song. Data from this bird are included with the males whose females were removed. We continued "postremoval" sampling on 4 mated males whose females could not be captured and who therefore remained mated throughout. To examine the change in song production after female removal relative to each bird's baseline song production, we calculated the ratio of mean postremoval song production to mean preremoval song production. Ratios were determined for the 6 males whose females were removed or left, for 7 unmated males sampled at comparable times in the season, and for 4 mated males. A Kruskal-Wallis one-way ANOVA revealed significant differences among the groups (H [one-tailed] = 4.95, $P < 0.025$). Pairwise comparisons indicated that the ratio of post- to preremoval song production was significantly greater in males whose females had been removed compared with both unmated males (Mated-removed = 3.16 ± 0.86; Unmated = 0.81 ± 0.10; U [one-tailed] = 7, $P < 0.03$; Fig. 1) and to mated males whose females were not removed (Mated: 0.83 ± 0.20; U [one-tailed] = 4, $P = 0.057$). However, the relative change in song produced before versus after capture in mated males whose females could not be captured did not differ from that of unmated males (U [one tailed] = 17, $P > 0.20$). The change in song production in birds whose females were removed occurred quickly. Comparison of mean song output in the last two samples before removal with the first two samples after removal indicated a rapid threefold increase in singing (means

= 7.75 versus 27.33 bins with song per sample). There-fore, variability across birds in the effect of removal is unlikely to be due to variable times at which males increased song production. Female-removed and un-mated males did not differ either before or after re-moval in average time per sample in which audio and visual contact with the focal bird was lost ($P > 0.20$), and there was no difference in total minutes of ob-servation per bird (485 ± 39.8 versus 446 ± 38.6).

One of the unmated males (Bird T) attracted a mate during precapture sampling. Data obtained on this bird were excluded from the above analyses, though several aspects of the sequence are of note. Our preex-perimental inventory indicated no sign of a second bird in the territory, and the male was classed as unmated. During the third of 17 behavioral samples, Bird T engaged in a courtship chase with an unbanded bird. Thereafter, an unbanded bird that was not chased out of the territory was seen on 8 of the 17 time samples. Comparison of the mean song production per sample in samples with the unbanded bird pres-ent ($n = 9$) versus those with no second bird present ($n = 8$) indicated a twofold increase in time spent in song in the absence of a second bird (30.22 versus 59.33 bins with song per sample). Four days after the first courtship chase, the unbanded bird fed in the territory, and on two of the final samples the un-banded bird sang in the territory with Bird T present. Though we cannot be certain that the unbanded bird observed on successive samples was the same bird each time, it would be extremely unlikely for a res-ident to allow a succession of intruders to remain in the territory undisturbed. If we assume that the un-banded bird was a single individual, these observa-tions confirm that mate attraction occurs naturally in autumn, and they illustrate that when a female is present there is a natural decrease in autumnal sing-ing. Moreover, the pattern of change described for this bird parallels that seen in a male that acquired his mate during the breeding season in south Florida (Breitwisch and Whitesides 1987).

Though autumnal song may function territorially, it is unlikely that the differences in song production were due to altered patterns of territoriality. The groups did not differ in mean number of territorial fights per sample either before (mated-removed = 0.20 ± 0.07; unmated = 0.38 ± 0.14; $U = 19$, $P > 0.20$) or after female removal (mated-removed = 0.20 ± 0.06; unmated = 0.43 ± 0.16; $U = 19$, $P > 0.20$). Sim-ilarly, there were no differences in average number of territorial fights per sample before versus after re-moval in males whose females were removed ($T = 3$, $P > 0.10$). Finally, following the removal of females the groups did not differ in other indices of aggres-sion, including the average production per sample of the chatburst call, known to function in territorial defense (Logan et al. 1983), or the average number of fights per sample with other species (all P values >0.20).

Though there is increasingly strong evidence for autumnal reproductive activity in several avian spe-cies (e.g. Bluhm 1988), we are aware of no prior dem-onstration that song functions in the formation of autumnal pairs in a temperate passerine. Hegner and Wingfield (1986) suggested that the annual cycle of reproductive activities may begin in passerines in au-tumn. House Sparrows (*Passer domesticus*) show two phases of reproductive development outside the breeding season proper: an autumnal phase from Oc-tober through January in which reproductive phys-iology changes very gradually, and a more rapid win-ter phase characterized by more complete gonadal function. During the earlier phase paired House Spar-rows showed defense of nest boxes and gradual in-creases in testis size and androgen secretion. We found that, like House Sparrows, mockingbirds may show reproductive behavior that includes song and mate attraction during a period roughly corresponding to the gradual autumnal phase.

Several potential advantages of winter pairing have been suggested in waterfowl, including earlier spring nesting, enhanced female nutrition and mate testing (Rohwer and Anderson 1988). Hegner and Wingfield (1986) add to these the advantage of a longer breeding season produced by earlier pairings in multibrooded species. In the spring, mockingbirds appear adapted for temporal efficiency in an already long breeding season (Zaias and Breitwisch 1989, Logan et al. 1990). Because they are perennially territorial and highly multibrooded, and may renest with the same partner season after season, mockingbirds are likely to benefit from the increased breeding time associated with ear-ly pairing. If males use song to acquire mates in au-tumn, nesting may begin the following spring as soon as weather permits, thereby further enhancing the temporal efficiency of spring and summer reproduc-tive efforts.

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Measurement Error of External and Skeletal Variables in Birds and Its Effect on Principal Components

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Assessment of measurement error is important for studies that use morphometric variables to make statistical inferences about biological phenomena (e.g. studies of adaptive radiation, taxonomic relationships, interspecific competition, age and sex determination, body condition, heritability, and growth). Use of variables with large measurement errors can result in Type II statistical errors (i.e. accepting false null hypotheses, see Toft and Shea 1983). The effect of measurement error, however, has been ignored in most morphometric studies. Those researchers that have assessed measurement error used techniques that identified interobserver or session biases (e.g. Nisbet et al. 1970, Zink 1983, Arendt and Faaborg 1989) or the absolute precision of particular measurements (e.g. Bortolotti 1984, Francis and Wood 1989). However, measurement error can be assessed properly only when it is evaluated *relative* to variation among individuals in a sample (Schluter and Smith 1986, Bailey and Byrnes 1990).

To assess relative measurement error of several external and skeletal measures in Rufous-collared Sparrows (*Zonotrichia capensis*), and external measures in American Coots (*Fulica americana*), we used repeated measurements and Model II analysis of variance

(Schluter and Smith 1986, Lessells and Boag 1987, Bailey and Byrnes 1990). In addition, we examined the effects of such error on principal component analysis using morphological variables.

The specimens used represent subsets of larger collections of birds obtained for other research objectives. The morphological variables were selected for these research objectives and were not chosen specifically for a study of measurement error. Before conducting the present study of measurement error, we had intended that all variables be included in our respective studies. Hence, our data are typical of "real world" avian morphological data, except that we measured individual specimens more than once.

Twenty-one male Rufous-collared Sparrows were mist-netted in Belen, Catamarca Province, Argentina (27°39′S, 67°02′W). Thirteen skeletal characters were measured three times on each sparrow: skull width, partial skull length (from the base of the maxilla to the foramen magnum), coracoid length, width of the proximal end of the scapula, scapula length, sternum length, keel depth, synsacrum width (distance between acetabulae), width of proximal end of femur, femur length, tibiotarsus length, humerus length, and ulna length (see Robins and Schnell 1971 for detailed