

Molt-Breeding Overlap in Northern Mockingbirds

JULIA ZAIAS¹ AND RANDALL BREITWISCH²

Department of Biology, University of Miami, Coral Gables, Florida 33124 USA

Molting and breeding are commonly thought to be mutually exclusive processes, because of the great physiological expense of each (Lofts and Murton 1968, Payne 1972, Skutch 1976, O'Connor 1984; however, see King and and Murphy 1985). This generalization appears to be true for most temperate species although exceptions exist (Newton 1966, Ligon and White 1974, Nolan 1978, Bancroft and Woolfenden 1982, Thompson and Slack 1983), especially in tropical species. Payne (1969) and Foster (1975) both reported low frequencies of molt-breeding overlap in large collections of African (3.8%) and Neotropical (10%) species. Both authors characterized molt and gonadal activity at the time of collection of the specimens. Payne and Foster indicate, however, that these are probably overestimates that are due to the difficulty of determining if the observed molt was scheduled and complete vs. replacement, interrupted (Payne 1969), or adventitious (Foster 1975).

Molt-breeding overlap is observed in arctic/subarctic species where resources are abundant for only a brief period (Pitelka 1958, Johnston 1961, Hunter 1984). Other species have arrested or protracted molts presumably to decrease physiological stress in unpredictable environments or while they breed (Miller 1961, Newton 1966, Payne 1972, Ligon and White 1974). Although many species have been noted to overlap molting and breeding, few studies have provided quantitative data. Snow and Snow (1964) presented data on 123 tropical passerines, where 41 (33%) species were observed to molt and breed in the same month. These were, however, general molt and breeding records for species and did not necessarily pertain to individuals.

We report molt-breeding overlap in individually color-banded Northern Mockingbirds (*Mimus polyglottos*) while they cared for fledglings. These data were part of a 7-year study of a population of mockingbirds on the main campus of the University of Miami, Dade County, Florida. Approximately 35 territories were monitored each year, and the population is continuous into surrounding suburbs. The campus is sparsely wooded, suburban lawn (for details of the study site, see Breitwisch et al. 1984). Mockingbirds in southern Florida are multibrooded. Typically, they build 3-6 nests in a breeding season, which begins in mid-March and extends through August (Breit-

wisch 1988, Zaias and Breitwisch 1989). This pattern of multiple nestings within a breeding season and instances of molt-breeding overlap is not unique to this population (observed in North Carolina, C. Logan pers. comm.). The characteristic pattern of molt for adult Northern Mockingbirds and their sympatric relatives (i.e. Gray Catbird, *Dumetella carolinensis*, and Brown Thrasher, *Toxostoma rufum*) in southern Florida is a single, complete postnuptial molt in late summer to early autumn (Bent 1948).

Mockingbirds in the University of Miami population were observed throughout the entire 1986 breeding season as part of a study on fledgling care and re-nesting behavior (Zaias and Breitwisch 1989). We conducted regular censuses of ca. 35 territories throughout the breeding season. Data presented are the subset of observations during which we monitored molt. Mockingbirds on seven territories were observed to molt while they cared for fledglings. In all cases, the overlap occurred during the last broods of the season (i.e. broods not followed by another nesting attempt). Most last broods were initiated between mid-July and mid-August.

We recorded a bird as being in molt if it was observed to be markedly disheveled in appearance of its torso and to have lost *paired* primaries and rectrices. Complete records of the extent and duration of molt were not obtained, but all molting birds were observed more than once over several days. We recorded whether the parent was molting and whether it fed fledglings. Occasionally, only one parent cares for fledglings of the last brood of the season (Zaias and Breitwisch 1989).

We recorded 9 of 14 individuals (64%) with molt-breeding overlap. The onset of molt varied between 15 July and 14 August. Four of seven (57%) males and five of six (83%) females molted while they cared for fledglings. Percentages did not differ between sexes (Fisher exact probability test, $P > 0.05$). Parents were first observed in molt a mean of 4.4 ± 3.4 (SD) days after young fledged (range: 2-11 days, $n = 9$). For the five females that fed fledglings, the mean day of first molt was 3.8 ± 2.5 days postfledging (range: 2-8). For the four males, the mean day of first molt was 4.8 ± 4.2 days postfledging (range: 2-11). These values for the sexes were not significantly different (randomization test $P > 0.05$).

Molt onset was synchronous within pairs (Kendall rank correlation, $S = 14$, $n = 6$ pairs, $P < 0.01$; Fig. 1). The mean calendar date of onset of molt for feeding males was 23 July, for feeding females was 28 July. The mean calendar date of molt onset for those birds not feeding was 4 August ($n = 4$).

In theory, the cost of rearing a brood increases with

¹ Present address: Department of Ecology, Ethology, and Evolution, University of Illinois, 606 East Healey, Champaign, Illinois 61820 USA.

² Present address: Department of Biology, University of Dayton, Dayton, Ohio 45469 USA.

brood size (Williams 1966). If there is a significant cost to molt-breeding overlap, then one might expect parents to delay molting until fledglings were independent (i.e. capable of flight and foraging on their own). We found no correlation between the first day the parent was observed in molt after the young fledged and the number of fledglings present. This was true for males, females, and both sexes combined (Kendall rank correlation; males: $S = -4, n = 7$; females: $S = -3, n = 6$; sexes combined: $S = -2, n = 6$ pair means, $P > 0.05$ for all).

Feeding rates of fledglings did not differ significantly from nestling feeding rates (Breitwisch et al. 1986, Zaias and Breitwisch 1989). This raises the question of why mockingbirds wait until after nestlings fledge to begin molt. Defense of nestlings is strong (Breitwisch 1988) and is greatest within the first week of the fledgling stage. Nearly all fledgling mortality occurs during this time before they can fly (Zaias and Breitwisch 1989), and molt might compromise flight maneuverability (Newton 1966, Hunter 1984) during attacks on potential predators. Adults may delay or be unable to initiate molt until fledglings are less vulnerable to predators. Although mean feeding rates per fledgling remain constant throughout the fledgling stage, the decreasing fledgling vulnerability might then allow parents finally to initiate molt.

Our observations of molt-breeding overlap are consistent with Foster's (1974) hypothesis that an overlap in molt and breeding effectively prolongs the potential breeding season of an individual, which increases the probability of producing offspring. In areas of high nest predation, such as the tropics, lengthening the breeding season may be advantageous (Foster 1975). Mockingbirds in Florida have <50% nest success, which is typical for a tropical open-cup nester (Ricklefs 1969). The birds use time-saving mechanisms in renesting in the form of a temporal division of labor and clutch overlap of eggs and fledglings (Zaias and Breitwisch 1989) as predicted by Burley (1980).

Molt-breeding overlap can occur only if energy and nutrients are adequate for both activities to occur simultaneously. Hypotheses to account for overlap include a dependence on nutrient reserves, a reduction or reallocation in energy or nutrient expenditures, or both (Foster 1974, 1975; King and Murphy 1985). Although there is no evidence of reduction in mockingbirds, there may be sufficient food resources available for overlap to occur even without a reduction in the levels of necessary nutrients. The long nesting period and rapid renesting in this population attest to the continued availability of food.

The range of days of onset of molt indicate that environmental factors may not be the only factors that influence initiation of molt. For instance, high levels of reproductive effort early in the season could affect timing of molt. This effort places the birds in an energy/nutrient deficit later in the season. Low

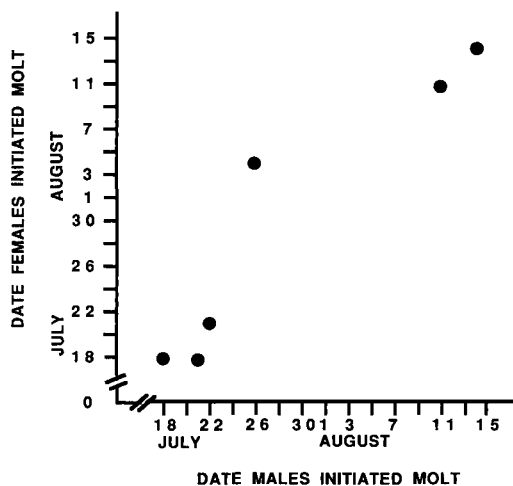


Fig. 1. Synchrony of initiation of molt within pairs in Northern Mockingbirds.

reproductive success early in the breeding season may also affect initiation of molt. These prior events can influence hormone levels and in turn influence molt. Demonstrated synchrony between mockingbird mates and in other species (Newton 1966), despite the wide range of dates for molt initiation among pairs, suggests that these factors may be important.

Cues that initiated molt differ among species and across habitats. Molt is induced hormonally in some species (Wright and Wright 1944, Payne 1972 and references therein). Molt in other species is independent of breeding schedules and cued by the environment (Keast 1968, Payne 1972 and references therein). It is possible, however, that molt schedules of species in stable environments may be influenced by their relative reproductive success or effort. It is increasingly apparent that no one factor functions as the same cue for initiation of molt in all species. Additional incidences of molt-breeding overlap in various stages of nesting may elucidate factors responsible for the onset of molt.

We thank B. Broussard, N. Burley, N. Solomon, and B. Steinly for helpful insight and revisions of an earlier version of this manuscript. This work was partially funded by grants to Breitwisch from Frank M. Chapman Memorial Fund of the American Museum of Natural History and Tropical Audubon Society.

LITERATURE CITED

BANCROFT, G. T., & G. E. WOOLFENDEN. 1982. The molt of Scrub Jays and Blue Jays in Florida. *Ornithol. Monogr.* 29.
 BENT, A. C. 1948. *Life Histories of North American nuthatches, wrens, thrashers, and their allies.* U.S. Natl. Mus. Bull. 195, Washington, D.C., Smithsonian Instit.

- BREITWISCH, R. 1988. Sex differences in defence of eggs and nestlings by Northern Mockingbirds, *Mimus polyglottos*. *Anim. Behav.* 36: 62-72.
- , P. G. MERRITT, & G. H. WHITESIDES. 1984. Why do Northern Mockingbirds feed fruit to their nestlings? *Condor* 86: 281-287.
- , ———, & ———. 1986. Parental investment by the Northern Mockingbird: male and female roles in feeding nestlings. *Auk* 103: 152-159.
- BURLEY, N. 1980. Clutch overlap and clutch size: alternative and complementary reproductive tactics. *Am. Nat.* 115: 223-246.
- FOSTER, M. S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. *Evolution* 28: 182-190.
- . 1975. The overlap of molting and breeding in some tropical birds. *Condor* 77: 304-314.
- HUNTER, S. 1984. Molt of the Giant Petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Ibis* 126: 119-132.
- JOHNSTON, D. W. 1961. Timing of annual molt in the Glaucous Gulls of northern Alaska. *Condor* 63: 474-478.
- KEAST, A. 1968. Molt in birds of the Australia dry country relative to rainfall and breeding. *J. Zool., London* 155: 185-200.
- KING, J. R., & M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *Am. Zool.* 25: 955-964.
- LIGON, J. D., & J. L. WHITE. 1974. Molt and its timing on the Pinon Jay, *Gymnorhinus cyanocephalus*. *Condor* 76: 274-287.
- LOFTS, B., & R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool. London* 155: 327-394.
- MILLER, A. H. 1961. Molt cycles in equatorial Andean sparrows. *Condor* 63: 143-161.
- NEWTON, I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41-67.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26.
- O'CONNOR, R. J. 1984. *The Growth and Development of Birds*. New York, Wiley-Interscience.
- PAYNE, R. 1969. Overlap of breeding and molting schedules in a collection of African birds. *Condor* 71: 140-145.
- . 1972. Mechanisms and control of molt. Pp. 104-155 in *Avian biology*, vol. 2 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- PITELKA, F. A. 1958. Timing of molt in the Steller Jays of the Queen Charlotte Islands, British Columbia. *Condor* 60: 38-49.
- RICKLEFS, R. E. 1969. The nesting cycle of songbirds in tropical and temperate regions. *Living Bird* 8: 165-175.
- SKUTCH, A. F. 1976. *Parent birds and their young*. Austin, Univ. Texas Press.
- SNOW, D. W., & B. K. SNOW. 1964. Breeding seasons and annual cycles of Trinidad land birds. *Zoologica* 49: 1-39.
- THOMPSON, B. C., & R. D. SLACK. 1983. Molt-breeding overlap and timing of pre-basic molt in Texas Least Terns. *J. Field Ornithol.* 54: 187-190.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100: 687-690.
- WRIGHT, P. L., & M. H. WRIGHT. 1944. The reproductive cycle of the male Red-winged Blackbird. *Condor* 46: 46-59.
- ZAIAS, J., & R. BREITWISCH. 1989. Intra-pair cooperation, fledgling care, and renesting by Northern Mockingbirds, *Mimus polyglottos*. *Ethology* 80: 94-110.

Received 30 January 1989, accepted 31 October 1989.

Sexual Differences in Nest Attendance and Chick-Feeding Rhythms of White Spoonbills

EDUARDO AGUILERA

Estación Biológica de Doñana, Apartado 1056, E-41080 Sevilla, Spain

Sexual separation of activity rhythms may be favored if each sex can forage either at night or during the day. This should be especially advantageous during reproduction, when breeding activities (pair formation, mate guarding, nest defense, incubation, etc.) compete with time for foraging, and overall energy demands are higher. Although there is extensive literature on feeding habits of wading birds, few studies focus on daily rhythms of foraging (reviewed in Kushlan 1978). Some typical night-herons, including

the Yellow-crowned Night-Heron (*Nyctanassa violaceus*) and the Black-crowned Night-Heron (*Nycticorax nycticorax*), also forage during the day (Mock 1975; Fasola 1982, 1984). On the other hand, Wood Storks (*Mycteria americana*), Great Blue Herons (*Ardea herodias*), Reef Herons (*Egretta sacra*), and Gray Herons (*Ardea cinerea*), mainly diurnal foragers, are reported to forage at night (Kahl 1964, Krebs 1974, Black and Collopy 1982, Draulans and van Vessem 1985, van Vessem and Draulans 1986). Knowledge of daily