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ECOLOGICAL CORRELATES OF MOLT IN MERLINS (*FALCO COLUMBARIUS*)

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ABSTRACT.—The energetic requirements of breeding can affect the ability of a bird to simultaneously undergo replacement of its feathers. From 1987 to 1994 we examined patterns of wing- and tail-feather molt in 286 Merlins (*Falco columbarius richardsonii*) captured in Saskatoon, Saskatchewan during the breeding season to investigate the relationship between these two events. Female Merlins had significantly higher molt scores than males, but among a variety of environmental variables, only capture date was significantly correlated with the extent of molt in female Merlins. In contrast, molt in male Merlins was correlated with capture date, the quality of the nest place, and the hatching date of the chicks. Nearly one-half of all males examined had an arrested molt pattern (i.e. molt stopped partway through), while less than 30% of females had arrested molt. Differences between the sexes may be related to their roles in reproduction. The fact that male Merlins provide most of the food for the pair and their young during the breeding season apparently necessitates slowing down and in some cases arresting molt. Females appear to arrest molt due to the greater demand of having more chicks. *Received 30 March 1995, accepted 20 August 1995.*

MOLT IN BIRDS is defined as the periodic shedding and replacement of feathers (Campbell and Lack 1985). As feathers become worn and broken, molting on a regular basis is necessary to maintain flight efficiency and insulative properties (Payne 1972). Because feathers are comprised largely of protein (i.e. keratin; Murphy and King 1982, 1986), molt is believed to be energetically costly (Payne 1972, Dolnik and Gavrilov 1979), and the relative costs to passerines apparently are much higher than those to nonpasserines (Wijnandts 1984, Dietz et al. 1992, Lindström et al. 1993). The costs of molt can be broken down into primary and secondary costs. The primary costs of molt are costs of feather synthesis and of maintaining the tissues necessary for feather production (Payne 1972, Dolnik and Gavrilov 1979, Lindström et al. 1993). The secondary costs of molt are reduced flight efficiency and ability to thermoregulate (Payne 1972, Tucker 1991). In most Temperate Zone bird species, molt and breeding are temporally separated, and it has been proposed that this is due to the high energy demands of these two activities (Payne 1972, Kendeigh 1973, Farner et al. 1980, Pietiäinen et al. 1984, Furness 1988). Diet also may influence the timing of molt. Dolnik and Gavrilov (1979) posited that the cystine content in birds' food rather than the energy content may limit the rate of molt (but see Murphy and King 1984).

For those species in which molt and breeding overlap, it has been suggested that this is the result of taking advantage of a periodic abundance of resources in high-latitude species (Johnstone 1961, Hunter 1984), or due to prolonged breeding seasons in tropical species (Payne 1972, Foster 1975, Thompson 1988). However, overlap in the timing of molt and breeding has now also been shown for a number of Temperate Zone species (Bancroft and Woolfenden 1982, Morton and Morton 1990, Zaias and Breitwisch 1990). King and Murphy (1985) suggested the overlap of molt and breeding may depend on nutrient reserves (i.e. continue molting by relying upon energy stores within the body) or a reallocation in energy or nutrient reserves (i.e. reduce the rate of molt and allocate more energy to breeding). If there is a significant trade-off between molt and breeding, one may expect some birds to have developed the ability to delay molting during particularly stressful periods of the breeding season. Such adaptations have been shown for Gadwalls (*Anas strepera;* Oring 1968), Yellow-nosed Albatrosses (*Diomedea chlororhynchos;* Furness 1988), Wandering Albatrosses (*Diomedea exulans;* Weimerskirch 1991), Northern Mockingbirds (*Mimus polyglottus;* Zaias and Breitwisch 1990), and Sparrowhawks (*Accipiter nisus;* Newton and Marquiss 1982).

The Merlin (*Falco columbarius*) is a small falcon that breeds throughout the northern forests and prairies of North America, Europe and Asia (Sodhi et al. 1993). Merlins are primarily monogamous and raise one brood each breeding season (Sodhi et al. 1992). During the incubation period, female Merlins are largely inactive, only leaving the nest for brief periods of time to feed. In contrast, males hunt for both themselves and the female throughout this period, bringing an average of three birds (prey items) per day to the female (Laing 1985). During the nestling period, males continue to provide all food (Sodhi et al. 1992), bringing an average of 10 birds per day to the nest (Laing 1985). Females in the population we studied do not usually hunt until the young fledge (Sodhi et al. 1992), but in some populations females may begin to hunt when chicks are about three weeks old (Temple 1972).

Molt overlaps extensively with the breeding season in Merlins (Sodhi et al. 1993), providing an opportunity through which to identify any ecological constraints of feather replacement in these birds. Moreover, because male and female Merlins allocate time and energy differently with respect to breeding and they are sexually dimorphic (Warkentin et al. 1992), we examined whether environmental factors affect the sexes differently with respect to the progression of molt.

METHODS

As part of a long-term population study, we recorded feather molt for 286 Merlins (109 males and 177 females) live-trapped during the nestling period of the breeding season (late June to early July) in Saskatoon, Saskatchewan, Canada (52°07′N, 106°38′W) between 1987 and 1994. For a description of the trapping methods and the study area, see James et al. (1989) and Warkentin and James (1988). Individuals trapped in different years were analyzed as independent data.

For our study, we examined the pattern of molt in both wing feathers (primaries) and tail feathers (rectrices) of Merlins. Molt scores for individuals were only recorded once within a breeding season. We considered only wing and tail molt because the replacement of these feathers requires a substantial proportion of the energy allocated to molting, and it is easier to quantify their growth as compared to body feathers (Ginn and Melville 1983). Primary feathers were numbered 1 to 10 from the proximal to the distal end of the wing, and rectrices 1 to 6 from the inner to the outer portion of the tail. Each feather was allocated a score depending on its state of growth, from zero (old or missing) to five (completely grown). Partially grown feathers were scored in fifths (e.g. feathers between three-fifths and four-fifths grown were scored as three). Adding the scores of the 10 primaries on the right wing (maximum 50) and the 12 rectrices (maximum 60) gave the molt score. Any birds which had a full complement of fully grown, new and old feathers were classified as having "arrested molt" (Newton and Marquiss 1982). We tested for differences between all molting and arrested Merlins in order to determine what factors influenced Merlins to arrest molt. To reduce the possibility that some of the molting birds may have arrested a few days after we captured them, we also compared arrested birds to molting individuals having a molt score equal to or greater than the arrested birds. We assumed that these molting birds had not arrested molt before we captured them.

Molt scores for both male and female Merlins were not normally distributed ($P < 0.05$, Kolmogorov-Smirnov tests), nor were those of transformed data ($\log_{10}[x + 1]$). Therefore, we used distribution-free tests for all analyses (Zar 1984, Siegel and Castellan 1988). For nonparametric correlations (Kendall's rank order), the independent variables included: date of capture, hatching date, bird age, habitat quality, brood size, and body size.

We determined the hatching date of a parent's chicks by backdating from the age of the chicks at the time of banding (for details on aging of chicks, see Sodhi et al. 1992). Because Merlins have nested continuously in Saskatoon since 1970 and a program of banding nestlings has been in operation within the city since 1971 (Oliphant and Haug 1985), we were able to determine the age of captured birds by comparing band numbers to banding records. In addition, we could distinguish between yearling and adult males not banded as chicks, based on plumage characteristics (see Temple 1972). Using these methods, we knew the ages of 81 males and 41 females.

Following Newton (1991), we assessed habitat quality based upon occupancy of nest places. We denoted nest-place occupancy by determining if a nest in a particular year was closer to a nest used in a previous year or to its nearest neighbor in the same year. If a nest was closer to an old nest site, it was then classified

TABLE 1. Kendall's tau correlations for molt in male and female Merlins.

	Males			Females		
Variable	*n*	tau	Z	*n*	tau	Z
Date of capture	109	0.173	2.66**	177	0.244	4.81**
Habitat quality	109	0.145	2.23*	177	−0.012	−0.23
Hatching date	108	0.228	3.50**	171	0.056	1.08
Brood size	108	−0.012	−0.18	175	−0.025	−0.49
Age	81	−0.082	−1.08	41	−0.003	−0.03
Size	106	0.004	0.07	176	−0.041	−0.81

*, $P < 0.05$; **, $P < 0.01$; others, $P > 0.05$.

as occupying that nest place. If a nest was closer to its nearest neighbor, we classified it as a new nest place. In order to account for changes in habitat over time, we graded each nest place by giving it a separate score for each year, depending on its occupancy in a moving five-year period, centered on the year in question (Newton 1991). For instance, nest places in 1987 were graded on a scale of one to five, based on their occupancy in the period 1985-1989. Nest places for the last two years of the study were graded on occupancy in the last five years of the study.

Body size was calculated by reducing six morphometric measurements using principal component analysis (PCA). The PCA was based on the correlation matrix of the raw measures. PCA done in this manner implies that the component scores are based on standardized data with a mean of zero and unit variance (see Pielou 1984). We used the individual component scores (PC1) generated by the analysis for all other analyses involving body size. The six measurements used in the PCA were: (1) cube root of body mass (mass measured to nearest gram using Pesola scale); (2) total length (from top of head to tip of tail); (3) tail length (base to tip); (4) wing chord of unflattened wing (measured to nearest millimeter using wing ruler); (5) bill length (from distal edge of cere to tip of bill, measured to nearest 0.1 millimeter with vernier caliper); and (6) tarsus length (measured to nearest 0.1 millimeter with vernier caliper).

RESULTS

As expected, wing and tail molt within individuals were correlated for both males ($\tau = 0.321$, $Z = 4.93$, $P < 0.01$, $n = 109$) and females ($\tau = 0.275$, $Z = 5.44$, $P < 0.01$, $n = 177$). There was, however, a significant difference between the molt scores of male and female Merlins, with females having higher scores than males (female median of 20 vs. male median of 10; Mann-Whitney *U*-test, $Z = -12.23$, $P < 0.01$, $n = 286$), despite the fact that there was no significant difference in the capture date for the two sexes (male and female median of 23 June; Mann-Whitney *U*-test, $Z = -0.352$, $P > 0.10$).

For males, date of capture, habitat quality and hatching date were positively correlated with molt score (Table 1). There were no significant correlations between any paired combination of these three variables (all $P > 0.10$, Kendall's tau). Kendall's partial-correlation analyses revealed that all three variables were still significantly correlated with molt when we controlled for each of the other variables (Table 2). Only capture date was significantly correlated with molt score for females (Table 1).

We found that 52 (48%) of the males exhibited arrested molt and, of these, 49 had fully replaced primaries 4 and 5, and had not lost any tail feathers. Of the other arrested males, one had replaced primaries 4 and 5 and had fully replaced one of the central tail ("deck") feathers. Two others had replaced only primary 4 and had not lost any tail feathers. When we compared arrested males to molting males, we found that arrested males bred earlier, had larger broods, and were older (Table 3). When we controlled for age by considering only two-year-old birds (i.e. the mode for arrested males) and then compared arrested to molting males (all variables except age), we found that there still was a significant difference in the hatching date

TABLE 2. Kendall's partial correlations for molt in male Merlins.

	Controlling for		
Variable	Date of capture	Habitat quality	Hatching date
Date of capture		0.177**	0.163*
Habitat quality	0.150*		0.136*
Hatching date	0.221**	0.238**	

*, $P < 0.05$; **, $P < 0.01$.

TABLE 3. Mann-Whitney U-tests between molting and arrested male and female Merlins. Median values are provided to indicate directions of differences.

	Males			Females		
Variable	Arrested molt (n)	Molting (n)	U	Arrested molt (n)	Molting (n)	U
Date of capture	23 June (52)	23 June (57)	1,300.5	25 June (50)	23 June (127)	2,290.5**
Habitat quality	3 (52)	3 (57)	1,468.5	3 (50)	3 (127)	2,878.0
Hatching date	12 June (51)	15 June (57)	964.5**	11 June (49)	13 June (122)	2,494.5
Brood size	5 (51)	4 (57)	1,134.5*	5 (50)	4 (125)	2,521.0*
Age	3 (35)	2 (46)	518.5**	3 (7)	2 (34)	90.0
Size	−1.30 (50)	−1.20 (56)	1,236.0	0.71 (49)	0.69 (127)	3,031.0

*, $P < 0.05$; **, $P < 0.01$; others, $P > 0.05$.

for the two groups, with arrested males ($n = 14$, median of 12 June) breeding earlier than molting males ($n = 14$, median of 15 June; Mann-Whitney U-test, $Z = -1.99$, $P < 0.05$). In addition, when we compared two-year-old arrested and molting males with molt scores equal to or greater than 10 (all variables except age), we again found that arrested males had chicks with significantly earlier hatching dates ($n = 13$, median of 11 June) than molting males ($n = 11$, median of 16 June; Mann-Whitney U-test, $Z = -2.62$, $P < 0.01$). All other tests between the two groups were non-significant ($P > 0.05$).

Arrested molt also was apparent in 50 (28%) of the female Merlins captured. All but two of the arrested females had replaced primaries 3, 4, 5, and 6, and had not molted any tail feathers. For the two other arrested females, one had a wing score of 40 (i.e. replaced eight primaries) and not molted her tail feathers, and the other had replaced primaries 3, 4, 5, and 6, and had fully replaced the two "deck" feathers. Comparisons between arrested and molting females revealed that arrested females had larger broods and were captured later than molting females (Table 3). In order to control for the date of capture, we compared arrested and molting females captured on 25 June (the mode for arrested and molting females); we still found a significant difference in the brood size of the two groups, with arrested females having larger broods (median of 5, $n = 7$) compared to molting females (median of 4, $n = 13$; Mann-Whitney U-test, $Z = -2.03$, $P < 0.05$). When we compared arrested and molting females having scores equal to or greater than 20, we again found that arrested females had significantly larger broods ($n = 50$, median of 5.0) than molting females ($n = 66$, median of 4.0; Mann-Whitney U-test, $Z = -2.28$, $P < 0.05$). All other tests between the two groups were nonsignificant ($P > 0.05$).

The frequency of arrested molt was greater among males than females ($X^2 = 11.13$, df = 1, $P < 0.01$). In addition, there was no significant mating association between arrested and molting birds (Fisher's exact test, two-tailed, $P = 0.08$).

DISCUSSION

Payne (1972) suggested that the degree of temporal overlap of breeding and molt in birds is influenced by several ecological circumstances, particularly the abundance and availability of food. Depending upon habitat and location, food resources may influence molt to differing degrees. For instance, food may be abundant year-round with little or no seasonal change, thus enabling birds to separate chronologically breeding and molt. A second possibility is that feathers are replaced over a long time period and relatively little energy input per day is allocated to feather growth (see Weimerskirch 1991). Finally, food may be relatively abundant for a short time period and in short supply during the rest of the year. Merlins appear to fit this last scenario. The timing and pattern of molt is of fundamental concern for Merlins (especially males), as they must maintain flight efficiency while at the same time renew their feathers and raise their offspring. For Merlins breeding in Saskatoon, food resources consist predominately of House Sparrows (*Passer domesticus*), which are at their highest concentrations during the summer (Sodhi and Oliphant 1993). In Saskatoon, House Sparrows start fledging young from mid-May, but fledgling numbers peak in early June and again in late July

(Sodhi et al. 1992). Thus, it appears that the Merlins are able to exploit this particularly vulnerable food supply (i.e. fledgling House Sparrows) and, thereby, simultaneously provide energy for molting and for their growing offspring.

The difference in the molt scores between male and females may be due to females starting molt earlier than males as suggested by Palmer (1988). This is partially substantiated by the fact that the first molted primaries we found near nests were always female. Similar conclusions have been drawn for Sparrowhawks (Newton 1986). For other species, differences in molt between males and females have been attributed to differing rates of feather replacement (Schmutz and Schmutz 1975, Schmutz 1992) or differing energy demands (Weimerskirch 1991), rather than different starting dates. In general, however, it appears that due to task division male Merlins have to meet both primary and secondary molt costs (especially flight costs), whereas females have more or less only to meet the primary costs of molt.

Molt in Merlins differs from that of the ecologically comparable Sparrowhawk (i.e. both are raptors of similar size, which predominately prey upon small passerines). For female Merlins, only capture date was related to molt score. Newton and Marquiss (1982) reported that, among female Sparrowhawks, molt was strongly correlated with date of egg laying; females that began laying later also molted later. In female Sparrowhawks, age also seems to influence molt. In male Merlins, it appears the high energy demands of providing food for himself, his mate and his chicks, allows several ecological factors to influence his molt. For male Sparrowhawks, neither laying date nor age influenced molt, but day length did (Newton and Marquiss 1982). Day length (i.e. photoperiod) is usually considered to be the main proximate factor influencing both breeding and molt in birds (Payne 1972, Dolnik and Gavrilov 1979, Campbell and Lack 1985). Perhaps these differences in molt between Merlins and Sparrowhawks are due to a higher concentration of vulnerable prey (i.e. House Sparrows) within Saskatoon (see Sodhi et al. 1992, Sodhi and Oliphant 1993). It may be that this concentration of food allows male Merlins to feed females and chicks at a rate that enables most females to continue molting during the breeding season.

It also appears that habitat quality influences molt in male Merlins. Male Merlins on higher-quality territories had higher molt scores, suggesting that they were able to molt at a faster rate or start at an earlier date than their counterparts on lower-quality territories. This may have been due to an increased availability of resources on higher-quality territories because of greater abundance of prey, better access, or some combination of the two. However, molt in female Merlins was not related to habitat quality, and there was no significant difference in the habitat quality between molting and arrested males. Thus, our findings on the effect of habitat quality on molt are not entirely conclusive.

Males breeding later had higher molt scores, suggesting that they were able to allocate more energy to feather growth until their chicks hatched. Further evidence that feeding chicks somehow influenced molt in males comes from our comparison of molting and arrested birds. On average, arrested males bred significantly earlier than molting males and, thus, had spent several more days providing food for offspring. It may be that male Merlins arrest molt in order to cope with the increased energetic costs of feeding chicks. Newton and Marquiss (1982) suggested that arrested molt in Sparrowhawks was influenced by the stage of breeding. Our results for Merlins support this notion. Because breeding male Merlins spend approximately 31% of their time hunting during the incubation period and 58% of their time is spent hunting during the nestling period (Sodhi et al. 1993), there may be a strong adaptive reason for a raptor to be able to arrest molt. Acquiring enough protein from their food for feather growth should not be a problem for Merlins, because they eat primarily small birds. However, male Merlins still face the energetic demands of catching enough prey, particularly during the nestling period.

Tucker (1991) and Masman et al. (1988) have shown that the flight performance of birds is negatively influenced by the loss of flight feathers. Because primaries are used predominately for propulsion (Welty and Baptista 1988), having a full complement of feathers may be a distinct advantage for a bird that generally catches prey in short, dashing flights (Sodhi et al. 1993). Male Merlins do all the hunting during the breeding season, and this may be the reason why more males than females show arrested molt. A second advantage is that by arresting molt for a short period of time, more energy and resources can be directed to raising the highest-quality offspring possible. Moreover, it may be advantageous for a female Merlin to have a mate with arrested molt, in order that she and her chicks can receive the maximum amount of food caught by the male, as an arrested male would require less food for self maintenance. However, we found no significant mating associations between male and female Merlins with respect to molt. Quite likely, several other factors also influence mate choice by females (Warkentin et al. 1992).

For females, the fact that molting birds had significantly smaller brood sizes than arrested birds suggests that they were able to acquire enough energy to continue feather growth, while at the same time feed and defend their chicks. Arrested females appear to have been unable to continue feather growth due to the increased food demands of having more chicks. Pietiäinen et al. (1984) found that Ural Owls (*Strix uralensis*) with an above average number of young, molted on average fewer feathers at a time. They proposed that the owls balanced molt energy demands against energy demands for reproduction. This also appears to be the case with female Merlins.

Perhaps the inability of some birds to arrest molt (e.g. White-crowned Sparrows, *Zonotrichia leucophrys;* Murphy et al. 1988) is related to the fact that their molt usually is mutually exclusive from breeding and, thus, there may be no selective advantage under these circumstances, to be able to arrest it. However, arrested molt is found quite frequently among birds where molt and breeding overlap (Newton and Marquiss 1982, Furness 1988, Zaias and Breitwisch 1990, Weimerskirch 1991), and may have adaptive significance in that it allows individuals of these species to cope with the competing energetic demands of these two activities.

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