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RESEARCH ARTICLE

The trade-off between molt and parental care in Hooded Warblers: Simultaneous rectrix molt and uniparental desertion of late-season young

Ronald L. Mumme

Department of Biology, Allegheny College, Meadville, Pennsylvania, USA
rmumme@allegheny.edu

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ABSTRACT

Temporal overlap between parental care and molt occurs frequently in birds, but few studies have examined how individuals manage conflicts between these 2 demanding phases of the annual cycle. The potential for trade-offs between molt and parental care is especially high in the Hooded Warbler (*Setophaga citrina*) because (1) all rectrices are replaced simultaneously during primary molt, leaving birds temporarily without a functional tail; and (2) the tail plays an important role in foraging, as birds use their white tail spots and tail-flicking behavior to startle insect prey. I examined how simultaneous rectrix molt affected late-season parental care in a color-banded population of Hooded Warblers in northwest Pennsylvania, USA. Of 62 adults initiating rectrix molt before the end of parental care, 43 (69%) deserted their late-season nestlings and fledglings, leaving the mate to provide all remaining parental care. Because females initiate rectrix molt significantly later than males, most instances of uniparental desertion involved molting males abandoning fledglings or nestlings, but rare cases of postfledging desertion by females also occurred. Although most molting parents deserted, the probability of desertion decreased significantly with brood age, presumably because the costs of providing parental care during molt decline as fledglings approach independence. The probability of desertion by the male also decreased significantly with male age, suggesting that more experienced males can successfully balance the dual demands of molt and late-season parental care. In females, however, the only instances of desertion involved unusually old females $\geq$5 yr old, which suggests that rare cases of female desertion may occur as a mechanism to reduce reproductive effort late in life. My findings indicate that conflicts between parental care and molt, and the strategies that individuals use to manage those conflicts, merit increased attention from ornithologists seeking to understand the full annual cycle of migratory songbirds.

Keywords: molt-breeding overlap, parental care, Parulidae, rectrix molt, *Setophaga citrina*, trade-offs, uniparental desertion

Solución de compromiso entre muda y cuidado parental en *Setophaga citrina*: Muda rectriz simultáneas y deserción uniparental en jóvenes de fines de estación

RESUMEN

La superposición temporal entre el cuidado parental y la muda ocurre frecuentemente en las aves, pero pocos estudios han examinado como los individuos manejan los conflictos entre estas dos fases demandantes del ciclo anual. La posibilidad de soluciones de compromiso entre la muda y el cuidado parental es especialmente alto en *Setophaga citrina* debido a que (1) todas las rectrices son reemplazadas simultáneamente durante la muda primaria, dejando a las aves temporalmente sin una cola funcional, y (2) la cola juega un rol importante en el forrajeo, ya que las aves usan sus manchas blancas de la cola y el comportamiento de parpadeo de la cola para ahuyentar los insectos presa. Examiné cómo la muda simultánea de las rectrices afectó el cuidado parental de fines de estación en una población de *S. citrina* marcada con anillos de color en el noroeste de Pensilvania. De los 62 adultos que iniciaron la muda de las rectrices antes del final del cuidado parental, 43 (69%) desertaron sus polluelos y volantones de fines de estación, dejando que el compañero de pareja brinde todos los cuidados parentales restantes. Debido a que las hembras inician la muda de las rectrices significativamente más tarde que los machos, la mayoría de las instancias de deserción uniparental involucró a machos que estaban mudando y que abandonaron a volantones o polluelos, pero también ocurrieron algunos casos raros de deserción post emplumamiento por parte de las hembras. Aunque la mayoría de los padres que estaban mudando desertaron, la probabilidad de deserción disminuyó significativamente con la edad de la nidada, presumiblemente debido a que los costos de brindar cuidado parental durante la muda disminuyen a medida que los volantones se acercan a su independencia. Para los machos, la probabilidad de deserción también disminuyó significativamente con la edad del macho, sugiriendo que los machos más experimentados pueden balancear exitosamente las demandas duales de la muda y el cuidado parental de fines la estación. En las hembras, sin embargo, las únicas instancias de deserción involucraron a individuos

llamativamente viejos de al menos cinco años de edad, sugiriendo que los casos raros de deserción de hembras pueden ocurrir como un mecanismo para reducir el esfuerzo reproductivo hacia el final de la vida. Mis hallazgos indican que los conflictos entre cuidado parental y muda, y que las estrategias que usan los individuos para manejar estos conflictos, merecen una mayor atención de parte de los ornitólogos que buscan entender el ciclo anual completo de las aves canoras migratorias.

Palabras clave: cuidado parental, deserción uniparental, muda de las rectrices, Parulidae *Setophaga citrina*, soluciones de compromiso, superposición de la muda y la cría

INTRODUCTION

Molt is one of the most demanding phases of the avian life cycle, one that exacts substantial physiological and behavioral costs. The energetic requirements of molt can lead to significant increases in metabolism and daily energy expenditure, especially in small birds (Murphy and King 1992, Lindström et al. 1993). Furthermore, because feathers are built from proteins and represent a significant fraction of a bird's body mass, feather replacement also requires major investment in protein synthesis (Murphy and King 1992, Cherel et al. 1994). To meet these nutritional challenges, birds in molt may need to increase their foraging effort and food intake (Bonier et al. 2007, Echeverry-Galvis and Hau 2012) while simultaneously dealing with deficits in flight performance that result from the replacement of multiple flight feathers (Swaddle and Witter 1997, Chai and Dudley 1999, Chai et al. 1999). Because of these varied physiological and behavioral demands, molt is generally segregated temporally from other challenging phases of the avian annual cycle, such as reproduction and migration. Exceptions to this generalization, however, are frequent, and temporal overlap between reproduction and molt occurs regularly in a wide diversity of avian taxa and environments (Foster 1975, Jenni and Winkler 1994, Howell 2010, Williams 2012).

When reproduction and molt overlap in time, individuals may be forced to make trade-offs between these 2 competing demands—for example, by slowing the growth of replacement feathers (Echeverry-Galvis and Hau 2012, Saino et al. 2014) or by temporarily suspending molt (Jenni and Winkler 1994, Howell 2010). One potential trade-off that might be expected during molt–breeding overlap is a behavioral trade-off with parental care; molting birds could reduce or modify their parental care behavior in response to the impaired flight performance and increased metabolic and nutritional demands associated with molt. Surprisingly, however, few studies have explicitly examined how molt influences parental care behavior. The best evidence of a behavioral trade-off between molt and parental care comes from Blue Tits (*Parus caeruleus*), in which molting males make a proportionally lower investment in nestling feeding than non-molting males (Svensson and Nilsson 1997). Other studies have also suggested that molt is associated with reduced provisioning of offspring but have not provided convincing evidence of such a relationship (e.g., Hemborg and Merilä 1998, Gow and Stutchbury 2013).

Another behavioral trade-off that is often hypothesized to occur when molt and parental care overlap is uniparental desertion. Studies of several songbird species have shown that individuals of one sex (invariably the males) may abandon nestlings or dependent fledglings late in the breeding season, leaving their mates to provide all remaining parental care. Because male desertion typically occurs at about the same time as molt, several authors have interpreted late-season uniparental male desertion as evidence of a behavioral trade-off between molt and parental care (e.g., Nolan 1978, Ezaki 1988, Morton and Morton 1990, Urano 1992, Hemborg 1999). The evidence, however, is largely circumstantial, and none of these studies has persuasively linked an individual's molt status to its desertion behavior.

A North American songbird in which trade-offs between parental care and molt seem especially likely is the Hooded Warbler (*Setophaga citrina*). This species is a long-distance Neotropical migrant with an unusually extended breeding season and a long period of postfledging parental care. In northwest Pennsylvania, USA, it is double brooded, and breeding pairs initiate nests from mid-May through late July (Evans Ogden and Stutchbury 1996, Chiver et al. 2011). Furthermore, because fledglings don't reach nutritional independence until 35–40 days after hatching (Chiver et al. 2011, Mumme 2014), many adults can be tending and feeding dependent young through late August and even into early September. Because August and early September is also when adults complete the annual prebasic molt prior to fall migration (Evans Ogden and Stutchbury 1996, Chiver et al. 2011), the potential for temporal overlap between parental care and molt is substantial in Hooded Warblers.

A second reason why trade-offs between molt and parental care are likely is that Hooded Warblers molt their rectrices more or less simultaneously, leaving molting individuals without a functional tail for a week or more (Howell 2010, Chiver et al. 2011). The pattern of rapid and nearly simultaneous rectrix loss is common, and perhaps even universal, in migratory warblers that breed in North America; it has been documented

multiple times across 3 parulid genera, including 4 *Oreothlypis* species (Foster 1967, Voelker and McFarland 2002, Rimmer and McFarland 2012), one *Parkesia* species (Mattsson et al. 2009), and 5 *Setophaga* species (Nolan 1978, Rimmer 1988, Ladd and Gass 1999, Chiver et al. 2011, Bocetti et al. 2014). Because simultaneous rectrix loss in warblers occurs concurrently with primary molt (Foster 1967, Nolan 1978, Rimmer 1988, Voelker and McFarland 2002, Rimmer and McFarland 2012), flight ability may be significantly compromised for warblers in tail molt (Swaddle and Witter 1997, Chai and Dudley 1999, Chai et al. 1999), making parental care even more demanding and costly than usual. Reduced flight ability during parental care is likely to present particular challenges to Hooded Warblers, because the breeding adults regularly employ aerial foraging maneuvers and provide significant numbers of flying insects to their dependent nestlings (Chiver et al. 2011, Mumme 2014). Moreover, while in simultaneous rectrix molt, Hooded Warblers behave in ways that appear to be incompatible with parental care—they typically seek out dense understory thickets, curtail their movements considerably, and become furtive and retiring (Evans Ogden and Stutchbury 1996).

A third reason why Hooded Warblers are likely candidates for trade-offs between molt and parental care is that adults in simultaneous rectrix molt are without the use of an important foraging adaptation. When foraging, Hooded Warblers use their white tail spots (Figure 1A) and their conspicuous tail-flicking behavior to startle potential insect prey; birds with experimentally darkened tail spots show significantly impaired foraging performance in relation to controls, primarily because of a reduced frequency of aerial prey attack maneuvers (Mumme 2014). Thus, as in redstarts (*Myioborus* spp.; Jabłoński 1999, Mumme 2002), the tails of Hooded Warblers constitute an important tool for flushing flying insects and enhancing foraging performance. This tool, however, is temporarily unavailable to birds in simultaneous rectrix molt, thereby increasing the potential for trade-offs between parental care and molt when these 2 activities overlap in time.

Here, I examine the conflicts and trade-offs between simultaneous rectrix molt and late-season parental care in Hooded Warblers. My focus is on 3 questions: (1) Is simultaneous rectrix molt associated with uniparental desertion of late-season young? (2) What factors determine whether a molting bird deserts or continues to provide parental care? (3) What are the survival costs and benefits of desertion and non-desertion for parents and their social mates? An examination of the effects of uniparental desertion on dependent young—including provisioning rates, nestling growth, fledging success, and postfledging survival—is deferred to a later analysis.

METHODS

Study Area and Field Methods

Data were collected at Hemlock Hill Field Station, Crawford County, Pennsylvania (41.8°N, 79.9°W), during the 5 yr period 2013–2017. A color-banded population of 50–60 nesting pairs of Hooded Warblers has been under continuous observation at Hemlock Hill since 2010 (Schaef and Mumme 2012, Mumme 2014), and Hemlock Hill has been the location of many previous studies of this species (e.g., Howlett and Stuchbury 2003, Chiver et al. 2008). Hooded Warblers at Hemlock Hill are socially monogamous, with female-only incubation and biparental care during the nestling and fledgling stages (Evans Ogden and Stutchbury 1997). Feeding of nestlings increases with nestling age, reaching ~4 feedings nestling^{-1} hour^{-1} at fledging, with males providing ~60% of all feeding visits. Provisioning rates during the fledgling stage are considerably higher, averaging 10 feedings fledgling^{-1} hour^{-1} for each parent (Evans Ogden and Stutchbury 1997). Although extrapair fertilizations occur regularly (Chiver et al. 2011), relatively little extrapair paternity occurs in the late-season nests that are the focus of the present study (Stutchbury et al. 1994, 1997).

Fieldwork was conducted during May–September each year, and intensive efforts were made to capture and color band all breeding adults, locate all nests, determine the identity of parents active at every nest, and color band all nestlings. Unbanded adult males and females captured for the first time were classified as either second-year or after-second-year using rectrix shape (Pyle 1997), a method that has been verified for Hooded Warblers with recaptures of previously banded birds (Evans Ogden and Stutchbury 1996). Nests were checked every 3–4 days until failure or success, and young fledged from successful nests when 8–9 days old (hatching = day zero; Chiver et al. 2011).

Beginning in late July each year, I made twice-weekly visits to nesting territories to search for the color-banded breeding pair and ascertain (1) their molt status, as determined by visual evidence of rectrix molt; and (2) whether they were still engaged in parental care behavior, either at active nests or with dependent fledglings 9–35 days old. I used rectrix molt as an indicator of molt status because loss of rectrices, particularly the nearly simultaneous loss of all rectrices, could be detected easily in the field and did not depend on capturing birds to determine molt score. Adults that were directly observed incubating, brooding, or carrying food to nestlings or fledglings were categorized as still engaged in parental care. However, if an adult failed to deliver food to nestlings or fledglings in ≥90 min of observation, and all parental care during that period was performed by its mate, I classified the bird as having deserted. Because deserting birds usually behaved very differently than active parents (i.e. deserters were often

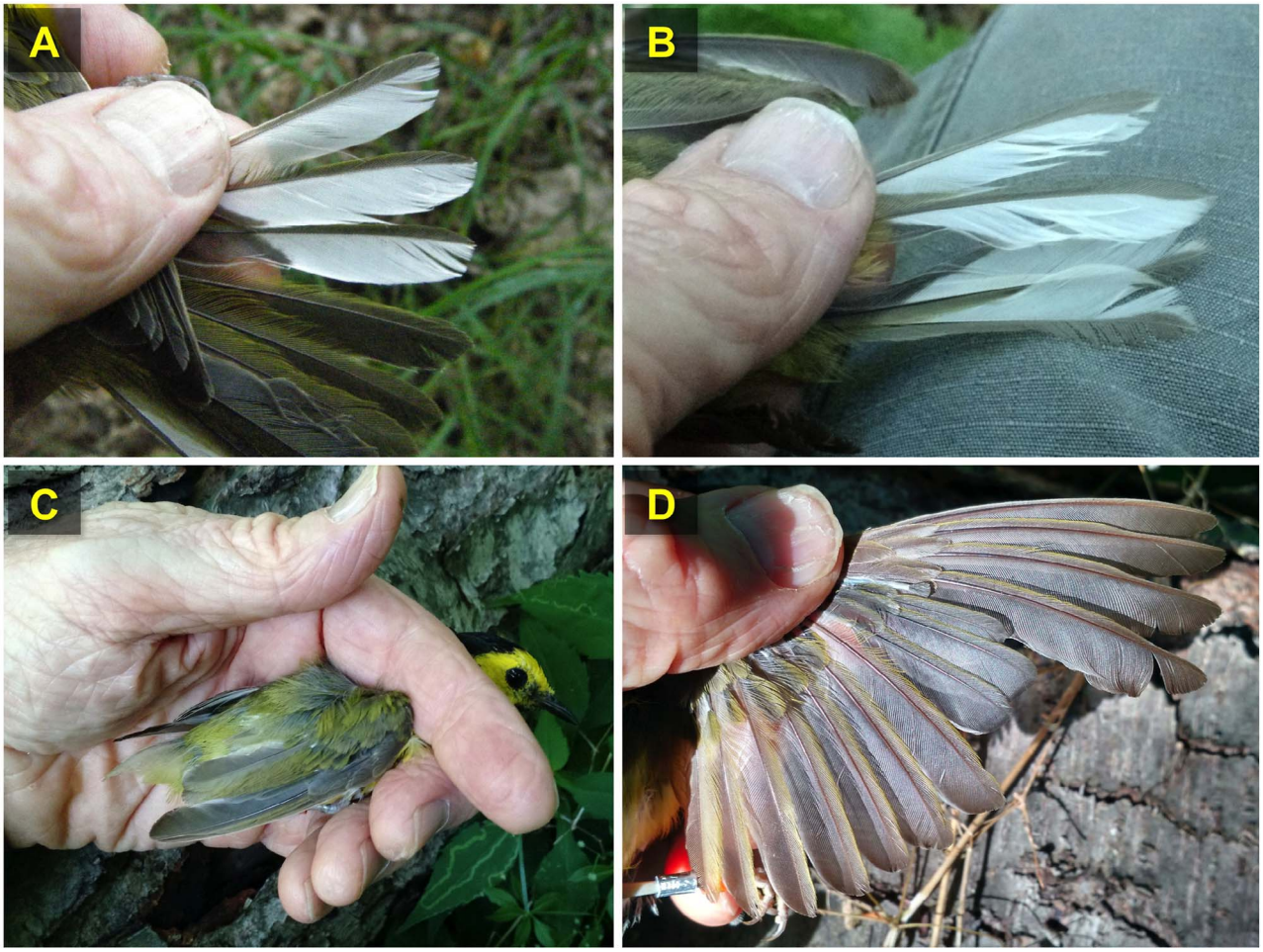

FIGURE 1. Rectrix and primary molt in male Hooded Warblers. (**A**) Typical tail pattern prior to molt, showing white tail spots on outer rectrices 4–6. (**B**) Male in early stages of rectrix molt; 8 inner rectrices (left and right 1–4) are missing, but the 4 outermost rectrices (left and right 5–6) remain. (**C**) Male in complete simultaneous rectrix molt; all 12 rectrices are either missing or small pin feathers. (**D**) Status of primary molt for the male shown in C; primaries 1–4 are new and growing, primary 5 is missing, and primaries 6–9 are old and not yet molted.

furtive and skulked in understory thickets far from the nest or fledglings), cases of desertion were nearly always unambiguous, and in no case was a judgment of desertion reversed by observations made in subsequent visits.

Although juvenile Hooded Warblers $\leq$50 days old occasionally may beg and be fed by parents (Evans Odgen and Stutchbury 1997), juveniles $>$35 days old are capable foragers that frequently operate independently of their parents (Mumme 2014). I therefore considered juveniles $>$35 days old to be independent, and parents that failed to feed such juveniles were not classified as having deserted.

In addition to recording the status of rectrix molt visually, I also made periodic efforts to mist net individuals in varying stages of molt to collect quantitative data on the timing and progression of rectrix and primary molt. For captured birds, I assigned all 12 rectrices and the 9 primaries of the right wing a molt score on a scale of 0–5, where 0 = old feather, 1 = missing feather, 2 = pin feather, 3 = emerged feather $<$50% grown, 4 = growing feather $>$50% grown, and 5 = fully grown new feather. Wing molt is symmetrical in Hooded Warblers, and molt score is usually identical for both the left and right wing (Evans Ogden and Stutchbury 1996). Because the molt of secondaries didn't begin until late in primary and rectrix molt, secondary molt is not considered here.

Data Analysis

The primary dataset for the analysis of the relationship between simultaneous rectrix molt and desertion consists of 62 Hooded Warblers (56 males and 6 females) that met 2 criteria: (1) they initiated rectrix molt before the end of parental care (day 35 after hatching) and (2) they initiated rectrix molt before their mate had already deserted. The second criterion was included because desertion is not a

viable option for a Hooded Warbler parent whose mate has already deserted. For the 56 males that met the inclusion criteria, I examined the factors contributing to desertion probability with logistic regression models, using desertion (yes or no) as the categorical dependent variable and 4 continuous predictive variables: (1) age of the brood at the time of initial rectrix loss, (2) minimum or known age of the male, (3) brood size at the time of initial rectrix loss, and (4) ordinal hatch date. Preliminary models revealed that neither brood size, which showed little variation and was 2 or 3 in 95% of the 56 cases, nor hatch date had significant effects on the probability of desertion, so these 2 predictor variables were excluded from the final logistic model. Because only 6 females met the inclusion criteria, a formal logistic regression model for female desertion was not possible.

I explored the fitness consequences of desertion for males by comparing apparent survival—return rate the subsequent year—between deserting and non-deserting males. Because successful return can be determined only in the year following the instance of desertion, this analysis was limited to 40 males (31 deserters and 9 non-deserters) that met the inclusion criteria during the first 4 yr of the study (2013–2016). Because so few females met the inclusion criteria, a comparable analysis for females is not possible; instead, I compiled data for all females that had active nests after July 15 and compared return rates for the 31 females that were deserted by their mates with those for the 19 females that were not deserted. I used chi-square tests to compare return rates of deserting and non-deserting males and to compare return rates of deserted and non-deserted females.

I used JMP Pro 12.1.0 (SAS Institute, Cary, North Carolina, USA) for all statistical analyses. Results are reported as means ± SD unless otherwise noted. For comparisons between 2 groups, I used paired or unpaired *t*-tests when the assumptions of normality and equal variance were satisfied, and Wilcoxon signed-rank tests when they were not.

RESULTS

Timing of Rectrix Loss and Primary Molt

Hooded Warblers molted rectrices from late July through September. Tail molt began with the central pair of rectrices (left and right rectrix 1) and progressed outward; most molting birds underwent a period of 2–4 days when 1–6 of the outermost rectrices (rectrices 4–6) remained (Figure 1A, 1B). Any remaining outer rectrices were dropped within 4–6 days of the onset of tail molt, resulting in a completely tail-less bird simultaneously replacing all 12 rectrices (Figure 1C). Molting birds lacked a visible tail for ~1 wk, after which regrowing rectrices began to extend past the tail coverts and became visible again. Tails were fully regrown ~3 wk after complete rectrix loss.

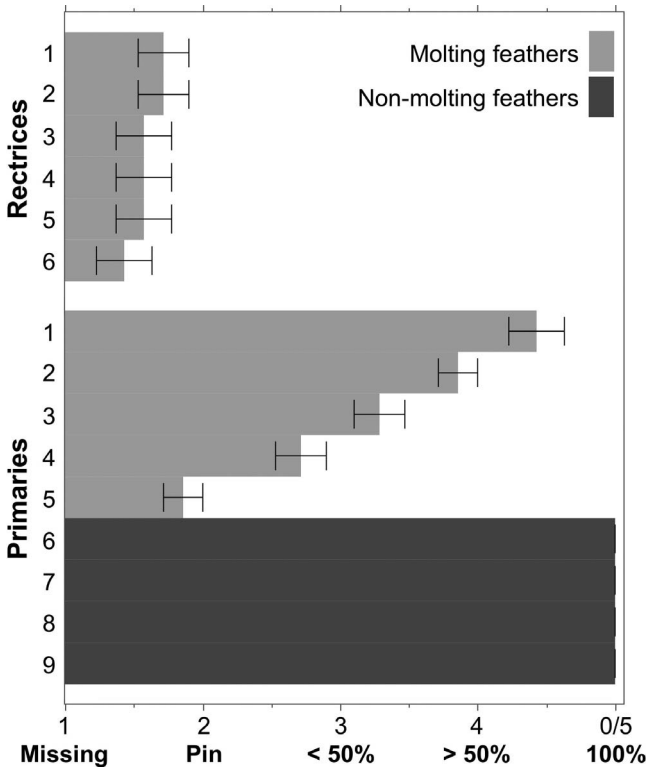

FIGURE 2. Molt scores of rectrices and primaries for 7 male Hooded Warblers captured soon after the complete loss of all rectrices. Error bars denote the standard error of molt score. Old (unmolted) primaries with molt score 0 are plotted as fully grown feathers with molt score 5 (fully grown) to more clearly illustrate the loss of flight-feather surface area during simultaneous rectrix molt and concurrent primary molt.

Complete loss of the tail feathers coincided with the approximate midpoint of primary molt; 7 males that had recently dropped all their rectrices were actively regrowing primaries 1–4, and primary 5 was either missing (recently dropped) or was a small pin feather (Figures 1D and 2). Thus, birds in complete rectrix molt were typically replacing 22 flight feathers simultaneously: all 12 rectrices plus 5 primaries on each wing (Figure 2).

Among 47 breeding pairs for which I had complete data on the timing of rectrix molt, males initiated rectrix molt 15.7 ± 12.6 days earlier than their mates (matched-pairs $t_{46} = 8.5$, $P < 0.001$; Figure 3). In only 5 (11%) of the 47 pairs did the female initiate rectrix molt before the male (sign test $P < 0.001$).

Uniparental Desertion of Late-Season Young

A total of 62 breeding adults (6 females and 56 males) initiated rectrix molt before the end of parental care and before their mate had already deserted. Of these, 43 (69%) deserted their late-season nestlings or fledglings (Table 1).

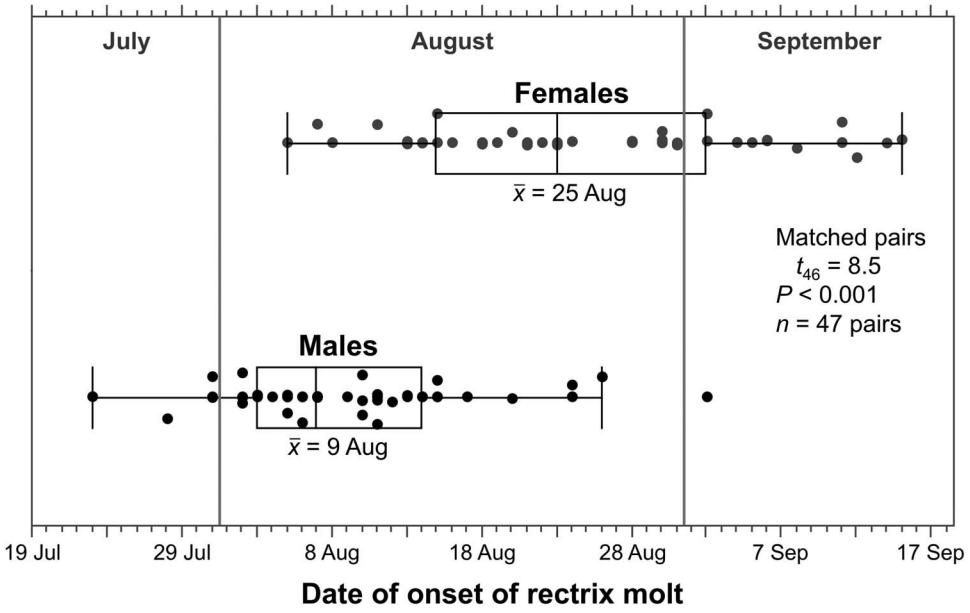

FIGURE 3. Box plots showing sex differences in the date of onset of rectrix molt for 47 mated pairs of Hooded Warblers in the study area in Pennsylvania, USA, 2013–2017. Mean (± SD) date of the onset of tail molt was August 9 ± 8 days for males and August 25 ± 11 days for females.

Most instances of uniparental desertion involved males deserting fledglings (28 of the 43 cases, or 65%), but prefledging desertion by males (13, or 30%) and postfledging desertion by females (2, or 5%) also occurred (Table 1).

For 26 deserting males, I obtained good estimates of the dates of both desertion and the onset of rectrix molt. For 17 (65%), desertion occurred at the same time or slightly after initial rectrix loss (Figure 4). Nine (35%), however, deserted 1–10 days in advance of rectrix molt, during the early stages of primary molt (Figure 4).

Factors Influencing Probability of Desertion

Logistic regression modeling shows that 2 factors are particularly important in determining whether a molting male deserts: (1) age of the brood at the onset of rectrix molt and (2) minimum age of the male (Figure 5A). Younger males with young nestlings and fledglings were more likely to desert than older males with older fledglings approaching independence (Figure 5A). Mean brood age at the onset of rectrix molt was 12.1 ± 10.4 days for deserters vs. 27.3 ± 5.3 days for non-deserters (Wilcoxon rank sum test $P < 0.001$; Figure 5B). The mean minimum age of deserting males was 2.2 ± 1.0 yr, compared with 3.3 ± 1.2 yr for non-deserters ($t_{54} = 3.49$, $P = 0.001$; Figure 5C). Neither hatching date nor brood size was a significant predictor of male desertion (both $P > 0.15$), and these factors were not included in the final logistic model (Figure 5A). Hatching date, however, may have had weak indirect effects on desertion via a strong negative relationship with

TABLE 1. Instances of uniparental desertion and non-desertion of late-season nestlings and fledglings by 62 Hooded Warblers (6 females and 56 males) that initiated tail molt before the end of parental care and before their mate had already deserted in the study area in Pennsylvania, USA, 2013–2017. Two (33%) of 6 females and 41 (73%) of 56 males showed uniparental desertion.

	Sex of deserting parent		
	Female	Male	Total
Cases of non-desertion	4	15	19
Cases of uniparental desertion			
Prefledging (young <9 days old)	0	13	13
Postfledging (young ≥9 days old)	2	28	30
Total uniparental desertion	2	41	43
Grand total	6	56	62

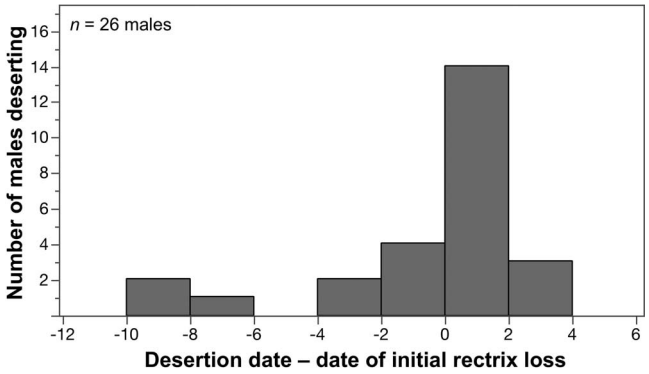

FIGURE 4. Frequency distribution of uniparental desertion in relation to the timing of initial rectrix loss for 26 male Hooded Warblers in the study area in Pennsylvania, USA, 2013–2017.

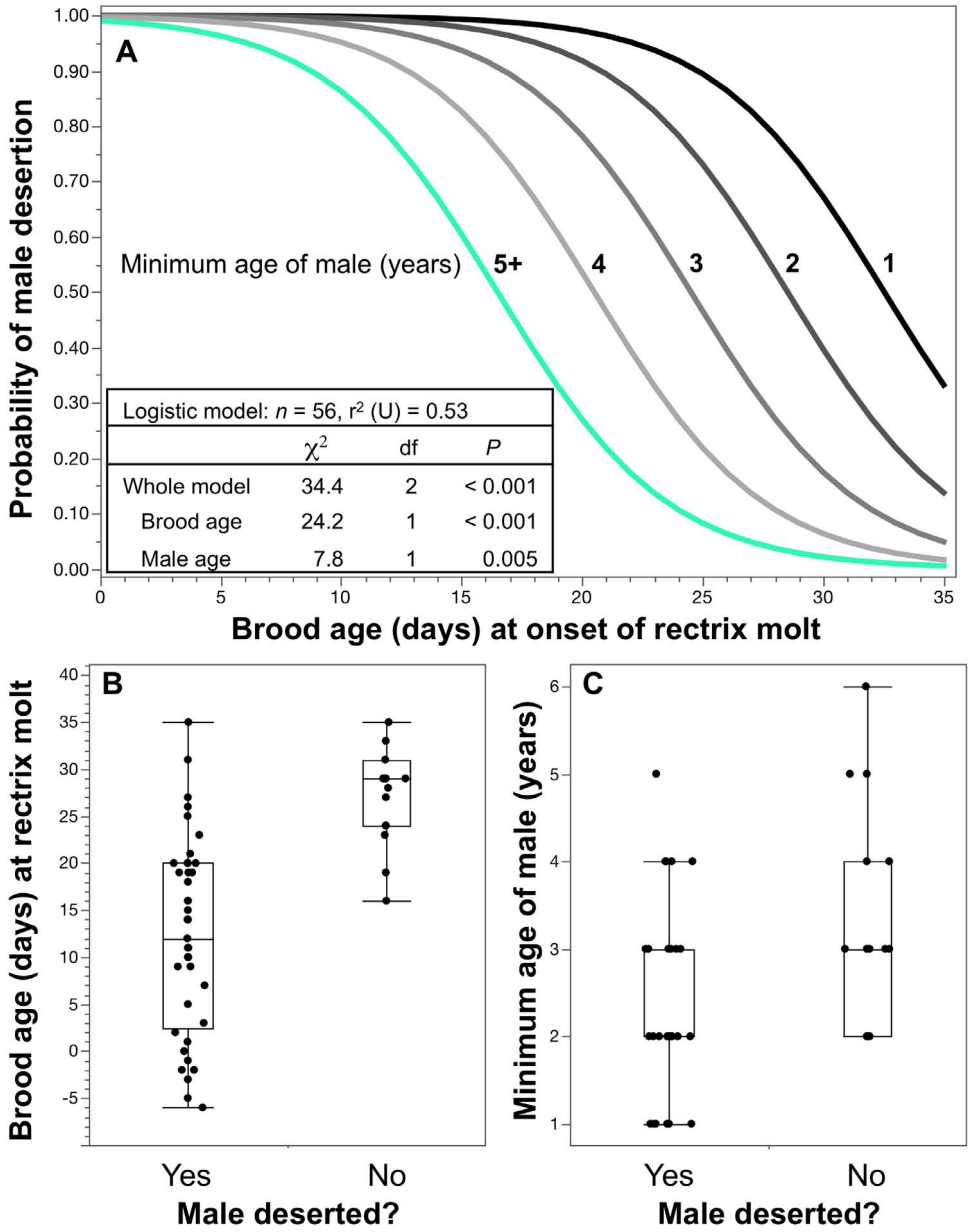

FIGURE 5. Factors contributing to uniparental desertion or non-desertion of late-season young by male Hooded Warblers in the study area in Pennsylvania, USA, 2013–2017. (**A**) Logistic regression model of male desertion in relation to age of the brood at the onset of rectrix molt and minimum age of the male. Curves represent the predicted probability of male desertion from the model. (**B**) Box plot showing the age of the brood at the onset of rectrix molt for deserting and non-deserting males. Hatching day is considered day zero, and negative ages indicate males that initiated rectrix molt during incubation. (**C**) Box plot showing the minimum age of deserting and non-deserting males.

brood age at the onset of rectrix molt (Figure 6); males at late-hatching nests were more likely to initiate rectrix molt during incubation or while tending nestlings and young fledglings, and such males nearly always deserted (Figures 5 and 6).

A comparable logistic regression analysis of factors contributing to female desertion is not possible because of small sample size; females molt significantly later than males (Figure 3), and only 6 females initiated rectrix molt before the end of parental care and before their mates had already deserted (Table 1). Nonetheless, the limited data suggest that the 2 factors important in male desertion—brood age at the onset of rectrix molt and minimum age of the parent—also play a role in the rare cases of female desertion. Mean brood age at the start of tail molt for the 2 deserting females was 17.5 ± 2.1 days, compared to 30.0

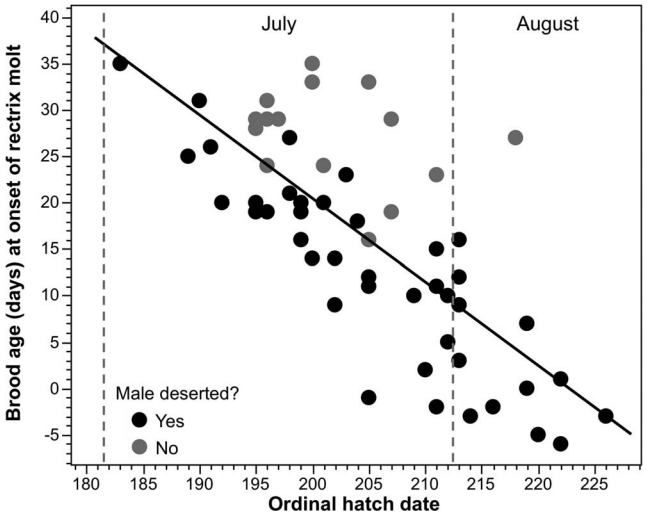

FIGURE 6. Relationship between ordinal hatch date and brood age at the onset of rectrix molt for deserting and non-deserting male Hooded Warblers in the study area in Pennsylvania, USA, 2013–2017 (linear regression $t_{54} = -8.3$, $P < 0.001$, $r^2 = 0.56$). Negative brood ages indicate males that initiated rectrix molt during incubation. Deserted and non-deserted nests did not differ significantly for hatch date (July 25 ± 10 days and July 21 ± 7 days, respectively, Wilcoxon rank-sum test $P = 0.15$).

± 2.6 days for the 4 non-deserters ($t_4 = 5.83$, $P = 0.004$). Unlike in males, however, deserting females were significantly older (minimum age = 5.0 ± 0.0 yr) than non-deserters (1.3 ± 0.5 yr; $t_4 = 10.0$, $P < 0.001$).

Desertion and Return Rate in Subsequent Year

The rate of return in the following year was slightly higher for deserting males than for non-deserting males, but not significantly so; 61% for 31 deserting males vs. 44% for 9 non-deserters ($\chi^2 = 0.8$, $P = 0.37$). Although a comparable analysis for deserting and non-deserting females is not meaningful because of small sample sizes (Table 1), return rates of females with late-season nests were similar for deserted (55% of 31) and non-deserted females (63% of 19; $\chi^2 = 0.3$, $P = 0.56$). Thus, desertion of late-season nestlings and fledglings appears to have little impact on the probability of returning the following year for either males or their mates.

DISCUSSION

Although potential conflicts between molt and parental care occur regularly in birds of both tropical (Foster 1975, Johnson et al. 2012) and temperate environments (Bancroft and Woolfenden 1982, Morales et al. 2007, Gow and Stutchbury 2013), only one previous study (Svensson and Nilsson 1997) has provided unambiguous evidence of a direct behavioral trade-off between molt and parental care. I investigated this issue in the Hooded Warbler because several aspects of its biology make conflicts between molt and parental care especially likely: a long period of postfledging parental care, an unusually prolonged nesting season that extends into late summer, simultaneous rectrix molt coupled with concurrent primary molt that also occurs in late summer, and the importance of the tail as a foraging adaptation. The 2 major findings of the present study are that uniparental desertion of late-season young occurs regularly in Hooded Warblers (Table 1) and that uniparental desertion is closely associated with the onset of simultaneous rectrix molt (Figure 4). Together, these results indicate a clear trade-off between molt and parental care and show that uniparental desertion is a frequent behavioral response to temporal overlap between these 2 demanding activities.

Previous studies have proposed 2 hypotheses to explain why molt may be associated with qualitative or quantitative reductions in parental effort: (1) that the energetic and metabolic demands of feather replacement may prohibit extensive simultaneous investment in offspring, and (2) that loss of flight feathers and compromised flight performance may make significant simultaneous investment in reproduction prohibitively costly or dangerous (Svensson and Nilsson 1997, Hemborg 1999). For Hooded Warblers, however, because the tail is an important foraging adaptation (Mumme 2014), a third hypothesis can be be added: (3) that simultaneous rectrix molt may compromise foraging performance and render adults incapable of obtaining sufficient food for both themselves and their dependent offspring. These 3 hypotheses are not mutually exclusive, and investigations of the metabolic rate, flight mechanics, and foraging performance of molting birds are needed to determine their relative importance in Hooded Warblers.

Most males that deserted their late-season young did so at the onset of rectrix molt (Figure 4). However, a significant fraction (35%; Figure 4) deserted 1–10 days in advance of rectrix molt, while they were molting primaries. It is not clear why some males desert early, but one untested possibility is that early desertion may be related to male body condition; as primary molt progresses and the number of flight feathers being replaced increases (Figure 2), males in relatively poor condition may be more likely to cross a "desertion threshold," leading to early desertion in advance of rectrix molt.

Effect of Brood Age and Parent Age on Desertion

For Hooded Warblers, the most important predictor of uniparental desertion of late-season young is age of the brood at the time of initial rectrix loss (Figure 5); broods with nestlings or young fledglings are much more likely to be deserted by a molting parent than broods with older fledglings approaching independence, and this is true for

both males (Figure 5) and females. I suggest 3 possible hypotheses for why desertion probability declines with brood age. First, molting parents may be sensitive to brood age because it accurately indicates the cumulative remaining costs of continuing parental care. Under this hypothesis, a molting parent may be willing to continue parental care if the period of remaining care is short and the cumulative remaining costs are small, but desert if they are not.

A second hypothesis for the decline in desertion probability with brood age is that the instantaneous costs of providing parental care during simultaneous rectrix molt may be relatively low if the dependent young are mobile, volant fledglings that can follow a molting adult and conform to its limited movements and constrained microhabitat preferences. Delivering food to largely or completely immobile young fledglings or nestlings, on the other hand, may be too dangerous or demanding for molting adults with limited flight and foraging abilities. In this context, it is notable that all 13 males that initiated rectrix molt during incubation or the nestling phase deserted (Table 1 and Figure 5B), which suggests that the mobility of dependent young may well be an important consideration in uniparental desertion.

A third hypothesis for the negative relationship between brood age and desertion probability is that the amount of food that must be provided to dependent young decreases as juveniles age. Although the provisioning rate of young by adults is significantly higher for fledglings than for nestlings (Evans Ogden and Stutchbury 1997), fledglings begin to catch prey on their own when they are 18–20 days old, and foraging performance increases steadily through day 35, after which performance becomes comparable to that of adults (Mumme 2014: fig. 4). Thus, it may be that birds in simultaneous tail molt can afford to provide care for older fledglings capable of meeting some of their nutritional needs on their own, but not for younger, more dependent and demanding offspring. These 3 hypotheses are not mutually exclusive, and it is possible that all 3 may play some role in explaining why desertion probability declines with brood age.

Age of the parent also had significant effects on the probability of desertion. Unexpectedly, however, these effects are in the opposite directions for males and females. For males, the probability of desertion decreases significantly with parental age (Figure 5), which suggests that older and presumably more experienced males are better equipped to deal with the dual demands of simultaneous rectrix molt and late-season parental care. Although the sample size of females is small (Table 1), it is nonetheless notable that the only 2 cases of female desertion involved unusually old females that were $\geq$5 yr old at the time of desertion; in addition, both of these deserting females survived and returned to nest the following year at age $\geq$6 yr, an exceptionally old age for Hooded Warblers of either sex at Hemlock Hill (Figure 5C). These observations suggest the possibility that rare cases of female desertion occur only in older presenescent females as a mechanism to reduce reproductive effort late in life.

An alternative hypothesis to explain the negative relationship between male age and probability of desertion is that if younger males are more likely to have nests with extrapair young, they may be more likely to desert during molt. Sexual conflict and extrapair matings are frequently hypothesized to explain why males of many species initiate molt before the end of parental care or reduce their parental investment late in the breeding season (e.g., Siikamäki et al. 1994, Svensson and Nilsson 1997, Hemborg 1999, Gow and Stuchbury 2013). For Hooded Warblers, however, 2 lines of evidence argue against a major role for paternity uncertainty in molt-related male desertion. First, extrapair paternity in Hooded Warblers is unrelated to either male age (Stutchbury et al. 1997) or male parental effort in feeding nestlings or fledglings (Stutchbury et al. 1994, 1997, Evans Ogden and Stutchbury 1997). Second, although the frequency of extrapair young is high early in the nesting season, it declines significantly as the season progresses, decreasing from ~40% of nestlings for nests initiated in late May to 15% of nestlings for nests initiated in late June (Stutchbury et al. 1997). Because nests where males ultimately desert are initiated even later (mean first egg date July 11 $\pm$ 10 days for the 41 cases described here), few extrapair young would be expected in the late-season nests, where male desertion is likely. Together, these 2 lines of evidence suggest that extrapair paternity is unlikely to be an important predictor of desertion by molting males.

Sex Differences in Timing of Molt and Desertion

Male and female Hooded Warblers differ strikingly in the timing of molt, with males initiating rectrix molt ~16 days earlier than females (Figure 3). The male–female difference in molt timing ultimately drives the pronounced sex difference in uniparental desertion; because very few females initiate rectrix molt before the end of parental care, molt-related desertion by females occurs only rarely (Table 1).

Sex differences in the timing of molt are common in passerines (e.g., Bancroft and Woolfenden 1982, Ezaki 1988, Morton and Morton 1990, Hemborg and Merilä 1998, Gow and Stutchbury 2013), but the ecological and behavioral factors that contribute to earlier male molt in Hooded Warblers are not entirely clear. Males arrive on the breeding grounds ~1 wk earlier than females (Chiver et al. 2011), so some of the difference in molt timing may reflect an endogenous rhythm that is set earlier in males than in females (Gwinner and Dittami 1990). The earlier molt of males might also be related to constraints on males

that favor early fall migration and an early arrival on their Caribbean wintering grounds (Evans Ogden and Stutchbury 1996). Both male and female Hooded Warblers defend individual feeding territories in their winter range, but the sexes differ considerably in their preferred habitat; males settle in closed-canopy tropical forest, whereas females prefer more open scrub habitat (Lynch et al. 1985, Morton 1990, Stutchbury 1994). Thus, in order to acquire wintering territories in high-quality forested habitats, males may be under selection to molt and migrate earlier than females (Evans Ogden and Stuchbury 1996). However, the behavior of many males at Hemlock Hill argues against this hypothesis; about half of all territorial males linger on their breeding territories into mid-September, and a few remain until early October, well after molt has been completed (R. L. Mumme personal observation). The existence of these lingering males suggests that selection for early male migration, if present, is by no means universal.

Desertion and Return Rates

Return rates for deserted females (55%) were slightly lower than those for non-deserted females (63%), but not significantly so. This suggests that male uniparental desertion of late-season young may not be especially costly to females, a conclusion that is also supported by the mate-choice decisions that deserted females make in the following year. I documented 11 instances of male desertion in which both the male and his deserted mate returned the following year, and in 6 (55%) of these cases the female settled with the same male again. These frequent repairings (see Howlett and Stutchbury 2003) suggest that deserted females do not discriminate against deserting males and support the conclusion that male desertion does not impose a severe fitness cost on females. This conclusion, however, is in sharp contrast to studies of *Ficedula* species showing that early male molt and uniparental male desertion can significantly reduce female survival (Hemborg and Merilä 1998, Hemborg 1999). Additional work is needed to clarify how female Hooded Warblers manage the costs of male desertion and adjust their molt and migration schedules accordingly.

Among males, return rates were higher for deserters (61%) than for non-deserters (44%), but because 73% of males that initiated rectrix molt before the end of parental care deserted, the sample size of non-deserters is small (Table 1) and the difference in return rate is not statistically significant. It seems likely that some benefit accrues to molting males that desert late-season young, while a corresponding cost is paid by males that continue to care for them (e.g., Urano 1992). These presumed benefits and costs, however, may not necessarily lead to strong differences in survival between deserting and non-deserting males; because molting males that elect not to desert are older and more experienced—and caring for less demanding older juveniles that are approaching independence (Figure 5)—males negotiating the trade-off between parental care and molt may be managing their risks and electing to continue to care for young only when the costs to future survival are relatively modest.

Mutual Interactions of Molt and Parental Care

Although the primary focus of the present study has been on how molt affects parental care in Hooded Warblers, I also have evidence that parental care affects molt, delaying its onset in both males and females. First, unpaired males with no parental responsibilities molt much earlier than paired males; 9 unmated males initiated rectrix molt on July 24 $\pm$ 8 days, 16 days earlier than the mean onset date of August 9 $\pm$ 8 days for 47 mated males ($t_{54} = 5.43$, $P < 0.001$; Figure 3). Second, 9 females deserted by males during incubation and forced to provide all parental care through successful fledging and independence initiated rectrix molt much later (September 6 $\pm$ 7 days) than the other 38 females shown in Figure 3 (August 19 $\pm$ 9 days; $t_{45} = 4.64$, $P < 0.001$). These observations suggest that parental care can delay the onset of molt in Hooded Warblers, a conclusion that has been reached in studies of many other species as well (e.g., Bancroft and Woolfenden 1982, Siikamäki et al. 1994, Hemborg 1999, Mitchell et al. 2012). Disentangling the complex ways in which parental care and molt influence each other, and the physiological mechanisms that regulate their mutual interactions, remains a significant challenge for future research (Dawson 2006, Williams 2012).

Conclusion

The Hooded Warbler has an unusual constellation of traits that makes conflicts and trade-offs between molt and parental care especially likely; it is a long-distance Neotropical migrant with an extended nesting season, a long period of postfledging parental care, simultaneous rectrix molt, and a tail that plays an important role in foraging. One of the major questions arising from the results presented here is whether Hooded Warblers are unique among the migratory warblers, or whether other species of Parulidae (Lovette et al. 2010) also show behavioral trade-offs between parental care and molt. Available evidence, although limited, suggests that Hooded Warblers may not be exceptional; simultaneous rectrix molt is widespread in migratory warblers that breed in North America (e.g., Foster 1967, Nolan 1978, Rimmer 1988, Mattsson et al. 2009), and some evidence in the literature suggests that molt-related uniparental desertion of late-season young occurs in other parulid species. For example, Holmes et al. (2017) reported that female Black-throated Blue Warblers (*Setophaga caerulescens*) are sometimes the only providers for fledglings produced

from late-season nests, which suggests that male Black-throated Blue Warblers, like male Hooded Warblers, may molt earlier than their mates and desert their fledglings while doing so. Similarly, Nolan (1978:429) recorded 11 cases of male desertion of late-season nests in the Prairie Warbler (*Setophaga discolor*) but found no link between male desertion and the simultaneous rectrix molt that he also observed (Nolan 1978:511).

Further work on the potential trade-offs between molt and parental care is clearly needed, not only in parulid warblers but also in other migratory songbirds that are highly constrained in their timing of reproduction, molt, and migration (e.g., Ezaki 1988, Gow and Stutchbury 2013). The transition from reproduction to molt is a critical and poorly understood phase of the avian annual cycle, one that has significant implications for understanding the complete annual cycle of migratory songbirds (Marra et al. 2015).

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