

CONSTRAINTS ON DOUBLE BROODING IN A NEOTROPICAL MIGRANT, THE HOODED WARBLER¹

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Abstract. We examined the constraints on double brooding in Hooded Warblers (*Wilsonia citrina*) to explain why 56% of females with successful first nests did not attempt second broods. Double brooded females fledged on average 1.9 more young than single brooded females. Double brooded females nested significantly earlier than single brooded females, but many females with early nests did not double brood. There were no significant differences among single and double brooded females in age, experience, body condition, or reproductive output at their first nest. Female breeding strategy did not depend on male age or male feeding effort at the first nest. Double brooded individuals were usually feeding fledglings while undergoing their pre-basic molt, and the main cost of being double brooded was a three week delay in molt compared with single brooded birds. This delay in molt could impose a high energetic cost due to the overlap of molt and fledgling care, and a time cost in terms of delaying migration and the acquisition of a winter territory.

Key words: double brooding; molt; Neotropical migrant; Hooded Warbler; *Wilsonia citrina*.

INTRODUCTION

Life history theory predicts that individuals may withhold reproductive effort to increase future survival or reproductive success (Charnov and Krebs 1974, Stearns 1976, Reznick 1985). Female birds can potentially increase reproductive effort dramatically by having multiple broods per breeding season (Holmes et al. 1992). However, there is much variability within populations in the reproductive effort of females. In many migrants, a large proportion of females produce only one brood of young despite having adequate time to renest (e.g. Nolan 1978, Petit 1989). Despite the interest in breeding productivity of Neotropical migrants due to declining populations of many species (Robbins et al. 1989, Askins et al. 1990, Hagan and Johnston 1992), relatively little is known about the factors that influence the number of broods produced by individuals in a population (Holmes et al. 1992).

Multiple brooding is more common among females nesting early in the season (Nolan 1978, Geupel and DeSante 1990, Holmes et al. 1992) and in years when food abundance is high (Holmes et al. 1992). This suggests that time and energy constraints at the time of nesting are the primary factors influencing female breeding

strategies. Older age, breeding experience, good body condition, and mates that contribute extensive parental care are all factors that may promote double brooding by females (Lindén 1988, Geupel and DeSante 1990, Holmes et al. 1992).

In this study we examine the costs and benefits of double brooding in the Hooded Warbler (*Wilsonia citrina*) to test why some females are double brooded whereas others are single brooded. Previous studies of double brooding have focused on time or energetic factors early in the breeding season that may constrain females from beginning a second brood (Lindén 1988, Geupel and DeSante 1990, Holmes et al. 1992). These early season factors can be categorized as female constraints (age, experience, body condition) and mate constraints (male age, male parental effort to first brood). Here, in addition to examining factors early in the season, we determine the effects of double brooding on the timing of molt late in the breeding season.

METHODS

We studied Hooded Warblers from 1991-1995 in a 150 ha mixed hardwood forest in Crawford County, Pennsylvania, USA (41° N, 79° W). The main study site of 100 ha had about 40 breeding pairs annually, and adjacent study areas (about 50 ha each) included in 1994 and 1995 had an additional 25 pairs. All individuals were banded with USFWS and color bands in unique com-

¹ Received 25 March 1996. Accepted 26 July 1996.

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binations. Females were aged by plumage coloration; second year (SY) birds have little or no black on the head and throat whereas older females (after second year, ASY) have moderate or extensive black (Evans Ogden and Stutchbury 1994). Males were aged using rectrix shape (Pyle et al. 1987), a method that proved reliable based on band returns. Most (94%; 59 of 63) males known to be ASY from band returns had rectrices scored as ASY. For males scored as SY based on rectrices, all (13 of 13) were scored as ASY the subsequent year.

We define double brooded pairs as those that initiated egg laying in a second nest after fledging young from a previous nest. Single brooded pairs were defined as pairs that did not initiate a second nest after successfully fledging young from their first nesting attempt. Nests were located at the building, egg-laying or incubation stage, usually by following the female to the nest. Nests were checked every 3–5 days to determine nesting success, and nestlings were banded. The effects of cowbird parasitism were minimal due to the removal of adult female cowbirds, resulting in a parasitism frequency of < 5% in most years (Stutchbury, in press). Cowbird eggs also were removed from nests.

Feeding rates to nestlings of single versus double brooded pairs were monitored using telescopes from a blind (1991) or video cameras (1992–1995) for a subset of 24 nests. All observations were made 5–9 days after hatching, and each nest was observed for 4–6 hr. Video cameras were placed 2 m from the nest, and feeding behavior was recorded for at least 45 min per day from 07:00–17:00. An analysis of feeding rate revealed that time of day did not significantly affect feeding rate (Pearson correlation, $r = 0.005$).

The furtive behavior of Hooded Warblers during molt precluded passive mist netting as a method of capturing birds. Molting birds were flushed toward a mist net by several people. This method of chasing molting birds into the nets proved very successful and allowed the molt stage of most individuals to be determined at least once during the molting period. We scored the degree of molt of flight feathers (wing and rectrices) by assigning a score from 0–5 for each feather based on its stage of growth (0: old feather; 1: missing feather or pin; 2: less than $\frac{1}{4}$ grown; 3: $\frac{1}{4}$ to $\frac{1}{2}$; 4: $\frac{1}{2}$ to $\frac{3}{4}$; 5: new feather over $\frac{3}{4}$ grown). Flight feather scores were taken for the left wing only (molt of the wings is fairly symmetrical) and

the left rectrices. The overall molt score was the sum of each score for the nine primaries, six secondaries, three tertials, and six rectrices (maximum score of 120 for birds that have completed molt).

We used indirect measures to assess nutritional stress of molting birds that were single versus double brooded. Subdermal fat levels in the furcular region were estimated based on an adaptation of the scoring system of Helms and Drury (1960). Nutritional state during molt can be estimated from the width of the growth bars on the rectrices (Grubb 1989). One rectrix feather (third from the inside) was plucked from each individual that had completed molt. Mitutoyo electronic calipers were used to take measurements (± 0.01 mm) of the width of a rectrix section containing five or more bars and average bar width was determined by dividing by the number of bars (Grubb 1989). Each feather was independently measured three times in order to assess measurement error. Feathers also were examined for the presence of fault bars, an indication of nutritional stress (Newton 1968a, 1968b).

All statistical tests are two-tailed unless otherwise noted. Values presented are means \pm SE.

RESULTS

BREEDING SUCCESS

Double brooding was rare among females whose first nest was preyed upon. Over the five year period, the first nesting attempt of 72 of 170 (42%) females was unsuccessful due to predation. Most of these unsuccessful females (75%; 54/72) re-nested on the same territory but only 6% (2/32) of females with successful re-nests produced a subsequent second brood. In contrast, 43.9% (43/98) of females with a successful first nest began a second brood. To compare the costs and benefits of double brooding, we compared only those females with successful first nests.

Single brooded females fledged an average of 3.1 young per breeding season (Table 1). Double brooded females on average fledged 3.0 young in their first brood, and an additional 1.9 young from their second brood (Table 1). Thus, a double brooded strategy increased annual reproductive success by 63%. This occurred despite the fact that 39% of second broods were preyed upon. Return rates for young hatched in the study area were low (0.9%; Evans Ogden and Stutchbury 1994), so we could not compare actual recruit-

TABLE 1. Clutch size, number of young hatched, and number fledged ($\bar{x} \pm SE$) for single brooded females ($n = 55$) and double brooded females ($n = 43$). By definition, single broods and first broods include only first nesting attempts that fledged at least one young. Number hatched and fledged for second broods is lower because they include nests that were preyed upon.

	Single brooded	Double brooded	
		First brood	Second brood
Clutch size	3.60 \pm 0.09	3.71 \pm 0.10	3.24 \pm 0.10
No. hatched	3.22 \pm 0.14	3.14 \pm 0.17	2.08 \pm 0.24
No. fledged	3.13 \pm 0.14	3.00 \pm 0.17	1.95 \pm 0.25

ment of young from single and double brooded pairs.

Although double brooding appears to have a large benefit, less than 50% of females with successful first nests attempted a second brood. Below we consider the constraints on double brooding for females.

FEMALE CONSTRAINTS

Double brooded females had a significantly (t -test, $t = 4.24$, $df = 96$, $P < 0.001$) earlier first nesting attempt than single brooded females (Fig. 1). For the first nesting attempt, the average first egg date for single brooded females was May 31 \pm 0.8 days, and May 26 \pm 0.8 days for females that subsequently had a second brood. Most (82%; 13 of 16) females who began egg laying by 23 May and did not experience predation were double brooded. The proportion of females that attempted second broods declined with later nesting attempts (Fig. 1). However, 46% of females

did not begin a second brood despite having first egg dates before 31 May.

We assessed female quality by comparing female age, experience, body condition, reproductive effort in the first season, and between-year return rate. Age and nesting date were correlated, because the earliest nesting females were primarily older females (Fig. 2). For each time period, there was no significant difference (Fisher's exact tests, $P > 0.5$) in female age class between single and double brooded individuals (Fig. 2). Thus female age does not explain why many females with successful first nests did not attempt a second brood.

Breeding experience could also affect the likelihood of double brooding. We compared the breeding strategy of individual females in two consecutive years. The return rate for females was relatively low (37%) and many first nests were preyed upon, so the sample size for this comparison is small. Of four females that were single brooded the first year, only one was double

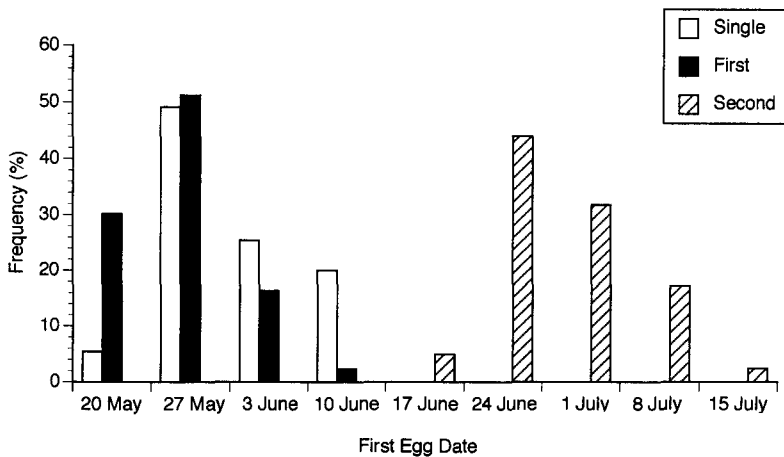


FIGURE 1. First egg dates for the nests of single brooded females ($n = 55$), and the first and second nests of double brooded females ($n = 43$).

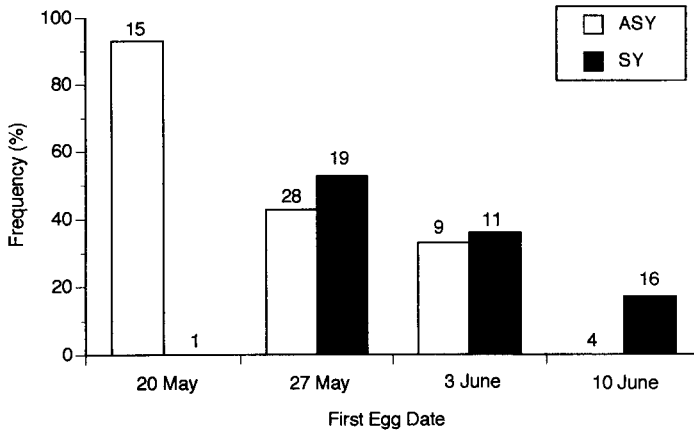


FIGURE 2. Frequency of double brooding versus date for young (SY) and old (ASY) females. Sample sizes are given above each bar.

brooded the subsequent year. Of six females that were double brooded the first year, four also double brooded the next year. These results suggest that experienced breeders are not more likely to double brood.

Body condition of females at the time they are feeding their first brood of nestlings could be an important indicator of energetic stress. Our measure of body condition was female mass divided by tarsus length, and we included data only for females measured while they were feeding at their first nest. There was no significant difference ($t = 0.90$, $df = 63$, $P = 0.37$) in body condition between single brooded ($\bar{x} = 0.499 \pm 0.005$, $n = 34$) and double brooded (0.506 ± 0.006 , $n = 31$) females.

Double brooding could be constrained by the reproductive effort of females during their first brood. However, double brooded females did not have significantly larger clutch size ($t = 0.82$, $df = 96$, $P > 0.40$), hatching success ($t = 0.37$, $P > 0.50$) or number of young fledged ($t = 0.58$, $P > 0.50$) in their first nest compared with single brooded females (Table 1).

The proportion of females that return to breed in subsequent years is an indirect measure of survivorship. Double brooded females had a return frequency of 35.5% (11 of 31) which did not differ significantly ($G = 0.05$, $P > 0.70$) from that of single brooded females (38.2%, 13 of 34).

In summary, we could find no evidence that female age, experience, body condition, fecundity early in the season or return rates differed between single and double brooded individuals.

MATE CONSTRAINTS

Females may be more likely to double brood if they are paired with a high quality mate. We assessed male quality by similar measures (age, return rate) and the degree of male parental care to the first brood of nestlings. For each time period we compared the frequency of double brooding by females mated to young versus old males. Females mated to SY males tended to be less likely to double brood (24–30 May: 3/10; 31 May–6 June: 1/7) than females mated to ASY males (14/27 and 4/10, respectively), but the differences were not significant (Fisher's exact tests, $P > 0.29$).

Feeding effort to nestlings varied widely among males (29–78% of feeding trips), so this could potentially affect a female's decision to start a second brood. However, there was no tendency for males to feed less at the nests of single brooded pairs (Fig. 3). The average feeding effort (% of trips by male) was $64 \pm 7\%$ for single brooded males ($n = 4$) and $55 \pm 4\%$ for double brooded males ($n = 13$).

There was no significant difference ($G = 0.24$, $P > 0.50$) in return rate for single brooded males (39.3%, 11/28) versus double brooded males (45.5%, 15/33).

MOLT CONSTRAINTS

Important constraints on double brooding may occur later in the breeding season, when adult Hooded Warblers must feed fledglings from late broods and undergo molt prior to migration

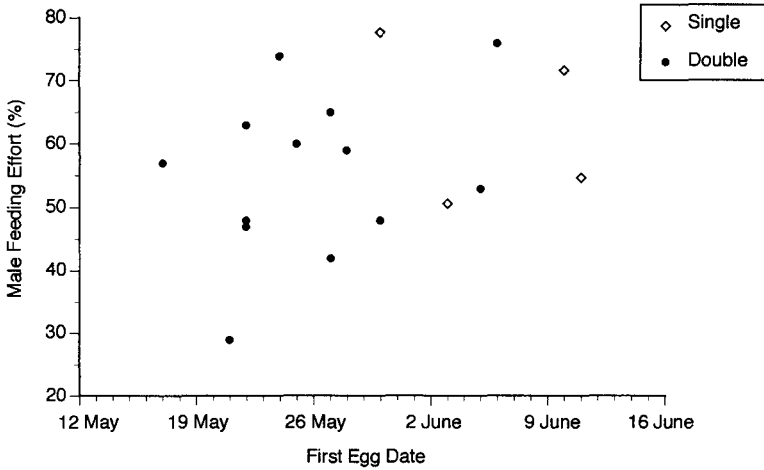


FIGURE 3. Male feeding effort (% of feeding trips) versus first egg date for single and double brooded pairs.

(Evans Ogden and Stutchbury 1994). The average first egg date for second broods was 29 June \pm 1.0 day, about 34 days after the first brood was started (Fig. 1). The average time from the first egg date to fledging young is 24 days, and parents usually feed fledglings for an additional 20–30 days (Evans Ogden 1994). Thus double brooded pairs that escape nest predation must provide parental care to young until at least mid-August. Approximately 50% of the population molted while still involved in parental care, and this could impose a large energetic cost or time cost on double brooding pairs.

We compared the average date of molt for individuals that were single versus double brooded. There were no significant differences between years (1992/1993) in the overall timing of molt for the population as a whole (ANOVA, $F_{1,73} = 1.03$, $P > 0.10$), so years were combined for analysis (but an individual was only included once). Double brooded individuals molted significantly later than individuals producing only a single brood (Fig. 4; ANCOVA, $F_{1,73} = 28.4$, $P < 0.01$). On average, double brooded individuals completed molt three weeks later than single brooded birds. Within double brooded pairs, males tended to complete molt earlier than females (ANCOVA, $F_{1,33} = 3.43$, $P = 0.08$).

We compared nestling feeding rates to the first and second brood to determine if parents reduce parental care to their second brood to compensate for the energetic demands of the molt period. In six of seven pairs, males reduced their feeding rate to nestlings of second broods (Fig. 5) which

resulted in an average decrease of 31% in male feeding effort to second broods. This pattern was strong but not statistically significant (Wilcoxon signed ranks test, $P = 0.06$, $n = 7$) perhaps due to the small sample size. Females did not appear to adjust for reduced male feeding effort, as female feeding rates did not differ significantly between broods (Wilcoxon signed ranks test, $P = 0.53$). The total feeding rate per nestling (male and female combined) to the second brood was lower than the first brood for six of seven pairs. However, this reduced feeding rate did not decrease fledging success of second broods relative to first broods. The mean number of young fledged from first broods (3.00 ± 0.17) did not differ from the mean number of young fledged from second broods that escaped predation (3.04 ± 0.14 , $n = 25$). Almost all nests that escaped predation fledged every young that hatched, for both first broods (40/43) and second broods (24/25). Return rates for nestlings were too low to test whether annual survival differs among nestlings from single versus double brooded parents.

We do not have a direct measure of energetic expenditure in single and double brooded individuals, but we indirectly estimated this using the fat scores and the width of growth bars during molt. Fat scores in all molting birds were low, with the highest scores being 2 out of a maximum of 5. Analysis of fat scores revealed no significant differences in the index of subcutaneous fat in double ($\bar{x} = 0.59$) versus single ($\bar{x} = 0.65$) brooded individuals undergoing molt ($t = 0.35$, $df = 32$, $P = 0.73$).

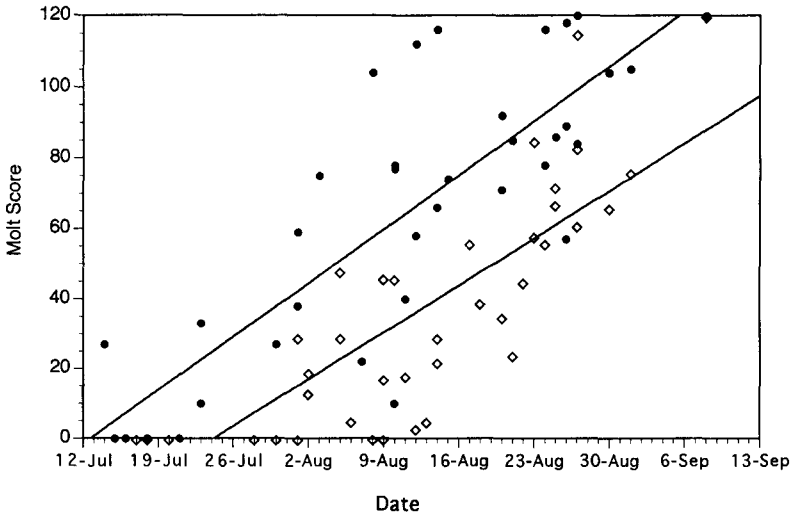


FIGURE 4. Molt score versus date for single (closed symbols; $n = 36$) and double brooded (open symbols; $n = 37$) males and females. A molt score of 0 indicates molt has not yet begun, and 120 indicates molt is complete. Each data point represents a different individual.

We used the width of growth bars on feathers collected after molt was complete to determine if overlapping molt with parental care increased nutritional stress. Growth bars were difficult to discern on the majority of feathers collected after molt, so sample sizes are small. There was no significant difference ($t = 0.66, df = 17, P > 0.10$) in the average width of growth bars from those individuals known to be overlapping molt with parental care ($\bar{x} = 2.76 \pm 0.41, n = 9$), versus

those with no overlap ($\bar{x} = 2.64 \pm 0.42, n = 10$). Fault bars were found on only 5 of 45 individuals, and two of these were from birds that did not overlap molt with parental care.

DISCUSSION

Our result that time is an important constraint on double brooding is consistent with studies of other species (Nolan 1978, Geupel and DeSante 1990, Holmes et al. 1992). The frequency of dou-

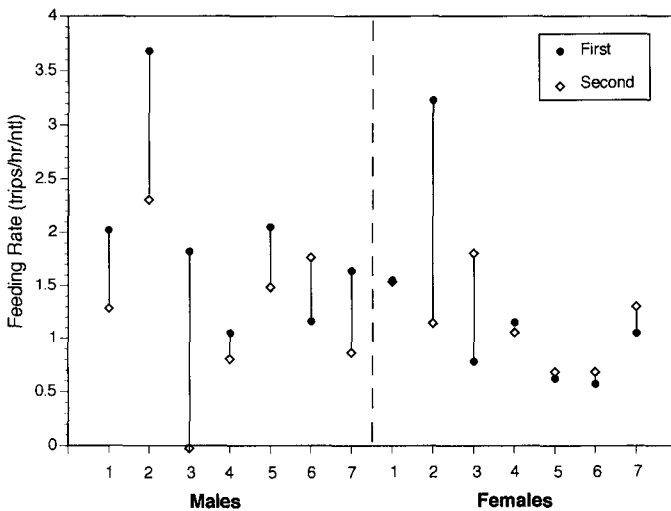


FIGURE 5. Male and female feeding rate for the first and second brood of seven pairs.

ble brooding declined as the season progressed (Fig. 1) and females who lost their first nest to predation were rarely double brooded. But time constraints early in the season cannot be the only factor, since 52% of females did not attempt a second brood despite adequate time to do so. This is surprising, because double brooding increased average reproductive success by about 60% within a breeding season (Table 1). There must be some important cost to double brooding that offsets the immediate reproductive advantage. We suggest that the main cost of double brooding is a three week delay in molt, which may have overwinter survival costs to adults and their young.

We first consider the evidence that female or male quality constrains the breeding strategy. Pairs that double brood are expected to be older, more experienced, or in better body condition (Holmes et al. 1992). However, we found that single and double brooded females did not differ significantly in age, breeding experience, body condition, reproductive ability, or return rates. The age of the female's mate, and the level of parental care provided by males to the nestlings did not differ between single and double brooded females. The results suggest that constraints imposed by the female or her mate early in the season do not affect breeding strategy.

We did not directly measure territory quality or food availability, both of which have been implicated as factors affecting breeding strategy (Holmes et al. 1992). Fledging success was uniformly high (94%) for nests escaping predation, and fledgling survival to independence was also high (Evans Ogden 1994). This suggests that food availability during the nestling period did not vary greatly among pairs.

MOLT CONSTRAINTS AND PARENTAL CARE

This is the first study to demonstrate molt constraints on double brooding in a Neotropical migrant. Double brooded parents molted about three weeks later than single brooded pairs (Fig. 3), which may be a strategy to minimize the overlap between molt and parental care. Because the pre-basic molt is completed prior to leaving the breeding grounds (Evans Ogden and Stutchbury 1994), double brooded pairs will overlap two energetically demanding activities, molt and feeding young. However, neither of our two measures of nutritional stress (subcutaneous fat,

growth bars on rectrix feathers) differed between individuals that were overlapping fledgling care and molt versus those that were not. A three week delay in the pre-basic molt may reduce the energetic costs on double brooded parents.

Parents may reduce their parental care to first broods in order to have a second brood (Geupel and DeSante 1990). However, the duration of fledgling care and fledgling feeding rates did not differ significantly between first and second broods (Evans Ogden 1994). We found that most males reduced parental care at the nest to second broods, although this did not affect nesting success. Within double brooded pairs males tended to complete their molt earlier than females. Males may be reducing their parental effort to second broods in order to initiate molt earlier, although this would have to be tested experimentally.

WINTER TERRITORY CONSTRAINT

The fitness consequences of a delayed molt may lie in the reduced likelihood of obtaining a good winter territory. Although individuals with second broods benefit from increased production of fledglings, the delay in molt may be costly for adults and their young if arrival on the wintering grounds is also delayed (Morton 1976, Smallwood 1988). Many Neotropical migrant songbirds are territorial on their wintering grounds (Greenberg 1986), so a late arrival may result in reduced ability to obtain a winter territory. Spring arrival times strongly affect an individual's ability to claim a breeding territory (Hill 1989, Stutchbury 1991) and competition for winter territories is likely analogous. Intense competition for winter territories resulting in non-territorial "floaters" has been shown for the Wood Thrush *Hylocichla mustelina* (Rappole et al. 1989, Winker et al. 1990), Hooded Warbler (Stutchbury 1994), American Redstart *Setophaga ruticilla* and Black-throated Blue Warbler *Dendroica caerulescens* (Marra et al. 1994). The only study to examine the survival consequences for non-territorial individuals found that "floaters" suffered a relatively high mortality rate (Winker et al. 1990).

Although we found no difference in return rates of single and double brooded adults, this is a relatively weak test due to small sample sizes. Non-territorial individuals on the wintering grounds tend to be yearlings (Marra et al. 1994, Stutchbury 1994), suggesting that late migration may be more costly for fledglings than their par-

ents. In Hooded Warblers, individuals begin establishing winter territories in Mexico during early September (Stutchbury 1994), at the same time that many double brooded individuals in Pennsylvania are still completing molt on their breeding territories. Testing the winter territory constraint hypothesis would require knowing the breeding strategy of an individual, its arrival time on the wintering grounds and its success in obtaining a territory. Satellite telemetry is being used for tracking migration of large birds (Weimerskirch et al. 1993) but its use for small songbirds is unlikely in the near future. Instead, interspecific comparisons could be used to test the prediction that species without winter territories will have a higher frequency of double brooding than territorial species.

ACKNOWLEDGMENTS

For excellent help with field work we thank Joan Howlett and Abby Neufeld who assisted with feeding rates and chasing molting birds. We also thank David Mark, Mark DeBoer, Owen Moore, and Trevor Pitcher for their field assistance, and Diane Neudorf and Scott Tarof for their research. Eugene Morton, Diane Neudorf, Scott Tarof, Richard Wagner, Geoffrey Geupel, Terri Donovan, and Geoff Hill provided comments on the manuscript. Statistical assistance was provided by Peggy Ng. LJEJO was supported by fellowships from the Smithsonian Migratory Bird Center, a Sigma-Xi Grant-In-Aid of Research, and the Frank M. Chapman Memorial Fund of the American Museum of Natural History. BJMS was supported by a research grant from the Natural Sciences and Engineering Research Council of Canada.

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