

## PARENTAL CARE IN THE MULTI-BROODED BLACK-THROATED BLUE WARBLER

KIRK W. STODOLA<sup>1,5</sup>, ERIC T. LINDER<sup>2</sup>, DAVID A. BUEHLER<sup>3</sup>, KATHLEEN E. FRANZREB<sup>4</sup>,  
AND ROBERT J. COOPER<sup>1</sup>

<sup>1</sup>Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602

<sup>2</sup>Department of Biological Sciences, University of Texas–Brownsville, Brownsville, TX 78520

<sup>3</sup>Department of Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN 37996

<sup>4</sup>USDA Forest Service, Southern Research Station, Southern Appalachian Mountains Cooperative  
Ecosystems Studies Unit, University of Tennessee, Knoxville, TN 37996

**Abstract.** Maximizing reproductive output often entails a trade-off between energy spent on current breeding attempts and that saved for future reproductive opportunities. For species with biparental care, energy spent on the current breeding attempt represents not only a trade-off with future breeding opportunities but also an interaction with the energetic effort of one's mate. In most songbird species, the female typically invests the most in the early stages of breeding. Consequently, the male's contribution to provisioning young may free the female from this energetically costly activity and aid her ability to attempt a second brood. We investigated parental provisioning in the Black-throated Blue Warbler (*Dendroica caerulescens*) to see if males and females altered their provisioning rates with respect to first and second broods. Using parental provisioning rates from 239 nests from three study sites over 6 years, we show that females provisioned young of first broods at a rate lower than that for second broods, while males' provisioning rate did not differ. Males' provisioning rate was inversely associated with that of females, with males increasing their provisioning when the number of young in a nest increased while females' provisioning decreased. Consequently, we believe our results highlight both the trade-off in energy females spend on current and future reproduction and the role of males' care in helping to maintain reproductive output through increased effort when conditions for feeding are difficult.

**Key words:** Black-throated Blue Warbler, *Dendroica caerulescens*, double brooding, parental provisioning, reproductive output.

### Cuidado Parental en *Dendroica caerulescens* con Crías Múltiples

**Resumen.** La maximización del rendimiento reproductivo generalmente implica un balance de costos y beneficios entre el gasto de energía para los intentos reproductivos en el presente y el ahorro de energía para oportunidades reproductivas futuras. Para las especies con cuidado biparental, la energía gastada en un intento reproductivo no sólo representa una solución de compromiso con las oportunidades reproductivas futuras, sino que también representa una interacción del esfuerzo energético entre los miembros de una pareja. En la mayoría de las aves canoras, la hembra invierte la mayor cantidad de energía en los periodos iniciales de la reproducción. Consecuentemente, la contribución de los machos durante la alimentación de los polluelos puede liberar a las hembras de esta actividad energéticamente costosa, ayudando a su habilidad de intentar una segunda cría. Investigamos el aprovisionamiento parental en *Dendroica caerulescens* para examinar si las hembras y los machos alteraban sus tasas de aprovisionamiento con relación a sus primeras y segundas nidadas. Utilizando tasas de aprovisionamiento parental de 239 nidos ubicados en tres sitios de estudio durante 6 años, mostramos que las hembras alimentaban a los polluelos de las primeras nidadas con una tasa menor que a los polluelos de las segundas nidadas, mientras que las tasas de aprovisionamiento de los machos no difirieron entre nidadas. La tasa de aprovisionamiento de los machos estuvo inversamente relacionada a la de las hembras, con un aumento en el aprovisionamiento por parte de los machos cuando aumentó el número de polluelos en un nido, mientras que la tasa de aprovisionamiento de las hembras disminuyó. Consecuentemente, creemos que nuestros resultados resaltan tanto la solución de compromiso con relación a la energía que las hembras gastan en la reproducción presente y futura, como también el papel del cuidado por parte de los machos en ayudar a mantener el rendimiento reproductivo a través del aumento del esfuerzo cuando las condiciones para la alimentación son difíciles.

## INTRODUCTION

Energy spent on reproduction should act to maximize lifetime reproductive output (Trivers 1972). Maximizing lifetime reproductive output often entails a trade-off between energy

spent on current breeding attempts and that saved for future opportunities, and numerous studies have demonstrated a negative correlation between current reproductive effort and future reproductive output (e.g., Bryant 1979, Verhulst 1998, Parejo and Danchin 2006). In species with biparental care, the

Manuscript received 3 November 2008; accepted 3 May 2009.

<sup>5</sup>E-mail: [stodolak@warnell.uga.edu](mailto:stodolak@warnell.uga.edu)

energy spent on the current breeding attempt represents not only a trade-off between current reproduction and future opportunities but also an interaction with the effort expended by each partner (Chase 1980; Winkler 1987), each acting to maximize lifetime reproductive output.

Theoretical models of biparental care focus on the conflict of interest between mates where each parent prefers the other to expend the most energy (Houston et al. 2005). These models predict that parental effort is inversely related to the effort of one's mate, and as one parent decreases investment, the other is forced to compensate to maintain fitness of offspring (Chase 1980, Winkler 1987). In most bird species the female invests most heavily in parental care—nest building, investing in eggs, incubation, and provisioning young (Ken-deigh 1952)—although the male may also play a large role, often in provisioning. Consequently, males' provisioning of young may have direct benefits to the female by allowing her to decrease her energetic investment in the current reproductive attempt and potentially reapportion that energy to future reproductive effort (Smith 1978, Smith et al. 1988).

To optimize reproductive output, short-lived species should attempt to maximize the number of young produced within one breeding season (Roff 2002), which may influence the amount of parental care provided to young. In short-lived species, optimizing reproductive output often entails increasing the number of attempts at breeding (Holmes et al. 1992, Dececco et al. 2000, Morrison and Bolger 2002). The opportunity for multiple broods has implications for the amount of care given to first and subsequent broods during a breeding season because the time and resources available for reproduction are finite. Thus breeding adults that attempt multiple broods may need to invest less in the current brood (Grüebler and Naef-Daenzer 2008). Because the female typically accrues the higher costs associated with breeding, and the ability to attempt a second brood ultimately resides with her, it stands to reason that her investment in a first brood may affect her ability to attempt a second brood, as well as the quantity or quality of young from the first. However, because the male's direct care occurs mainly during the provisioning stage, male care of first broods may affect not only the quantity or quality of young in the first brood but also the ability of the female to attempt a second brood by allowing her to decrease provisioning and save energy.

Many studies have investigated the factors affecting double brooding in a multitude of species. These studies have consistently found that food resources (Hussell 1972, Morrison and Bolger 2002, Nagy and Holmes 2005a) and length of breeding season (Verboven and Verhulst 1996, Verhulst et al. 1997) play a role in determining the number of breeding attempts. Taken together these studies suggest the ability to provision young is influential in determining overall reproductive output. However, little information exists pertaining to the allocation of parental effort, in the form of parental provisioning,

into investments in the current brood and investments into multiple breeding attempts within a season (Grüebler and Naef-Daenzer 2008). Consequently, we were interested in assessing the role of female and male provisioning as it pertains to multiple brooding and clutch size in the socially monogamous, facultatively double-brooded Black-throated Blue Warbler (*Dendroica caerulescens*).

Specifically, we investigated sex-specific differences in parental provisioning with respect to first and second broods. We predicted that females provision first broods less than they do second broods because of the energetic costs associated with double brooding, while males should provision first broods more to offset any reduction in female care. Finally, we predicted that male and female provisioning interact, with male provisioning being inversely related to female provisioning.

## METHODS

### STUDY SPECIES

Our model species for examining parental care was the Black-throated Blue Warbler, a sexually dichromatic 10-g nearctic–neotropical migrant passerine (Holmes et al. 2005). Most individuals are socially monogamous (Holmes et al. 2005), but in New Hampshire Chuang et al. (1999) found approximately a quarter of all young were fathered by extra-pair males. In this species only the female builds nests and incubates, whereas both parents feed nestlings (Holmes et al. 2005). All young in a clutch hatch within the same day, typically 12 days after the last egg in the clutch is laid (KWS, pers. obs.). The normal period of fledgling dependency is 2–3 weeks, although young have been observed being fed by parents for 4–5 weeks (Holmes et al. 2005; KWS, pers. obs.). Over a 7-year study in New Hampshire, Nagy and Holmes (2005b) found that the frequency of females attempting a second brood after successfully fledging a first ranged from 0 to 87%. Although Holmes et al. (2005) reported three broods there as well, two was the maximum observed in our study. Black-throated Blue Warblers nest at the shrub level, with 95% of all 563 nests we found at heights between 0.95 and 1.30 m. They forage mainly in the understory of temperate deciduous woods, with larvae of Lepidoptera constituting >80% of the prey items taken (Robinson and Holmes 1982) and 60–87% of the estimated biomass fed to nestlings (Goodbred and Holmes 1996).

### STUDY AREA

We conducted the study between May and August of 2003–2008 within the Nantahala National Forest in the southern Appalachian Mountains, Macon County, North Carolina (35.1° N, 83.4° W). We established three study plots at elevations of 1050, 1200, and 1350 m, all within 15 km of one another and within contiguous forest. Cove hardwood and northern hardwood forest predominate (Day et al. 1988), with *Rhododendron*

*maximum* and *Kalmia latifolia* prevalent in the understory (Day and Monk 1974).

#### STUDY POPULATION AND REPRODUCTIVE INFORMATION

To facilitate nest finding and to allow us to follow individual pairs throughout the breeding season, we attempted to band all breeding individuals. Although not every territorial male and female was banded, unbanded individuals were typically surrounded by color-banded ones and were therefore easy to identify. We attempted to follow 10, 15, and 15 pairs at the 1050-, 1200-, and 1350-m study plots, respectively, in each year and made an effort to locate all nests these pairs attempted. We were on all plots nearly every day (days of inclement weather excluded), so we believe we found most attempted nests. This intensive monitoring allowed us to estimate the numbers of nests and broods attempted per breeding pair. We monitored nests every 2–4 days to ascertain the date of clutch initiation, clutch size, start of incubation, hatching date, and number of young fledged. We backdated nests found with completed clutches by using an incubation period of 12 days and under the premise that Black-throated Blue Warblers lay one egg per day until the clutch is completed (Holmes et al. 2005). We included only nests of known age, given the assumptions above, in our analyses.

#### PARENTAL PROVISIONING

We observed and recorded parental provisioning rates on day 7 of the nestling cycle (hatch day = day 0). We focused our efforts on this day because it represents a time when demands for feeding are relatively high and provisioning stress should be high as well. Furthermore, Black-throated Blue Warbler nestlings often fledge on day 8, so day 7 was the last day we could reliably obtain provisioning rates comparable between the sexes. We used hand-held video recorders (>8× zoom) mounted on a tripod and placed 5–10 m from the nest to record parental provisioning rates. The cameras did not appear to affect parental behavior, and after 7 years of observation we state this with confidence. If we noticed any behavior indicating an effect of the video cameras (e.g., scolding at cameras, constant chipping around the nest, prolonged vigilance) we removed the camera and repositioned it until we no longer observed such behavior. This effect was rare (<5%), and for statistical analyses we included nests only where we found no observable effect of the camera. While transcribing the video recordings we noted the sex of the parent. We standardized parental provisioning rates by number of nestlings in a nest to obtain an estimate of rate per hour per nestling. KWS transcribed all video recordings.

#### STATISTICAL ANALYSES

We analyzed parental provisioning rates, female and male visits per hour per nestling, from 239 nests across all years and sites

by using a repeated-measures analysis in Proc Mixed (SAS Institute 2006). We implemented a repeated-measures framework in order to avoid pseudoreplication due to 54 nests coming from 27 pairs, of which 25 attempted a second brood after fledging a first brood and two attempted a replacement brood after the first brood was depredated. We incorporated year and site as nuisance variable fixed effects because food provisioning can differ by year and site (Stodola 2004). We also incorporated number of nestlings as a fixed effect because the number of visits to feed nestling may not be related linearly to the number of nestlings (Nur 1984, Grundel 1987). Finally, to ascertain differences in food provisioning with respect to brood, we included brood number—following a successful first brood (2) or not (1)—as a fixed effect. We also wanted to determine if there was an association between males' and females' provisioning rates. We used the same repeated-measures analysis used to determine differences in females' provisioning rate with respect to brood but included males' visits per hour per nestling. Sample sizes for years, sites, and number of nestlings are in Table 1.

Pairs that attempt second broods may be of higher quality than pairs that do not attempt a second brood and may provision young differently. Consequently, we also analyzed differences between first and second broods in females' and males' provisioning by using a paired *t*-test analysis on the 25 pairs for which we had information on provisioning of both broods within a season.

#### RESULTS

The mean date of clutch initiation was 26 May (SE = 1) for first broods and 25 June (1.4) for second broods. We have observed active nests as late as 8 August, but most nests are typically concluded by the end of July. The average number of nestlings was 3.39 (0.06) for first broods, 3.23 (0.09) for second broods. On average, females made 0.72 fewer visits per hour per nestling to first broods than to second broods, irrespective of site, year, or number of nestlings, while males made 0.32 more visits per hour per nestling to first broods than to second broods, irrespective of site, year, or number of nestlings (Figure 1).

Females provisioned young of first broods less than those of second broods (Table 2). In addition, females' provisioning differed by year, site, and number of nestlings (Tables 1 and 2). Estimated female provisioning from the repeated-measures analysis indicated that females made 0.84 (95% confidence interval 0.26–1.43) fewer visits per hour per nestling to first broods than to second broods. Furthermore, females that fed two broods within a season made 0.90 (0.15–1.66) fewer visits per hour per nestling to first broods than to second broods ( $t_{24} = 2.5$ ,  $P = 0.02$ ). All other parameter estimates are in Table 1.

Males' provisioning of young did not differ by year, site, or brood, although males' provisioning increased with number of nestlings (Tables 1 and 2). Estimated male provisioning from the repeated-measures analysis indicated

TABLE 1. Parameter estimates for repeated measures analysis of female and male provisioning (visits per hour per nestling on day 7 of the nestling period) along with 95% confidence intervals.

Parameter	<i>n</i>	Female			Male		
		Estimate	95% Confidence interval		Estimate	95% Confidence interval	
			Lower	Upper		Lower	Upper
Intercept		2.87	0.00	5.74	0.84	-1.14	2.82
Year 2003	31	-1.00	-1.64	-0.35	0.21	-0.24	0.65
Year 2004	36	-1.24	-1.85	-0.63	-0.42	-0.85	0.00
Year 2005	35	-0.69	-1.30	-0.07	-0.11	-0.53	0.32
Year 2006	47	-0.89	-1.47	-0.32	-0.12	-0.52	0.28
Year 2007	42	-0.26	-0.85	0.34	0.19	-0.22	0.60
Year 2008	48	—	—	—	—	—	—
Site 1050	57	-0.70	-1.16	-0.25	-0.01	-0.33	0.30
Site 1200	72	-0.22	-0.64	0.20	0.28	-0.02	0.57
Site 1350	110	—	—	—	—	—	—
Nestlings 1	10	4.35	1.43	7.27	-0.23	-2.25	1.78
Nestlings 2	22	2.54	-0.30	5.38	0.60	-1.37	2.56
Nestlings 3	78	1.52	-1.29	4.33	0.84	-1.10	2.78
Nestlings 4	128	0.87	-1.91	3.66	0.82	-1.11	2.74
Nestlings 5	1	—	—	—	—	—	—

that males made 0.27 (-0.13–0.67) more visits per hour per nestling to first broods than to second broods. Males that fed two broods within a season did not vary their provisioning rate between broods ( $t_{24} = 0.5$ ,  $P = 0.65$ ), making on average 0.11 (-0.38–0.59) more visits per hour per nestling to first broods than to second broods. All other parameter estimates are in Table 1. Finally, males' and females' provisioning rates were negatively associated ( $F_{1,225} = 23.4$ ,  $P < 0.001$ ), with an increase of one male visit per hour per nestling corresponding to 0.43 (0.26–0.61) fewer female visits per hour per nestling.

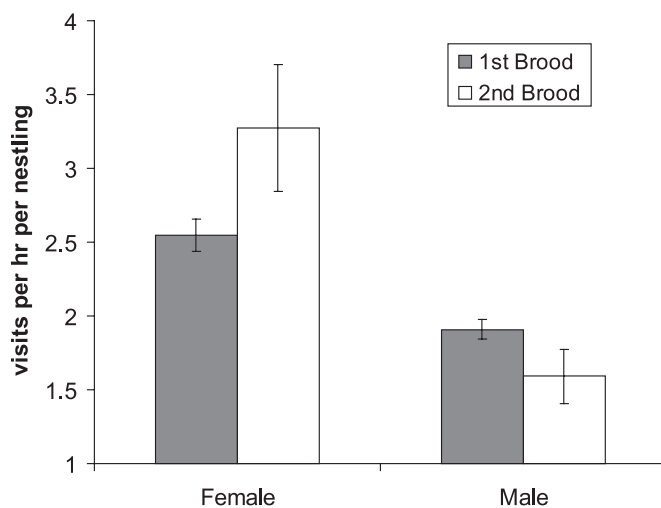


FIGURE 1. Average number of feeding visits per hour per nestling, irrespective of site, year, and number of nestlings, to first and second broods for both females and males. Error bars represent 1 SE.

## DISCUSSION

We believe our results highlight the trade-off between energy spent on current reproduction and future reproductive output in the Black-throated Blue Warbler and that this trade-off is most reflected in the investment by females. For songbirds breeding in the temperate zone, especially migratory songbirds, the time and resources available for a second brood within a breeding season are finite (Verboven and Verhulst 1996, Verhulst et al. 1997, Nagy and Holmes 2005b). Because the female invests most heavily in reproduction early in the breeding process (Clutton-Brock 1991) it is necessarily the sex whose difference in investment among broods is largest. In doing so, the female Black-throated Blue Warblers we studied reduced care to young of first broods by provisioning these young at a rate much lower than their rate for second broods.

Nest building and egg laying are energetically demanding processes (Clutton-Brock 1991) that necessitate a reduction in

TABLE 2. Results of parental provisioning (visits per hour per nestling on day 7 of the nestling period) related to year, site, brood, and number of nestlings.

Parameter	df	Female provisioning		Male provisioning	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Year	5226	4.6	0.001	2.0	0.08
Site	2226	4.6	0.01	2.1	0.13
Brood	1226	8.1	0.005	1.7	0.19
Nestlings	4226	18.9	<0.001	3.1	0.02

energy allocated to other aspects of life history (e.g., Evans Ogden and Stutchberry 1996, Gruebler and Naef-Daenzer 2008). We found that female Black-throated Blue Warblers tackle this dilemma by decreasing provisioning to first broods of the season, potentially to save energy for a second brood. Gruebler and Naef-Daenzer (2008) demonstrated that Barn Swallows (*Hirundo rustica*) provision fledglings of the first brood less than those of the second brood. Although their results are similar to ours, we demonstrate that this trade-off occurs even before young fledge from the nest; in essence, females are counting their fledglings before they are fledged. Anecdotally, we have noticed this trade-off in the field, where we have observed females building nests for a second brood while young of the first brood are still in the nest.

Contrary to our prediction, we failed to detect an increase in males' provisioning of first broods even though female care of these broods decreased and there was a negative association between males' and females' provisioning. In this species resource availability influences the ability of the female to attempt a second brood (Rodenhouse and Holmes 1992, Nagy and Holmes 2005b). Thus, for a female to attempt a second brood, feeding conditions must be good, and increased male care may not be necessary. For instance, in 2007 we failed to detect any double brooding by females, irrespective of the amount of care provided by males, and food availability in that year was the lowest we observed over the 6 years of this study (KWS, unpubl. data). Therefore, we may not have observed a substantial increase in male care of first broods over that of second broods, even though female care decreased, because resources were sufficient to enable females to provide for young of first broods and attempt a second brood.

Although we did not find any difference between broods in males' provisioning rate, males' provisioning is clearly influential when the pair is caring for young, especially when feeding conditions become difficult. Male Black-throated Blue Warblers' provisioning rate per nestling increased with increasing number of nestlings, while females' provisioning rate per nestling decreased. This difference suggests that females may be working at a maximum rate and changes in demand may affect their ability to provision. Males, on the other hand, may have more discretionary energy that they can reallocate from territory defense and singing to provisioning when conditions make provisioning young more difficult. Thus, when nestling demand increases, male care may be needed to offset any deficiency in female care. This finding agrees with other studies that have shown that male care increases when feeding is difficult (Wittenberger 1982, Breitwisch et al. 1986, Grundel 1987). If males are able to increase their parental care under difficult conditions then they may be able to offset any decrease in provisioning provided by females when conditions warrant. We believe the association between males' and females' provisioning rates, of males provisioning young at a greater rate when females' provisioning decreased, supports this.

In order to maintain constant reproductive output, theoretical models of parental care predict an inverse relationship in the sexes' effort (Chase 1980, Winkler 1987). However, evidence for this association has often been equivocal, with some studies finding an interaction (Sanz et al. 2000, Hinde and Kilner 2007), but most others either showing no relationship within a pair (Moreno et al. 1997, Lozano and Lemon 1998, Siikamaki et al. 1998) or a positive relationship (Wittenberger 1982, Sundberg and Larsson 1994, Clotfelter et al. 2007). Although we failed to find an increase in males' provisioning of first broods while females' provisioning decreased, we did find an inverse relationship between males' and females' provisioning, which was especially apparent with increasing number of young. While this inverse relationship has been predicted on theoretical grounds, Clotfelter et al. (2007) argued that a positive covariation may be more likely due to the similar response of each sex to food availability, energetic demands, and nestling demands. However, not only did we find an inverse relationship between males' and females' provisioning, but females appeared to respond more to changes in environmental conditions than did males, as evidenced by the influence year and site had on males' and females' provisioning. Thus we found little evidence for positive covariation with respect to environmental conditions and some evidence for negative covariation with respect to nestling demand, as predicted on theoretical grounds.

The majority of yearly variation in the Black-throated Blue Warbler's reproductive output comes from successfully fledging a second brood (Holmes et al. 1992). In addition, in this species the probability of second broods is influenced by food availability and its effect on nestling condition (Rodenhouse and Holmes 1992, Nagy and Holmes 2005b), suggesting a link between ability to provision nestlings and annual reproductive output. In our population, females provisioned young of first broods less frequently than they did second broods, while males' provisioning did not differ, suggesting that variation in reproductive output is dominated by the decisions of the female. However, we did find an inverse relationship between females' and males' provisioning rates, and male care was important when nestling demand increased. Furthermore, our previous research with this species demonstrates that increases in male care directly influence offspring size, while female provisioning has little effect (Stodola et al., unpubl. data). Consequently, we believe our results highlight both the trade-off in energy spent on current and future reproduction by the female and the role of male care in helping to maintain reproductive output through increased effort when conditions are difficult.

#### ACKNOWLEDGMENTS

We thank the Coweeta Hydrologic Laboratory, along with the Wayah and Highlands ranger districts of the U.S. Forest Service, for providing access to study sites. The USDA Forest Service Southern Research Station, National Science Foundation, Award 0342750, and the Georgia Ornithological Society provided for funding for this

project. D. Kim helped immensely in the initial stages of this project. Thanks to the Cooper Lab, P. Gowaty, and K. Nooker, whose comments greatly improved the manuscript. Finally, this project also would not have been possible without all the dedicated people who worked with us in the field but are too numerous to name, although we give a special thanks to K. Leavelle, L. Willenbring, A. Mahoney, P. Scarr, and B. Maley for their help over multiple years.

## LITERATURE CITED

- BREITWISCH, R., P. G. MERRITT, AND G. H. WHITESIDES. 1986. Parental investment by the Northern Mockingbird—male and female roles in feeding nestlings. *Auk* 103:152–159.
- BRYANT, D. M. 1979. Reproductive costs in the House Martin (*Delichon urbica*). *Journal of Animal Ecology* 48:655–675.
- CHASE, I. D. 1980. Cooperative and noncooperative behavior in animals. *American Naturalist* 115:827–857.
- CHUANG, H. C., M. S. WEBSTER, AND R. T. HOLMES. 1999. Extrapair paternity and local synchrony in the Black-throated Blue Warbler. *Auk* 116:726–736.
- CLOTFELTER, E. D., C. R. CHANDLER, V. NOLAN, AND E. D. KETTERSON. 2007. The influence of exogenous testosterone on the dynamics of nestling provisioning in Dark-eyed Juncos. *Ethology* 113:18–25.
- CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, NJ.
- DAY, F. P. J., AND C. D. MONK. 1974. Vegetation patterns on a southern Appalachian watershed. *Ecology* 55:1064–1074.
- DAY, F. P. J., D. L. PHILLIPS, AND C. D. MONK. 1988. Forest communities and patterns, p. 141–149. *In* W. T. Swank, and D. A. J. Crossley [EDS.], *Forest hydrology and ecology at Coweeta*. Springer-Verlag, New York.
- DECECCO, J. A., M. R. MARSHALL, A. B. WILLIAMS, G. A. GALE, AND R. J. COOPER. 2000. Comparative seasonal fecundity of four neotropical migrants in middle Appalachia. *Condor* 102:653–663.
- EVANS OGDEN, L. J., AND B. J. STUTCHBERRY. 1996. Constraints on double brooding in a neotropical migrant, the Hooded Warbler. *Condor* 98:736–744.
- GOODBRED, C. O. N., AND R. T. HOLMES. 1996. Factors affecting food provisioning of nestling Black-throated Blue Warblers. *Wilson Bulletin* 108:467–479.
- GRÜEBLER, M. U., AND B. NAEF-DAENZER. 2008. Postfledging parental effort in Barn Swallows: evidence for a trade-off in the allocation of time between broods. *Animal Behaviour* 75:1877–1884.
- GRUNDEL, R. 1987. Determinants of nestling feeding rates and parental investment in the Mountain Chickadee. *Condor* 89:319–328.
- HINDE, C. A., AND R. M. KILNER. 2007. Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B—Biological Sciences* 274:53–60.
- HOLMES, R. T., N. L. RODENHOUSE, AND T. S. SILLETT. 2005. Black-throated Blue Warbler (*Dendroica caerulescens*), no. 87. *In* A. Poole (ED.), *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, NY. <<http://bna.birds.cornell.edu/>>.
- HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. E. PETIT. 1992. Multiple brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109:321–333.
- HOUSTON, A. I., T. SZÉKELY, AND J. M. MCNAMARA. 2005. Conflict between parents over care. *Trends in Ecology & Evolution* 20:33–38.
- HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. *Ecological Monographs* 42:317–364.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. *Illinois Biological Monograph* 22:1–358.
- LOZANO, G. A., AND R. E. LEMON. 1998. Parental-care responses by Yellow Warblers (*Dendroica petechia*) to simultaneous manipulations of food abundance and brood size. *Canadian Journal of Zoology* 76:916–924.
- MORENO, J., J. POTTI, AND S. MERINO. 1997. Parental energy expenditure and offspring size in the Pied Flycatcher *Ficedula hypoleuca*. *Oikos* 79:559–567.
- MORRISON, S. A., AND D. T. BOLGER. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia* 133:315–324.
- NAGY, L. R., AND R. T. HOLMES. 2005a. Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* 86:675–681.
- NAGY, L. R., AND R. T. HOLMES. 2005b. To double-brood or not? Individual variation in the reproductive effort in Black-throated Blue Warblers (*Dendroica caerulescens*). *Auk* 122:902–914.
- NUR, N. 1984. Feeding frequencies of nestling Blue Tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. *Oecologia* 65:125–137.
- PAREJO, D., AND E. DANCHIN. 2006. Brood size manipulation affects frequency of second clutches in the Blue Tit. *Behavioral Ecology and Sociobiology* 60:184–194.
- ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918–1931.
- RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357–372.
- ROFF, D. A. 2002. *Life history evolution*. Sinauer Associates, Sunderland, MA.
- SANZ, J. J., S. KRANENBARG, AND J. M. TINBERGEN. 2000. Differential response by males and females to manipulation of partner contribution in the Great Tit (*Parus major*). *Journal of Animal Ecology* 69:74–84.
- SAS INSTITUTE. 2006. SAS 9.1.3 help and documentation. SAS Institute, Cary, NC.
- SHIKAMAKI, P., J. HAIMI, M. HOVI, AND O. RATTI. 1998. Properties of food loads delivered to nestlings in the Pied Flycatcher: effects of clutch size manipulation, year, and sex. *Oecologia* 115:579–585.
- SMITH, H. G., H. KALLANDER, K. FONTELL, AND M. LJUNGSTROM. 1988. Feeding frequency and parental division of labor in the double-brooded Great Tit *Parus major*—effects of manipulating brood size. *Behavioral Ecology and Sociobiology* 22:447–453.
- SMITH, J. N. M. 1978. Division of labour by Song Sparrows feeding fledged young. *Canadian Journal of Zoology* 56:187–191.
- STODOLA, K. W. 2004. Spatio-temporal variation in prey abundance and its impacts on two migratory songbirds. M.Sc. thesis, Mississippi State University, Mississippi State, MS.
- SUNDBERG, J., AND C. LARSSON. 1994. Male coloration as an indicator of parental quality in the Yellowhammer, *Emberiza citrinella*. *Animal Behaviour* 48:885–892.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136–179. *In* B. Campbell [ED.], *Sexual selection and the descent of man*. Aldine, Chicago.
- VERBOVEN, N., AND S. VERHULST. 1996. Seasonal variation in the incidence of double broods: The date hypothesis fits better than the quality hypothesis. *Journal of Animal Ecology* 65:264–273.
- VERHULST, S. 1998. Multiple breeding in the Great Tit, II. The costs of rearing a second clutch. *Functional Ecology* 12:132–140.
- VERHULST, S., J. M. TINBERGEN, AND S. DAAN. 1997. Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts? *Functional Ecology* 11:714–722.
- WINKLER, D. W. 1987. A general model for parental care. *American Naturalist* 130:526–543.
- WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. *Condor* 84:22–39.