



## Relative influence of male and female care in determining nestling mass in a migratory songbird

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Biparental care is common in birds, with the allocation of effort being highly variable between the sexes. In most songbird species, the female typically provides the most care early in the breeding cycle with both parents providing care when provisioning young. Food provisioning should be directly related to offspring quality; however, the relative influence each parent has on offspring quality has rarely been assessed at the nest level. Consequently, we were interested in assessing the relative influence male and female provisioning has on one measurement of offspring quality, nestling mass, in the black-throated blue warbler *Dendroica caerulescens*. Over a six year period, 2003–2008, we collected information on average nestling mass per brood on day 6 of the nestling cycle and parental provisioning rates on day 7 of the nestling cycle from 182 first brood nests on three different study plots. We found that average nestling mass was directly related to male provisioning rate, while it was not related to female provisioning rate. On the other hand, estimated biomass provisioned had little influence on average nestling mass, calling into question its utility in assessing parental quality. Finally, there was some indication that parental influence on average nestling mass was dependent on the other parent's provisioning rate, suggesting that parents work in concert to influence nestling quality.

Biparental care in birds is the norm rather than the exception (Lack 1968), with the allocation of parental care between the sexes being highly variable (Carranza 2000). In most bird species, the female invests most heavily in parental care (Kendeigh 1952), yet this may not be the case when provisioning young (Wittenberger 1982, Grundel 1987, Moreno et al. 2006). Consequently, the influence each parent imparts on nestling growth and size may not be equal. Trivers (1972) suggested that females should invest more in provisioning young due to their prior investment in egg laying and incubation. However, male provisioning may be more influential in determining offspring quality because males may increase their relative contribution when food availability is scarce (Wittenberger 1982) or when nestling demand increases (Breitwisch et al. 1986, Grundel 1987), and individual variation in paternal quality is influential in other stages of breeding as well (Kleindorfer et al. 1995, Lislevand et al. 2004). Furthermore, the influence of each parent may be dependent on the influence of the other as theoretical models predict that parental effort is directly related to the effort of one's mate (Chase 1980, Winkler 1987). Thus, understanding how and when female and male care occurs and interacts may help us better

understand parental care in general (Gowaty 1996, Houston et al. 2005).

Food provisioning is often used to evaluate parental care (Omland and Sherry 1994, Sætre et al. 1995, Moller and Thornhill 1998) because it is easily measured and represents one type of parental energy allocation. Food provisioning, and more specifically biomass provisioned, should be directly related to offspring quality with each parent able to increase offspring quality by increasing its own investment. This relationship is best demonstrated in removal studies (from Table 8.3, p. 142, in Clutton-Brock 1991), and from studies where parental effort is manipulated (Wright and Cuthill 1989, Markman et al. 1995). However, these studies provide little information pertaining to the relative influence of each parent and to the best of our knowledge, few studies have investigated the direct link between parental provisioning at a nest and offspring size at that nest. Moreover, the majority of studies that have investigated the link have failed to demonstrate any relationship between parental provisioning of either parent and offspring quality (Rytönen et al. 1995, Sætre et al. 1995, Brodmann et al. 1997, Freeman-Gallant 1998, Moreno et al. 2006). Thus, the utility of measuring parental provisioning could be called into

question if such measurements have no detectable influence on offspring.

Parental care should be influential in determining both offspring quantity and quality, and the relative influence of each parent may be different. We have already demonstrated in the well-studied migratory black-throated blue warbler *Dendroica caerulescens* that the relative contribution of males and females when provisioning young differs with the quantity of young in a nest (Stodola et al. 2009). However, as previously mentioned, the relative influence each parent has in determining offspring quality is still relatively unknown, whether it be with respect to the black-throated blue warbler, or birds in general. The influence that each parent imparts on nestling quality is an important facet of avian biology because nestling mass is related to recruitment in songbird species (Blancher and Robertson 1987, Kremenetz et al. 1989, Monros et al. 2002), suggesting a link between parental care, offspring quality, and realized reproductive output. Consequently, we were interested in assessing the relative influence male and female parental provisioning rates and biomass brought to the nest imparted on one measure of offspring quality, average nestling mass per brood, in the afore mentioned, black-throated blue warbler.

## Methods

### Study species

The black-throated blue warbler is a sexually dichromatic, 10 g Nearctic–Neotropical migrant passerine (Holmes et al. 2005). Most individuals of the species are socially monogamous (Holmes et al. 2005). Nest building and incubation in this species are conducted solely by the female, while both parents feed nestlings (Holmes et al. 2005). Hatching of all young in a clutch occurs within the same day, typically 12 days after the last egg in the clutch is laid (Stodola 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, Stodola pers. obs.). Frequency of females attempting a second brood after successfully fledging a first ranged from 0–87% over a seven year period in a study in New Hampshire (Nagy and Holmes 2005b), and while three broods have been reported there as well (Holmes et al. 2005), we have observed a maximum of two in our study area. Black-throated blue warblers nest at the shrub level with 95% of all nests found in our study area ( $n = 563$  nests), occurring between 0.95–1.30 m high. They forage mainly in the understory of temperate deciduous woods, with Lepidoptera larvae comprising >80% of the prey items taken (Robinson and Holmes 1982) and 60–87% of the estimated prey 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 a.s.l., all within 15 km of one another and within contiguous forest. Cove hardwood and northern hardwood forest vegetation dominate the canopy (Day et al. 1988), while *Rhododendron maximum* and *Kalmia latifolia* dominate the understory (Day and Monk 1974).

### Brood mass and parental provisioning

We measured nestling mass on day 6 of the nestling cycle (hatch day = day 0), which is believed to be the last day nestlings can be handled without premature fledging (Rodenhouse 1986, Stodola pers. obs.). We weighed nestlings before 1200 hrs, weather permitting. We averaged weights across the entire brood to obtain an average nestling mass per brood. Because parental provisioning rates may differ between first and second broods (Stodola et al. 2009), we constrained our analysis to only first broods within a season. We observed and recorded parental provisioning rates on day 7 because this day represented a time when feeding demands were relatively high and provisioning stress should be high as well. Furthermore, Black-throated blue warbler nestlings often fledged on day 8 of the nestling cycle, thus day 7 was the last day we could reliably attain provisioning rates comparable between the sexes. We recorded each nest using handheld video recorders (8× zoom) mounted on a tripod and placed 5–10 m from the nest. The cameras did not appear to affect parental behavior and after six 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 nest, prolonged nest vigilance) we removed the camera and repositioned it until we no longer observed such behavior. This occurrence was rare (<5%) and for statistical analyses we only included nests where we found no observable effect of the camera.

While transcribing the video recordings, we noted the sex of the parent and estimated prey size in relation to bill size (Simons and Martin 1990). The visible portion of the black-throated blue warbler bill is approximately 9 mm allowing the length of prey brought to the nest to be placed into one of four size classes: 1) 0–7 mm, 2) >7–14 mm, 3) >14–21 mm, and 4) >21 mm. We placed food brought to the nest into these size classes following previous research on parental provisioning in this species (Goodbred and Holmes 1996) and also to help minimize any discrepancies in measuring prey size. We then used these size classes to estimate biomass brought to nestlings following Goodbred and Holmes (1996), where size class to biomass conversion was 1, 2, 8, and 20 mg, respectively for the four size classes. Average recording time was 120 min and 95% of all recording time between 117 and 122 min. 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. In total, our measurements of parental provisioning rate was based on 182 nests from six years across three study plots. There were four nests where we were unable to estimate prey load size due to the approach angle of feeding adults. Consequently, the analysis

of the influence of biomass provisioned was based on 178 nests. Sample sizes for each year and study plot can be viewed in Appendix A and B.

## Statistical analyses

To describe how provisioning rate is related to estimated biomass provisioned we investigated the correlation between feeding rate (visits per hour per nestling), average prey size brought to the nest, and estimated biomass provisioned per hour per nestling using Proc Corr SAS v. 9 (SAS Inst. 2006). We then analyzed the influence of parental provisioning, visits per hour per nestling and estimated biomass brought to the nest, on average nestling weight per brood using the maximum likelihood specification in Proc Mixed SAS v. 9 (SAS Inst. 2006). We incorporated year and site as nuisance variable fixed effects because provisioning rates can differ between years and sites (Stodola et al. 2009). We also incorporated number of nestlings as a fixed effect because feeding visits and average nestling weight per brood may not be linearly related to number of nestlings (Nur 1984, Grundel 1987, Stodola et al. 2009).

## Results

Average (SE) nestling mass per brood was 7.43g (0.05) irrespective of year, site, or number of nestlings, although mass differed by year and site (Table 1, 2a, Fig. 1a–c). Increases in male provisioning rate were associated with increased average nestling mass per brood (Table 2a, 3, Fig. 2), while female provisioning rate appeared to have little influence (Table 2a, 3, Fig. 2). There was also some indication that male and female provisioning interacted in determining average nestling mass per brood (Table 2a, 3, Fig. 2). Surprisingly, neither male nor female estimated biomass (mg) provisioned per hour per nestling was related to average nestling mass per brood (Table 2b, 3). There was also no indication that male and female estimated biomass provisioned influenced average nestling mass (Table 2b, 3).

Both females and males brought smaller items to the nest when feeding more frequently (Fig. 3a,  $r = -0.34$ ,  $p < 0.001$  and Fig. 3b,  $r = -0.30$ ,  $p < 0.001$ , respectively), which may explain why feeding frequency was not related to estimated biomass provisioned per hour per nestling for either females or males (Fig. 4a,  $r = 0.09$ ,  $p < 0.23$ , and Fig. 4b,  $r = 0.01$ ,  $p < 0.90$ , respectively). Females made on average 0.72 more visits per hour per nestling than males, irrespective of year, site, or number

of nestlings (Table 1) while males provisioned 0.20 more mg of estimated biomass per hour per nestling than females irrespective of year, site or number of nestlings (Table 1). Parental provisioning rates for year, site, and number of nestlings can be viewed in Appendix A. Average biomass provisioned per hour per nestling for year, site, and number of nestlings can be viewed in Appendix B.

## Discussion

Male parental care is common in birds (Silver et al. 1985); however, the specific role that males play is highly variable and their influence on young is still ambiguous. We demonstrate that in the black-throated blue warbler, male provisioning late in the nestling stage is more influential in determining average nestling mass per brood than female provisioning. Males of other species take on a greater role in provisioning young when conditions are more difficult, i.e. when nestlings are growing faster (Breitwisch et al. 1986), nestling demand is greater (Grundel 1987), or food is scarce (Wittenberger 1982), presumably to help maintain offspring quality. In a related study, we found that males at our study site take on a greater role in provisioning when brood size increases, presumably to help offset a decrease in female provisioning (Stodola et al. 2009). Here, we demonstrate that male care is not only influential when feeding conditions become more difficult, but their influence is more important than female provisioning when determining offspring size.

Male provisioning has a positive influence on offspring size, even while environmental conditions may dictate the larger framework under which male provisioning acts. Average nestling mass per brood differed by years and sites suggesting that climatic and habitat conditions are important determinants of offspring size. Food availability within a season can influence parental provisioning, which in turn can influence offspring size (Naef-Daenzer and Keller 1999). Large-scale climate factors can determine food availability over broad spatial scales and between years (Jones et al. 2003), and differences in habitat, due to changes in elevation between our study sites, may have likely caused differences between years and sites in the food breeding adults had available to provision young. Our own assessment of caterpillar numbers, the major prey item fed to nestlings, show great variation between years and sites (Stodola unpubl.). Thus, food availability likely dictates adult provisioning to young, which was reflected in the differences we found in offspring size between years and

Table 1. Average nestling mass (g) on day 6 of the nestling cycle and parental provisioning rate (visits per hour per nestling) on day 7 of the nestling cycle from 182 first brood black-throated blue warbler nests, and estimated biomass (mg) brought per hour per nestling from 178 first brood nests, irrespective of year, site, or number of nestlings. Confidence intervals (95%) and minimum (min) and maximum (max) values are provided as well.

	Mean	Confidence interval	Min	Max
Average nestling mass	7.43	7.34–7.52	4.75	8.85
Male visits	1.88	1.73–2.04	0.00	5.21
Female visits	2.60	2.37–2.83	0.00	12.30
Male biomass	0.86	0.75–0.97	0.00	5.69
Female biomass	0.66	0.59–0.73	0.00	3.31

Table 2a. Results from a linear model relating average nestling brood mass on day 6 of the nestling cycle to parental provisioning rates (visits per hour per nestling) on day 7 of the nestling cycle, year, site, and number of nestlings for black-throated blue warblers.

	DF	F	p
Male provisioning	1,167	7.15	0.008
Female provisioning	1,167	0.52	0.471
Male × Female provisioning	1,167	3.23	0.074
Year	5,167	10.77	<0.001
Site	2,167	6.91	<0.001
Nestlings	4,167	0.79	0.530

sites. However, even when controlling for these environmental factors (year and site), we found that male provisioning rate was still influential in determining offspring size.

Surprisingly, we found that estimated biomass provisioned had little influence on average nestling mass per brood. While we found that male feeding rate was associated with offspring size, estimated biomass provisioned was not, and neither was biomass provisioned by the

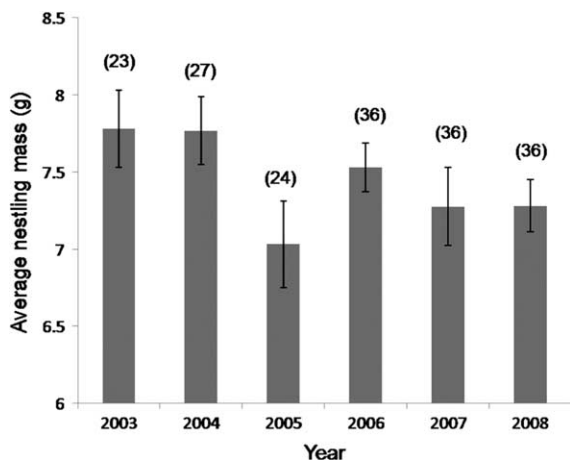


Figure 1a. Average nestling mass per brood (g) by year, along with 95% confidence intervals. Sample sizes provided in parentheses.

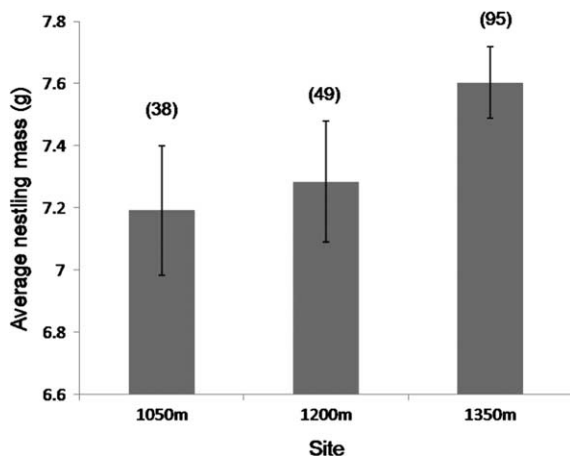


Figure 1b. Average nestling mass per brood (g) by site, along with 95% confidence intervals. Sample sizes provided in parentheses.

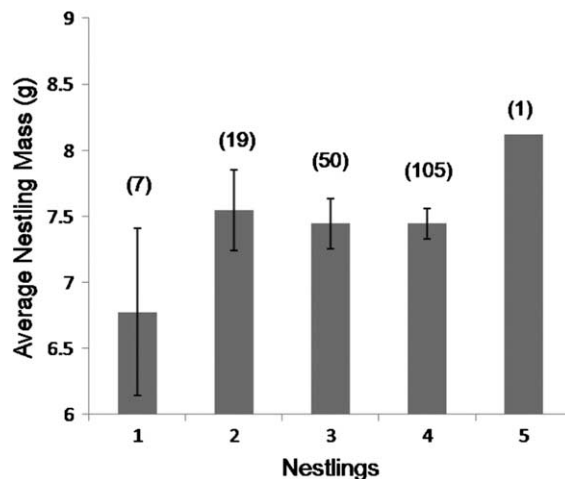


Figure 1c. Average nestling mass per brood (g) by number of nestlings in a nest along with 95% confidence intervals. Sample sizes provided in parentheses.

female. Most surprising of all, total biomass delivered (males + females) did not influence nestling mass (parameter estimate for total biomass delivered when controlling for year site and nestling was 0.063 with a 95% confidence interval of  $-0.037, 0.16$ ). Biomass provisioned should influence nestling mass because energetic intake, and not the rate of food items brought, should determine growth, yet this was not the case. The use of estimated biomass to assess parental quality is common in the ornithological field and has been used with numerous species (Omland and Sherry 1994, Sejberg et al. 2000, Schaefer et al. 2004, Tremblay et al. 2005). However, we believe our results highlight the difficulty in estimating biomass through visual inspection of prey size and corresponding conversion to biomass. It is particularly difficult to estimate prey size when multiple items are delivered in a visit and imprecision also arises from estimating biomass using one conversion factor for all taxa. Biomass equations are typically developed at the family level using freshly collected specimens; sometimes the best fitting models use insect width as well as length (Sample et al. 1993). Here, we used prey size categories, based solely on length for all taxa. We therefore suggest caution in the use of this practice, unless the true value of the food delivered can be ascertained.

In contrast to male provisioning rate, female provisioning was not related to average nestling mass per brood, and we believe there are two possibilities why this was the case. One possibility is a trade-off between rate of provisioning, size, and quality of prey brought. Not all items brought to

Table 2b. Results from a linear model relating average nestling brood mass on day 6 of the nestling cycle to estimated biomass (mg) provisioned per hour per nestling on day 7 of the nestling cycle, year, site, and number of nestlings for black-throated blue warblers.

	DF	F	p
Male biomass	1,163	0.01	0.921
Female biomass	1,163	1.96	0.164
Male × Female biomass	1,163	0.01	0.914
Year	5,163	9.50	<0.001
Site	2,163	5.32	<0.001
Nestlings	4,163	1.51	0.202

Table 3. Model coefficients and 95% confidence intervals from linear model relating average nestling brood mass on day 6 of the nestling cycle to parental provisioning rates (visits per hour per nestling) on day 7 of the nestling cycle and biomass brought (estimated biomass, mg, brought per hour per nestling) on day 7 of the nestling cycle for black-throated blue warblers. Sample sizes were 182 nests for parental provisioning rate and 178 nests for estimated biomass brought.

	Estimate	Confidence interval
Male provisioning	0.21	0.06-0.36
Female provisioning	0.03	-0.05-0.12
Male × Female provisioning	-0.04	-0.08-0.00
Male biomass	0.01	-0.21-0.23
Female biomass	0.20	-0.08-0.48
Male × Female biomass	-0.01	-0.16-0.14

nestlings are of similar quality (Brodmann et al. 1997, Wright et al. 1998) and it may be advantageous to bring fewer, larger, higher-quality items to nestlings to reduce the risk of predation caused by activity around the nest (Mullin and Cooper 1998, Martin et al. 2000). Other species bring larger items when feeding less frequently (Liffield and Slagsvold 1988) and we found a similar result with both male and female black-throated blue warblers. However, we may not have been able to observe this trade-off's affect on offspring size because of our inability to adequately assess biomass brought to the nest.

The second possibility is that female provisioning is unrelated to offspring size due to the influence that males have; the interaction in female and male provisioning may support this. Females that provision more must do so by reducing other aspects of parental care, most notably brooding nestlings. Black-throated blue warbler nestlings are unable to fully thermoregulate when still in the nest and females will brood seven-day-old nestlings (KWS pers. obs.). Time spent foraging and provisioning young will necessarily detract from time spent brooding. Thus, the energetic gains from additional food delivered

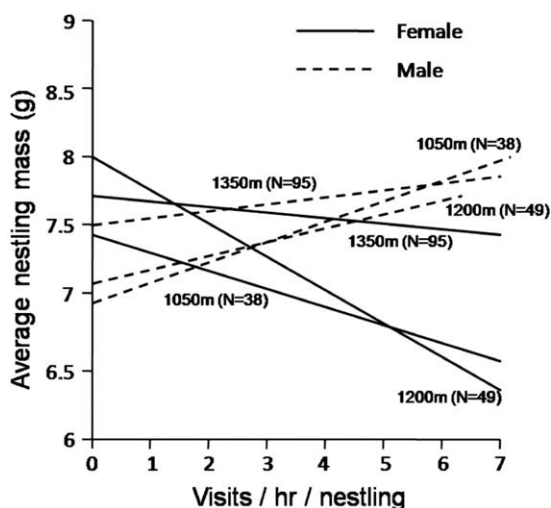


Figure 2. Depiction of the relationship between average nestling mass per brood (g) to female and male provisioning rates (visits per hour per nestling) using the best-fit trend lines for the three study plots, irrespective of year. Data points are removed for clarity. Study site and sample sizes (in parentheses) are included.

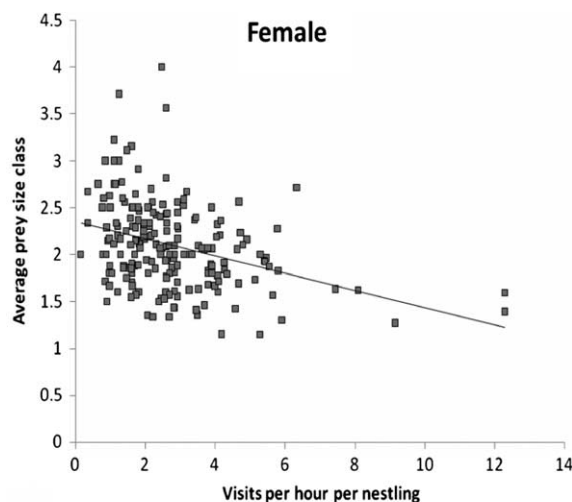


Figure 3a. Female feeding rate (visits per hour per nestling) in relation to average prey size class per visit, along with best-fit trend line.

by the female may be offset by an increase in energy expenditure for thermoregulation. Increases in male provisioning may allow the female to provision less and instead expend energy on other aspects of parental care, such as brooding. Consequently, increases in male care may not only directly affect offspring quality but also indirectly affect it by influencing the role of female care.

Male parental care in black-throated blue warblers is more influential in directly determining one measurement of offspring quality, even when controlling for environmental factors, yet increased male care may have additional benefits. Successful second broods constitute the majority of yearly variation in black-throated blue warbler reproductive output (Holmes et al. 1992). Food availability and its influence on nestling mass affect the probability of second broods in this species (Nagy and Holmes 2005a), suggesting a link between the ability to provision nestlings and annual reproductive output. Nest building and egg laying are

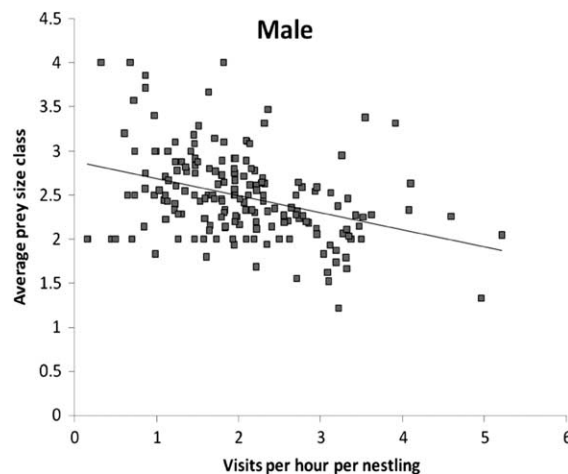


Figure 3b. Male feeding rate (visits per hour per nestling) in relation to average prey size class per visit, along with best-fit trend line.

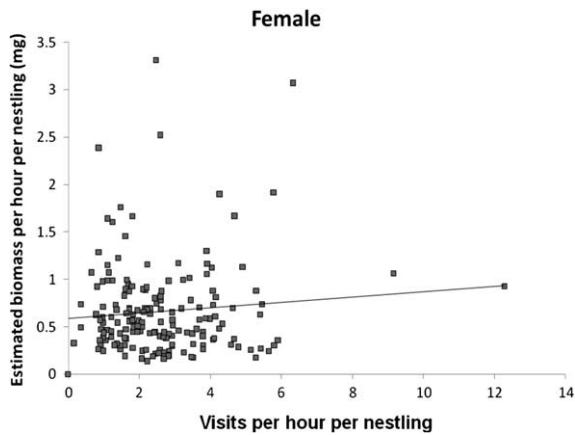


Figure 4a. Female feeding rate (visits per hour per nestling) in relation to estimated biomass (mg) provisioned per hour per nestling, along with best-fit trend line.

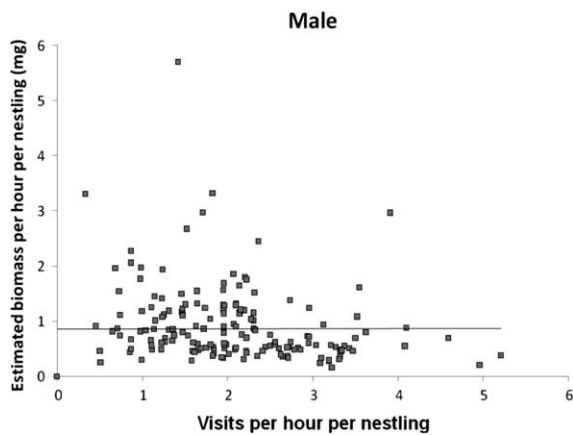


Figure 4b. Male feeding rate (visits per hour per nestling) in relation to estimated biomass (mg) provisioned per hour per nestling, along with best-fit trend line.

energetically demanding processes (Clutton-Brock 1991) and female black-throated blue warblers reduce the amount of care provided to first broods (Stodola et al. 2009), presumably to allocate that energy towards a second brood. If male care can increase nestling mass, as we have demonstrated, then females may be more apt to attempt a second brood, and males in this species may not only be influential in determining offspring quality, but may also be influential in determining overall reproductive output.

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## References

- Blancher, P. J. and Robertson, R. J. 1987. Effect of food supply on the breeding biology of western kingbirds. – *Ecology* 68: 723–732.
- Breitwisch, R., Merritt, P. G. and Whitesides, G. H. 1986. Parental investment by the northern mockingbird – male and female roles in feeding nestlings. – *Auk* 103: 152–159.
- Brodmann, P. A., Reyer, H.-U., Bollmann, K., Schlapfer, A. R. and Rauter, C. 1997. The importance of food quantity and quality for reproductive performance in Alpine water pipits *Anthus spinoletta*. – *Oecologia* 109: 200–208.
- Carranza, J. 2000. Environmental effects on the evolution of mating systems in endotherms. – 14th course of the Int. School of Ethology. World Scientific Printers, Singapore.
- Chase, I. D. 1980. Cooperative and noncooperative behavior in animals. – *Am. Nat.* 115: 827–857.
- Clutton-Brock, T. H. 1991. The evolution of parental care. – Princeton Univ. Press.
- Day, F. P. J. and Monk, C. D. 1974. Vegetation patterns on a southern Appalachian watershed. – *Ecology* 55: 1064–1074.
- Day, F. P. J., Phillips, D. L. and Monk, C. D. 1988. Forest communities and patterns. – In: Swank, W. T. and Crossley, D. A. J. (eds), *Forest hydrology and ecology at Coweeta, Ecological Studies* 66. Springer, pp. 141–149.
- Freeman-Gallant, C. R. 1998. Fitness consequences of male parental care in savannah sparrows. – *Behav. Ecol.* 9: 486–492.
- Goodbred, C. O. N. and Holmes, R. T. 1996. Factors affecting food provisioning of nestling black-throated blue warblers. – *Wilson Bull.* 108: 467–479.
- Gowaty, P. A. 1996. Field studies of parental care in birds. New data focus questions on variation among females. – In: Rosenblatt, J. S. and Snowdon, C. T. (eds), *Advances in the study of behavior*. Academic Press, pp. 476–531.
- Grundel, R. 1987. Determinants of nestling feeding rates and parental investment in the mountain chickadee. – *Condor* 89: 319–328.
- Holmes, R. T., Sherry, T. W., Marra, P. P. and Petit, K. E. 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.
- Holmes, R. T., Rodenhouse, N. L. and Sillert, T. S. 2005. Black-throated blue warbler *Dendroica caerulescens*. – In: Poole, A. (ed.), *The birds of North America*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Houston, A. I., Székely, T. and McNamara, J. M. 2005. Conflict between parents over care. – *Trends. Ecol. Evol.* 20: 33–38.
- Jones, J., Doran, P. J. and Holmes, R. T. 2003. Climate and food synchronize regional forest bird abundances. – *Ecology* 84: 3024–3032.
- Kendeigh, S. C. 1952. Parental care and its evolution in birds. – *Illinois Biol. Monogr.* 22: 1–358.
- Kleindorfer, S., Fessl, B. and Hoi, H. 1995. More is not always better – male incubation in two *Acrocephalus* warblers. – *Behaviour* 132: 607–625.
- Krementz, D. G., Nichols, J. D. and Hines, J. E. 1989. Postfledgling survival of European starlings. – *Ecology* 70: 646–655.
- Lack, D. 1968. *Ecological adaptations for breeding in birds* – Methuen and Co. Ltd.

- Lifjeld, J. T. and Slagsvold, T. 1988. Effect of energy costs on the optimal diet: an experiment with pied flycatchers *Ficedula hypoleuca* feeding nestlings. – *Ornis Scand.* 19: 111–118.
- Lislevand, T., Byrkjedal, I., Gronstol, G. B., Hafsmo, J. E., Kallestad, G. R. and Larsen, V. A. 2004. Incubation behaviour in northern lapwings: nocturnal nest attentiveness and possible importance of individual breeding quality. – *Ethology* 110: 177–192.
- Markman, S., Yomtov, Y. and Wright, J. 1995. Male parental care in the orange-tufted sunbird – behavioral adjustments in provisioning and nest guarding effort. – *Anim. Behav.* 50: 655–669.
- Martin, T. E., Scott, J. and Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. – *Proc. R. Soc. Lond. B* 267: 2287–2293.
- Moller, A. P. and Thornhill, R. 1998. Male parental care, differential parental investment by females and sexual selection. – *Anim. Behav.* 55: 1507–1515.
- Monros, J. S., Belda, E. J. and Barba, E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. – *Oikos* 99: 481–488.
- Moreno, J., Morales, J., Lobato, E., Merino, S., Tomas, G. and la Puente, J. M. D. 2006. More colourful eggs induce a higher relative paternal investment in the pied flycatcher *Ficedula hypoleuca*: a cross-fostering experiment. – *J. Avian Biol.* 37: 555–560.
- Mullin, S. J. and Cooper, R. J. 1998. The foraging ecology of the gray rat snake *Elaphe obsoleta spiloides* – visual stimuli facilitate location of aboreal prey. – *Am. Midl. Nat.* 140: 397–401.
- Naef-Daenzer, B. and Keller, L. F. 1999. The foraging performance of great and blue tits *Parus major* and *P. caeruleus* in relation to caterpillar development, and its consequences for nestling growth and fledgling weight. – *J. Anim. Ecol.* 68: 708–718.
- Nagy, L. R. and Holmes, R. T. 2005a. Food limits annual fecundity of a migratory songbird: an experimental study. – *Ecology* 86: 675–681.
- Nagy, L. R. and Holmes, R. T. 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.
- Omland, K. E. and Sherry, T. W. 1994. Parental care at nests of two age classes of male American redstart: implications for female mate choice. – *Condor* 96: 606–613.
- Robinson, S. K. and Holmes, R. T. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. – *Ecology* 63: 1918–1931.
- Rodenhouse, N. L. 1986. Food limitation for forest passerines: effects of natural and experimental food reductions. – Dartmouth College, Hanover, New Hampshire, USA.
- Rytönen, S., Orell, M., Koivula, K. and Soppela, M. 1995. Correlation between 2 components of parental investment – nest defense intensity and nestling provisioning effort of willow tits. – *Oecologia* 104: 386–393.
- Sætre, G.-P., Fossnes, T. and Slagsvold, T. 1995. Food provisioning in the pied flycatcher: do females gain direct benefits from choosing bright-coloured males? – *J. Anim. Ecol.* 64: 21–30.
- Sample, B. E., Cooper, R. J., Greer, R. D. and Whitmore, R. C. 1993. Estimation of insect biomass by length and width. – *Am. Midl. Nat.* 129: 234–240.
- Schaefer, R. R., Conner, R. N., Rudolph, D. C. and Saenz, D. 2004. Red-cockaded woodpecker nestling provisioning and reproduction in two different pine habitats. – *Wilson Bull.* 116: 31–40.
- Sejberg, D., Bensch, S. and Hasselquist, D. 2000. Nestling provisioning in polygynous great reed warblers *Acrocephalus arundinaceus*: do males bring larger prey to compensate for fewer nest visits? – *Behav. Ecol. Sociobiol.* 47: 213–219.
- Silver, R., Andrews, H. and Ball, G. F. 1985. Parental care in an ecological perspective – a quantitative-analysis of avian sub-families. – *Am. Zool.* 25: 823–840.
- Simons, L. S. and Martin, T. E. 1990. Food limitation of avian reproduction: an experiment with the cactus wren. – *Ecology* 71: 869–876.
- Stodola, K. W., Linder, E. T., Buehler, D. A., Franzreb, K. E. and Cooper, R. J. 2009. Parental care in the multi-brooded black-throated blue warbler. – *Condor* 111: 497–502.
- Tremblay, I., Thomas, D., Blondel, J., Perret, P. and Lambrechts, M. M. 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican blue tits *Parus caeruleus*. – *Ibis* 147: 17–24.
- Trivers, R. L. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed.), *Sexual selection and the descent of man*. Aldine, pp. 136–179.
- Winkler, D. W. 1987. A general model for parental care. – *Am. Nat.* 130: 526–543.
- Wittenberger, J. F. 1982. Factors affecting how male and female bobolinks apportion parental investments. – *Condor* 84: 22–39.
- Wright, J. and Cuthill, I. 1989. Manipulation of sex-differences in parental care. – *Behav. Ecol. – Sociobiol.* 25: 171–181.
- Wright, J., Both, C., Cotton, P. A. and Bryant, D. 1998. Quality vs quantity: energetic and nutritional trade-offs in parental strategies. – *J. Anim. Ecol.* 67: 620–634.

Appendix A. Average nestling mass per brood (g) on day 6 of the nestling cycle, and parental provisioning rate (visits per hour per nestling) on day 7 of the nestling cycle for black-throated blue warblers for each year, site, and number of nestlings in a brood, along with 95% confidence intervals.

	n	Female provisioning		Male provisioning	
		Mean	Confidence interval	Mean	Confidence interval
Year 2003	23	2.44	1.91–2.97	2.06	1.66–2.46
Year 2004	27	1.95	1.45–2.44	1.41	1.05–1.76
Year 2005	24	3.16	2.40–3.93	1.67	1.20–2.13
Year 2006	36	2.10	1.75–2.44	1.90	1.59–2.20
Year 2007	36	2.76	2.22–3.31	2.23	1.83–2.62
Year 2008	36	3.15	2.46–3.84	1.92	1.57–2.28
Site LOW	38	2.07	1.62–2.53	1.86	1.50–2.21
Site MID	49	2.92	2.55–3.29	1.99	1.70–2.28
Site HIGH	95	2.65	2.28–3.01	1.84	1.63–2.06
Nestling 1	7	6.70	3.90–9.50	0.55	0.00–1.71
Nestling 2	19	3.23	2.40–4.06	1.80	1.27–2.33
Nestling 3	50	2.61	2.22–3.00	2.00	1.69–2.30
Nestling 4	105	2.22	2.02–2.43	1.95	1.77–2.13
Nestling 5	1	0.78	.	0.68	.

Appendix B. Average estimated biomass brought (mg) per hour per nestling on day 7 of the nestling cycle for black-throated blue warblers for each year, site, and number of nestlings, along with 95% confidence intervals.

	n	Female biomass		Male biomass	
		Mean	Confidence interval	Mean	Confidence interval
Year 2003	23	0.63	0.51–0.74	1.09	0.78–1.40
Year 2004	27	1.07	0.78–1.35	1.26	0.90–1.62
Year 2005	24	0.85	0.61–1.09	0.80	0.34–1.26
Year 2006	34	0.67	0.57–0.77	0.99	0.81–1.17
Year 2007	35	0.49	0.32–0.66	0.69	0.54–0.84
Year 2008	35	0.40	0.32–0.49	0.48	0.35–0.60
Site LOW	38	0.66	0.47–0.84	0.88	0.66–1.09
Site MID	46	0.68	0.54–0.82	0.79	0.62–0.96
Site HIGH	94	0.65	0.56–0.75	0.89	0.72–1.05
Nestling 1	7	1.39	0.62–2.16	0.21	0.00–0.55
Nestling 2	18	0.79	0.54–1.04	1.47	0.77–2.17
Nestling 3	50	0.75	0.59–0.90	1.01	0.82–1.20
Nestling 4	102	0.55	0.47–0.62	0.71	0.62–0.80
Nestling 5	1	0.62	.	1.96	.