Do Digestive Contents Confound Body Mass as a Measure of Relative Condition in Nestling Songbirds?

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ABSTRACT Relative nestling condition, typically measured as nestling mass or as an index including nestling mass, is commonly purported to correlate with fledgling songbird survival. However, most studies directly investigating fledgling survival have found no such relationship. We weighed feces and stomach contents of nestling golden-winged warblers (*Vermivora chrysoptera*) to investigate the potential contribution of variation in digestive contents to differences in nestling mass. We estimated that the mass of a seventh-day (near fledging) nestling golden-winged warbler varies by 0.65 g (approx. 9% of mean nestling mass) depending on the contents of the nestling's digestive system at the time of weighing, and that digestive contents are dissimilar among nestlings at any moment the brood is removed from the nest for weighing. Our conservative estimate of within-individual variation in digestive contents equals 72% and 24% of the mean within-brood and population-wide range in nestling mass, respectively. Based on our results, a substantive but typically unknown amount of the variation in body mass among nestlings is confounded by differences in digestive contents. We conclude that short-term variation in digestive contents likely precludes the use of body mass, and therefore any mass-dependent index, as a measure of relative nestling condition or as a predictor of survival in golden-winged warblers and likely in many other songbirds of similar size. © 2014 The Wildlife Society.

KEY WORDS digestive contents, feces, fledgling survival, golden-winged warbler, nestling mass, stomach contents, *Vermivora chrysoptera*.

Nestling mass and numerous indices combining mass and linear body measurements are commonly purported to be indicators of relative nestling condition and thus predictors of fledgling songbird survival (Suedkamp Wells et al. 2007, Schwagmeyer and Mock 2008, Chalfoun and Schmidt 2012). Although some studies report such relationships (e.g., Perrins 1965, Magrath 1991, Monros et al. 2002, Mitchell et al. 2011), most recent studies directly monitoring individual fledgling survival found no correlation between nestling mass and fledgling survival (e.g., Anders et al. 1997,

Berkeley et al. 2007, Hovick et al. 2011, Jackson et al. 2011, McKim-Louder 2011, Vitz and Rodewald 2011). Possible explanations for failures to observe the presumed relationship between nestling condition and fledgling survival include age-related effects unaccounted for when birds are measured at different ages (Jackson et al. 2011); stabilizing selection from predation on lighter and heavier fledglings, which favors intermediate fledgling mass (Adriaensen et al. 1998); violation of one or more assumptions inherent to mass–length residual indices (Green 2001); or failure to employ appropriate body-condition indices (Peig and Green 2010). A basic but previously unquestioned assumption inherent in all such indices is that mass—the proverbial common denominator and literal common numerator in most body condition indices—is related in some way to nestling condition. However, it is possible that frequent ingestion of large prey mass (relative to body mass) and defecation of

large fecal sacs causes short-term variation in nestling mass that obfuscates meaningful differences in the mass of muscle or fat stores (Streby and Andersen 2013a). For some relatively large animals, digestive contents might be a negligible proportion of body weight, but this may not be the case in small songbirds.

Nestling songbirds grow quickly and are typically fed at short time intervals. Adult Nashville warblers (*Oreothlypis ruficapilla*) bring food to the nest 5–10 times/hour and more often during morning and evening hours (Knapton 1984). Adult ovenbirds (*Seiurus aurocapilla*) bring food up to 67 times/fledgling/day (Vander Haegen and DeGraaf 2002). Because nestlings within a brood are typically on staggered feeding and defecating schedules (i.e., adults do not feed all nestlings in one visit, and typically remove only one fecal sac per visit; Whittingham et al. 2003, Guigueno and Sealy 2012), the contents of each nestling's digestive system are likely not similar at any moment. These differences in digestive contents could confound measures of nestling mass intended to represent relative nestling condition.

As part of a larger demographic study, we monitored survival of golden-winged warbler (*Vermivora chrysoptera*) nestlings and fledglings. During handling of nestlings and recovery of dead nestlings and fledglings, we collected and weighed feces and stomach samples. Here, we assess the potential influence of variation in nestling mass related to stomach contents and feces evacuation on the utility of body mass as an index of nestling condition. Specifically, we first video-monitored nestling feeding and defecation rates to confirm that nestling digestive contents differed at any given time, and then we used the ranges of mass in stomach contents and fecal sacs to estimate the extent to which differences in digestive contents might confound among-nestling comparisons in body mass.

STUDY AREA AND SPECIES

We studied golden-winged warblers during May–July 2011 and 2012 at Rice Lake National Wildlife Refuge (NWR) and Tamarac NWR in northern Minnesota, USA, and at Sandilands Provincial Forest in southeastern Manitoba, Canada. Golden-winged warblers are a species of conservation concern in the United States and they are listed as Threatened under the Species at Risk Act in Canada. Although numbers are declining moderately-to-dramatically throughout most of this species' breeding range, golden-winged warbler abundance is relatively stable in Minnesota and Manitoba (Buehler et al. 2007).

METHODS

Because it was important to confirm that nestlings within each brood differed in digestive contents at any moment, as suggested by reports of feeding and defecation rates in other species (Knapton 1984, Neudorf and Pitcher 1997, Lang et al. 2002, Guigueno and Sealy 2012), we video-monitored 5 golden-winged warbler nests, each containing 4 nestlings ≤4 days prior to fledging. We recorded 40 hours of food delivery and fecal sac removal between dawn and noon, the

period of interest during which we planned to handle, weigh, and band nestlings.

Nestling golden-winged warblers typically fledge on Day 8–10 (and rarely on Day 7 or 11), with hatching as Day 1. On the morning (0600–1200 hr) of Day 7, we removed all nestlings and carried them in a soft cloth bag to a banding location 10–20 m from the nest. To avoid age-related differences in nestling mass, we included in our analyses only broods for which exact hatching day was identified during nest monitoring. We weighed each nestling to ±0.01 g using a digital scale (Fig. 1). We banded all nestlings with U.S. Geological Survey aluminum leg bands and attached 0.40-g radiotransmitters (Blackburn Transmitters, Nacogdoches, TX) to 1–5 (usually 2) randomly selected nestlings per brood using a figure-eight harness design modified from Rappole and Tipton (1991) with elastic leg loops to allow for ease of fitting and growth. We placed each brood back in its nest <15 minutes after removal.

We collected fecal samples (*n* = 89) from nestlings that defecated during our weighing, banding, and transmitter-fitting activities. Of those samples, 51 were from known individuals (i.e., we directly observed a nestling defecating) and 38 were found in holding bags that had contained >1 nestling from a brood. Some nestlings that defecated during handling likely did so prematurely in response to stress, resulting in the collection of many (approx. 25% of total) atypically small samples that were not encased in fecal sacs. Rather than exclude these samples, we included them to ensure that our estimate of mean fecal mass was conservative.

After returning broods to their nests, we monitored each nest until it failed or succeeded. We monitored the fate of each radiomarked nestling/fledgling using standard radio-telemetry techniques (Streby and Andersen 2013b). We collected stomach samples from radiomarked nestlings and fledglings that died either due to predation that left stomachs intact (*n* = 28) or apparent exposure (*n* = 5) 8–12 days after hatching. Nestlings fledged 7–11 days after hatching and
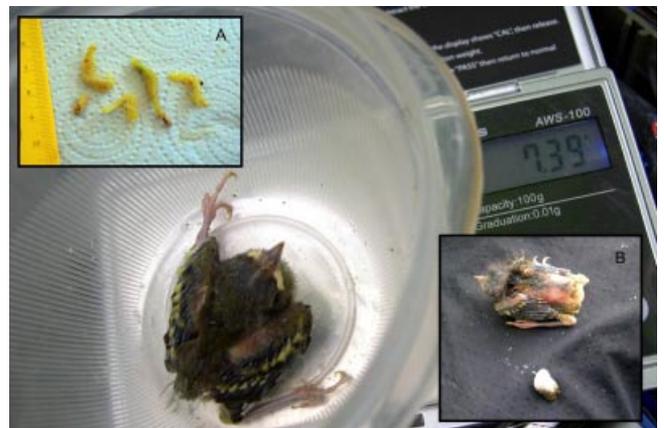
Figure 1. A seventh-day nestling golden-winged warbler in June, 2012 at Tamarac National Wildlife Refuge, Minnesota, USA. The nestling weighed 7.39 g, including an unknown quantity of recently consumed food (e.g., A; 5 leafroller caterpillars) weighing 0.00–1.90 g and an unknown quantity of feces (e.g., B) weighing 0.00–0.59 g.

there was no apparent change in diet composition or stomach-sample mass associated with fledging. We determined time and cause of mortality during radiotracking. For example, a bird found buried in a chipmunk burrow was assumed depredated by an eastern chipmunk (*Tamias striatus*) within the 24 hours since the last time we tracked it. Importantly, none of the birds that died from exposure during cold and wet nights had an empty stomach, so our sample was not biased downward by empty stomachs from starved birds. The empty stomachs we recovered were from birds that were cached by predators after we observed the bird alive within the past 24 hours, and we assumed those stomachs were empty because of normal variation in digestive contents.

We use the term stomach to refer to the cardiac stomach, or gizzard. The esophagus, proventriculus, and small intestine are small in insectivorous passerines, especially in juveniles, and the crop is so small it is often not included in descriptions of passerine digestive tracts (Ricklefs 1996). The contents of juvenile golden-winged warbler digestive tracts outside the stomach were negligible (0.00–0.05 g) for the first 5 birds we sampled, so we did not sample them from other birds. In 2011, we removed stomachs in the field, stored them in 70% ethanol solution, and examined the contents of each stomach in the laboratory after the field season. We identified invertebrate prey items to Family or Genus for each stomach sample. We counted and weighed non-animal items in each stomach, but did not identify seeds taxonomically or stones by geological origin. Because we stored those stomachs in solution, we could not measure their natural wet mass. In 2012, we extracted, identified, and weighed stomach contents from dead nestlings and fledglings in the field. We determined the mean unit mass of each item type from 2012, counted each item from 2011, and extrapolated estimates of 2011 stomach sample masses.

Analysis
We report mean food delivery and fecal sac removal rates as events per hour ± 1 standard deviation (SD), and then used these rates to estimate how often each nestling was fed and defecated. For example, if 4 fecal sacs were removed per hour from a nest with 4 nestlings, we assumed each nestling defecated once per hour. We report masses of nestlings and fecal samples as mean ± SD. The distribution of stomach content samples was skewed by a few relatively heavy samples, resulting in SD larger than the mean, so we report stomach content mass as median and interquartile (first and third quartiles) range. We report within-brood range and population-wide range in nestling mass including and excluding runt nestlings. We considered a bird with a mass <80% of the next smallest broodmate to be runt; we identified 7 (2%) of 305 nestlings as runts. We report results with and without runts because ranges in nestling mass differed considerably depending on the inclusion of the small number of runts. We calculated a conservative estimate of the within-individual variation in digestive contents by subtracting the values of a relatively empty digestive system (i.e., first quartile of stomach sample mass and no feces

immediately after defecating) from the values of a relatively full digestive system (i.e., third quartile of stomach sample mass and 1 SD above the mean fecal mass). We calculated the maximum possible within-individual range in nestling mass as the difference between an entirely empty digestive system (0 g) and the sum of the largest observed stomach sample and fecal sac mass. We handled, banded, and attached transmitters to birds following University of Minnesota Institutional Animal Care and Use Committee protocol no. 1004A80575.

RESULTS

From the 5 video-monitored nests, we observed that adults removed 4 (±1.9) fecal sacs/hour and delivered food (nearly always leafroller caterpillars [*Archips* sp.]; hereafter, leafrollers) 10 (±4.1) times/hour between dawn and noon. Assuming one nestling was fed during each visit, we estimated that each nestling was fed 2.5 times/hour (or every 24 min) and defecated once per hour. Fecal sac removal rates indicated that at any moment we chose to extract the brood for weighing, at least one nestling had defecated <15 minutes earlier and at least one nestling had not defecated for >45 minutes. These estimates were supported by our collection of 89 fecal samples while handling 72 broods (i.e., usually only 1 and sometimes 2 nestlings from each brood defecated during handling). Similarly, based on food delivery rates, we estimated that ≥1 bird had been fed in the 5 minutes prior to extraction from the nest and ≥1 bird had not been fed for >15 minutes prior to extraction. Our estimates were consistent with feeding rates (Knapton 1984, Neudorf and Pitcher 1997) and fecal sac removal rates (Lang et al. 2002, Guigueno and Sealy 2012) reported for other songbirds, and demonstrated that digestive contents differed among broodmates when we extracted each brood for weighing.

Seventh-day nestling golden-winged warblers ($n = 305$) from 72 broods weighed 7.36 (±0.64) g. Fecal samples ($n = 89$) ranged from 0.14 g to 0.59 g ($\bar{x} = 0.27 ± 0.10$) and stomachs samples ($n = 33$) weighed 0.00–1.90 g (median = 0.23, interquartile range = 0.28). Leafrollers constituted 89% of the mass in nestling and young fledgling stomachs; other food items included small land snail shells (Discidae; 5%), ants (Formicidae; 3%), and seeds (1%). We also found several small stones in each of 5 stomachs, constituting approximately 2% of the total sample mass.

A nestling golden-winged warbler with a relatively full stomach of 0.39 g (third quartile of stomach-sample mass) and not having defecated recently (1 SD above mean fecal mass = 0.37 g) would weigh 0.65 g (approx. 9% of mean nestling mass) more than the same nestling immediately after defecating (i.e., containing 0 g of feces) and with a relatively empty stomach of 0.11 g (first quartile of stomach-sample mass). The mean within-brood range ($n = 72$ broods) in nestling mass was 0.90 (±0.44) g including runts, and 0.80 (±0.33) g excluding runts. Therefore, our conservatively estimated range in digestive system contents was equal to 72% of total within-brood range in nestling mass, and 81% of the range excluding the few runts. Population-wide nestling

mass ranged from 5.12 g to 8.77 g (range = 3.65 g), and from 6.07 g to 8.77 g (range = 2.70 g) when runts were excluded (n = 298). Therefore, our conservatively estimated range in the mass of digestive contents was equal to 18–24% of the population-wide range in nestling mass depending on inclusion of runts. For a less conservative measure, the heaviest fecal sac and stomach sample together weighed 2.58 g. If digestive contents within an individual nestling varied from 0 g to 2.58 g, that variation would equal approximately 3 times the mean within-brood range with or without runts, and 71% (including runts) and 96% (excluding runts) of the population-wide range in nestling mass. This does not suggest that up to 96% of the range in nestling mass is attributable to differences in digestive contents. Rather, it suggests that much of the observed range in nestling mass is confounded by unknown differences in digestive contents.

DISCUSSION

The common use of nestling mass as an indicator of relative condition inherently assumes that heavier nestlings are heavier because they are developmentally superior in some way (i.e., more muscle and/or more fat stores) that will help them avoid predation, the primary source of mortality in fledgling songbirds, or survive exposure to weather after thermoregulatory independence from the nestling brood (Peig and Green 2010). We found that roughly a quarter of the range in nestling mass in golden-winged warblers, and most of the within-brood range, can be confounded by relative contents of nestling digestive systems. Our results demonstrate that mass is not a reliable measure of relative nestling condition because an unknown but substantive proportion of each nestling's mass is food and feces that varies considerably depending on timing. Consequently, attempts to correlate such unreliable measures of body mass or indices including mass to other parameters, such as survival, are equally unreliable. Indeed, despite some highly cited empirical support for its existence (e.g., Perrins 1965, Magrath 1991, Monros et al. 2002), a positive relationship between nestling mass and fledgling survival in songbirds typically is not observed when fledgling survival is directly monitored in small birds like our study species (Moreno et al. 2005, Ausprey and Rodewald 2011, Jackson et al. 2011, Hovick et al. 2011, McKim-Louder 2011; but see Vitz and Rodewald 2011) or in birds of greater mass (Anders et al. 1997, Brown and Roth 2004, Schmidt et al. 2008, Balogh et al. 2011, Richmond 2011).

Many authors attempt to explain why they found no relationship between nestling mass and fledgling survival (Anders et al. 1997, Brown and Roth 2004, Balogh et al. 2011, Jackson et al. 2011). However, we are unaware of a case in which alternative explanations are discussed when such a relationship is observed, despite the existence of plausible alternatives. For example, relationships between nestling mass and subsequent survival are potentially confounded by sexual size dimorphism and sex-specific survival rates or dispersal patterns. A strong positive relationship between nestling mass and first-year survival

has been reported for great tits (*Parus major*; Monros et al. 2002) and for savannah sparrows (*Passerculus sandwichensis*; Mitchell et al. 2011). However, males of both species are larger than females (Rising 1987, Oddie 2000) and female great tits disperse farther than males (Verhulst et al. 1997), suggesting that larger (i.e., male) nestlings are more likely to be subsequently encountered as adults in a repeatedly sampled breeding population. Although female savannah sparrows apparently do not disperse farther than males, substantially more males are re-sighted in subsequent years after being marked as juveniles (Fajardo et al. 2009), likely resulting in a similar effect.

A relationship between nestling mass and fledgling survival can also be confounded by weighing nestlings at different ages. Naef-Daezner et al. (2001) found mass at time of fledging was associated with survival of great tits, but not coal tits (*Periparus ater*), and Vitz and Rodewald (2011) found a similar relationship in ovenbirds. In addition to the sexual size dimorphism issue in great tits described above, it is unclear when Naef-Daezner et al. (2001) weighed birds, but they imply that they weighed them at the time of banding and transmitter attachment, which varied among broods from 3 days before fledging to 1 day after fledging. Vitz and Rodewald (2011) also weighed some birds as nestlings and some shortly after they fledged. The strongest predictor of juvenile songbird survival is usually age, with mortality being highest in the first hours and days outside the nest (Ricklefs 1968, Anders et al. 1997, Powell et al. 2000, Berkeley et al. 2007, Streby and Andersen 2011), as was the case in Naef-Daezner et al. (2001) and Vitz and Rodewald (2011). Therefore, heavier (i.e., older) birds may have already survived some portion of the highest mortality period, possibly contributing to the observed relationship between mass and survival. None of this is to say the conclusions of these studies are incorrect; it is only to say there are additional factors potentially explaining their results.

Future studies investigating condition-survival relationships in juvenile songbirds might benefit from considering other indicators of nestling condition, which could be species-specific. It is possible that measures such as immune function (Moreno et al. 2005) and baseline corticosterone (Rivers et al. 2012) are more reliable than body mass as indicators of nestling condition. Perhaps particular linear body measurements or rates of feather development will work with some species. Or perhaps studies directly monitoring fledgling songbirds will continue to find that survival is more strongly affected by nest location and post-fledging habitat use than by their body condition as nestlings (Berkeley et al. 2007; Jackson et al. 2011, 2013; Streby and Andersen 2011, 2013a).

IMPLICATIONS

Although there may be some relationship between relative nestling condition and fledgling survival, we conclude that mass and mass-dependent body condition indices are unreliable measures of relative nestling condition in golden-winged warblers and likely in many other songbirds. However, the most important implication from this study

might be that any measure of nestling condition used to predict fledgling survival will likely not be as informative to management and conservation planning as directly monitoring fledgling songbirds and identifying the extrinsic factors to which most fledgling mortality can be attributed.

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