

5-2016

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## Recommended Citation

Perlut, Noah G. and Strong, Allan M., "Comparative Analysis Of Factors Associated With First-Year Survival In Two Species Of Migratory Songbirds" (2016). *Environmental Studies Faculty Publications*. 30.

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## Comparative analysis of factors associated with first-year survival in two species of migratory songbirds

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A complete understanding of the annual life cycle remains a mystery for most migratory species (Faaborg et al. 2010). In particular, gaps in understanding survival is especially evident for the most tenuous part of the life-cycle – the first year (Faaborg et al. 2010). The transitional period between fledging and independence from parents is associated with high mortality rates (Cox et al. 2014, Martin 2015); therefore, population models using estimates of birth rates based on the number of young fledged likely overestimates the recruitment pool (Streby and Anderson 2011, Streby et al. 2014a, 2014b). Consequently better estimates of first-year survival are critical in modeling populations and understanding environmental, temporal, and spatial variation in demographic rates (Ringsby et al. 1999, Adams et al. 2006).

For migratory species, first-year survival rates are difficult to assess due to high rates of mortality in the first few weeks of the post-fledging period (Adams et al. 2006, Hovick et al. 2011) and the inability to distinguish between emigration and death due to low philopatry (Cooper et al. 2008). Detection probability of natal dispersers is at least partially influenced by a species' migration strategy. For resident songbird species, young banded as nestlings show greater philopatry (median: 6.3%; range 0–39.7%) to study areas than nestlings of migratory species (median: 2.6%; range 0–13.5%; Weatherhead and Forbes 1994). Weatherhead and Forbes (1994) identified only 35 datasets that described return rates in migratory songbirds; Maness and Anderson's (2013) literature review of studies that investigated factors influencing first-year survival included studies of only 22 passerine species that spanned  $\geq 1$  yr in duration. Given the lack of field data, some researchers have incorporated a combination of integrated field and published data to estimate first-year survival (Ekman and Askenmo 1986). For example, Reilly and Reilly (2009) combined field estimates of adult survival rates with published survival rates for juveniles on the nonbreeding quarters and estimates of the costs of migration to calculate a first-year survival estimate. However, this type of creative approach is rare, largely due to the lack of precise survival estimates during any period of the life-cycle.

Here we used a long-term dataset (2002–2012) to assess the factors that are associated with first-year apparent survival for two migratory grassland songbird species breeding in the same agricultural habitats, the bobolink *Dolichonyx oryzivorus* and the Savannah sparrow *Passerculus sandwichensis*. These species use similar breeding sites (Perkins et al. 2013) and food resources (Strong unpubl.). However, they differ with respect to migratory behavior, which affects reproductive effort and timing of fledging (Perlut et al. 2006). Bobolinks spend the non-breeding period in southern South America, arrive on the breeding grounds in mid- to late May, and begin migration in early August (Renfrew et al. 2013). Because they are on the breeding grounds for such a short period, bobolinks are generally single brooded. Savannah sparrows spend the non-breeding period in the southern United States and Mexico,

arrive on the breeding grounds in late April, and can remain there through September (Wheelwright and Rising 2008). This comparatively short migration provides Savannah sparrows with enough time to attempt multiple broods in a season (up to six nesting attempts in our study system); therefore, fledging tends to be more asynchronous for Savannah sparrows than bobolinks.

Using 10 yr of mark–recapture data, we were able to assess associations among migratory strategy (species), ecological factors (variation in habitat quality [e.g. field treatment], fledge date), nest-based factors (nestling body mass, # of young fledged) and first-year apparent survival. Despite data suggesting that > 85% of the annual mortality occurs during the migratory period (Sillett and Holmes 2002) there has been little research into the consequences in variation in migration distance on survival rates. For example, variation in annual cycle bottlenecks in the red knot *Calidris canutus* suggested that subspecies with longer migration pathways showed greater temporal overlap in nutritional and energetic bottlenecks (Buehler and Piersma 2008), but empirical tests are lacking. Therefore, we first predicted that the Savannah sparrow, with the shorter migration distance, would show greater annual survival rates than the bobolink.

Our data were collected on two study sites that varied with respect to management regime: fields harvested early in the nesting season, and fields harvested after the nesting season was over (see below for description of management). As a result of variation in intensity of management, these fields differ in 1) the amount of food available to nestlings and juveniles (Zalik and Strong 2008), where greater intensity of management resulted in less food, and 2) the timing of fledging, where greater intensity of management caused birds to fledge later in nesting season (Perlut et al. 2006). Therefore, our second prediction was that field treatment would lead to greater apparent survival on less-intensively managed fields. Third, we predicted greater apparent survival rates in males than females. This prediction is based on studies that have found higher male post-fledgling survival (Green and Cockburn 2001) as well as sex-specific segregation on the wintering grounds, where males occupied higher quality habitat (Parrish and Sherry 1994, Marra 1999). Fourth, birds fledging earlier in the nesting season have been shown to have greater apparent survival than later fledging birds (Bryant 1988, Magrath 1991, Monros et al. 2002, Cleasby et al. 2010, Molina-Morales et al. 2012, McKim-Louder et al. 2013), as they have more time to prepare for migration or dispersal. Therefore, given the migratory life history strategy of both of our study species, we predicted that earlier fledging would be associated with greater apparent survival. Fifth, apparent survival can be negatively impacted by increasing brood size (Magrath 1991, Tarof et al. 2011), likely reflecting the costs of parental care. We predicted that an increasing number of young fledged within a given brood would be negatively associated with apparent survival. Finally, we predicted that earlier hatching date and larger nestling body mass would be positively associated with greater first-year survival rates (Bryant 1988, Brown and Brown 1996, Tarof et al. 2011, Tarwater et al. 2011, Molina-Morales et al. 2012, McKim-Louder et al. 2013). Although some studies have found that strong variation in nestling body mass is a result of variation in digestive tract contents (Streby et al. 2014a, 2014b), there is general support for this hypothesis (Maness and Anderson 2013). Here, we expect that heavier birds fledging earlier in the nesting season will have more time to develop foraging and predator avoidance skills and be better prepared physiologically for fall migration.

## Methods

### Field methods

#### Study site

Our research took place in two hayfields in Shelburne, Vermont, USA, located within the Champlain Valley (44.39°N, 73.27°W), which contains 146 000 ha of managed grasslands (NASS 2010). The majority of hayfield habitat in this region is harvested during the breeding season (Perlut et al. 2006). One field (hereafter 'late-hayed'; 17.7 ha) was harvested no earlier than two weeks after the last nest fledged (~ mid-August to mid-September). The vegetation in this field was primarily grass-dominated, including orchard grass *Dactylis glomerata*, timothy *Phleum pretense*, bluegrass *Poa* sp., reed canary grass *Phalaris arundinacea*, as well as vetch *Vicia* sp., sedges *Carex* spp. and bedstraw *Galium* sp. The second hayfield (hereafter 'early-hayed'; 18.5 ha) was first harvested between 15 May and 11 June. In 2002–2007 these fields were harvested a second time 34–52 d after the first cut; in 2008–2012, they were harvested no earlier than 65-d after the first harvest – a change that significantly increased nest productivity (Perlut et al. 2011). The dominant vegetation on these fields were alfalfa *Medicago sativa*, red clover *Trifolium pratense*, white clover *Trifolium repens*, dandelion *Taraxacum officinale*, orchard grass, and reed canary grass. These sites were intentionally located in proximity (1.5 km apart, separated by small forest fragments), increasing the probability of detecting natal dispersers.

#### Field sampling

We collected morphological, reproductive and recapture data for both species from early-May (range 7–15 May) until the last nest fledged or failed (late-July to mid-August) each year. We spent the first two weeks of each field season blanket-netting both study fields (20–30 12 m mist-nets, at least two days per field per year, between the hours of 04:30 and 13:00) attempting to capture each breeding bird, particularly first-year birds returning to the study site. Birds passively flew into nets, we walked through fields flushing birds into nets, and birds were caught responding to playbacks of conspecific song from recorders placed in front of mist-nets. Adults were banded with three colored and a single U.S. Geological Survey band and we measured their wing length, tarsus, bill length, and body mass (NGP took > 99% of all measurements). We located nests through behavioral observations and attempted to find every nest by every female on our study fields. Nests were visited every one to two days to assess their status until fledging or failure. Young were considered to have fledged if nestlings remained in the nest for at least nine days and parents were later seen provisioning young. Nestlings were banded with a single U.S. Geological Survey band, weighed, and blood samples were collected (20–60 µl); 86% of nestlings were weighed one time between days 5 and 7; because of the timing of when we found the nest, or to minimize disturbance at the nest, < 1% were sampled on days 3 and 10. We aged nestlings based on hatch date (if the nest was found during the egg stage, as nests were checked at least every two days) or feather growth (if the nest was found during the nestling stage). Blood was placed on Whatman filter paper and frozen at –80°C until analyzed.

Capture histories were built for each nestling with a combination of three data sources: banding records, nest association records and resight records. We maintained resight records throughout the

season, recording color banded birds as we searched for nests each day. In addition, in 2005–2012, we searched all fields for banded birds within 1.5 km of our study fields once during the breeding season. These off-site searches increased apparent survival estimates, especially for male Savannah sparrows (Perlut et al. 2008).

#### Molecular analysis of sex

We used molecular techniques to determine the sex of all nestlings included in this study. DNA was extracted from blood samples using a Qiagen DNeasy Kit and then underwent polymerase-chain-reaction (PCR) amplification of sex-specific DNA markers using primers described by Han et al. (2009). Gels were visualized and photographed under UV illumination and scored by eye. Males could be identified by single (Z-linked) bands whereas females were identified by double (Z- and W-linked) bands. Each gel included one adult male and female for comparison.

#### Survival analysis

We evaluated apparent survival for first-year birds ( $\phi_{1st}$ ) with Cormack–Jolly–Seber (CJS) models in Program MARK (White and Burnham 1999). These models were time dependent and detection probability was partitioned into two time periods (no off study field searches 2002–2004; yes off study field searches 2005–2012). In addition to species, sex and treatment, we tested the effect of number of young fledged from a brood, nestling mass relative to the other nestlings in the brood, and fledge date. Nestling mass was standardized around zero within a given nest. This ensured that species did not become an implicit component of this covariate. We included all three way additive and two-way interactive models (for all seven covariates).

#### Results

We banded 1624 nestlings, including 759 bobolinks (184 female, 575 male) and 865 Savannah sparrows (330 female, 535 male). Of the nestlings banded in 2002–2011, we recaptured 83 (12.5%) bobolinks and 62 (7.5%) Savannah sparrows in 2003–2012. The mean (SD) and median dispersal distance for bobolinks was 1287.2 m (1146.9) and 1037.1 m and 1426.2 m (400.7) and 1001.3 m for Savannah sparrows, respectively. Of the recaptured birds, 22% of bobolinks and 29% of Savannah sparrows returned to their natal field.

In explaining variation in apparent survival, the top ranked model, with  $\omega_i = 0.88$ , was the interaction between fledge date and body mass (see Supplementary material Appendix 1 for full model set). Species was a factor in the second ranked model (interaction between species and the number of young fledged), although this model explained little of the variation in the data ( $\omega_i = 0.04$ ;  $\Delta AIC_c = 5.98$ ). Therefore, values presented for  $\phi_{1st}$  are for both bobolinks and Savannah sparrows. Across the ten yearly estimates,  $\phi_{1st}$  averaged 0.412 (range 0.322–0.577; Fig. 1). The detection probability for first-year birds (in the top ranked model) was 0.10 in 2002–2005 and 0.31 in 2006–2012.

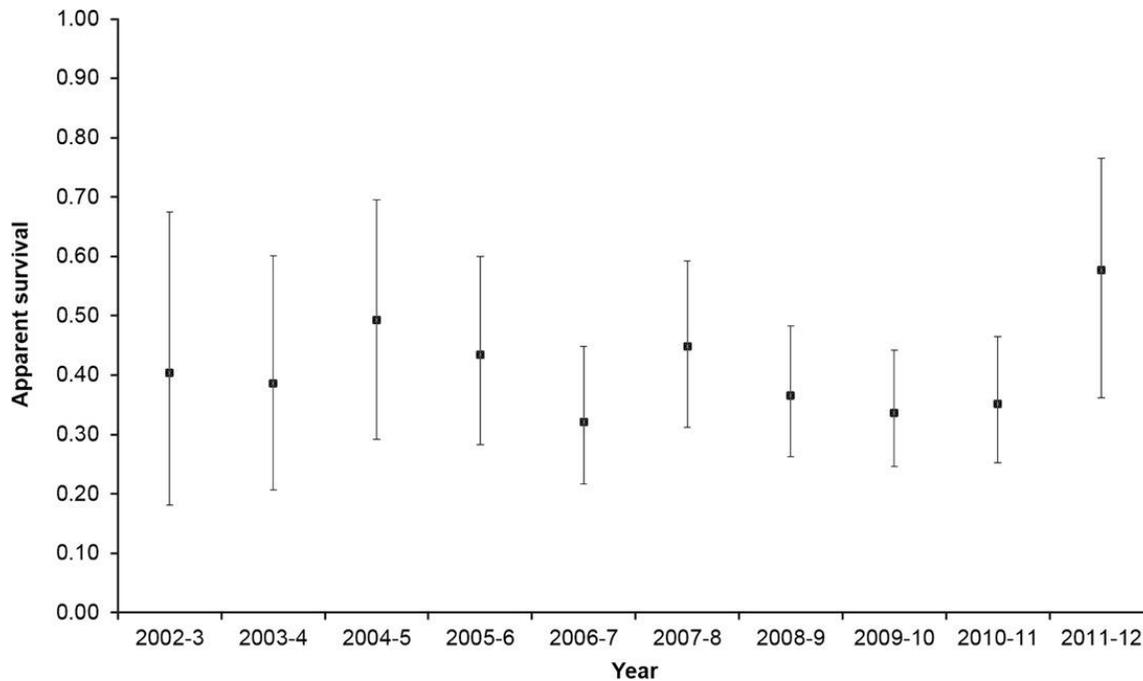


Figure 1

Apparent survival for 1st year bobolinks and Savannah sparrows breeding in the Champlain Valley of Vermont, USA, 2002–2012. Error bars indicate 95% confidence intervals. These values do not include the effects of covariates.

The seasonal distribution of fledging varied across years, although the majority of birds fledged in the first half of the season. Across all years, 32.9% of young fledged in the first three weeks, where  $\phi_{1st}$  varied from 0.215 to 0.532, while only 2.4% fledged in the final three weeks, where  $\phi_{1st}$  varied from 0.030 to 0.113. Compared to fledge date, the distribution of nestling mass was consistent across years. The standardized distribution of nestling mass ranged from  $-1.55$  to  $1.67$ . Birds whose body mass was average or greater than average within-brood showed declines in apparent survival with later fledge dates. Birds whose body mass was less than average within their brood showed increases in apparent survival with later fledging dates (Fig. 2); after week 3, birds with the lightest body masses showed the greatest apparent survival rates.

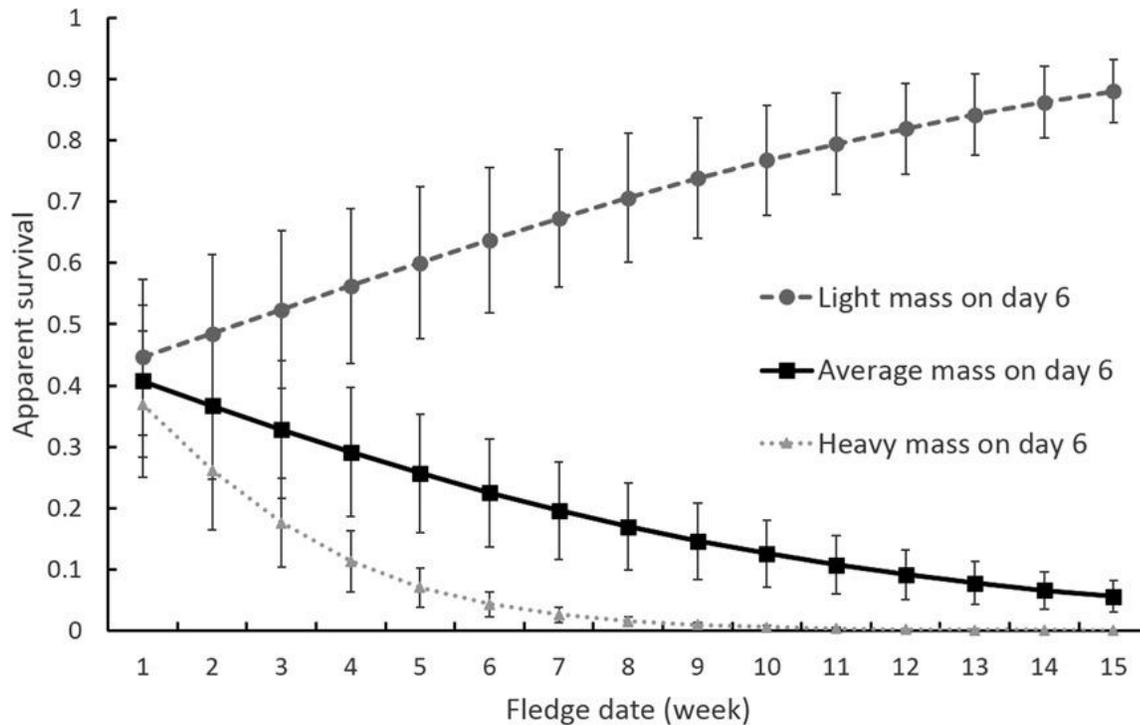


Figure 2  
 Apparent survival for 1st year bobolinks and Savannah sparrows breeding in the Champlain Valley of Vermont, USA, 2002–2012 was greater for nestlings that fledged earlier in the breeding season; the interaction effect between fledge date and mass showed differential effects on 1st year apparent survival based on nestling body mass.

### Discussion

While recent advances in inexpensive technologies like geolocators (Stutchbury et al. 2009) and stable isotopes (Chamberlain et al. 1996, Hobson and Wassenaar 1996) are beginning to fill knowledge gaps on avian migration timing and movement, some of the most basic demographic parameters, in particular, first-year survival, remain poorly understood. Although more studies of first-year survival are being published, there are still few studies that estimate this parameter over multiple years with a relatively full complement of individual covariates. In this study, first-year apparent survival of migratory bobolinks and Savannah sparrows was best explained by the interaction between date of fledging and body mass. Body mass at fledging has been assumed to be a strong predictor of survival, as greater fat reserves (presumably correlated with body mass) would provide a buffer for birds with limited experience in foraging independently (Lack 1966). This result has received support in the literature (Maness and Anderson 2013) although there are studies that have shown no relationship between body mass and survival (Styrsky et al. 2005, Gruebler and Naef-Daenzer 2008). Fledging earlier in the breeding season may allow offspring to forage during periods of resource abundance and provide more time to acquire fat reserves prior to migration. Again, this result has received relatively strong support (see Maness and Anderson 2013 for review). Monros et al. (2002) also found that date of fledging and nestling mass affected great tit *Parus major* first-year survival; however, the direction of the effect

changed in some years, where survival was sometimes greater for birds that fledged later rather than earlier, suggesting stabilizing selection. Tarof et al. (2011) found that fledge date and brood size both negatively affected first-year survival of purple martins *Progne subis*. However, in our study, the interaction effect between fledge date and mass showed differential effects on apparent survival based on nestling body mass: average or heavy nestlings had greater apparent survival when they fledged earlier in the summer, while for lighter nestlings, apparent survival increased in later fledging nests. For average and heavy nestlings, this result matched predictions suggesting that earlier fledged young have more time to prepare for migration and therefore have greater survival rates (Suedkamp et al. 2007, Vitz and Rodewald 2011, McKim-Louder et al. 2013). However, the pattern we documented for nestlings with lower body mass was unexpected, with these birds showing greater apparent survival overall (after week four) and apparent survival increasing with later fledging dates. Only 2% of all nestlings fledged within the last three weeks of the breeding season, thus although these birds show high rates of apparent survival, they are relatively rare in the population. Zalik and Strong (2008) found that on most of these study sites, insect biomass increased 100–500% between week 4 and week 11 of the breeding season, with prey biomass staying constant or declining through week 15. Yackel Adams et al. (2006) found a similar pattern in shortgrass prairies in Colorado. They suggested this pattern in prey availability led to greater survival rates for lark buntings *Calamospiza melanocorys* that fledged later in the breeding season. They also found a significant interaction between apparent survival and body mass during a year with drought conditions, but the response was opposite to our results (decreased survival of lighter birds). That increased prey biomass late in the nesting season would have differential effects on apparent survival across a body mass gradient is difficult to explain based on environmental factors.

An alternative explanation is that the result is a product of differential patterns of natal dispersal as a result of body mass and fledging date. Heavier birds that fledge earlier in the season have a longer window of opportunity to disperse and evaluate potential breeding sites; therefore, these birds may show greater natal dispersal distances and effectively remove themselves from our sample. Similarly, lighter birds may have to spend more time on self-maintenance and consequently have less time to disperse and evaluate potential future breeding habitat. As a result, these birds may show greater fidelity to their natal region (and be available for detection), as they are most familiar with its resources and potential breeding opportunities (Green and Cockburn 2001, Middleton and Green 2008). However, we found no relationship between dispersal distance and body mass ( $r^2 = 0.0075$ ) or fledging date ( $r^2 = 0.0033$ ). Thus, within our search radii, it is unlikely that these covariates influenced detection probability.

Our results showed no direct effect of brood size, although the fact that nestling mass was important for survival suggests that there are within brood effects on survival, perhaps via density dependence. However, we did not have data to test other potentially important factors related to parental care such as hatching order (although hatching is fairly synchronous) or nestling growth rate (Martin 2015). Our first-year survival models did not support sex as an important factor although including sex within a broader model set is known to provide greater detail in understanding how body size may affect survival (Maness and Anderson 2013). For example, Cleasby et al. (2010) found greater first-year survival in female house sparrows *Passer domesticus*. In our study population, for both species, male nestlings are

significantly heavier than female nestlings (Perlut et al. 2014), however our results showed limited support for an effect of sex on apparent survival.

We found no species-specific differences in first-year survival. Again, this did not match our predictions as we assumed that the greater migration distance of bobolinks would lead to greater mortality during the migratory period (Sillett and Holmes 2002). Mortality between initial departure from the nest and initiation of migration is significant (Cox et al. 2014) and thus body mass (or condition) may be a better indicator of an individual's ability to survive this period. However, Mitchell et al. (2011) showed that mass during the pre-migratory period can carry-over to affect survival to subsequent years. Because we did not follow fledglings after they left the nest, our next contact with these individuals was not until the subsequent breeding season(s). Thus, we cannot partition mortality factors more finely. Working with barn swallows *Hirundo rustica*, Gruebler et al. (2014) showed that differences between adult and first-year survival could be explained by a significant three week bottleneck during the post-fledging period; survival rates were similar for the two groups during the remainder of the annual cycle. Other studies have shown similar results for passerines, with the period of greatest mortality occurring immediately after fledging, but prior to becoming independent from adults (Anders et al. 1997, Yackel Adams et al. 2006, Vitz and Rodewald 2011). This pattern could explain similarities in first-year survival rates between Savannah sparrows and bobolinks. If mortality rates are greatest during the period immediately following fledging, survival during migration may be similar between the two species.

For Savannah sparrows, the factors associated with first-year survival were similar to those found for an isolated population on Kent Island, NB, Canada (~ 520 km east of our study sites), where first-year survival was negatively related to the timing of nesting and positively related to nestling mass (Mitchell et al. 2011). The fact that survival rates in our mainland population showed similar associations with these two covariates is surprising given that natal philopatry varies strongly with isolation of the population (Weatherhead and Forbes 1994). However, similar results between the two studies may be indicative of the strong generality of the results. Despite recapturing a relatively large sample of first-year birds, our detection probability was low (0.31). Thus, that our results showed similar patterns to other studies with an order of magnitude greater sample size are suggestive of a general ecological pattern. Given the advantages that may be accrued through greater statistical power in these isolated habitats, we encourage more researchers to take advantage of these study sites.

To our knowledge this is the first test of the effect of varying habitat quality on first-year survival. No effect of treatment in explaining variation in apparent survival is notable given our previous work showing strong variation for adult survival (Perlut et al. 2008). The lack of effect by treatment was potentially confounded by fledge date, as the mean fledge date on the early-hayed field was slightly later (fledge week  $7.02 \pm 3.11$  SD versus fledge week  $6.41 \pm 2.12$ ) than on the late-hayed field. However, the average difference (4 d) seems unlikely to lead to biologically meaningful effects on survival. Although Zalik and Strong (2008) found notable differences in food biomass between these sites, neither the average nestling mass or mass of the lightest nestling differed between sites, suggesting that adults found ways to compensate for biomass differences (likely by increasing time spent foraging). Likewise, previous work in this system found no effect of treatment in explaining natal dispersal distances (Fajardo et al. 2009, Cava pers. comm.).

Our results provide a long-term assessment of the covariates associated with first-year survival in two species of migratory birds. Although we did not find significant differences in first-year survival rates between the two species, this finding in and of itself was notable. This result suggests that the selection pressures associated with distance traveled during migration may not act along a continuum, but rather migration itself is the driver. Additional experimental work is necessary to elucidate the causal mechanisms behind this result.

#### Acknowledgements

This project was supported by the Univ. of New England, the Rubenstein School of Environment and Natural Resources, and the Initiative for Future Agricultural and Food Systems and the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service, grant numbers 2001-52103-11351 and 03-35101-13817, respectively and the U.S. Dept of Agriculture/National Inst. of Food and Agriculture Managed Ecosystems Program (award no. 2009-35304-05349). Additional funding was provided by the Natural Resource Conservation Service's Wildlife Habitat Management Inst. and the Galipeau family. We thank Shelburne Farms, the Galipeau, Ross, Maile and Stern families for generous access to their land. Thanks to each summer's army of research assistants for their excellent work.

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