IBIS The International Journal of Avian Science BOU
Ibis (2012), **154**, 325–337

Short- and long-term costs of reproduction in a migratory songbird

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Costs of reproduction represent a common life-history trade-off. Critical to understanding these costs in migratory species is the ability to track individuals across successive stages of the annual cycle. We assessed the effects of total number of offspring fledged and date of breeding completion on pre-migratory body condition, the schedule of moult and annual survival in a migratory songbird, the Savannah Sparrow *Passerculus sandwichensis*. Between 2008 and 2010, moult was delayed for individuals that finished breeding later in the breeding period and resulted in reduced lean tissue mass during the pre-migratory period, suggesting an indirect trade-off between the timing of breeding completion and condition just prior to migration. Lean tissue mass decreased as the number of offspring fledged increased in 2009, a particularly cool and wet year, illustrating a direct trade-off between reproductive effort and condition just prior to migration in years when weather is poor. However, using a 17-year dataset from the same population, we found that parents that fledged young late in the breeding period had the highest survival and that number of offspring fledged did not affect survival, suggesting that individuals do not experience long-term trade-offs between reproduction and survival. Taken together, our results suggest that adult Savannah Sparrows pay short-term costs of reproduction, but that longer-term costs are mitigated by individual quality, perhaps through individual variation in resource acquisition.

Keywords: carry-over effects, d-separation, fat mass, individual quality, lean mass, life-history stages, life-history trade-offs, migration, moult.

Reproductive costs occur when time or energy is invested in reproduction at the expense of growth, maintenance, storage or future reproduction (Williams 1966, Reznick *et al.* 2000, Ricklefs & Wikelski 2002) and result in one of the most prominent life-history trade-offs observed in nature (Stearns 1989, Jönsson & Tuomi 1994, Reznick *et al.* 2000). The annual cycle of migratory animals is organized into a series of unique life-history stages, each defined by distinct behaviours, physiological processes and energetic demands (Jacobs & Wingfield 2000, Wingfield 2008). Although reproductive costs are initiated during breeding, they may not be realized until a later life-history stage. Therefore, the ability to track individual success across life-history stages is critical to understanding life-history trade-offs in migratory animals (Norris & Marra 2007, Harrison *et al.* 2011).

In migratory birds, reproduction is typically followed by a pre-migratory period in which individuals accumulate lean tissue and fat for migration and complete an energetically demanding moult (Baggot 1975, Murphy & King 1992, Lindström & Piersma 1993, Rubolini *et al.* 2002, Bauchinger & Biebach 2006). However, reproduction can be costly in terms of both time and energy

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(reviewed by Martin 1987, see also Merilä & Wiggins 1997, Hemborg & Lundberg 1998, Hemborg 1999, Sanz 1999, Murphy 2000) and, as a result, reproductive effort and timing may carry over to influence body condition (e.g. the quantity of lean tissue and fat) and the timing of moult during the pre-migratory period. To date, understanding how breeding events influence condition and moult during the pre-migratory period has been challenging because individuals often disperse from their breeding site prior to migration and can be difficult to catch because they are no longer responsive to conspecific playbacks of songs (Cherry 1985, Wingfield & Monk 1992, Vega Rivera *et al.* 1998).

We addressed multiple hypotheses relating to the costs of reproduction in an island-breeding population of Savannah Sparrows *Passerculus sandwichensis* using two measures of body condition and body moult scores taken repeatedly throughout the autumn pre-migratory period from 2008 to 2010. We also used a 17-year dataset to examine the effect of number of offspring produced and timing of breeding completion on annual survival. First, we expected that individuals trade off the number of offspring produced with body condition during the breeding period (Nur 1984, Martin 1987, Merilä & Wiggins 1997, Sanz 1999, Murphy 2000) and predicted that condition carries forward into the pre-migratory period (Martin 1987), so that higher breeding effort results in poorer pre-migratory body condition. Secondly, as migratory preparations begin once breeding is complete (Hahn *et al.* 1992, Ricklefs & Wikelski 2002, Wingfield 2008), we expected that timing of breeding affects body condition (Heise & Moore 2003) and timing of moult (Siikamäki *et al.* 1994, Ogden & Stutchbury 1996, Siikamäki 1998, Hemborg 1999, Flinks *et al.* 2008), and predicted that body condition would be lower and moult would be delayed for late breeders relative to early breeders. Thirdly, we expected that the number of offspring produced and the timing of breeding completion affect annual survival (Nilsson & Svensson 1996, Wiggins *et al.* 1998, Hemborg 1999) due to the energetically demanding nature of migration (McWilliams *et al.* 2004, Weber 2009) and the reduction in favourable conditions for migration as the autumn season progresses (Alerstam *et al.* 2003, Newton 2006, 2007). We predicted that individuals that fledge a larger number of offspring and late breeders would be less likely to return the following year.

METHODS

Study site and species

Fieldwork was conducted on Kent Island, an isolated 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35′N, 66°45′W). The northern third of the island comprises spruce-fir forest (*Picea glauca*, *Picea rubens* and *Abies balsamea*) and the southern two-thirds are characterized by old-field habitat. We studied a population of migratory Savannah Sparrows inhabiting a 10-ha old-field located in the centre of the island. Savannah Sparrows are grassland songbirds that breed in the northern United States and across Canada and winter mainly in the southern United States (Wheelwright & Rising 2008). On Kent Island, median clutch size is four eggs (mean = 4.17, sd = 0.62, $n = 1667$ clutches; Wheelwright & Schultz 1994, Nathaniel T. Wheelwright, unpubl. data) and median adult body mass during the breeding period is 20 g for males and 19 g for females (males: mean = 20.19, sd = 1.32, $n = 1071$; females: mean = 19.03, sd = 1.85, $n = 1207$; Freeman-Gallant 1996, Nathaniel T. Wheelwright unpubl. data). Females provide more parental care at the nest than males (60–76% of feeding trips) but both sexes provide equal amounts of parental care to fledglings (Freeman-Gallant 1998, Wheelwright *et al.* 2003). Historically, 15–43% of males in a given year are polygynous (Wheelwright *et al.* 1992). Both sexes depart the island between mid-September and late October (Greg W. Mitchell & D. Ryan Norris unpubl. data).

Kent Island represents an ideal study site to investigate costs of reproduction in a migratory songbird for several reasons. First, a moderate number of nests are predated and replaced every breeding season (predation rate = 23%; Wheelwright & Rising 2008), resulting in natural variation in timing of breeding completion. Secondly, there is natural variation in clutch size, resulting in variation in breeding effort (Dixon 1978, Wheelwright & Schultz 1994). Thirdly, approximately 30% of females are double-brooded, creating additional variation in breeding effort and timing (Wheelwright *et al.* 1992, Wheelwright & Mauck 1998). Fourthly, the island's small size facilitates the capture of individuals prior to migration and results in high breeding philopatry (median distance between nests in successive years = 32 m; Wheelwright & Mauck 1998), which allows for a robust assessment of annual apparent survival.

Breeding data

Nests were found between 30 May and 25 July by observing adult females during the nest-building and incubation stages. Adults were captured on their breeding territories with mist-nets. At the time of capture, unflattened wing-chord and tarsus length (± 1 mm) were measured according to Pyle (1997) and mass (± 0.1 g) was measured using an electronic top-loading balance. Sex was assigned based on the presence or absence of a brood patch or cloacal protuberance and was later confirmed with observations of breeding behaviour (e.g. singing males, incubating females, copulation, mate-guarding). Nests were visited every 2 days until nestlings were 7 days old to monitor nest fate.

Timing of breeding completion was calculated as the fledging date of the last nest in a season plus 14 days, which is the average time to parental independence (Wheelwright & Templeton 2003). All individuals attempted to breed, but one individual in each year did not successfully fledge a nest. For these individuals, date of breeding completion represents the date at which their last nest was found predated. Total number of offspring fledged was taken as the sum of the number of offspring fledged for each nest for a given individual in a single year.

Pre-migratory data

Short-term costs of reproduction were assessed in 2008, 2009 and 2010 (7 August – 30 September in 2008, 1 September–10 October in 2009, and 18 August – 3 October in 2010). Adults were captured in and around their breeding territories by flushing individuals from within a randomly chosen 50 × 50-m quadrat (29 in total) bordered on three sides by mist-nets ($n = 30$ captures of 21 males, $n = 40$ captures of 25 females; Supporting Information Table S1). For females, only the primary social mate of males was included in analyses. Netting took place between 07:00 and 17:00 h, Atlantic Standard Time. Following capture, the same morphological measurements described above were repeated along with measurements of total body water and fat mass (described below). Moult progression was also assessed using the completeness of feather growth on the stomach and flanks and was scored as an ordinal variable (1 = ≤ 25%: feather sheaths and initial emergence of feathers, 2 = 25–49% of each feather grown in, 3 = 50–74% of each feather grown in, 4 = ≥ 75% of each feather grown in, up to the completion of moult). Feather growth on the stomach and flanks was measured because body feathers comprise 70% of a bird's total plumage mass and are therefore most likely to affect protein stores during moult (Newton 1966, Chilgren 1977, Murphy & King 1991, 1992) and because body feathers help birds maintain fat through insulating the body (Bonier *et al.* 2007). Body moult progression was linearly and positively correlated with the progression of primary feather moult ($\beta = 0.46$, $t_{65} = 12.7$, $P < 0.001$; Supporting Information Fig. S1).

Assessing condition

Condition during the breeding period was measured as the residual from a regression of mass on tarsus (for the path analysis this relation was: $\beta = 0.93$, $t_{44} = 3.9$, $P < 0.001$, $R^2 = 0.24$; for the annual survival analysis this relation was: $\beta = 0.70$, $t_{631} = 9.1$, $P < 0.001$, $R^2 = 0.12$; see below for details of statistical analyses). For both analyses, this relationship was linear (Supporting Information Fig. S2). Condition during the pre-migratory period was assessed using (1) total body water, a surrogate for lean tissue mass (muscle + organ mass), and (2) an index of fat mass. Total body water was measured using heavy water dilution (Karasov & Pinshow 1998, Speakman *et al.* 2001, Eichhorn & Visser 2008) following the methods of Rae *et al.* (2009). Fat mass was assessed using the residuals of the regression between body mass and total body water while controlling for tarsus length ($\beta = 0.73$, $t_{119} = 3.9$, $P < 0.001$, $R^2 = 0.51$).

In 2008, 2009 and 2010, all but six birds were fitted with radio-transmitters (0.62 g; Lotek, Newmarket, ON, Canada) as part of a larger study on migratory movements but these had no effect on total body water or the quantity of fat for adults in this population during the pre-migratory period (Rae *et al.* 2009).

Apparent annual survival

We measured apparent survival between breeding seasons for individuals following their first (individuals that were 1 year of age at breeding; *n* = 633, Table S1) and second breeding seasons (individuals that were 2 years of age at breeding; *n* = 177).

Hypotheses and predictions: breeding period

We tested the hypothesis that body condition during breeding affects the number of offspring produced and the timing of breeding completion because it is indicative of endogenous energy reserves (Tinbergen & Dietz 1994, Martin *et al.* 2006). We predicted that birds in better condition would fledge more offspring and have later dates of breeding completion relative to individuals in poorer condition through having larger clutches, producing a second brood, or being more likely to re-nest after having multiple failed nesting attempts. We also hypothesized that the number of offspring produced would be higher and timing of reproduction would be later for older individuals owing to improvement of reproductive performance between the first and second breeding seasons (Wheelwright & Schultz 1994). Age was classified as a two-level factor: 1 = adults that were 1 year of age and 2 = adults that were 2 years of age or older (*n* = 8). Two-way interactions between year and body condition were also assessed with respect to total number of offspring fledged and timing of breeding completion because temperature was lower and rainfall amounts were higher during the breeding period in 2009 relative to the other two years (average temperature: 2008 = 16.5 °C, 2009 = 14.7 °C, 2010 = 16.7 °C; average rainfall: 2008 = 81.7 mm, 2009 = 163.4 mm, 2010 = 131.5 mm; http://www.climate.weatheroffice.gc.ca). Interactions were fitted one at a time and only significant interactions were included in the final path model (Supporting Information Table S2).

Hypotheses and predictions: pre-migratory period

Hypotheses and predictions regarding costs of reproduction are outlined in the introduction. We also hypothesized that moult progression would affect an individual's total body water given increased protein demands for feather synthesis (Murphy & King 1991, 1992, Pérez-Tris *et al.* 2001, Bauchinger & Biebach 2006), as well as their fat stores because new feathers may improve insulation and reduce energy loss (Baggot 1975, Klaassen 1995, Pérez-Tris *et al.* 2001, Rubolini *et al.* 2002, Bonier *et al.* 2007). We predicted a negative relationship between moult progression and total body water and a positive relationship between feather growth and fat storage.

Additional covariates in our models of total body water and fat included age, sex, tarsus length, time of day captured, date captured and year. The last two covariates were also included in our model of moult progression. Detailed hypotheses and predictions related to each variable are given in the Supporting Information (Data S1). We assessed two-way interactions between sex with total offspring fledged and timing of breeding completion because costs of reproduction may be stronger in females than males, given higher provisioning rates of females during the nestling stage (Freeman-Gallant 1998). Similarly, we assessed the two-way interaction between sex and timing of breeding completion with respect to moult progression because males of other species often begin moulting while still provisioning young, whereas females do not (Hemborg 1999, Hemborg *et al.* 2001, Rubolini *et al.* 2002, Flinks *et al.* 2008). Last, we assessed two-way interactions between (1) year and total offspring fledged and (2) year and timing of breeding completion with respect to their association with total body water and fat mass, and the two-way interaction between year and timing of breeding completion with respect to its association with moult progression. Interactions were assessed one at a time and only significant interactions were included in the path model (Table S2).

Hypotheses and predictions: apparent annual survival

We tested the hypothesis that the total number of offspring fledged affects survival through its effect on pre-migratory body condition. We also tested the hypothesis that timing of breeding completion affects survival through its effect on the timing of moult and the ability to build sufficient lean mass and fat stores prior to migration, concurrent with a decrease in favourable conditions for migration as the autumn season progresses (Alerstam *et al.* 2003, Newton 2006, 2007). Individual quality was controlled using body condition. Year was included as a random effect to control within-year autocorrelation with respect to probability of survival. Two-way interactions between sex and both total number of offspring fledged and timing of breeding completion were assessed for the same reasons detailed above. Interactions were assessed simultaneously and significance was evaluated using likelihood ratio tests (Supporting Information Table S3).

Statistical analyses and structure of path model

All modelling was conducted in R version 2.8.1 using the 'stats' and 'lme4' packages (R Development Core Team 2008, Bates *et al.* 2011). Costs of reproduction during the pre-migratory period were assessed in a path modelling framework using the concept of d-separation (d-sep test; Shipley 2000). Path models fitted using d-sep tests are ideal for situations in which sample sizes are small, data are non-normally distributed, or when functional relationships are non-linear (Shipley 2000). Model fit is evaluated using a set of (k) mutually independent claims of probabalistic independence that must be true if the structure of the hypothesized path model is correct. The probabilities (P) from these k tests are used to derive Fisher's C statistic: $C = -2\sum \ln(P)$, which follows a chi-squared distribution with $2k$ degrees of freedom (Shipley 2000). The null hypothesis is that the proposed correlational structure of the model does not differ from the observed correlational structure in the data, and therefore $P \leq 0.05$ indicates the proposed causal structure is incorrect (Shipley 2000).

To account for repeated measures on individuals (Table S1), a random effect was initially specified for each path, where appropriate. However, exact restricted likelihood ratio tests (10 000 simulations; 'RLRsim' package; Scheipl 2010) indicated that this term was not significant in any case and it was therefore removed. This meant that all paths were fitted using linear multiple regression models. Prior to model fitting, potential curvilinear relationships were visually assessed using scatter plots fitted with LOESS lines. Model fit was visually assessed using residual plots. Correlations between predictors were evaluated through the variance-covariance matrix of the fitted model, where correlation coefficients ≥ 0.7 represented highly correlated variables (McGarigal *et al.* 2000). For the path analysis, each variable was standardized (value $- \bar{X}$)/sd) such that path coefficients represent standardized partial regression coefficients, or the standard deviation change in y when x is increased or decreased by 1 sd (Shipley 2000). The significance of all statistical tests was evaluated at $\alpha = 0.05$.

Significant two-way interactions were initially assessed using the cross products of the terms involved in the interaction (Tables S2 and S3). Significant interactions were then re-evaluated using the cross-product residuals according to Lance (1988). This procedure eliminates covariances between the cross product term and the main effects (Lance 1988), thus reducing the number of paths included in the path model. For significant interactions involving year, data were collapsed across years where the pattern was similar to further reduce the number of parameters and paths in the final model.

RESULTS

Breeding period

For 2008–2010, the average number of offspring fledged per individual over the course of a breeding season was 4.4 (sd = 2.2) and the average date of breeding completion was 19 July (sd = 16.9 days). The average capture date for individuals was 8 June (sd = 13.9 days) and the average mass at capture was 20.2 g (sd = 0.88 g) for males and 19.2 g (sd = 1.5 g) for females. Median age in years was 1 (range = 1–4).

The correlational structure of our path model (Fig. 1) was consistent with the correlational structure of the data (61 tests of probabilistic independence; Fisher's $C_{122} = 124.6$, $P = 0.417$; implied independencies did not differ from those observed). As expected, individuals that fledged the largest number of offspring were also the last to finish breeding ($t_{40} = 3.3$, $P = 0.002$) and males had significantly longer tarsi than females ($t_{44} = 2.7$, $P = 0.011$). We also found that body condition was higher in 2010 than in 2008 ($\beta = 0.68$, $t_{43} = 2.0$, $P = 0.054$; Fig. 1), but no difference was observed between 2008 and 2009 ($\beta = 0.33$, $t_{43} = 0.9$, $P = 0.383$). Rejecting six of our hypotheses, neither the timing of breeding completion nor the number of offspring fledged was dependent on body condition (timing of breeding completion: $\beta = 0.16$, $t_{40} = 1.1$, $P = 0.268$; number of offspring fledged: $\beta = 0.15$, $t_{41} = 0.4$, $P = 0.378$), age (timing of breeding completion: $\beta = 0.46$, $t_{40} = 1.3$, $P = 0.207$; number of offspring fledged: $\beta = 0.16$, $t_{41} = -0.3$, $P = 0.737$), or year (timing of breeding completion: 2009: $\beta = -0.47$, $t_{40} = -1.3$, $P = 0.186$,

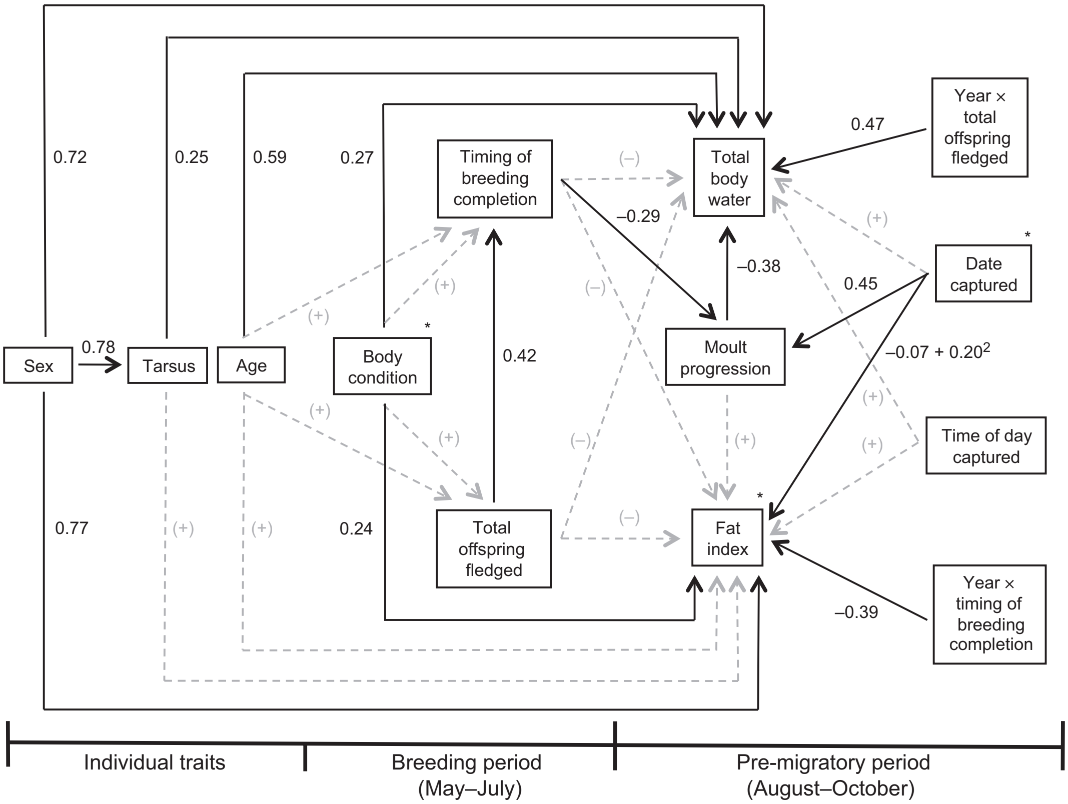

Figure 1. Path model depicting relationships between timing of breeding completion and total offspring fledged with pre-migratory body condition. Solid black arrows represent significant causal relationships and the hatched grey lines represent hypothesized causal relationships that were not statistically significant ($P > 0.05$). The sign inside the parentheses associated with each grey arrow represents the predicted direction of the relationship. Numbers associated with each solid line represent standardized path coefficients. The asterisks indicate significant year effects.

2010: $\beta = -0.45$, $t_{40} = -1.3$, $P = 0.192$; number of offspring fledged 2009: $\beta = -0.05$, $t_{41} = -0.11$, $P = 0.915$, 2010: $\beta = 0.30$, $t_{41} = 0.3$, $P = 0.737$).

Pre-migratory period

The average number of captures per individual during the pre-migratory period was 1.4 (sd = 0.7, $n = 21$) for males and 1.6 (sd = 0.8, $n = 25$) for females. Mean date of capture was 7 September (sd = 14.3 days, $n = 70$) and the average number of days since breeding completion at capture was 49 days for both sexes (males: sd = 24, $n = 30$; females: sd = 20, $n = 40$). Average mass at capture was 20.4 g (sd = 1.4 g) for males and 18.5 g (sd = 1.4 g) for females.

Several lines of evidence suggest that there were short-term costs of reproduction. As predicted, total body water decreased as the number of offspring fledged increased, but only in 2009 (main effect: $\beta = -0.04$, $t_{57} = -0.4$, $P = 0.691$; interaction with year: $t_{57} = -3.7$, $P = < 0.001$; Figs 1 and 2, Table 1). Moult progression was also delayed for late breeders ($t_{65} = -2.8$, $P = 0.006$; Fig. 3a) and total body water decreased as moult progressed ($t_{57} = -4.3$, $P = < 0.001$; Fig. 3b), resulting in an indirect effect of timing of breeding completion on total body water through the path: timing of breeding completion → moult progression → total body water (Fig. 1). However, there was no evidence of a direct effect of timing of breeding completion on total body water ($\beta = 0.12$, $t_{57} = 1.3$, $P = 0.216$), for total offspring fledged on fat mass ($\beta = -0.07$, $t_{55} = -0.8$, $P = 0.429$), or for moult progression on fat mass ($\beta = 0.10$, $t_{55} = 1.1$, $P = 0.285$). Contrary to our prediction, fat mass was positively correlated with timing of breeding completion in 2008 and 2009, but not in 2010 (main effect: $\beta = 0.11$, $t_{55} = 1.1$, $P = 0.284$; interaction with year $t_{55} = -2.1$, $P = 0.038$; Supporting Information Fig. S3).

Table 1. Structural equations detailing the effects of individual traits, breeding variables and pre-migratory variables on (1) total body water, (2) quantity of fat and (3) the progression of moult, for adult Savannah Sparrows on Kent Island, NB, 2008–2010.

Model	Model term	β	*t*	df	*P* (*t*)
(1) Pre-migratory body water	Age: ≥ 2 years of age	0.89	2.58	57	0.012*
	Sex: males	1.09	4.10	57	<0.001*
	Tarsus length	0.55	2.92	57	0.005*
	Breeding body condition	0.36	3.24	57	0.002*
	Timing of breeding completion	0.01	1.25	57	0.216
	Total offspring fledged	−0.03	−0.04	57	0.691
	Moult progression	−0.65	−4.26	57	<0.001*
	Time of day captured	0.06	1.28	57	0.207
	Date captured	0.002	0.27	57	0.789
	Year: 2009	0.48	1.50	57	0.139
	Year: 2010	−0.57	−1.96	57	0.055
	Year *X* total offspring fledged	−0.43	−3.71	57	<0.001*
(2) Pre-migratory fat index	Age: ≥ 2 years of age	−0.37	−1.34	55	0.186
	Sex: males	0.91	4.60	55	<0.001*
	Tarsus length	−0.16	−1.05	55	0.298
	Breeding body condition	0.25	2.98	55	0.004*
	Timing of breeding completion	0.007	1.08	55	0.284
	Total offspring fledged	−0.04	−0.80	55	0.429
	Moult progression	0.13	1.08	55	0.285
	Time of day captured	0.05	1.35	55	0.183
	Date captured	−0.58	−2.87	55	0.006*
	Date captured^{a}	0.001	2.86	55	0.006*
	Year: 2009	−0.79	−3.15	55	0.003*
	Year: 2010	0.14	0.62	55	0.539
	Year × timing of breeding completion	−0.03	−2.12	55	0.038*
(3) Pre-migratory progression of body moult	Timing of breeding completion	−0.02	−2.82	65	0.006*
	Date captured	0.03	4.01	65	<0.001*
	Year: 2009	0.01	0.03	65	0.973
	Year: 2010	0.29	1.33	65	0.188

Parameter estimates are for unstandardized data.
^{a}Indicates a curvilinear term.
*Indicates statistically significant terms ($P < 0.05$).

Together, our models explained 70, 67 and 32% of the observed variation in total body water, fat and moult progression, respectively.

Apparent annual survival

On average, 51% of adults returned after their first year of breeding and 47% of adults returned after their second year of breeding. Contrary to our prediction, individuals with later dates of breeding completion during their first breeding season were more likely to return the following year relative to earlier-breeding birds ($\beta = 0.02$, likelihood-ratio test: $\chi^2_1 = 6.9$, $P = 0.008$; Fig. 4). However, there was no evidence of a relationship between annual survival and timing of breeding completion for adults during their second breeding season ($\beta = 0.01$, likelihood-ratio test: $\chi^2_1 = 0.6$, $P = 0.448$). There was also no evidence in either age group for a relationship between survival and total offspring fledged (1-year-olds: $\beta = -0.03$, likelihood-ratio test: $\chi^2_1 = 1.2$, $P = 0.264$; 2-year-olds: $\beta = 0.04$, likelihood-ratio test: $\chi^2_1 = 0.2$, $P = 0.650$), body condition during the breeding period (1-year-olds: $\beta = -0.06$, likelihood-ratio test: $\chi^2_1 = 0.9$, $P = 0.336$; 2-year-olds: $\beta = 0.04$, likelihood-ratio test: $\chi^2_1 = 0.1$, $P = 0.734$), or sex (1-year-olds: $\beta = -0.40$, likelihood-ratio test: $\chi^2_1 = 3.3$, $P = 0.071$; 2-year-olds: $\beta = -0.40$, likelihood-ratio test: $\chi^2_1 = 1.2$, $P = 0.278$).

DISCUSSION

In songbirds, there is generally little overlap between breeding and moult because of competing energetic demands (Hahn *et al.* 1992, Hemborg & Lundberg 1998, Ricklefs & Wikelski 2002). Our results support these observations: individuals that continued breeding later into the season had

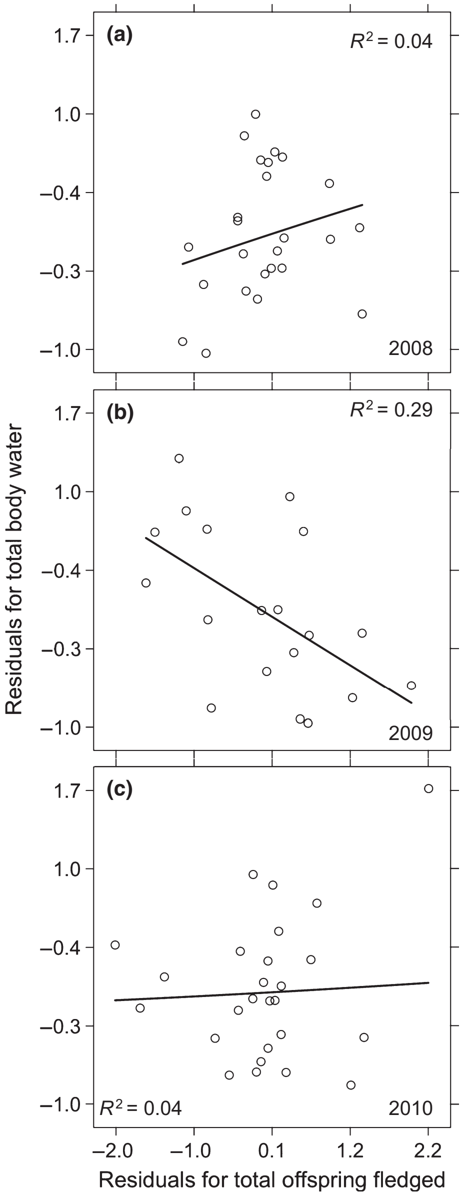

Figure 2. Partial regression plots illustrating interaction between total offspring fledged and year with respect to total body water (a = 2008, b = 2009, c = 2010). Trends illustrated with locally weighted regression lines. In panels a and c, there is no relationship between total body water and total offspring fledged, whereas in panel b there is a significant negative relationship between total offspring fledged and total body water.

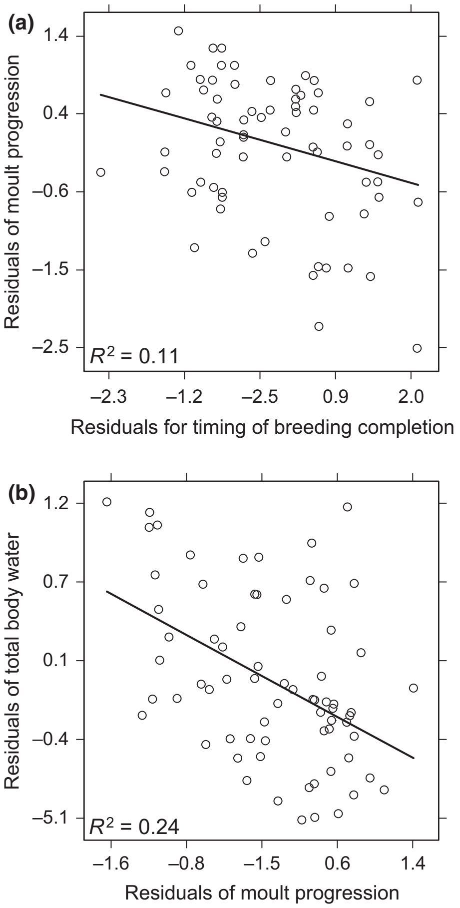

Figure 3. Partial regression plots illustrating relationships between (a) progression of body moult with timing of breeding completion, and (b) total body water with progression of body moult. Trends illustrated with locally weighted regression lines. In panel a, as the date of breeding completion increases, the schedule of moult is significantly delayed. In panel b, as moult progresses, total body water significantly decreases. Together, both effects illustrate an indirect relationship between timing of breeding and total body water.

delayed moult schedules relative to individuals that bred earlier. In migratory species, delayed moult may have important consequences over the longer term. For example, it may result in individuals being obliged to moult during migration, which has been shown negatively to affect feather coloration and sexual attractiveness (Norris *et al.* 2004). Alternatively, feathers of late-moulting individuals may grow more quickly, impairing structural quality, which in turn can increase thermoregulatory costs and decrease flight performance (Nilsson & Svensson 1996, Swaddle *et al.* 1996, Dawson *et al.* 2000). Both of the latter effects may be particularly costly during migration.

In addition to affecting plumage quality, delays in moult may also affect an individual's ability to prepare for migration. We found that as moult progressed, total body water (an index of lean tissue mass) declined. This relationship probably

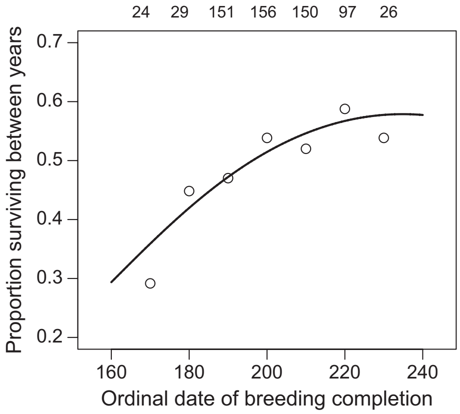

Figure 4. Scatter plot illustrating relationship between timing of breeding completion and annual survival for 1-year-old birds. Numbers above points represent sample sizes for each proportion. Numbers along *x*-axes represent the centre values of bins for date. Trend illustrated with fitted values from a logistic regression model with a curvilinear term for timing of breeding completion and a random effect for year. Survival increases as date of breeding completion increases.

reflects increased protein demands associated with feather synthesis (Murphy & King 1991, 1992, Bauchinger & Biebach 2006). It also results in an indirect link between timing of breeding completion and lean mass, wherein late-breeding individuals pay the costs of moulting later in the pre-migratory period. Lean mass plays an important role in migration, providing metabolic intermediates for the Krebs cycle and gluconeogenesis, water for hydration and the muscular machinery needed to fly (Klaassen 1995, Jenni & Jenni-Eiermann 1998, McWilliams *et al.* 2004). If late-moulting individuals are unable to compensate for these costs and depart for migration in poor condition, survival may be compromised. Alternatively, if migratory departure is delayed in order to replenish moult-induced losses of lean mass, individuals may be more likely to encounter inclement weather and diminished resources during migration, again compromising survival (Alerstam *et al.* 2003, Newton 2006, 2007). Thus, delays in moult may affect survival through several different mechanisms.

We found that as total number of offspring fledged increased, total body water decreased, but only in 2009, a relatively wet and cool breeding season. Poor weather during the breeding period may have affected lean tissue mass through several different mechanisms. First, parents may have had to increase provisioning rates and energy expenditure to meet increased energy demands of nestlings. Secondly, thermoregulatory demands of parents themselves may have increased. Last, prey availability may have been lower. Regardless of the exact mechanism, our results suggest that costs of reproduction may only be apparent when weather conditions during the breeding period are particularly unfavourable.

Despite the costs of reproduction discussed above, empirical evidence of survival costs is mixed. For example, Hemborg (1999) found that late-breeding and moulting female Pied Flycatchers *Ficedula hypoleuca* had reduced annual survival relative to early-breeding and moulting individuals. However, Flinks *et al.* (2008) found no effect of prolonged breeding and delayed moult on annual survival in European Stonechats *Saxicola rubicola*. In contrast to both these studies, we found a positive correlation between timing of breeding completion (and thus timing of moult) and annual survival in first-year breeders. Thus, our results indicate that short-term effects associated with delayed moult in Savannah Sparrows, on average, do not translate to longer-term survival costs.

The absence of long-term survival costs, and the positive correlation between timing of breeding completion and breeding effort, suggest that individuals investing more in reproduction are also high-quality individuals (and thus are better able to acquire resources). Specifically, when genetic variation exists for acquisition of resources, but little variation exists for allocation of those resources (i.e. regardless of energy intake, individuals divide up their energy budgets in a similar way), breeding investment will be positively correlated with survival. Conversely, if genetic variation for acquisition of resources is low but variation for allocation is high, survival costs of reproduction should be apparent (Van Noordwijk & de Jong 1986, Stearns 1989, Reznick *et al.* 2000). Our results are most consistent with the predictions of the former hypothesis and suggest that high-quality individuals are able to mitigate short-term costs associated with delayed moult through the acquisition of resources. This hypothesis is also supported by the largely positive relationship between timing of breeding completion and fat mass that we observed in 2008 and 2009.

In a separate analysis (Mitchell *et al.* 2011), we found that juvenile Savannah Sparrows fledging in lower body condition had less fat during the pre-migratory period and were less likely to survive until the following breeding season than were individuals fledging in higher body condition. In the current study, adults with lower body condition during breeding had less lean tissue and fat during the pre-migratory period compared with individuals in better condition, but we also found that condition did not affect annual survival, suggesting that migration is not costly for experienced adults or that adults are able to compensate for individual differences in condition during migration. With respect to the former possibility, total migration distance for Savannah Sparrows is relatively short compared with many other passerine species (e.g. neotropical migrants; Odum *et al.* 1961), which may reduce many of the energetic demands associated with migration. With respect to the latter possibility, most fat accumulation may occur en route (Odum *et al.* 1961), providing individuals in poor condition with an opportunity to catch up with conspecifics already in good condition. Regardless of the exact mechanism, our results highlight important age-specific differences in long-term individual success with respect to breeding season events.

Although our results suggest that short-term costs of reproduction are on average mitigated by individual quality, this does not preclude the possibility that the short-term costs we observed have long-term consequences in other species (e.g. Hemborg 1999), or that survival costs are more apparent under different environmental circumstances that occur only rarely (Reznick *et al.* 2000, Kingsolver *et al.* 2001, Siepielski *et al.* 2009). It also suggests that in Savannah Sparrows, costs of reproduction are borne more by offspring (see also Mitchell *et al.* in press). Overall, our results suggest the importance of examining differences in resource acquisition and allocation among individuals (see also Van Noordwijk & de Jong 1986, Reznick *et al.* 2000) when assessing life-history trade-offs in migratory birds.

Thanks to A. Newman, C. Cooper-Mullin, E. Graff, H. Harwood, L. Rae, M. Janssen, P. Erickson, R. Mauck, S. Brough, S. Nichols, E. Christiansen, B. Dossman and T. Winegard for their assistance in the field. Thanks to A. Gerson for help and advice with heavy water processing and spectrometry. Our gratitude is also extended to R. Mauck and D. Gannon for access to the study site and advice in the field. This paper benefited from the critical comments of Richard Inger, one anonymous reviewer, and Alistair Dawson, associate editor. Funding for this study was provided by the American Ornithologist's Union (G.W.M.), the Animal Behavior Society (G.W.M.), the Global Forest Science (GFS-18-210-229; G.W.M.), the Society of Canadian Ornithologists (G.W.M), the American Museum of Natural History (G.W.M), the Natural Sciences and Engineering Research Council (D.R.N., C.G.G.), the Canada Foundation for Innovation (D.R.N., C.G.G.), the Ontario Research Fund (D.R.N., C.G.G.), and the University of Guelph (D.R.N., G.W.M.). This represents Bowdoin Scientific Station contribution no. 231. All procedures were approved by the Animal Care Committees at the University of Guelph and Bowdoin College in accordance with Canadian Council on Animal Care guidelines (permit number: 08R061) and met the legal requirements of the Canadian Wildlife Service (banding permit number: 10789; scientific permit number: SC2732).

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Received 14 March 2011;
revision accepted 30 December 2011.
Associate Editor: Alistair Dawson.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Scatter plot illustrating positive linear relationship between body moult progression and primary moult progression for adult Savannah Sparrows during the pre-migratory period on Kent Island, NB, 2009–2010.

Figure S2. Scatter plots illustrating positive linear relationships between mass (g) and tarsus length (mm) for adult Savannah Sparrows during the breeding period on Kent Island, NB, (A) 2008–2010 and (B) 1987–2004.

Figure S3. Partial regression plots illustrating the interaction between timing of breeding completion and year with respect to quantity of fat for adult Savannah Sparrows during the pre-migratory period on Kent Island, NB, 2008–2010.

Table S1. Sample sizes for each analysis stratified by year and sex.

Table S2. Linear model results (interactions only; no main effects) for two-way interactions hypothesized to affect (1) total offspring fledged, (2) timing of breeding completion, (3) total body water, (4) fat mass and (5) the progression of body moult.

Table S3. Likelihood ratio test results for interactions hypothesized to affect the annual survival of (1) first- and (2) second-year breeders.

Data S1. Additional covariates for pre-migratory total body water, fat mass and moult.