Non-breeding season events influence sexual selection in a long-distance migratory bird

Matthew W. Reudink\textsuperscript{1,2,*}, Peter P. Marra\textsuperscript{2}, T. Kurt Kyser\textsuperscript{3}, Peter T. Boag\textsuperscript{1}, Kathryn M. Langin\textsuperscript{1,†} and Laurene M. Ratcliffe\textsuperscript{1}

\textsuperscript{1}Department of Biology, and \textsuperscript{2}Department of Geological Sciences and Geological Engineering, Queen’s University, Kingston, Ontario, Canada K7L 3N6, \textsuperscript{3}Smithsonian Migratory Bird Center, 3001 Connecticut Avenue NW, Washington, DC 20008, USA

The study of sexual selection has traditionally focused on events and behaviours immediately surrounding copulation. In this study, we examine whether carry-over effects from the non-breeding season can influence the process of sexual selection in a long-distance migratory bird, the American redstart (\textit{Setophaga ruticilla}). Previous work on American redstarts demonstrated that overwintering in a high-quality habitat influences spring dates from the wintering grounds, advances arrival dates on the breeding grounds and increases apparent reproductive success. We show that the mixed-mating strategy of American redstarts compounds the benefits of overwintering in high-quality winter habitats. Males arriving to breed in Canada from high-quality winter habitats arrive earlier than males from poor-quality habitats, resulting in a lower probability of paternity loss, a higher probability of achieving polygyny and ultimately higher realized reproductive success. Such results suggest that the process of sexual selection may be influenced by events interacting throughout the annual cycle.

\textbf{Keywords:} non-breeding; sexual selection; American redstart; carry-over; extra-pair paternity; polygyny

\section{1. INTRODUCTION}

For long-distance migratory birds, individual life history, ecology and behaviour are shaped by events and selective pressures acting throughout the annual cycle (Greenberg & Marra 2005). The challenge in understanding seasonal interactions lies in the inherent difficulty of tracking individuals and tracing the impacts of carry-over effects (i.e. events occurring during one season that carry over to influence an individual's or population's performance in subsequent seasons; Marra et al. 1998) between the phases of the annual cycle, often between continents. Until recently, making connections between breeding and wintering populations and detecting potential carry-over effects has remained elusive. However, advances in the utilization of naturally occurring biochemical markers, such as stable isotopes, in animal tissues have allowed us to begin making connections throughout the annual cycle (Webster et al. 2002; Rubenstein & Hobson 2004). Studies using stable-isotope hydrogens have revealed connections between wintering and breeding populations (Webster et al. 2002), use of migratory stopover sites (e.g. Yohannes et al. 2007) and patterns of migration (e.g. Kelly et al. 2002). This technique has also revealed previously unknown carry-over effects. Studds et al. (2008) recently demonstrated that natal dispersal is influenced by conditions during the non-breeding season, whereby individuals overwintering in high-quality habitats disperse south of their natal origin, while individuals in low-quality winter habitats migrate much further and ultimately breed north of their natal origin. Indeed, carry-over effects from the non-breeding period have now been shown to impact many aspects of individual life history in a variety of species.

In European barn swallows (\textit{Hirundo rustica}), favourable winter conditions in Africa (inferred by the normalized difference vegetation index, NDVI) advance population-level arrival onto the breeding grounds in Italy (Saino et al. 2004a). Furthermore, NDVI in winter is positively correlated with population-level breeding success and the length of tail streamers, a sexually selected trait that is moulted on the wintering grounds (Saino et al. 2004b). At the individual level, territory acquisition in high-quality winter habitats can have significant fitness consequences. American redstarts (\textit{Setophaga ruticilla}) holding winter territories in high-quality habitats have higher annual return rates (Marra & Holmes 2001), are in better condition (Marra & Holberton 1998; Studds & Marra 2005) and ultimately depart the wintering grounds earlier than individuals holding territories in low-quality habitat (Marra et al. 1998; Studds & Marra 2005). Moreover, these consequences can carry over to subsequent seasons. Stable-carbon isotope analysis has revealed that the quality of an individual's winter habitat can influence condition during migration (black-throated blue warblers (\textit{Dendroica caerulescens}); Bearhop et al. 2004) and the timing of arrival on breeding areas (American redstarts; Marra et al. 1998; Norris et al. 2004). Norris et al. (2004) demonstrated that carry-over effect of winter habitat on arrival date ultimately predicted apparent reproductive success, with early arriving birds fledging more offspring. However, the carry-over effects may also influence whether males achieve polygyny as well as within-pair (WP) and extra-pair (EP) paternity—processes that are important drivers of sexual selection in many songbirds (Webster et al. 2007). Thus, examining the carry-over effects using only apparent reproductive success

\textsuperscript{*}Author for correspondence (mattreudink@gmail.com).

\textsuperscript{†}Current address: Department of Biology, Colorado State University, Fort Collins, CO 80523, USA.
mixed-deciduous forest, dominated by sugar maple (Acer saccharum). Recently begin singing for territory advertisement and to attract females. Each year, from May 1 to 31, we surveyed our 60 ha study area daily from 06.00 to 12.00, detecting males by the presence of singing and subsequent visual identification. Arrival date was standardized as the number of days after the first male arrived (first-male arrival date = 0). All adults were captured in mist-nets within 7 days of arrival by simulating territorial intrusions using song playbacks accompanied with a decoy. Once captured, American redstarts were individually marked with a single Canadian Wildlife Service aluminium band and two to three colour bands. We then extracted 50 μl of blood for paternity analysis by piercing the brachial vein and clipped 2–3 mm of the central claw for stable-isotope analysis (2006 and 2007 only).

Upon arrival, all males were observed and mapped for at least 20–30 min d−1 throughout the breeding season to determine territory boundaries and pairing date. Females typically begin nest building within a few days of pairing. Once nest building began, we monitored nest status every other day, noting the onset of egg laying, number of eggs laid, hatching and fledging success. Males were monitored daily to detect individuals that paired with secondary females (i.e. polygynous mating). At day 5 after hatching, we banded nestlings with a single aluminium band and collected 15–20 μl of blood for paternity analysis. Offspring from nests that were too high to access on day 5 were captured on the day of fledging.

American redstart males exhibit delayed plumage maturation, wherein males resemble females during their first breeding season and do not mature into the full adult breeding plumage until their second prebasic moult, which follows their first breeding season. Owing to the differences in plumage, and the fact that the first-year American redstarts have greatly reduced reproductive performance (Sherry & Holmes 1997; M. W. Reudink 2007 unpublished data), we limited our analyses to only adult (after second-year or ASY) males.

2. MATERIAL AND METHODS
(a) Field data collection
Fieldwork was conducted in May–July 2004–2007 at Queen’s University Biological Station, Chaffey’s Lock, Ontario, Canada (44°34’N, 76°19’W). Our study area is composed of mixed-deciduous forest, dominated by sugar maple (Acer saccharum) and Eastern hop hornbeam (Ostrya virginiana). When males arrive on the breeding grounds, they immediately begin singing for territory advertisement and to attract females. Each year, from May 1 to 31, we surveyed our 60 ha study area daily from 06.00 to 12.00, detecting males by the presence of singing and subsequent visual identification. Arrival date was standardized as the number of days after the first male arrived (first-male arrival date = 0). All adults were captured in mist-nets within 7 days of arrival by simulating territorial intrusions using song playbacks accompanied with a decoy. Once captured, American redstarts were individually marked with a single Canadian Wildlife Service aluminium band and two to three colour bands. We then extracted 50 μl of blood for paternity analysis by piercing the brachial vein and clipped 2–3 mm of the central claw for stable-isotope analysis (2006 and 2007 only).

Upon arrival, all males were observed and mapped for at least 20–30 min d−1 throughout the breeding season to determine territory boundaries and pairing date. Females typically begin nest building within a few days of pairing. Once nest building began, we monitored nest status every other day, noting the onset of egg laying, number of eggs laid, hatching and fledging success. Males were monitored daily to detect individuals that paired with secondary females (i.e. polygynous mating). At day 5 after hatching, we banded nestlings with a single aluminium band and collected 15–20 μl of blood for paternity analysis. Offspring from nests that were too high to access on day 5 were captured on the day of fledging.

American redstart males exhibit delayed plumage maturation, wherein males resemble females during their first breeding season and do not mature into the full adult breeding plumage until their second prebasic moult, which follows their first breeding season. Owing to the differences in plumage, and the fact that the first-year American redstarts have greatly reduced reproductive performance (Sherry & Holmes 1997; M. W. Reudink 2007 unpublished data), we limited our analyses to only adult (after second-year or ASY) males.

(b) Winter habitat quality and stable-carbon isotope analysis
American redstarts are widespread across Central America, northern South America, and are especially abundant throughout the Caribbean (Sherry & Holmes 1997). Although the specific overwintering location of our breeding population is unknown, stable-hydrogen isotope analysis indicates that birds breeding in southeastern Ontario probably overwinter in the Caribbean (Norris et al. 2006).
Table 1. American redstart microsatellite data characterization from CERVUS v. 2.0 (Marshall et al. 1998) over the 4 years of this study (2004–2007).

<table>
<thead>
<tr>
<th>locus</th>
<th>no. of alleles</th>
<th>expected heterozygosity (he)</th>
<th>observed heterozygosity (ho)</th>
<th>probability of maternal exclusion</th>
<th>probability of paternal exclusion</th>
<th>null allele frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dpu01</td>
<td>29</td>
<td>0.945</td>
<td>0.866</td>
<td>0.789</td>
<td>0.885</td>
<td>+0.043</td>
</tr>
<tr>
<td>Dpu03</td>
<td>13</td>
<td>0.479</td>
<td>0.460</td>
<td>0.133</td>
<td>0.302</td>
<td>+0.018</td>
</tr>
<tr>
<td>Dpu15</td>
<td>27</td>
<td>0.949</td>
<td>0.824</td>
<td>0.808</td>
<td>0.894</td>
<td>+0.070</td>
</tr>
<tr>
<td>Dpu16</td>
<td>19</td>
<td>0.880</td>
<td>0.772*</td>
<td>0.611</td>
<td>0.759</td>
<td>+0.065</td>
</tr>
<tr>
<td>all loci</td>
<td>21 (avg)</td>
<td>0.831</td>
<td>0.764</td>
<td>0.671</td>
<td>0.804</td>
<td>+0.002</td>
</tr>
</tbody>
</table>

*Significantly different from expected (goodness-of-fit test: \( X^2 = 31.90, p < 0.001 \)).

(c) Paternity analysis
We collected blood samples from putative parents and offspring and stored the samples in Queen's lysis buffer (Seutin et al. 1991; 2005–2007) or on blotting paper (2004). DNA was extracted using an Invitrogen Blood and Tissue Kit. gDNA was then quantified via agarose gel electrophoresis and diluted or concentrated to approximately 10 ng \( \mu l^{-1} \). All loci were amplified using a Biometra Thermogradient or Biometra UNOII PCR machine under the following conditions: 94°C for 3 min followed by 35 cycles of 94°C for 15 s, 58°C for 15 s, 72°C for 30 s, and a final extension of 72°C for 10 min. Each sample included 1 \( \mu l \) DNA (10 ng \( \mu l^{-1} \)), 1 \( \mu l \) Qiagen PCR buffer, 0.03 \( \mu l \) (100 mM) dNTPs, 0.03 \( \mu l \) (100 \( \mu M \)) forward primer, 0.03 \( \mu l \) (100 \( \mu M \)) reverse primer, 0.25 \( \mu l \) M13 F 700IRD licor primer, 0.005 \( \mu l \) (5 U \( \mu l^{-1} \)) Taq polymerase, brought up to 10 \( \mu l \) total volume with sterile ddH2O. Amplified samples were run on a Licor IR2 Global Sequencer and allele scoring was conducted by a trained observer blind to the identity of individuals.

Paternity analysis was conducted using five microsatellite loci (Dpu01, Dpu03, Dpu05, Dpu15 and Dpu16) originally isolated from yellow warblers (Dendroica petechia, Dawson et al. 1997, table 1). Over the 4 years of this study, we analysed DNA from 265 offspring from 75 nests and all putative parents. The use of five highly variable microsatellite loci ensured a high probability of paternity exclusion (>0.999, table 1). Owing to limitations in detecting 2 bp differences and the relatively high frequency of null alleles, we followed the conservative approach of Reudink et al. (2006): offspring were excluded only if they mismatched the putative sire at more than 2 bp and at two or more loci. All EPO were then compared with all sampled potential sires in the population to assign paternity using CERVUS v. 2.0 (Marshall et al. 1998). All assignments were then double-checked by hand by two trained, independent observers. EP paternity was assigned when the putative sire matched at least four out of five loci within 2 bp. Mismatches at single loci were only allowed when the mismatch was due to a likely null allele. Total fertilization success was calculated as the number of WP offspring at the primary and secondary (if polygynous) nests and the number of EPO sired. Some offspring died prior to fledging and we were unable to ascertain the identity of all fledged offspring. Thus, we calculated genetic fledging success by multiplying the number of offspring fledged by the proportion of WP offspring for the primary and secondary nests and added the number of EPO \( \times \) proportion fledged at the EP nest.

(d) Predicting paternity and polygyny
To illustrate the potential carry-over effects resulting from holding a territory in tropical winter habitats that vary in quality, we created a simple model based on \( \delta^{13}C \) signatures of tissues from individuals collected in four different winter habitats (wet forest, mangrove, citrus and scrub; sensu Norris et al. 2004). Because winter habitat quality is unlikely to influence paternity directly, but rather through factors associated with arrival timing (see Norris et al. 2004), we first predicted average arrival dates for birds arriving from

---

Winter events influence sexual selection  M. W. Reudink et al.
those four winter habitat types based on the regression of δ13C on arrival. Next, calculated the probability of polygyny, proportion paternity and realized fledging success based on regressions of polygyny, proportion paternity and realized fledging success on arrival.

(e) Statistical analysis
All statistical analyses were performed in JMP v. 5.1 (SAS Institute 2006) and SAS v. 8.2 (SAS Institute 1999). We used a mixed model with individual as a random effect and δ13C and year as main effects to test the relationship between δ13C and arrival. Because some individuals were present in multiple years, we tested whether arrival date predicted binary reproductive variables (EP paternity (y/n) and polygyny/monogamy) using logistic regression with individual as a repeated measure and year as a random effect. To test whether arrival date predicted linear response variables (fertilization success and fledging success), we used a mixed model with the reproductive variable as the response, year as a random effect, individual as a repeated measure and standardized arrival date as a linear covariate. If year was not found to have a significant effect on the model, we excluded the year term and used a mixed model with individual as a random effect and standardized arrival date as a linear covariate. To test for a relationship between the arrival date and the proportion of WP offspring, we used a non-parametric mixed model with proportion paternity as a response variable, year as a random effect, individual as a repeated measure and standardized arrival date as a linear covariate (PROC MIXED in SAS). It was necessary to take a non-parametric approach as our proportion paternity data were highly skewed and could not be transformed. Comparisons between WP and EPO were analysed using matched-pairs t-tests.

3. RESULTS
(a) Winter habitat quality and arrival date
Adult males that overwintered in high-quality habitats (more negative claw δ13C signatures) in 2006–2007 arrived on the breeding grounds earlier than males that overwintered in low-quality habitats (mixed model: claw δ13C: n = 43, F = 7.56, p = 0.009; year: n = 43, F = 0.36, p = 0.55; figure 2a).

(b) Paternity
Out of the 75 nests analysed, 32 (43%) contained one or more EPO and 56 out of the 239 (23%) offspring analysed were EP. A subset of males (9/75) was polygynous, but there was no significant difference in paternity at the nest of the primary female or the secondary female (first females: 28 out of 66 (42%) of nests contained EPO, 52 out of 209 (25%) of offspring were EPO; second females: 4 out of 9 (45%) of nests contained EPO, 4 out of 30 (13%) of offspring were EPO; Fisher’s exact probability test for the presence of EPO: n = 9, r² = 0.42, p = 0.17; paired t-test for proportion EPO: n = 9, t = 0.58, p = 0.58). Realized success (WP offspring at each nest + EPO sired) for 62 adult males with complete reproductive data ranged from zero to seven offspring (mean = 3.13 ± 0.24 s.e.).

(c) Arrival date and paternity
Adult males that sired all the offspring at their own nest arrived earlier on the breeding grounds than males that

Figure 2. Significant relationships between standardized arrival date (number of days after first male to arrive) on the breeding grounds and (a) claw δ13C, (b) proportion of offspring sired by the social male at a nest and (c) total genetic fledging success (within pair + EPO).

lost paternity (logistic regression with correlated data; arrival: n = 64, z = 2.00, p = 0.045; year: n = 64, z = −0.65, p = 0.52). Arrival date of adult males was also significantly correlated with the proportion of a WP offspring male sired (non-parametric random effects mixed model: n = 64, χ² = 5.95, p = 0.01; figure 2b). At nests that lost paternity, EP sires arrived on average 4.19 ± 1.83 s.d. days earlier than the males they cuckolded (matched-pairs t-test: n = 26, t = −2.28, p = 0.03). However, an examination of all adult males revealed no difference in arrival date between males that sired EPO and those that did not (logistic regression: arrival: n = 115, χ² = 0.53, p = 0.47; year: n = 115, χ² = 2.59, p = 0.11).

(d) Arrival date and polygyny
Males that achieved polygyny arrived significantly earlier than males who remained socially monogamous (logistic regression with correlated data; n = 115 (86 monogamous, 29 polygynous), arrival: z = −2.04, p = 0.04; year: z = −1.78, p = 0.08; figure 3). These results did not change qualitatively when we removed the non-significant year effect (z = −2.59, p = 0.01).
We calculated the average (mean total fledging success (model; n covariate, we found that males that arrived earlier had using individual as a random effect and arrival as a linear realized fertilization success and realized fledging success effects and tested the relationships between arrival and figure 2). When we removed the non-significant year effects and tested the relationships between arrival and realized fertilization success and realized fledging success using individual as a random effect and arrival as a linear covariate, we found that males that arrived earlier had significantly higher fertilization (mixed model; n=65, F=3.45, p=0.017) and fledging success (mixed model; arrival: n=65, F=3.50, p=0.09; year: n=65, F=2.08, p=0.17; figure 2c). When we removed the non-significant year effects and tested the relationships between arrival and realized fertilization success and realized fledging success using individual as a random effect and arrival as a linear covariate, we found that males that arrived earlier had significantly higher fertilization (mixed model; n=65, F=4.03, p=0.05) and realized fledging success (mixed model; n=65, F=7.52, p=0.008).

(f) Predicting paternity, polygyny and total fledging success
We calculated the average (mean ± s.e.) δ13C signatures of the American redstarts from four tropical habitat types (from wet to dry: wet forest (δ13C=-24.35±0.11; n=15), mangrove (δ13C=-22.80±0.16; n=34), citrus (δ13C=-22.16±0.20; n=16), scrub (δ13C=-21.69±0.16; n=24); Marra et al. 1998; Norris et al. 2004; Marra unpublished data). We then calculated the average (mean ± s.e.) arrival dates for birds arriving from those four habitat types, based on the regression of δ13C on arrival date for birds arriving on the breeding grounds (figure 2a). Next, we used those four arrival dates (days 4.61±0.29, 8.83±0.44, 10.55±0.55 and 11.83±0.43) to predict the proportion of offspring an individual was likely to sire based on the regression of the proportion of WP offspring on the arrival date (figure 2b). We then predicted the probability of being polygynous based on a regression of the probability of polygyny on the arrival date. Finally, we predicted realized fledging success based on a regression of realized fledging success on the arrival date (figure 2c). Our model suggests that males arriving on the breeding grounds from high-quality winter habitats sire 14 per cent more offspring at their primary nest and are 19 per cent more likely to be polygynous than males arriving later from low-quality habitats (figure 4a,b). Ultimately, males overwintering in the high-quality winter habitats fledge approximately one additional offspring than birds overwintering in the poor-quality habitats (figure 4c).

4. DISCUSSION
Our results indicate that arrival timing on the breeding grounds, driven by conditions that experienced thousands
of kilometres away on tropical wintering grounds, may influence the rates of polygyny and EP paternity in American redstarts, suggesting that non-breeding season events may carry over to influence the process of sexual selection. Specifically, we demonstrate that not only does winter territory quality influence apparent success through arrival timing (wherein variation in apparent success is driven largely by predation; Norris et al. 2004), but also carry-over effects from winter may influence behavioural processes such as female mate choice and male–male competition. Males overwintering in high-quality habitats arrive earlier on the breeding grounds than males overwintering in low-quality habitats (inferred by stable-carbon isotope analysis). In turn, early arriving males sire a higher proportion of their own offspring, sire EPO in the nests of late-arriving males, are more likely to achieve polygyny and ultimately fledge a greater number of genetic offspring. These results suggest that early male arrival, driven by winter habitat quality, has the potential to directly influence evolutionary processes (Spottiswoode et al. 2006).

Several species of migratory birds are returning earlier to the breeding grounds and recent work has suggested that long-distance migrants breeding in Scandinavia have advanced arrival dates as a result of rapid, climate-driven evolutionary change (Jonzen et al. 2006; but see Both 2007). Our data indicate that early arriving males may increase fledging success by approximately 25 per cent through variation in polygyny and EP paternity, suggesting that early arrival is strongly favoured by selection and may be a mechanism by which rapid evolutionary change may occur.

Previous studies of American redstarts on the wintering grounds have shown that individuals holding territories in poor-quality habitats delay their spring departure northwards from the wintering grounds (Marra et al. 1998; Studds & Marra 2005), and arrive on the breeding grounds later (Marra et al. 1998; Norris et al. 2004; this study) and in poorer condition (Marra et al. 1998). Obtaining a territory in high-quality habitat during the winter is to some degree driven by individual quality, which could suggest that the relationship between winter territory quality and reproductive success is driven, at least in part, by individual quality rather a carry-over effect of winter habitat quality. However, Studds & Marra (2005) provided strong experimental evidence showing that American redstarts overwintering in low-quality habitats can ‘turn into’ high-quality birds through an experimental upgrade in habitat quality. When birds were removed from high-quality habitats that were subsequently resettled by birds from low-quality habitats, those new settlers were in better condition throughout the overwinter period and ultimately advanced their spring departure dates relative to birds that remained in low-quality habitats (Studds & Marra 2005). While disentangling the effects of individual quality from the effects of habitat quality is onerous, these data strongly support the idea that spring departure and subsequent arrival on the breeding grounds are influenced by ecological conditions during winter, not just individual condition/quality. Future studies that track individuals throughout the annual cycle will allow us to explicitly identify the impacts of altering territory quality on arrival date and eventual reproductive success.

While previous work on our breeding population of American redstarts has shown that late arrival is associated with reduced apparent reproductive success (Norris et al. 2004), our study demonstrates a strong relationship between winter territory quality and rates of EP paternity and polygyny through variation in arrival scheduling and suggests that non-breeding season events may influence sexual selection. While experimental work is still needed, we suggest that the costs of wintering in a low-quality territory are compounded by the mixed-mating strategy employed by American redstarts. Late arrival on the breeding grounds appears to lead not only to a shortened breeding season and higher probability of nest predation (Lozano et al. 1996; Norris et al. 2004), but also to an increased probability of cuckoldry from early arriving males. Furthermore, late-arriving males are less likely to mitigate the costs of lost paternity through either EP copulations or polygyny. Our model suggests that the acquisition of a poor-quality territory during winter may result in a paternity loss of approximately 14 per cent and a 19 per cent lower probability of polygynous mating, ultimately resulting in an over 25 per cent reduction in total fledging success, or one less successful offspring fledged per season (figure 4c). To our knowledge, this is the first study to demonstrate that genetic success may be influenced by non-breeding season events in a migratory songbird.

Previous studies have suggested that protandry and early male arrival is favoured by sexual selection (Thusius et al. 2001; Coppack et al. 2006; Kokko et al. 2006; Spottiswoode et al. 2006), where early arriving individuals increase their probability of obtaining mates (Lozano et al. 1996), achieving polygyny (Hasselquist 1998) and increasing reproductive performance (Norris et al. 2004; Smith & Moore 2005). Early arrival may also influence EP paternity through density-dependent effects and breeding synchrony/asynchrony (Westneat et al. 1990; Birkhead & Møller 1992; Chuang et al. 1999; Lindstedt et al. 2007). However, these studies have generally assumed that individual variation in the arrival date is dependent on individual quality and condition during migration, largely ignoring the factors affecting variation in arrival scheduling, such as non-breeding season carry-over effects. Ample evidence has now accumulated, which suggests that spring migration scheduling and condition during migration are influenced by the conditions experienced during the non-breeding season (Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004; Saino et al. 2004a; Studds & Marra 2005). We suggest that processes that can influence the opportunity for sexual selection, such as variation in EP paternity and polygyny (Andersson 1994), should be viewed not only in terms of the events and processes occurring during the breeding season, but rather as a continual process that may be influenced by events occurring throughout the annual cycle.

All methods in this study complied with the laws of Canada.

We gratefully acknowledge the many field assistants who contributed to this study. R. Reudink, R. Germain, A. McKellar, C. Studds, A. Tøttrup, S. Bearhop and an anonymous reviewer provided insightful comments on this manuscript. C. Studds provided invaluable statistical help. K. Klassen and A. Vuletich provided critical isotope analysis assistance and we thank C. Scott for molecular assistance. Funding was provided by the Natural Sciences and
REFERENCES


