Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat

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Although predicted some time ago, there has been little success in demonstrating that the overall fitness of migratory birds depends on the combined influences of their experiences over all seasons. We used stable carbon isotope signatures (δ13C) in the claws of migrating black-throated blue warblers Dendroica caerulescens to infer their wintering habitats and investigated whether winter habitat selection can be linked to condition during migration. Resident bird species with low δ13C corresponded to selection of more mesic habitats, and migrating birds with low δ13C were in better condition than conspecifics with higher δ13C signatures. These findings concur with empirical observations on the wintering grounds, where dominants (mostly males) tend to exclude subordinates from mesic areas (considered to be high-quality habitats). We believe that variation in condition during migration may be one of the key factors determining differences in arrival times and condition at the breeding areas, which in turn have a major influence on reproductive success.

Keywords: migration; condition; seasonal interaction; stable isotope

1. INTRODUCTION

It is generally agreed that early arrival on the breeding grounds and good body condition are important determinants of fitness in migratory birds (e.g. Lundberg & Alatalo 1992). Fretwell (1972) suggested that, in seasonal environments, events throughout the year might interact to produce these patterns. However, because of the difficulty in tracking such animals, it is unclear to what extent interactions among seasons may impact upon migratory species, particularly during migration (Webster et al. 2002).

Recent developments in the use of stable isotopes have allowed researchers to investigate, for the first time, seasonal interactions in migrant songbirds. Marra et al. (1998) demonstrated that American redstarts Setophaga ruticilla wintering in mesic, high-quality habitats were not only in better condition and migrated earlier than conspecifics wintering in poorer xeric habitats, but they arrived earlier on the breeding grounds (inferred from comparatively lower stable-carbon-isotope signatures in their pectoral muscle).

Stable isotope ratios in the environment vary according to several well-established processes and thus can be used as local habitat or broad-scale geographical markers in the study of migration (Hobson 1999). For example, the ratio of 13C: 12C (expressed as δ13C) in consumer tissues varies according to the proportions of C3, C4 and CAM plants within the foraging area (Hobson 1999). Tissues that remain metabolically inert after formation (e.g. feather or claw) will hold these habitat signatures indefinitely (Hobson & Clark 1992; Bearhop et al. 2002). Therefore sampling of claw material in spring can allow inferences to be made about winter habitat selection (Bearhop et al. 2003).

We examine whether seasonal interactions explain variability in the condition of black-throated blue warblers Dendroica caerulescens (BTBWs) during spring migration. Breeding in eastern North America, the BTBW is a small, insectivorous passerine that winters in the northern Caribbean. We predicted that birds in better condition during northwards migration had wintered in more mesic habitats (high-quality wintering sites). Thus, condition should be negatively correlated with stable carbon isotope signatures of claws, because low δ13C values tend to indicate more mesic habitats.

The BTBW is ideally suited to a study of this nature. Its breeding and wintering ecology are relatively well known (e.g. Sillet & Holmes 2002), studies have already reported values for δ13C in this species (Chamberlain et al. 1997; Rubenstein et al. 2002) and it has a relatively small wintering range almost entirely in the Greater Antilles with a small population in the Yucatan peninsula. This is beneficial, since changes in the proportions of C3, C4 and CAM plants produce large-scale spatial variation in δ13C (Still et al. 2003) and can confound smaller-scale habitat-specific signals when examining tissues synthesized away from the sampling site.

2. METHODS

We trapped 25 BTBWs on North Andros, Bahamas (24°50′N 77°53′W) in mist nets, during 2 days in April 2000 when adverse weather produced a ‘fall’ of migrant birds. Few birds were likely to have wintered locally, since no BTBWs were caught in the area on the 2 days preceding the fall and only one on the day following. Each individual was weighed (to the nearest 0.5 g) and measured (maximum wing chord, to the nearest millimetre). Subcutaneous fat reserves were estimated via examination of the tracheal pit using a six-point scale and birds were also assigned one of four pectoral muscle scores, both adapted from Redfern & Clark (2001). A length of claw (1–2 mm) was clipped from each individual. Bearhop et al. (2003) demonstrated that claws grow at ca. 0.04 mm d−1 and that there was no correlation between δ13C values of BTBW claw collected during the spring and those in tertials grown in the breeding season the previous autumn. Thus, claw tips in spring probably reflect winter habitat selection. The third tertial of one wing was also clipped by 4–10 mm in each individual. Since they were grown during the post-breeding moult, δ13C in these feathers reflects habitat selection during the previous (1999) breeding season.

To determine habitat-specific isotope signatures, claws were clipped from insectivorous thick-billed vireos Vireo crassirostris (TBV), a resident found in the same types of habitat as BTBWs.

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during winter. The size of TBVI home range is unknown, but a resident congener in the Yucatan is known to defend territories throughout the year (Greenberg et al. 1993). Samples were collected at multiple sites on three islands separated by almost 4° of latitude (Long Island: 22°52′ N, 74°58′ W; Andros and Abaco: 26°31′ N, 77°11′ W) and assigned one of two habitat types (scrub, with a high prevalence of xerophytic shrubs, and pine forest Pinus caribaea). To ensure that they were isotopically representative of the sampling habitat, claw δ¹³C of TBVIs from pine were compared with those collected from resident species found only in this habitat; Bahama yellowthroat Geothlypis rostrata, olive-capped warbler Dendroica pittispila, yellow-throated warbler Dendroica dominica (Bahamian subspecies only) and pine warbler Dendroica pinus. TBVIs were the only exclusively resident species captured in scrub.

Isotopic analyses of claws and feathers were conducted using the protocol described in Bearhop et al. (2003). Repeat analysis of an internal standard showed that δ¹³C can be measured with accuracy and a precision of 0.2 % or less.

Data from resident birds were analysed using a generalized linear model (GLM) with claw δ¹³C as the dependent variable, latitude of the sampling locality as a covariate and habitat as a factor (scrub or pine). A measure of ‘migratory condition’ was derived from a principal components analysis using the correlation between fat and muscle score. Principal component 1 (PC1) accounted for 85% of the variance and was selected as a condition index (factor loadings for fat and muscle score). Principal component 1 (PC1) was significantly related to δ¹³C (claw) (GLM, F₁,₁₂ = 16.48, p = 0.001). There was no significant relationship between δ¹³C of tertial feathers and migratory condition (F₁,₁₁ = 2.95, p = 0.11), with no significant association between age and migratory condition (F₁,₁₁ = 0.27, p = 0.61).

There was no significant relationship between δ¹³C of tertial feathers and migratory condition (F₂,₁₅ = 0.69, p = 0.414). Standard errors indicate that we could detect relationships with slopes of less than −0.039 or greater than 0.401 and, with a sample size of 25, relationships with r²-values as low as 0.15 would have been significant.

4. DISCUSSION

BTBWs that had wintered in habitats with lower δ¹³C signatures were in better body condition during migration with respect to fat reserves and pectoral muscle mass (figure 2), implying that individuals in better condition spent the winter in more moist forest habitats, as has been found in American redstarts (Marra et al. 1998).

There are two lines of complementary evidence to support our interpretation:

(i) stable isotope signatures in the claws of resident Bahamian birds, where TBVIs from relatively mesic pine forest had lower mean δ¹³C values (figure 1) than those caught in drier scrub;
(ii) studies of BTBWs in their wintering areas indicate that dominant individuals tend to displace subordinates from forest into scrub habitats (Wunderle 1995; Sherry & Holmes 1996).

By implication, mesic forest is the better wintering habitat for this species. The consequences for individuals wintering in sub-optimal habitats may be higher mortality or poorer condition (Marra et al. 1998; Sillet & Holmes 2002).

Studies have also shown that winter habitat segregation in BTBWs is often sex biased, with males dominant in primary forest and females and subordinates occupying drier scrub (e.g. Wunderle 1995). Indeed, in our analyses, males were in better condition than females, although we detected no direct effect of sex on winter habitat use as inferred from δ¹³C (possibly owing to lack of statistical power).

Birds in better condition during migration may benefit over conspecifics in several ways. First, these individuals probably have more resources to devote to reproduction when they arrive on the breeding grounds. However, it may also permit shorter inward migration times and earlier arrival on the breeding grounds, allowing access to the highest-quality territories. This is because birds in high migratory condition can spend less time refuelling during stopovers (Gannes 2002) or make longer continuous migration flights.

Marra et al. (1998) suggested that dominance-mediated habitat segregation during winter influences the time of arrival of American redstarts at breeding grounds and condition on arrival. Since individuals wintering in lower-quality habitats were in poorer breeding condition on arrival, winter habitat may be a limiting factor for this species. Our study provides evidence that such habitat forcing may also occur with BTBWs, suggesting that the results of Marra et al. (1998) have some generality for migratory Dendroica warblers.

However, it is important that we consider factors that may confound our interpretation. As we are inferring habitat selection remotely, we cannot directly demonstrate that the observed variation in condition is a consequence of differences in winter habitat use.

Variation in δ¹³C occurs as large-scale latitudinal trends, as well as local habitat-related variability owing to changes in the proportions of C3, C4 and CAM plants. Thus, the relationship shown in figure 2 could be a consequence of large-scale gradients in δ¹³C signatures, whereby sites further south in the wintering range have higher δ¹³C, independent of local habitat. In this scenario, birds in poorer condition during migration through the Bahamas would simply have been migrating for longer, from more Southerly wintering sites, and hence would have used up a larger proportion of their initial energy reserves. This is unlikely to be the case for two reasons.

(ii) studies of BTBWs in their wintering areas indicate that dominant individuals tend to displace subordinates from forest into scrub habitats (Wunderle 1995; Sherry & Holmes 1996).

However, large-scale longitudinal variability in δ¹³C may exist across the wintering range (Still et al. 2003). Since the birds were sampled in the central–northern part of the wintering range, the winter residence could have been in a range of longitudes further east. Breeding season δ¹³C values covary with wintering longitude (Rubenstein et al. 2002). In our study, there was no significant relationship between individual condition and δ¹³C values representative of the previous breeding season (from tertial feathers), despite considerable statistical power. The absence of any such relationship suggests that our observed results cannot be driven by large-scale longitudinal gradients. Moreover, breeding season δ¹³C also covaries with breeding latitude and thus the non-significant relationship also indicates that birds in better condition were not carrying more reserves because they had further to travel to their breeding areas.

Marra et al. (1998) demonstrated that winter habitat selection could influence fitness in migratory birds. Here, we have demonstrated a mechanism that may be one of the drivers of this phenomenon: variation in winter habitat results in systematic variation in condition during return migration. This in turn is likely to result in differences in arrival date at the breeding grounds and in condition on arrival, both of which influence fitness. This paper demonstrates the strong connectivity between wintering and breeding season ecology in many migratory species, and provides rare evidence of the applicability of the seasonal interaction ideas of Fretwell (1972) to migratory birds. Our research emphasizes the need to consider winter ecology and habitat use in population models and ultimately in conservation management of such species.

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