BLACKPOLL WARBLER (*DENDROICA STRIATA*) FAT DEPOSITION IN SOUTHERN NOVA SCOTIA DURING AUTUMN MIGRATION

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ABSTRACT — There is considerable evidence that the Blackpoll Warbler (*Dendroica striata*) undertakes a non-stop, transoceanic, fall migration from New England and Atlantic Canada to South America. However, this unique migration strategy is not yet clearly understood. Based on flight range estimates, Blackpoll Warblers must require large amounts of fat for this flight. I captured Blackpoll Warblers during fall migration on Bon Portage Island, a small island off southern Nova Scotia, to determine if Blackpoll Warblers either arrive with, or remain on the island and deposit, the large fat reserves necessary for their migration. Most Blackpoll Warblers did not arrive at Bon Portage with sufficient fat reserves to complete transoceanic migration from Nova Scotia to South America. Furthermore, although young Blackpoll Warblers did show moderate rates of diurnal fat deposition while on Bon Portage, most did not remain long enough to accumulate the necessary fat reserves for transoceanic migration. I conclude then, that Bon Portage Island is not one of the final sites for Blackpoll fat deposition, and I discuss several possible explanations for these results.

INTRODUCTION

The migration of landbirds over the western Atlantic coast has been studied in great detail using weather radar (e.g., Able 1974; Drury and Nisbet 1964; Richardson 1972, 1976, 1978a, 1978b, 1980; Williams et al. 1977). Thus the general patterns of migration in this area are well documented. Using radar, Richardson (1972, 1976, 1980) found that the majority of fall migrants fly southwest, approximately parallel to the northeast-southwest axis of eastern North America (see Fig. 1). Similar orientation has also been observed in landbird migrants over northern New England (Drury and Keith 1962). A smaller group of landbird migrants migrate in a mainly south-southeast direction from Nova Scotia and New England (Richardson 1972, 1976, 1978a, 1978b, 1980; Williams et al. 1977; Williams and Williams 1978; see Fig. 1), and are the subject of my study.

The trajectory of the smaller group of landbirds upon departure from Nova Scotia and New England implies that they make a non-stop,

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"transoceanic" flight over the Atlantic Ocean to their wintering grounds in South America (Richardson 1972, 1976). In Nova Scotia, transoceanic migrants usually departed from all land areas of the province. Some individuals initiated the flight from as far north as New Brunswick and continued flying past the southern tip of Nova Scotia. However, few birds began the flight from more than 150 km inland from the coast of New Brunswick or Maine (Richardson 1976). The Blackpoll Warbler is currently the only species that most authors agree to be a transoceanic migrant (Nisbet et al. 1995, but see Murray 1989). The evidence for this is mostly indirect, but substantial (summarized by Nisbet et al. 1995).

Blackpoll Warblers must require large amounts of fat, which is used as fuel during migration, to allow a transoceanic migration initiated from Nova Scotia. Based on calculations by Pennycuick (1975), a bird the size of a Blackpoll Warbler (approx. 10-12 g fat-free) would need approximately 50% of its body weight as fat to make a non-stop flight (in still air) of over 3000 km. This may be an overestimate of the fat required by Blackpolls departing from Nova Scotia, since these birds are able to exploit moderately strong tailwinds during flight (Richardson 1972, 1976). Nonetheless, from Nova Scotia to the northernmost coast of South America is over 4000 km, so a value of 50% may be at least close to the actual amount required. Furthermore, based on his radar observations, Richardson (1976) also suggested that Blackpolls may require as much as 50% of their body weight when they depart from Nova Scotia. This is equivalent to approximately 5-6 g of fat for a 10-12g Blackpoll Warbler. In addition, by examining Blackpoll Warbler

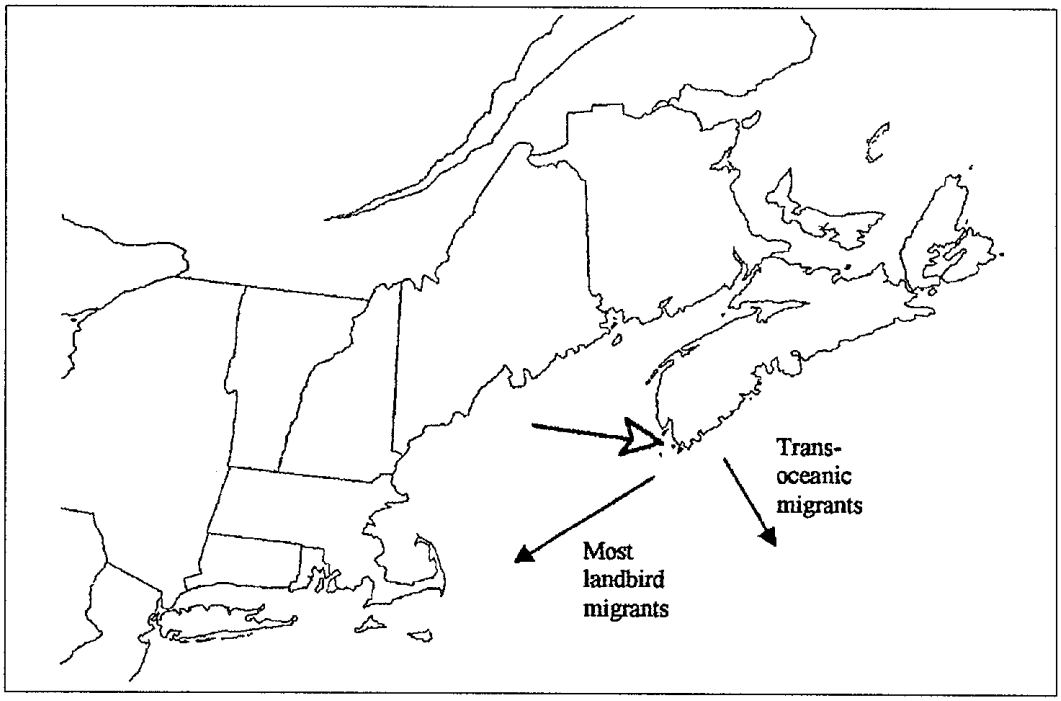

Figure 1. General directions of fall migration in Atlantic Canada. Location of Bon Portage island also shown (open arrow).

weights, Nisbet et al. (1963) found that Blackpoll Warblers left Massachusetts after fattening to 20-23 g. Therefore, it is not unreasonable to assume that Blackpolls need to be approximately 20 g or more to make a transoceanic flight from an area on the north Atlantic coast.

Blackpoll Warblers, like all migrants, require areas where they can feed and deposit fat along their migration routes. Whether a species deposits fat at a site is commonly used as an index of the site quality for the species in question (e.g., Dunn 2000). Furthermore, a site can be suitable for mass gain by certain species but not others (e.g., Davis 1999, Morris et al. 1996), probably because of the species' differences in habitat or food preferences during migration. Identifying important fattening sites for landbirds along their migration routes has recently received much attention (Davis 1999, Dunn 2000, Morris et al. 1994, Winker et al. 1992, Winker 1995, Yong et al. 1998). Blackpoll Warbler stopover sites have been studied in the northeastern United States (Drury 1979, Nisbet et al. 1963), and in the Dominican Republic (Latta and Brown 1999). However no sites in Atlantic Canada, where Blackpolls would be in the earlier stages of their migration, have been studied.

Bon Portage Island, located approximately 3 km off the southwestern shore of Nova Scotia (Fig. 1), is an ideal site to study the fat deposition of Blackpoll Warblers before the start of their main overwater flight. Since Richardson (1972, 1976) showed that transoceanic migrants fly south to southeast in southern Nova Scotia, Bon Portage may represent at least one of the last land areas where they can stop to either rest or deposit fat. Blackpolls may then use the island as a final stopover site before the main transoceanic flight. If so, then Blackpolls captured on Bon Portage may either have already accumulated the large fat reserves necessary for this flight, or they may remain on Bon Portage until they have accumulated the necessary fat reserves. I captured and examined the fat deposits of Blackpoll Warblers during stopover on Bon Portage Island, to determine which, if either, of these two descriptions is true.

STUDY SITE AND METHODS

Study Site

Bon Portage Island (43°28'N, 65°44'W), is a 150 ha island situated approximately 3 km off the southwestern tip of Nova Scotia (Fig. 1). It is one of two sites that make up the Atlantic Bird Observatory, the other being Seal Island, which is approximately 10 km southwest of Bon Portage Island. Bon Portage is elongated, being 600 m wide and 3 km long, with an overall north-south orientation (Johnson 1984). The island has two forested sections separated by a floating bog. Bon Portage is forested with white spruce (*Picea glauca*), black spruce (*P. mariana*), and balsam fir (*Abies balsamea*), with some mountain ash (*Sorbus*

americana) and white birch (*Betula papyrifera*). Along the edge of the forest on the eastern side of the island are small stands of speckled alder (*Alnus rugosa*). A fire burned across a section on the southern end where there is now new vegetation with wild raisin (*Viburnum cassinoides*) and various other small shrubs. In the early 1980s, there was an infestation of hemlock looper (Order Lepidoptera, *Lambdina fiscellaria*), which caused a dramatic change in the vegetation of certain areas of Bon Portage Island (R. Milton, pers. comm.). In these areas, most of the forest softwood is now dead, creating openings in the once-dense evergreen canopy. The early successional forest floor in these areas is composed of small hardwood saplings such as white birch and mountain ash, mixed in with dense patches of Canada yew (*Taxus canadensis*) and raspberry (*Rubus* sp.).

Field Methods

From 12 August to 2 November in 1995, and from 12 August to 20 October in 1996, a set of standard 12 m x 2.5 m, 30 mm mesh, nylon mist nets was operated daily on Bon Portage Island. The number of nets operated each day varied with the weather conditions (e.g., exposed nets were not opened on days with high winds, and none were opened during rain), with at least 12 nets operated on most days and up to 21 nets when feasible. Nets were opened by 20 minutes after sunrise, and operated continuously for 5 hours in 1995 and 6 hours in 1996. In the fall of 1995, I conducted all of the banding myself, but was helped by two field assistants in 1996.

Each open net was checked at intervals of no longer than 30 minutes. Birds were removed from the nets, placed in cloth bags, transported to a central banding laboratory, processed and released. Processing entailed the following: each bird was banded with an aluminum USFWS leg band, aged, sexed (according to Pyle et al. 1987), weighed, had its unflattened wing chord measured, and was assigned a 0-5 fat score following Helms and Drury (1960). This fat scoring system was recorded as follows: "0" = no visible trace of fat showing in the bird's furcular hollow; "1" = a trace of fat showing in the furculum; "2" = furcular hollow half-filled or more; "3" = fat just filling furculum; "4" = fat overflowing furculum and continuous with abdominal fat; and "5" = furculum, abdomen and "armpits" completely filled and continuous. All birds were aged by skulling, whereby hatch-year birds are identified based on partially ossified skulls, following Pyle et al. (1987). Further, for all birds the interval between net extraction and release was approximately 40 minutes. So as not to bias observations, all recaptured birds were processed exactly the same as initially captured birds without referring to the original capture data.

In 1995, Blackpoll Warblers were weighed using a 50 g Pesola spring scale (with 0.5 g graduations) and their weight was estimated to the nearest 0.25 g. In 1996, an electronic balance was used and all weights were recorded to the nearest 0.1 g. Since two methods were used to measure the weights of Blackpolls, I tested for differences between these two methods *a posteriori* by weighing 35 objects, of weights varying between 5 g and 50 g, with both scales. A paired t-test revealed a significant difference between the two methods of measurement ($t=2.14$, $df=34$, $p=0.03$). Thus, in the analysis of Blackpoll Warbler weights where the data from both years were pooled (below), I included a dichotomous dummy variable to account for this difference. Unfortunately, using a different weighing method each year means that I could not control for possible effects of annual variation on the weights of migrants.

There is evidence that some species display sex-related differences in stopover ecology (e.g., Morris et al. 1996, Yong et al. 1998). Unfortunately, it was rarely possible to sex hatch-year or even after-hatch year Blackpoll Warblers in the hand on Bon Portage. Thus, examination of sex-specific differences in Blackpoll fat deposition on Bon Portage was not possible.

Fat deposition analysis

To determine if a species deposits fat while at a stopover site, the weights of recaptured individuals at final capture are compared to those at first capture using one-tailed, paired t-tests (e.g., Morris et al. 1994). However, too few Blackpoll Warblers were recaptured in this study for such an analysis. Therefore, to determine the extent of daily fat deposition by Blackpoll Warblers on Bon Portage, I used a linear regression method similar to Winker et al. (1992). Winker et al. (1992) proposed that a bird that gains weight at a site should show a positive relationship between weight and time of capture. This method allows all birds to be analyzed, no matter how many were recaptured. However, Winker (1995) also found that there were significant positive relationships between body size (indicated by wing and tail measurements) and time of day. This was a bias that Winker et al. (1992) did not consider. Nor did Winker et al. (1992) account for the effects of seasonal variability in the weights of migrants.

To determine the relationship between weight and time of capture (i.e., to determine if Blackpolls gain weight during the day), I used a modification of the method of Winker et al. (1992). I performed a forward stepwise linear regression where I first had as explanatory variables wing length (to account for effects of body size on weight), date of capture (to account for any variation in the weights of migrants

within a season; in number of days since Jan. 1) and a dichotomous dummy variable to account for the differences in weighing methods. I then forced time of capture into the model. In 1995, individuals that did not have their wing chords measured were excluded. All p-values in these regressions were adjusted for multiple tests using a sequential Bonferroni technique following Rice (1989).

In all tests in this study, significance was accepted when $p < 0.05$.

RESULTS

A total of 245 Blackpoll Warblers was captured on Bon Portage in 1995 and 1996 combined. Blackpoll Warblers were the second most numerous species captured on Bon Portage, with Yellow-rumped Warblers (*Dendroica coronata*) the most frequently captured (Table 1). Of the total Blackpolls, there were 54 known after-hatch year (AHY), 142 known hatch-year (HY), and 49 individuals that could not be accurately aged. Of these, only 4 HY individuals were later recaptured, while no AHY birds were later recaptured. Three of the recaptured HY individuals were recaptured 1 day after initial capture, while the fourth was recaptured later the same day. This lack of recaptures and the short stopover length of the few recaptured individuals both suggest that most Blackpoll Warblers did not remain longer than 1 day on Bon Portage.

The sample sizes of both HY and AHY birds were large enough to allow for separate examinations of the fat reserves of each of these age classes. There was no significant difference between the average weights of AHY birds and HY birds in 1995 (two-tailed t-test, $n = 89$, $p = 0.510$; Table 2). However, in 1996 there was a significant difference in average weight between the age classes (two-tailed t-test, $n = 106$, $p = 0.041$). The lack of a difference in weights in 1995 may have been because the pesola

Table 1. Capture totals of the 10 most abundant species on Bon Portage in 1995 and 1996 combined.

Common Name	Latin Name	N
Myrtle Warbler	*Dendroica coronata*	545
Blackpoll Warbler	*Dendroica striata*	245
Red-eyed Vireo	*Vireo olivaceus*	163
Golden-crowned Kinglet	*Regulus satrapa*	147
White-throated Sparrow	*Zonotrichia albicollis*	126
Northern Waterthrush	*Seiurus noveboracensis*	110
Black-and-white Warbler	*Mniotilta varia*	109
Black-throated green Warbler	*Dendroica virens*	94
Yellow-bellied Flycatcher	*Empidonax flaviventris*	88
Magnolia Warbler	*Dendroica magnolia*	71

scale used that year was not sensitive enough. The 1996 difference (when an electronic balance was used), however, may suggest age-related differences in foraging abilities or migration strategies, and justifies examining each age class separately.

In both age classes, the majority of Blackpolls captured on Bon Portage did not appear to be already carrying large fat reserves. The distribution of original weights (i.e., not corrected for size of birds) of known AHY and known HY birds is graphed in Figure 2. From these distributions it is evident that the majority of individuals of both age classes on Bon Portage weighed between 10 and 14 g, while few individuals of either age class weighed above 18 g (Fig. 2). Furthermore, the average weight of Blackpolls that were assigned 0 fat scores (i.e., individuals with no visible fat reserves) was 11.25g (± 0.29g) for AHY birds and 10.81g (± 0.25g) for HY birds (Table 3). Thus, the majority of Blackpolls that were captured on Bon Portage did not weigh substantially more than those that had little or no visible fat reserves.

Table 2. Summary of Blackpoll Warbler weights by age class and year.

Year	Age	N	Mean Weight (g)	Standard Deviation
1995	AHY	31	11.59	2.29
	HY	58	11.28	1.99
1996	AHY	23	13.91*	2.29
	HY	83	12.95	1.94

* Significant difference ($p < 0.05$) between AHY and HY weights.

Table 3. Average weights of AHY (top) and HY (bottom) Blackpoll Warblers in each fat class on Bon Portage Island in 1995 and 1996 (pooled).

Fat Score	N	Average Weight (g)	Standard Error (g)
0	8	11.25	0.29
1	12	11.05	0.32
2	14	11.74	0.35
3	11	12.52	0.66
4	4	16.85	0.64
5	4	17.43	0.72

Fat Score	N	Average Weight (g)	Standard Error (g)
0	20	10.81	0.25
1	34	11.30	0.23
2	50	11.73	0.16
3	14	12.71	0.36
4	14	15.03	0.36
5	9	17.09	0.64

In the multiple regression analyses of Blackpoll Warbler weights, there was a significant effect of year ($p < 0.001$), but after correcting for multiple tests, there was no significant effect of time of day ($p = 0.144$) on the weights of AHY Blackpoll Warblers ($n = 40$, $r^2 = 0.465$, $p < 0.001$). Adult Blackpolls then, did not appear to be depositing fat on Bon

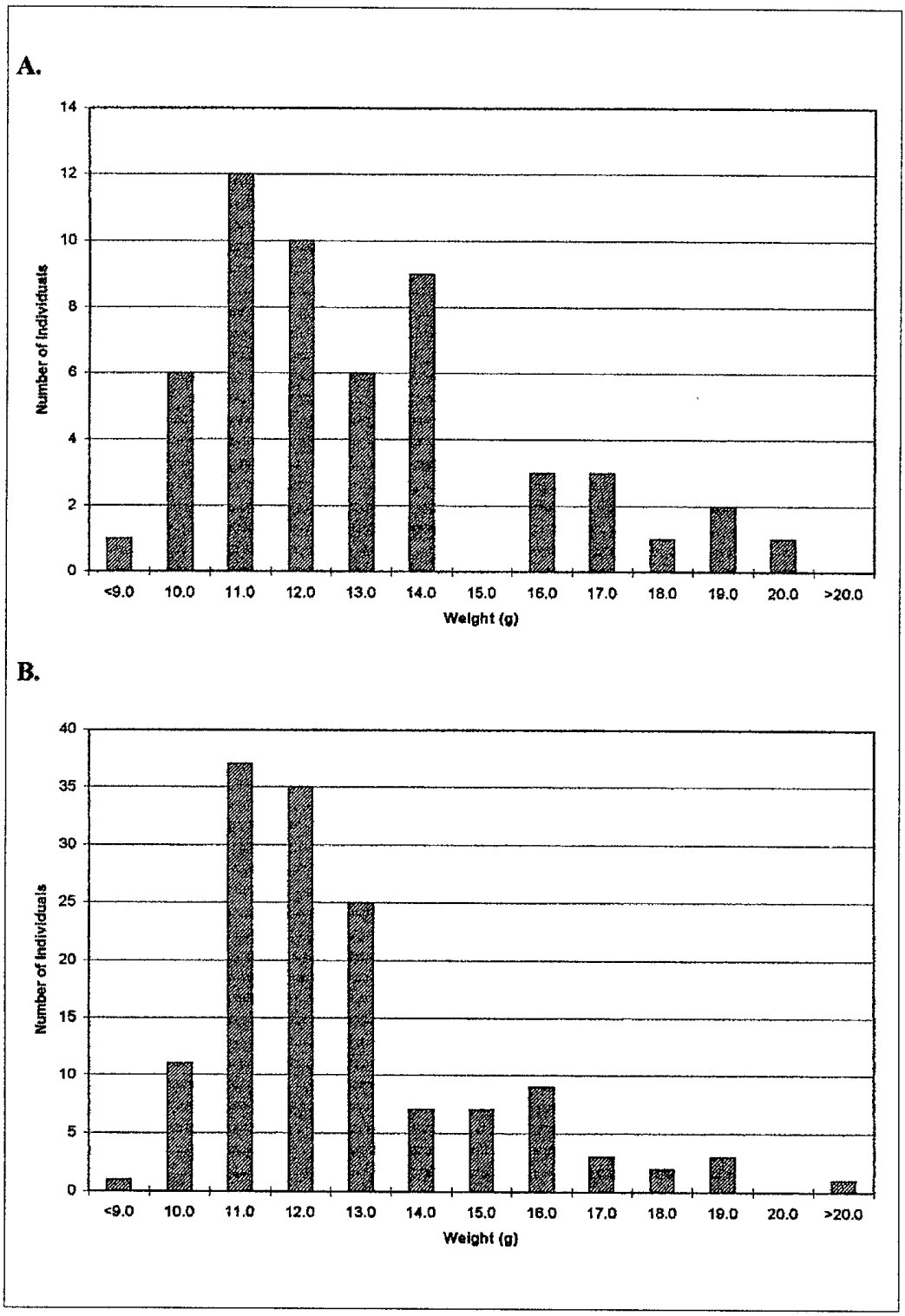

Figure 2. Distribution of known after-hatch year (A.) and known hatch-year (B.) Blackpoll Warbler original weights on Bon Portage in 1995 and 1996 (pooled).

Portage (Fig. 3A). The same analysis of HY individuals resulted in significant effects of date ($p < 0.001$), year ($p < 0.001$), wing ($p = 0.002$), and time ($p < 0.001$) on weight ($n = 101$, $r^2 = 0.495$, $p < 0.001$). For HY birds, the significant effect of time indicates that there was a tendency to catch heavier birds later in the day, suggesting that indi-

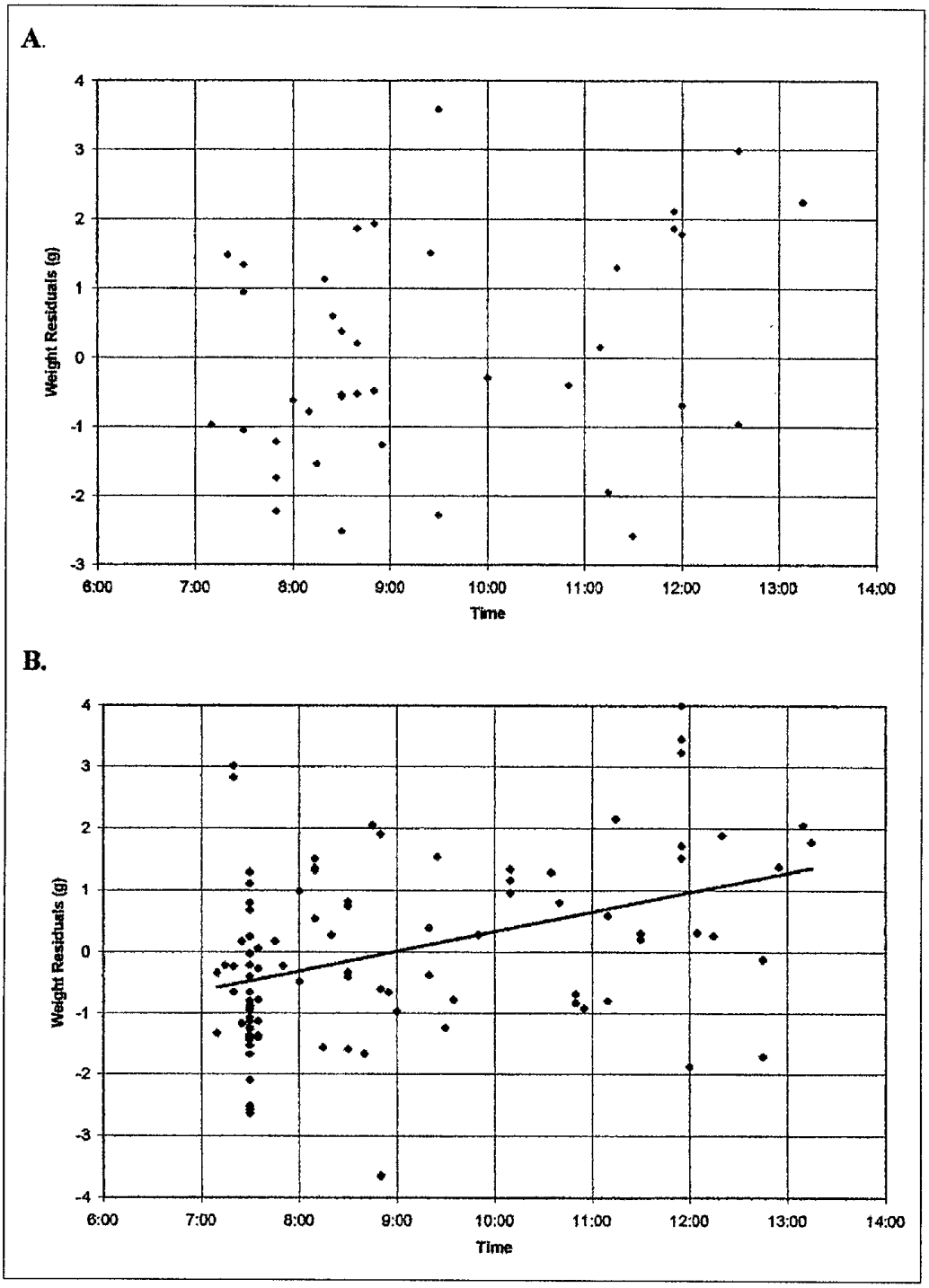

Figure 3. Weights (regression residuals shown) of known after-hatch year (A.) and known hatch-year (B.) Blackpoll Warblers on Bon Portage in 1995 and 1996 (pooled). Trend line is shown in 3B indicating a significant positive effect of time.

viduals were depositing fat during the day (Fig. 3B). However, the short stopover lengths I observed suggest that most individuals did not stay long enough to deposit substantial amounts of fat.

In summary, most Blackpoll Warblers apparently did not deposit sufficient fat reserves on Bon Portage Island for transoceanic migration departing from Nova Scotia. The majority of individuals captured did not appear to be already carrying the large fat reserves I estimated to be necessary for transoceanic migration.

DISCUSSION

Young Blackpoll Warblers appeared able to deposit fat on Bon Portage. In Fig. 3B the residuals from the multiple regression model are used to illustrate the diurnal weight gains. The slope of the trendline for HY birds indicates weight gains of approximately 2 g per day. If I consider this value as a rough estimate of the rate of fat deposition HY Blackpolls are capable of on Bon Portage, then it appears that HY Blackpoll Warblers may have been capable of depositing the required amount of fat on Bon Portage in only a few days. The few recaptured HY individuals, however suggest that most did not stay long enough to do so.

Adult Blackpolls did not appear to deposit fat on Bon Portage. However, although not significant after adjusting for multiple tests, the p-value of 0.144 does indicate a slight tendency to catch heavier individuals later in the day. The sample size ($n = 40$) of known adult Blackpolls (with wing chord measurements) may not have been large enough to determine if an effect were present. Alternatively, it may be that adult Blackpolls differ in either their migration strategy or fat-depositing from young Blackpolls. Future study and additional data from Bon Portage may help to elucidate which of these cases is true.

If any Blackpolls were using Bon Portage as a fattening site as in Nisbet et al. (1963), then I should have observed higher recapture rates; if most individuals were present over several days, the probability of recapture would be higher. There is the possibility that some Blackpolls did stay long enough to deposit sufficient fat stores, and simply never were recaptured. Nevertheless, this is inconsistent with what I observed while banding each fall. When I observed large numbers of Blackpoll Warblers on the island, mist net captures were high, and when few or no individuals were captured, I did not see large numbers of Blackpolls in any other areas on the island.

The fact that most Blackpoll Warblers that stopped on Bon Portage did not appear to remain and deposit the large amounts of fat needed for their transoceanic migration, nor were they already carrying these fat

reserves, was unexpected. Since it is known from radar studies that at least some migrant landbirds (presumably Blackpoll Warblers) commence their transoceanic flight from southern Nova Scotia (Richardson 1972, 1976), I expected that Bon Portage Island would be one of the final fat deposition areas for this species, and I would therefore encounter many fat Blackpoll Warblers on the island, or many individuals lingering and fattening. However, that was not the case. Since Nisbet et al. (1995) provided convincing evidence for the transoceanic migration of Blackpolls, I therefore suggest that Bon Portage Island is not one of the final fat-deposition sites for Blackpolls before their main transoceanic flight. Bon Portage may simply be a rest area for Blackpolls on their way to an area where they are able to remain and deposit the necessary fat reserves.

The above statement raises an important question: if Bon Portage Island is not one of the final fat deposition sites for Blackpolls in southern Nova Scotia, then where, if anywhere, are the final sites in Nova Scotia? One possible explanation is that there are none, at least in southern Nova Scotia. The transoceanic migrants observed via radar over Nova Scotia (Richardson 1972, 1976) may have initiated their flight from farther inland and continued past Bon Portage. Richardson (1976) observed many such departures from as far inland as the coast of New Brunswick. These birds flew south, over the southern coast of Nova Scotia and continued out to sea, without changing course. If this is true, however, what becomes of those Blackpolls that land on Bon Portage? One possibility is that Blackpolls depart Bon Portage and then fly southwest to areas in New England where they then put on the fat they need. From radar observations, it is known that a large number of landbirds depart southern Nova Scotia and fly across the Gulf of Maine (Richardson 1972, 1976). It may be that some of these landbirds are also Blackpoll Warblers that originated from Bon Portage, which are heading to more favorable stopover areas, such as those described by Nisbet et al. (1963).

Alternatively, if Blackpoll Warblers do require a stop in southwestern Nova Scotia to fatten before their main transoceanic flight, it may be that upon their arrival at Bon Portage Island, they find that it is not suitable for depositing large amounts of fat. This could explain why the majority of Blackpolls do not remain long on Bon Portage. In support of this idea, Nisbet et al. (1963) found that some immature Blackpoll Warblers tended to settle in marginal habitats where they deposited fat more slowly. These individuals then departed their study site in Massachusetts weighing between 13.5 and 19.5 grams. This may also be the case on Bon Portage. The difference in HY and AHY average weights and the diurnal weight gains of HY but not AHY birds on Bon Portage

does suggest age-related differences in migration patterns at this site. Although HY Blackpolls may be able to remain on the island and deposit small amounts of fat, they may do so at a sub-optimal rate. However, it is not known whether this suboptimal fattening rate causes Blackpolls to depart with insufficient fat for their migration, or if they simply move to an area where they can deposit more adequate fat loads.

At Island Beach, New Jersey, Murray (1979) also found that very few Blackpolls departed that site with sufficient fat stores for a transoceanic flight. Murray (1979, 1989) interpreted this as partial evidence against the idea that Blackpoll Warblers complete a transoceanic flight. However, the evidence for Blackpoll Warblers making a transoceanic flight is substantial (Nisbet et al. 1995), which is why I suggest that Bon Portage is not one of the the final stopover areas for Blackpoll Warblers before their transoceanic migration. Future explorations of other areas in southern Nova Scotia may reveal areas where Blackpolls remain for longer periods than on Bon Portage, and where they gain the necessary amounts of fat. If no such areas are found, it may be that Blackpoll Warblers find a suitable area to deposit the necessary fat reserves on the other side of the Gulf of Maine.

Understanding the migration strategies of long-distance migrants such as Blackpoll Warblers is an important step in understanding their complete life-cycle. Specifically, knowledge of their migration routes will help to determine the locations of important stopover areas, which may be crucial to this species in particular. All landbirds, especially long-distance migrants, require places along their migration routes where they can not only stay and deposit fat, but also simply rest for short periods, as Blackpoll Warblers do on Bon Portage Island. However, because of its long overwater migration strategy, Blackpoll Warblers presumably use certain key fattening sites before the main overwater flight begins. Such places need to be identified and studied so that we can determine if conservation measures, for this species in particular, are warranted.

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