# BODY SIZE, BREEDING HABITAT, AND WINTER EXPLOITATION SYSTEMS IN *DENDROICA*

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ABSTRACT.—Body size varies considerably among species of *Dendroica*. Larger species are nearly restricted to breeding in coniferous forests and woodlands. Among the largest warblers are species breeding in taiga and species specializing, at least in eastern North America, on spruce budworm outbreaks. On the wintering grounds large coniferous breeders may often display features of opportunistic exploitation systems: intraspecific gregariousness and labile foraging behavior. A detailed comparative study of *Dendroica pensylvanica* and *D. castanea* supports this general conclusion. Small body size is probably an adaptation to specialized foliage insectivory. If conifer foliage is easily exploited, if insect abundance cannot support specialization on foliage insects, or if food often occurs in abundant, easily used patches, then larger body size may evolve in response to counterselective factors. These factors might include resistance to starvation or cold stress. I propose that current coniferous-restricted species are members of species groups that evolved in association with coniferous forest, first as residents and later as migrants. Migration evolved in response to late Tertiary and Quaternary climate cooling. Perhaps generalist coniferous-breeding *Dendroica* were preadapted for roles as opportunists on their wintering ranges. *Received 20 October 1978, accepted 8 June 1979.*

THE 16 species of the genus *Dendroica* breeding in eastern North America are similar in basic body plan. Within this group ecological divergence has been thought to be largely behavioral. Bill dimensions are strikingly similar for syntopic species (MacArthur 1958, Schoener 1965), although small variations in bill length may occasionally be important (Ficken et al. 1968).

Still, given the diversity in habitat selection and microhabitat use on the breeding range, some significant interspecific variation in morphology should occur. In addition, *Dendroica* differ in many aspects of their winter exploitation systems, and this should also select for divergent morphology. In this paper I will explore the relationship between body size, as indicated by skeletal measurements, and foraging style, habitat selection, and winter exploitation systems in eastern *Dendroica*. I will examine basic models of speciation and distribution changes to see whether breeding or wintering ground factors seem primarily responsible for the observed suites of characters.

## METHODS

I measured skeletons of 178 males (7–15 per species) of 16 species of eastern *Dendroica*. Specimens were broadly distributed geographically to minimize the effects of geographic variation within species. I measured bony wing length (excluding the manus, which was often broken) and sternum length. These measurements will be used to index core body size. Ideally, fat-free weight should be used, but lacking these data for most of the species, these two skeletal measurements are probably an adequate substitute. Sternum length is a linear measurement of a large portion of the body cavity, and both wing bones and sternum support the mass of flight muscles that constitute a large portion of the total body weight.

I compiled information on breeding habitats and winter ecology of *Dendroica* from a search of available literature. I also briefly summarize data I have gathered on *D. pensylvanica* and *D. castanea* in Panama during the winter from December 1976 to May 1979.

## RESULTS AND DISCUSSION

*Body size variation.*—*Dendroica* vary considerably in sternum length, from *D. discolor* (1.07 cm) to *D. kirtlandii* (1.37 cm). Bony wing length ranges from 2.88
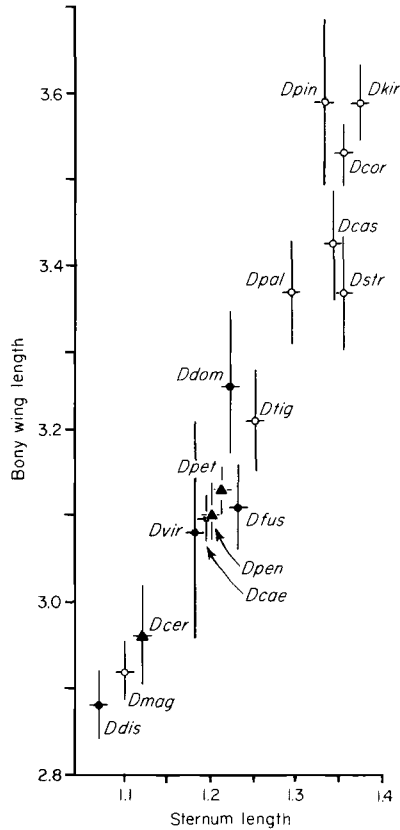
Fig. 1.   Regression of bony wing length on sternum length. Y = .77 + 3.23X. Symbols indicate mean values, and lines encompass two standard errors. (▲) are deciduous forest breeders; (●) are mixed decid-uous-coniferous forest breeders, and (○) are coniferous forest breeders. (See text for explanation of habitat classes.) Abbreviations: *D. caerulescens* =Dcae (n = 14), *D. castanea* = Dcas (n = 13), *D. cerulea* = Dcer (n = 7), *D. coronata* = Dcor (n = 14), *D. discolor* = Ddis (n = 9), *D. dominica* = Ddom (n = 11), *D. fusca* = Dfus (n = 12), *D. kirtlandii* = Dkir (n = 8), *D. magnolia* = Dmag (n = 14), *D. pal-marum* = Dpal (n = 10), *D. pensylvanica* = Dpen (n = 12), *D. petechia* = Dpet (n = 13), *D. pinus* = Dpin (n = 8), *D. striata* = Dstr (n = 12), *D. tigrina* = Dtig (n = 12), and *D. virens* = Dvir (n = 10).

cm in *D. discolor* to 3.57 cm in *D. pinus* and *D. kirtlandii.* Sternum length is highly correlated with bony wing length interspecifically (Kendall's $\tau$ of species means = 0.91, $P < 0.001$). These two variables define a size gradient for the species of *Den-droica* (presented in Fig. 1) that will be related to breeding habitat and winter exploitation systems.

*Breeding habitats.*—I separated the *Dendroica* species into three breeding habitat classes: deciduous forest and scrub, coniferous forest, and mixed (use of both decid-uous and coniferous habitats). I based the classifications (Fig. 1) largely on Mengel (1964), supplemented with additional information from Todd (1940), Kendeigh (1945), Brooks (1947), Griscom and Sprunt (1957), Burleigh (1958), Stewart and Robbins (1958), and Mengel (1965). Those species that Mengel (1964) designated as restricted taiga breeders I consider to be in the coniferous group, with two additions: *D. pinus,* which is restricted to pine forests within the deciduous forest biome, and

TABLE 1. The comparative behavior of two tropical wintering *Dendroica* species.

| Behavior | *D. pensylvanica* | *D. castanea* |
|---|---|---|
| Dominant foraging substrate | Leaf bottoms | Leaf tops |
| Foraging strata | Mid-level | Variable and seasonal |
| Ground foraging | Never | Rare |
| Frugivory | Rare (wet season), uncommon (dry season) | Uncommon (wet) common (dry) |
| Search behavior | Branch changes common | Rapid creeping |
| Single-species flocking | Extremely rare | Common; 2–25 individuals |
| Mixed-species flocking | Persistent, mainly with antwrens | Fairly common, more common in dry season; often in canopy flocks. |
| Spacing behavior | Small exclusive home-ranges | Large overlapping home-ranges (?) |

*D. magnolia,* which is only rarely found away from coniferous forests or woodlands or the coniferous understory of mixed forest. The mixed group has several species that have populations that are restricted to coniferous forests but occupy deciduous or mixed mesophytic habitats in some portion of the breeding range. Several boreal spruce or spruce-hemlock species (Erskine 1977), including *D. fusca* and *D. virens,* can be found to varying degrees in nonconiferous habitats in the Appalachian Mountains or southeastern lowlands (Todd 1940, Kendeigh 1945, Brooks 1947, Mengel 1964, 1965). *Dendroica dominica* also shows strong geographic variation in habitat selection (Mengel 1965, Ficken et al. 1968); some populations (such as *D. dominica stoddardi* and *D. d. flavescens*) may be restricted to pine forests.

One more comment concerning breeding habitat use is necessary. The boreal forests are often occupied by both coniferous and mixed *Dendroica* species (Kendeigh 1945, MacArthur 1958, Morse 1976a, Erskine 1977); several species classified in the mixed group are actually found predominantly in these forests. The coniferous and the mixed group contrast, however, in several ways in their basic ecological relations. The coniferous species can be characterized in one of the following two ways. First, species (with the exception of *D. magnolia*) tend to occupy the low diversity portions of the boreal forest, such as taiga (low stature spruce savannah) or bogs [*D. striata, D. coronata,* and *D. palmarum* (Erskine 1977)]. Where *D. coronata* occurs in the more species-rich southern boreal forest, it has large territories and is an opportunistic species fluctuating in abundance inversely with behaviorally dominant and more stereotyped warblers such as *D. virens* and *D. magnolia* (Morse 1976a). Second, species exploit gradations of the spruce budworm (*Chirostoneura fumiferana*) (Kendeigh 1945, Morris et al. 1958, MacArthur 1958, Erskine 1977). This includes *D. castanea* and *D. tigrina,* although *D. fusca* may show a numerical response to an outbreak (Morris et al. 1958, Erskine 1977). The mixed species, *D. virens, D. fusca,* and *D. caerulescens,* are restricted to the southern portion of the boreal forest, which is structurally and floristically diverse (Erskine 1977), and where at least the first two species act as microhabitat specialists (Morse 1971).

*Body size and breeding habitats.*—Variation in body size is strongly related to breeding habitats. In the basic size gradient presented in Fig. 1, the coniferous *Dendroica* are generally larger than species of the other two habitat groups, which themselves are indistinguishable. The exception to this relationship is *D. magnolia,*

TABLE 2. Opportunistic foraging behavior in wintering *Dendrocia*.

| Species | | Opportunistic foraging behavior | Reference |
|---|---|---|---|
| *D. caerulescens* | | None | Lack and Lack 1972, Emlen 1978 |
| *D. castanea* | C[a] | Ground foraging, limb foraging, frugivory | pers. obs. |
| *D. coronata* | C | Ground foraging, sallying, limb foraging, nectivory, frugivory | MacArthur 1958, pers. obs. |
| *D. discolor* | | None | Lack and Lack 1972 |
| *D. dominica* | | None | Lack and Lack 1972 |
| *D. fusca* | | None | Chipley 1974 |
| *D. kirtlandii* | C | Ground foraging, limb foraging | Ficken and Ficken 1962, Mayfield 1960 (not wintering data) |
| *D. magnolia* | | None[b] | pers. obs. |
| *D. palmarum* | C | Nectivory, ground foraging | Lack and Lack 1972, Emlen 1978 |
| *D. pensylvanica* | | None[b] | pers. obs. |
| *D. petechia* | | None[b] | Lack and Lack 1972, pers. obs. |
| *D. pinus* | C | Ground foraging, sallying, limb foraging | J. Greenberg (pers. comm.) |
| *D. striata* | C | Ground foraging | Meyer de Schauensee and Phelps 1978 |
| *D. tigrina* | C | Nectivory and frugivory | Bond 1957, Eaton 1953, Lack and Lack 1972 |
| *D. virens* | | None[b] | pers. obs., Lack and Lack 1972 |

[a] Coniferous group.
[b] Rarely frugivorous.

which has a small body size and is almost completely restricted to coniferous forest. One quality that distinguishes *D. magnolia* from other species restricted to breeding in coniferous forest is that it may have more restricted microhabitat preferences (Morse 1971).

*Winter exploitation systems.*—I studied in detail the overall exploitation systems of the large coniferous-breeding *D. castanea* and the smaller deciduous scrub-breeding *D. pensylvanica* where they winter together in central Panama. A suite of characters distinguishes the winter behavior of these two species (Table 1). *Dendroica castanea* is less agile and switches from foliage insectivory to bark insectivory and frugivory more readily. *Dendroica castanea* appears to have large overlapping home-ranges and often occurs in flocks of up to 25 individuals. In contrast, *D. pensylvanica* is almost invariably solitary and occupies small territories throughout the winter.

While the subtleties of winter exploitation systems require careful study, certain pivotal features of winter behavior may be examined more generally. These features include the lability of winter foraging behavior and intraspecific gregariousness. From the fragmentary data reviewed below, an intriguing pattern emerges. Species that are opportunistic and gregarious have large bodies and are restricted to breeding in coniferous forests. *Dendroica magnolia,* the small coniferous breeder, seems to behave like other small *Dendroica*.

If foraging opportunism is operationally defined to be the incorporation of tactics

TABLE 3. Occurrence of single-species flocks of wintering *Dendroica*.

| Species | | Single-species flocks common | Reference |
|---|---|---|---|
| *D. caerulescens* | | no? | Eaton 1953 |
| *D. castanea* | C[a] | yes | pers. obs. |
| *D. coronata* | C | yes | pers. obs. |
| *D. discolor* | | ? | |
| *D. dominica* | | ? | |
| *D. fusca* | | no | Chipley 1974 |
| *D. kirtlandii* | C | ? | |
| *D. magnolia* | | no | pers. obs. |
| *D. palmarum* | C | yes | Eaton 1953 |
| *D. pensylvanica* | | no | pers. obs. |
| *D. petechia* | | no | pers. obs., Morton 1976 |
| *D. striata* | C | yes | Meyer de Schauensee and Phelps 1978 |
| *D. tigrina* | C | ? | |
| *D. virens* | | rare | pers. obs. |

[a] Coniferous group.

or food types widely divergent from the modal foraging style of a species (in this case foliage insectivory), a dichotomy emerges among the eastern *Dendroica* on their winter ranges. One group is commonly opportunistic, either by incorporating diverse behaviors such as hawking aerial insects or gleaning limbs or ground, or by the extensive use of fruit and nectar (although many birds will be frugivorous rarely, particularly in the tropics). The less opportunistic group, in contrast, remains relatively constant in foraging behavior throughout the winter. Table 2 characterizes the relative opportunism that has been observed in *Dendroica* species on the wintering range. While the data are few, all species that are noted for having labile foraging behavior are members of the coniferous group. Members of the mixed or deciduous group appear to be more constant in their foraging behavior (i.e. more restricted to foliage insectivory). My impression, based on 10 days of observation of *D. magnolia* where it is common (Guatemala) and three winters where it is uncommon (Panama), is that it is a relatively restricted foliage insectivore like other small *Dendroica*.

Table 3 lists the *Dendroica* that are commonly found in single species flocks. The four species that are known to form integrated single species flocks (where the members forage and move together) are also members of the coniferous group. From this brief overview it appears that some species often travel in flocks and are not restricted to foliage insectivory, whereas other species may remain intraspecifically solitary, searching foliage for their arthropod prey throughout the winter. This pattern and its relationship to body size and breeding habitat, while poorly documented with current data, bears further investigation.

*Advantages of small or large body size.*—Small size allows the exploitation of certain microhabitats by permitting the use of smaller branches and facilitating agility. This can be exemplified by returning to the example of *D. castanea* and *D. pensylvanica* in Panama. *Dendroica pensylvanica* is similar to many mid-level insectivores, such as the Dot-winged Antwren (*Microrhopias quixensis*) and Lesser Greenlet (*Hylophilus decurtatus*), in its specialization on leaf bottoms. This microhabitat is more difficult to exploit, but richer in insects, than leaf tops (Greenberg MS). These species pick skulking insects from the undersurface of leaves by leaping from small branches. *Dendroica castanea* forages like the omnivorous forest tanagers, such as Blue Dacnis (*Dacnis cayana*) and White-shouldered Tanager (*Tachyphonus luctuosus*), which glean insects mainly from leaf tops.

If small body size confers advantages to birds exploiting foliage insects, under what circumstances might large body size be advantageous? First, adaptations for foliage insectivory might be the same for both coniferous and nonconiferous warblers, but some overriding factor might counterselect for larger size in the coniferous group. Because all ecological factors are equivalent by this view, a physiological mechanism such as Bergmann's Rule could be operating. Second, foliage insectivory might be qualitatively different for the two groups in two ways: the structure of the foliage might make the agility allowed by small body size less useful in coniferous habitats, or coniferous species might be less specialized for foliage insectivory than the nonconiferous group. In either of these cases some advantage may select for larger body size in the absence of strong selection for small body size; the counterselective forces may function in either breeding ecology, winter ecology, or both.

Large body size may be an adaptation to conserve energy in physically stressful environments. This could occur by reducing the surface to volume ratio and, hence, the rate of heat loss per unit weight, or it might be a result of an absolute increase in insulation found in larger birds (Kendeigh 1969). The simplest hypothesis is that Bergmann's Rule is operating among the species, irrespective of the habitat or foraging differences, so that species living at higher altitudes and latitudes should be larger. As most *Dendroica* populations are migratory, I will examine both breeding and winter distributions. Most of the large *Dendroica,* such as *D. striata, D. coronata, D. castanea, D. palmarum,* and *D. tigrina,* are northerly breeders, but there are obvious exceptions (*D. pinus* and *D. kirtlandii*); *D. petechia* is a small northerly breeder. I can find even less support for large *Dendroica* wintering farther north, as the large *D. striata* and *D. castanea* winter in South America. While it is true that the largest *Dendroica* either breed farthest north or winter farthest north, this hypothesis does not explain the most striking features of the largest *Dendroica.* All of the species are restricted to breeding in coniferous forests and probably have opportunistic winter strategies. Because Bergmann's Rule fails to account for these unifying features, I do not think it is the primary selective factor for large body size.

The second hypothesis proposes that if small size allows increased maneuverability in foliage, then circumstances that confer no advantage to increased maneuverability could allow counterselective forces to operate and large body size to evolve. The following factors might decrease the advantage of small size (1–3) or increase the advantage of large size (4–5).

(1) Coniferous trees, with needle clusters near stout branches, could allow efficient foliage insectivory without high maneuverability.

(2) A foliage-gleaning species restricted to coniferous forest may find no single microhabitat productive enough, on a predictable basis, for the species to specialize on foliage insectivory. To exacerbate the situation, conifer foliage, particularly that of pines, is generally sparse compared with other vegetation types (MacArthur 1959). This might select for conifer forest residents having a diverse array of foraging tactics to allow switching to bark, ground, or aerial insects in between foliage foraging bouts.

The opportunism that is often extreme in winter-foraging repertoires is often present in breeding-season repertoires as well: *D. coronata* readily switches from foliage-gleaning to sallying for aerial insects, hawking, and gleaning ground insects and probing bark for insects and sap (MacArthur 1958, pers. obs.); *D. tigrina* often switches to sallying for aerial insects (MacArthur 1958); *D. palmarum* frequently
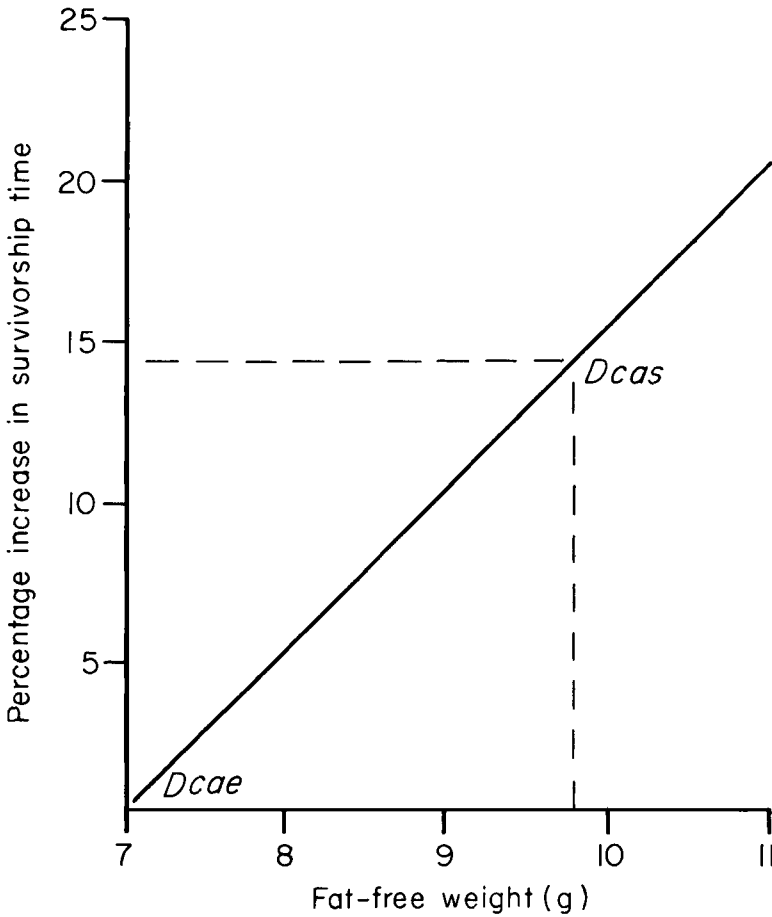
Fig. 2.   Percent increase in survivorship time in birds larger than 7 g. Survivorship time ratios $(Ts_i/Ts_j)$ given by the formula $W_iW_j^{.69}/W_jW_i^{.69}$ (see text). Fat-free weight (and corresponding increase in survivorship time) is indicated for *D. castanea* on the basis of Connell et al. (1960).

forages on or near the ground (Erskine 1977); *D. pinus* and coniferous populations of *D. dominica* forage for aerial insects and bark insects on large limbs or trunks (Ficken et al. 1968); and *D. kirtlandii* often forages on the ground and on limbs (Mayfield 1960).

This diverse array of tactics may be necessary for the occupation of some conifer habitats during periods of bad weather. Ficken and Ficken (1962) observed that ground foraging was employed by *D. pinus, D. palmarum,* and *D. coronata* in cold weather during migration. *Dendroica coronata* and *D. pinus* will forage in open areas with flocks of bluebirds (*Sialia*) during the cold winter months. For migratory forms, diversity of tactics may allow the early occupancy of temperate breeding grounds when the weather is unpredictable (although *D. striata* and *D. castanea* are late spring migrants). It also follows that in resident forms the ability to diversify tactics allows occupation of habitats with periodic cold weather.

(3) A species that depends upon a locally abundant food supply and specializes in locating and dominating that food source may find little advantage in using highly specialized foraging behaviors to obtain prey items. Two divergent examples come

to mind. Species that display a sharp numerical response to gradients of the spruce budworm may act as microhabitat generalists to obtain the abundant food from a large array of easily exploited situations. Similarly, species that employ opportunistic strategies on the wintering grounds may specialize in locating rich patches of food that, once located, do not require use of specialized foraging behavior.

(4) Warblers exploiting food that is abundant but patchy in time or space may gain advantages by decreasing the risk of food deprivation between foraging bouts. Relative (weight-specific) metabolism is lower in larger birds (Kendeigh 1969), and they can survive longer on the same proportional fat load. The argument is as follows: if $F$ is proportion of body weight $(W)$ in fat, $aW^{.69}$ is existence energy for unspecified time interval, 9.5 Kcal is number of Kcal/g of fat, and $Ts$ is time of survivorship (with subscripts for two species), then $Ts_i = FW_i\ 9.5/aW_i^{.69}$, and $Ts_j = FW_j\ 9.5/aW_j^{.69}$, so $Ts_i/Ts_j = FW_i 9.5aW_j^{.69}/FW_j 9.5aW_i^{.69} = W_i(W_j^{.69})/W_j(W_i^{.69})$. The actual magnitude of the survivorship-time ratios $(Ts_i/Ts_j)$ is explored in Fig. 2. A 7-g bird (fat-free mean weight of *D. caerulescens,* Connell et al. 1960) is compared to a bird ranging from 7.1 to 11 g. A 10-g bird has about a 15% advantage over a 7-g bird (9.9 g is the mean fat free weight of *D. castanea*).

I would expect that this advantage would be particularly significant for species that harvest from one or more patchily distributed food types: on the breeding range as an insectivore using variable insect emergences, or on the wintering ground as a species switching from fruit or nectar to insects.

(5) Larger animals are often socially dominant to smaller species and may gain in obtaining access to a portion of the resource spectrum (Morse 1974). Social dominance has been shown to be important in allowing warbler species to use certain optimal habitats (Morse 1971, 1974, 1976a, 1976b). It may also be important in allowing budworm specialists to dominate outbreak areas. *Dendroica castanea, D. tigrina,* and *Vermivora peregrina* comprised an impressive 98% of the breeding warblers on one mature forest plot under seige by budworms (Kendeigh 1947), and populations of nonbudworm *Dendroica* have been found to remain stable or even decrease (Kendeigh 1947, Morris et al. 1958). No direct evidence, however, implicates behavioral dominance of larger budworm-exploiting species over smaller *Dendroica* as the cause of this pattern. For other *Dendroica* the prediction that larger birds will dominate smaller birds has not been borne out. While *D. pinus* is dominant to the smaller *D. dominica* (Ficken et al. 1968), *D. coronata* is subordinate to the smaller *D. virens* and *D. magnolia. Dendroica fusca* is subordinate to all other spruce forest *Dendroica* (Morse 1976b).

The situation is not well studied for the wintering grounds. *Dendroica coronata* and *D. palmarum* (pers. obs.; Eaton 1953) tend not to travel in mixed-species flocks, so interspecific social dominance may be unimportant. *Dendroica coronota* is only sympatric with another equally large warbler, *D. pinus,* over much of its winter range. My studies of *D. castanea* indicate that while it often occurs in mixed-species flocks and fruiting aggregations, it is dominant only over other migrant parulids (*D. pensylvanica* and *V. peregrina*). This interspecific dominance is probably not a primary selective factor for body size in *D. castanea,* as its range only narrowly overlaps these smaller parulid species. It appears that interspecific social dominance is not a consistent result of large body size.

To summarize, if a warbler species is no longer committed to specialized broad-leafed foliage-insectivory, then other factors can operate to increase optimal body

size. Resistance to cold and starvation appear to be the most likely counter selective factors.

*The evolution of coniferous forest* Dendroica.—These arguments suggest that selection for larger body size occurs on both the breeding and wintering grounds. Because most migrant coniferous *Dendroica* are boreal, their origins become central to determining the importance of selection at different seasons. Two alternative models for the origin of current boreal forest species reflect this.

Model I. Recent ancestors could have originated in deciduous or mixed mesophytic forests. These ancestors would presumably have been neotropical migrants throughout the cool Quaternary period. Those migrants with opportunistic winter strategies could have been preadapted for roles as generalists or opportunists in boreal forests.

Mengel (1964) suggested a model for the Pleistocene speciation of warblers by successive isolation of protospecies in western glacial refugia. The primary elegance of this model is the explanation of the origin of western species, particularly those closely related to *D. virens* and *Vermivora ruficapilla*. The origin of the current species that are restricted to the boreal forest is only briefly discussed. He suggests that these species adapted to boreal forest during the glacial maxima and expanded in range with the expanding boreal forest. By this scheme, *D. tigrina*, *D. castanea*, and *D. striata* are closely related and may have been derived from a deciduous forest ancestor, perhaps similar to the extant *D. pensylvanica*.

This model requires a large number of invasions and extinctions, because the origin of the diversity of boreal species without close vicariants in the deciduous forest cannot otherwise be explained. The reason for isolation between boreal and deciduous populations, even during the glacial maxima, is not clear, as both forest types existed in contact throughout the Pleistocene (Martin 1958). A current view is that deciduous elements had a local distribution among pine-spruce forest during glacial advances (Davis 1976).

Model II. Ancestors could have originated in less seasonal coniferous forests, similar to current southeastern pine forests or Central American montane forests, and evolved autochthonously with more seasonal coniferous forests during the cooling of the late Tertiary and early Quaternary.

This model has been developed for only some of the boreal *Dendroica*, the *D. coronata* complex (Hubbard 1969). Hubbard suggests that a cordilleran forest protospecies colonized the northern boreal forest, and speciation occurred as the range became fragmented in various glaciations. The glacial refugia include an eastern boreal refugium (*D. coronata coronata*, *D. palmarum*, *D. castanea*), a possible Beringian refugium (*D. striata*), and a cordilleran refugium (*D. coronata auduboni*). While not explicitly stated by Hubbard, the species complex (*D. coronata* and allies) could have originated in the Tertiary when, in response to mountain uplifting and climatic cooling, the cordilleran and boreal forests developed.

Rather than a recent invasion of boreal forest, *Dendroica* could have had a long association with conifer habitats dating back into the Tertiary. Current species may be associated with climatic changes and Pleistocene isolation, but the species groups may have had a less dynamic history. The extant resident forms, *D. coronata goldmani* and southern populations of *D. pinus*, allow us to visualize the possibility of a resident coniferous ancestor for these groups. A Tertiary origin was proposed for

the *D. graceae-D. dominica* species group (Mengel 1964), and this group differs from the species groups discussed in not occupying more seasonal boreal forests.

By this model, the boreal forest had two sources for its *Dendroica* species. Coniferous ancestors in the *D. pinus* and *D. coronata* groups became the opportunistic and generalist species, and *Dendroica* associated with mixed mesophytic forests became the microhabitat specialists of the rich southern portion of the boreal forest. When the larger, generalist species began to migrate out of the more seasonal boreal forests, they were forced to occupy broad-leafed habitats for which they were poorly adapted. Their larger body size, lack of agility, and inappropriate searching behavior both required and allowed these species to undertake the opportunistic strategies of food location so prevalent among tropical forest residents (*Dacnis, Tachyphonus,* etc.).

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## SPECIFIC NAME OF THE INDIGO BUNTING CONSERVED

The International Commission on Zoological Nomenclature, by exercise of its plenary power (Opinion 1126; Bull. Zool. Nomencl. vol. 36, pt. 1: 24–26, July 1979), has conserved the long used name *Passerina cyanea* (Linnaeus 1766) for the Indigo Bunting, by suppressing the same specific name, as published in *Loxia cyanea* Linnaeus 1758, for the South American Ultramarine (or Blue) Grosbeak, usually called *Cyanocompsa cyanea*. Paynter merged *Cyanocompsa* in *Passerina* in a recent "Peters" Check-list volume, and, but for the application to suppress the older name, this would have required a confusing transfer of names. The specific name *brissonii* (based on *Fringilla brissonii* Lichtenstein 1823) becomes the name of the South American species, regardless of the genus in which it is placed, with type locality fixed as Bahia, Brazil.—E. EISENMANN.