

Extralimital Nesting of Bay-breasted Warblers: Response to Forest Tent Caterpillars?

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The Bay-breasted Warbler (*Dendroica castanea*) normally breeds in the coniferous forests of north-eastern and northcentral North America. Its numbers during the breeding season vary locally, often in response to localized outbreaks of spruce budworm (*Choristoneura fumiferana*) (see Kendeigh 1947, Morris et al. 1958, Mook 1963) and black-headed budworm (*Acleris variana*) (Gage et al. 1970). The species has been cited often by ecologists as exhibiting numerical response (Holling 1959) to such sudden increases in prey density (Stewart and Aldrich 1951; MacArthur 1958; Morse 1971, 1976) by laying larger clutches (MacArthur 1958, Cody 1966, Zach and Falls 1975).

During the summer of 1976, a small population of Bay-breasted Warblers nested on the Delta Beach Ridge, about 5 km west of Delta (50°11'N, 89°19'W), Manitoba. Here a narrow ridge of trees separates Lake Manitoba and the Delta Marsh (see MacKenzie 1979). The woody vegetation includes sand-bar willow (*Salix interior*), peach-leaved willow (*S. amygdaloides*), Manitoba maple (*Acer negundo*), eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), red-berried elder (*Sambucus pubens*), pincherry (*Prunus* sp.), and dogwood (*Cornus stolonifera*). Conifers are absent. The Bay-breasted Warbler is normally only an uncommon spring and fall migrant through the ridge (Criddle 1922, Hochbaum 1971) between 17 May and 3 June (extreme spring dates for 1973–76). In 1976, however, six active and four unfinished nests were found here. These extralimital nestings (see Appendix) coincided with the first year of an outbreak of the forest tent caterpillar (*Malacosoma disstria* Hbn.).

The infestation of forest tent caterpillars in 1976 (Fig. 1) was the first recorded on the ridge (V. Hildahl, pers. comm.). Small caterpillars were available in large numbers to migrating Bay-breasted Warblers. Defoliation was severe and widespread. Possibly as a result of a warmer and drier spring in 1977 (see Hildahl and Campbell 1975), the chronology of caterpillar development on the study area was about 1 week earlier than in 1976. Defoliation was localized and not severe, and Bay-breasted Warblers did not nest.

Bay-breasted Warblers were seen feeding on newly hatched, clustered forest tent caterpillars in late May (two males) and on 11 June (one female). Most larvae were about 20 mm long by the latter date (Fig. 1) and were apparently not taken by the birds. Most observed prey items of the nesting birds were unidentified winged insects, probably chironomids, which are extremely abundant on the ridge (Busby 1978). Stomachs from one male and one female Bay-breasted Warbler, taken on 17 May and 24 May, respectively, contained mostly chironomids. The male had also taken 1 mirid, 1 chrysomelid, 1 ichneumonid, and an unidentified Mallophaga. The female had also ingested 2 chrysomelids, 1 ichneumonid, and 8 seeds. Other studies (Mitchell 1952, Morse 1978) have shown that during outbreaks of the spruce budworm the apparently superabundant budworms do not provide a complete diet for Bay-breasted Warblers and that other foods may still be important in their diets during such outbreaks.

All but 1 of the 6 active nests and the 4 unfinished nests were placed in Manitoba maples; 1 active nest was in a green ash. The mean (\pm SD) height of active nests (measured with a Haga altimeter) was 4.6 ± 1.8 m in trees that averaged 9.8 ± 5.3 m. The mean height of the unfinished nests was 3.1 ± 1.1 m in trees that averaged 7.2 ± 4.6 m. The outer shells of two active nests and one unfinished nest were composed of willow twigs. The active nests were lined mainly with wild cucumber (*Echinocystis lobata*) and grasses. The nests were clumped, except for one nest (D) situated by itself 510 m west of the clump. Despite intensive searching and much time spent mist-netting in about 3,000 m of the ridge, only these nests were found. Nesting chronology is summarized in Fig. 1.

The non-random and dense placement of most of the nests poses interesting questions. Although the tree species composition on the ridge is not uniform (MacKenzie 1979), habitat similar to that selected by the Bay-breasted Warblers was generally available. The clumping of the nests, then, may have been caused by a tendency of the birds to aggregate, as has been suggested by Mayfield (1960: 52–53) for the Kirtland's Warbler (*Dendroica kirtlandii*). Irrupective species such as the Piñon Jay (*Gymnorhinus cyanocephalus*), Clark's Nutcracker (*Nucifraga columbiana*), and Red Crossbill (*Loxia curvirostra*) are gregarious and often nest in clumps or colonies (Bailey and Niedrach 1953, Balda and Bateman 1971), despite widespread though local distributions of their food.

Two males were temporarily monogamous. One male was mated until at least 12 June to a female that was constructing Nest B. The female then disappeared, and the male was discovered on 23 June with an unmarked female at Nest E, which contained three warbler eggs and two Brown-headed Cowbird

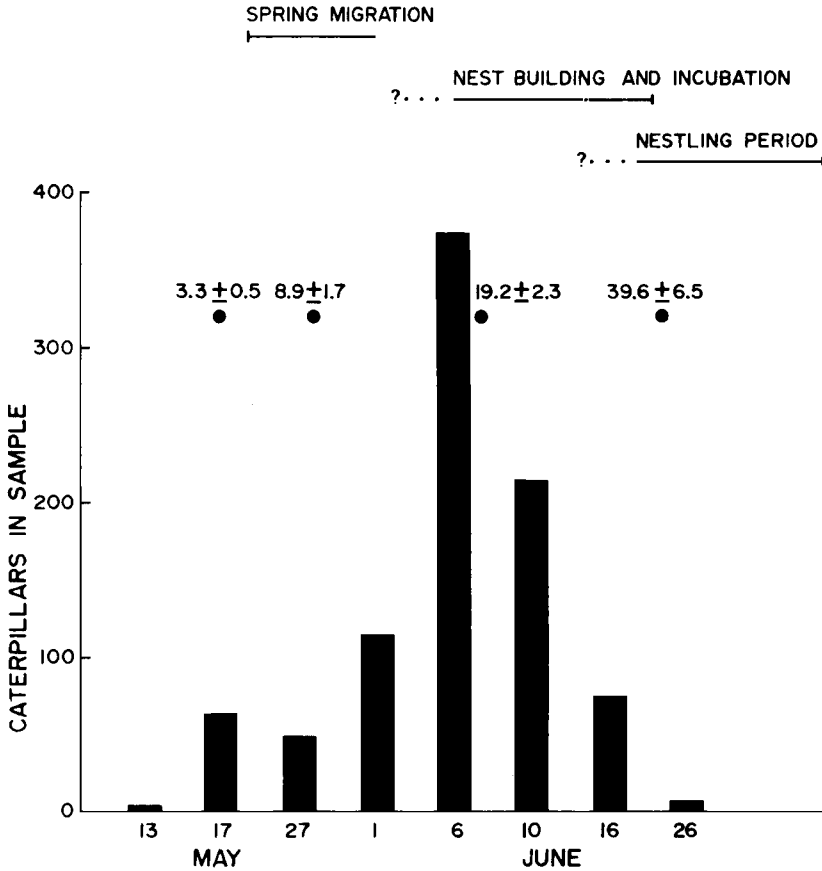


Fig. 1. Abundance and development of forest tent caterpillar larvae and chronology of Bay-breasted Warbler nesting in 1976. Insect abundance is based on data from standard insect sweep samples by Busby (1978) on the Delta Beach Ridge in 1976. Pupae were first encountered on 16 June, and adult moths were taken in the sweep samples by 1 July. Total length of 10 larvae ($\bar{x} \pm SD$, mm) is indicated for each of four dates, 17 and 28 May and 8 and 17 June (dates indicated by solid dots).

(*Molothrus ater*) eggs. This male had probably been mated to this female by at least 18 June (the date by which the first egg must have been laid, assuming the two cowbird eggs equal two warbler eggs). It is even possible that this male was polygynous and had copulated simultaneously with both of these females.

The second male was mated until 12 June with a female that was then constructing Nest H. Nest H was abandoned (unfinished) when this female took over the partially constructed Nest B with yet another male. The original male at Nest H moved to another nest (F) and was noted with another female. Copulation was never witnessed, so that statements that birds were mated are based on their general behavior toward each other. The flexibility of Bay-breasted Warbler relationships is evident. The pair bonds are quickly and perhaps opportunistically established and may be quite transitory.

Clutch size was difficult to determine because of cowbird parasitism. Two unparasitized nests had three eggs each. Nest E received 5 eggs, if the 2 cowbird eggs do indeed represent 2 ejected warbler eggs (see Rothstein 1975). Nest B fledged two young warblers, but no other active nests produced warbler young. Four nests were parasitized by cowbirds; one of these (E) fledged a single cowbird.

Cody (1966) suggested that clutch size is inversely related to nest predation pressure. The relatively large clutches usually reported for the Bay-breasted Warbler may be possible because of the safety of nesting in conifers, as pointed out by Zach and Falls (1975) and Nice (1954). Clutch size may have been

small in the population on the ridge because of the deciduous habitat used and possibly because of the intense cowbird parasitism. Mayfield (1977) speculated that some forest bird species cannot sustain their populations in the presence of the cowbird. The Bay-breasted Warbler may be one such species; with the small sample, however, no conclusion can be drawn. The breeding ranges of the Bay-breasted Warbler and Brown-headed Cowbird generally do not overlap. There are only 3 previously published records of cowbird parasitism of the Bay-breasted Warbler, 2 from Quebec (Friedmann 1963) and 1 from Alberta (Jones 1965).

The Bay-breasted Warbler depends largely on an unstable food supply and rapidly invades areas where irregular increases in food occur. The observations presented here reveal just how rapid such a response may be and confirm the observations of Morris et al. (1958). Clutch initiation at northern points in this species' range appears not to begin until mid- to late June, based on one record from Alberta and six from Ontario. It started as early as 6 June on the Delta Beach Ridge in 1976.

The Bay-breasted Warbler has not been reported as a predator of tent caterpillars (Witter and Kulman 1972), and previously reported episodes comparable to the present one have been limited to rapid colonization of coniferous or mixed woods in apparent response to budworm populations. The apparent responses to tent caterpillars and the use of deciduous tree habitat reveals an unrecognized plasticity in the Bay-breasted Warbler's selection both of prey and of habitat, even considering that Kendeigh (1947) described this species as opportunistic.

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APPENDIX

Breeding status of the Bay-breasted Warbler in Manitoba.—Most of the breeding evidence from Manitoba is circumstantial. No nests have been found outside those described here. Godfrey (1966: 337) showed the southern limit of the breeding range of the Bay-breasted Warbler in Manitoba extending from southeastern Manitoba (49°33'N, 95°09'W), where there is evidence of breeding (Rowan 1922), directly northwestward (including the Delta Beach Ridge) to Riding Mountain National Park (50°50'N, 100°00'W), where Godfrey (1953: 227) "heard singing [Bay-breasted Warblers] until July 15, 1938." Godfrey (1966) did not cite Thompson (1891), who referred vaguely to the Bay-breasted Warbler as a rare summer resident at Winnipeg and Portage la Prairie. A singing male was observed by Shortt and Waller (1937) on 17 June 1934 farther north near Lake St. Martin (51°46'N, 98°21'W). W. J. Walley (in litt. 1977) saw a pair of adult Bay-breasted Warblers on 21 July 1971 near East Blue Lake (51°17'N, 98°02'W) in the Duck Mountain area but was unable to determine their status. Two adults in the Royal Ontario Museum (nos. 82508-9) were taken on 11 and 16 July 1925 near Steep Rock (51°26'N, 98°48'W). Neither Soper (1951) nor Walley (1973) recorded it during their extensive work in Riding Mountain National Park. All of the above sites are in coniferous or mixed wooded areas.

Although evidence for Bay-breasted Warbler breeding in Manitoba is sparse, it appears that the southern limit of its usual Manitoba range as shown by Godfrey (1966) is misleading and that the nestings on the Delta Beach Ridge in 1976 are indeed extralimital.—Received 14 March 1978, accepted 21 February 1979.