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Catharus bicknelli

Bicknell's Thrush

FRENCH: *Grive de Bicknell*
SPANISH: *Zorzal migratorio (Hispaniola), Tordo de Bicknell (Cuba)*

15.375 X 21.375 PICAS

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The song is in a minor key, finer, more attenuated, and more under the breath than that of any other thrush. It seemed as if the bird was blowing in a delicate, slender, golden tube, so fine and yet flute-like and resonant the song appeared. At times it was like a musical whisper of great sweetness and power.

Burroughs 1904: 51

. . . only a freak ornithologist would think of leaving the trails [on Mt. Mansfield] for more than a few feet. The discouragingly dense tangles in which Bicknell's Thrushes dwell have kept their habits long wrapped in mystery.

Wallace 1939: 285

The nasal, gyrating song and plaintive calling of Bicknell's Thrush are familiar to few birders or ornithologists. The species' remote, inhospitable montane and maritime forest habitats, its penchant for dusk and dawn activity, and its reclusive behavior underscore its status as one of the least-known breeding birds in North America. It is also among the most rare and, possibly, most threatened. Breeding from the northern Gulf of St. Lawrence and easternmost Nova Scotia southwest to the Catskill Mountains of New York State, Bicknell's Thrush probably numbers no more than 50,000 individuals across its naturally fragmented breeding range. The species inhabits an even more restricted winter range, occurring regularly on only four islands in the Greater Antilles. Habitat loss and degradation at both ends of its migratory spectrum suggest a tenuous conservation status for Bicknell's Thrush, which is ranked as the Nearctic-

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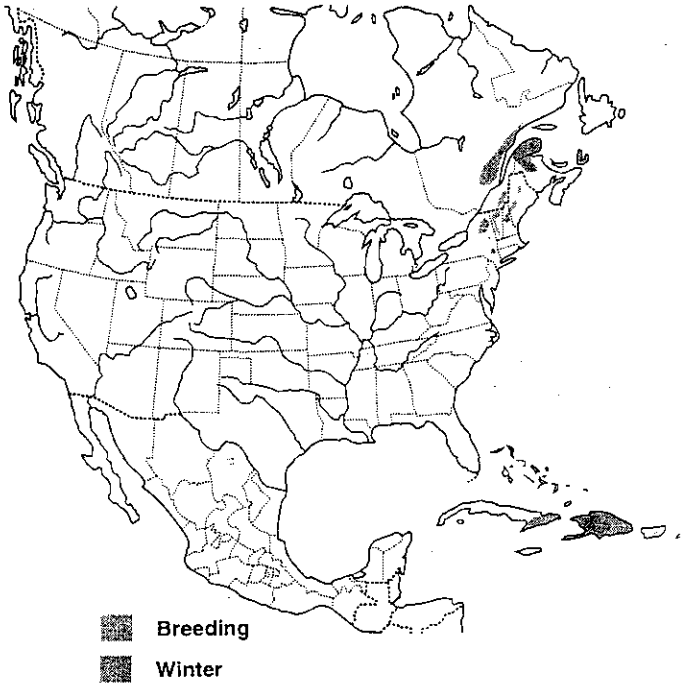

Figure 1.
Distribution of Bicknell's Thrush. Patchy distribution in both parts of its range makes exact delineation difficult.

Neotropical migrant of highest conservation priority in the Northeast (Rosenberg and Wells 1995, Pashley et al. 2000).

Following its discovery in 1881 by Eugene Bicknell on Slide Mountain in New York's Catskill range, Robert Ridgway named and described Bicknell's Thrush in 1882, then classified it as a subspecies of Gray-cheeked Thrush (*Catharus minimus*). George Wallace's (1939) classic natural-history study and a careful taxonomic assessment by Henri Ouellet (1993) led to specific recognition in 1995 (Am. Ornithol. Union 1995). Although reliable field identification of Bicknell's and Gray-cheeked thrushes remains dubious at best, marked morphological, vocal, and biochemical differences between the two taxa support this designation. The ranges are completely allopatric, with Gray-cheeked breeding farther north (Newfoundland to Siberia) and wintering farther south (Panama through northwestern Brazil and Colombia) than Bicknell's Thrush. The recent elevation of Bicknell's Thrush to full species status has heightened interest and concern among birders, scientists, land-use planners, and conservationists.

Bicknell's Thrush is adapted to naturally disturbed habitats. Historically, the species probably selected patches of regenerating forest caused by fir waves, wind throw, ice and snow damage, fire, and insect outbreaks, as well as chronically disturbed, stunted altitudinal and coastal conifer forests (Ouellet 1993, Nixon 1999, Vermont Institute of Natural Science [VINS]). In addition to these natural successional habitats, Bicknell's Thrush has recently been discovered in areas disturbed by timber harvesting, ski trail and road construction, and other human activities (Ouellet 1993, VINS). Evidence of local declines and extinctions in "traditional" breeding habitats may indicate either a shift in habitat use or increasing populations (Ouellet 1993, 1996), but more likely reflects the species' opportunistic use of disturbed habitats. Extensive loss and degradation of the primary forests that Bicknell's Thrush appears to prefer in winter pose the greatest threat to the species' long-term viability.

Despite detailed studies by Wallace (1939), VINS, and others, few concrete data are available by which to assess the conservation status of Bicknell's Thrush. The species is poorly monitored by traditional sampling methods, and its unusual spacing and mating system makes estimation of breeding densities unreliable at best. Current range-wide population estimates represent little more than educated guesses. Knowledge of the species' wintering ecology and demography is fragmentary, and its migratory routes and stopover ecology are poorly known. Recent research on the breeding and behavioral ecology of Bicknell's Thrush has documented a strongly male-biased sex ratio, with 2 to 4 males feeding young at 75% of nests and multiple paternity of most broods. Possible sexual habitat or geographic segregation on wintering grounds may cause differential survivorship of females and promote skewed breeding sex ratio, but firm evidence is lacking. Much work remains to be done on Bicknell's Thrush at all stages of its annual cycle and in all parts of its range.

DISTINGUISHING CHARACTERISTICS

Medium-sized thrush (16–17 cm, 26–30 g), but smallish and slender for a *Catharus*. Generally wary and hard to observe, occasionally sings on exposed song-post. Field identification subtle and difficult under best circumstances. Plumage separation from very similar Gray-cheeked Thrush relies on slight color differences and contrasts (e.g., tail versus lower back), less useful than soft part color and morphometrics (Ouellet 1993, Knox 1996). Body coloration of both species varies across respective breeding ranges, obscuring differences in all but extreme variants. Most Bicknell's have olive-brown or brown dorsal coloration, whereas most Gray-cheeked have olive-gray or olive (Ouellet 1993). In comparison to Gray-cheeked, Bicknell's shows contrast between chestnut-tinged tail and wings, and rest of upperparts. This may be obscured by worn, dull tail and wings, or low contrast in warmest brown birds. Also shows warmer brown upperparts and a lighter buffy wash on the breast (underlying the dark spots) than continental subarctic Gray-cheeked Thrush (*C. m. aliciae*). This, combined with bright yellow to yellow-orange basal half or more of lower mandible, provides a subtle but generally reliable method of separating Bicknell's from *aliciae* Gray-cheeked Thrush. Potential confusion with Gray-cheeked Thrushes of Newfoundland and nearby St. Lawrence estuary coasts (*C. m. minimus*), which show some chestnut edging on wings and tail, are generally warmer brown than the more olive-gray *aliciae*, and often have extensive pale yellow on the lower mandible, although apparently not as bright as Bicknell's (McLaren 1995). In Bicknell's, color of legs purplish flesh, with toes darker than tarsi and soles of feet flesh to dull pale yellow; in Gray-cheeked, tarsi lighter flesh color, with toes invariably much darker and soles of feet brighter yellow than in Bicknell's (Ouellet 1993).

Bicknell's Thrush best identified in hand on basis of size and relative wing shape (Pyle 1997). Usually smaller than Gray-cheeked, although considerable overlap in measurements exists. Wing-chord of adult Bicknell's 82–100 mm (n = 415; VINS), of Gray-cheeked 93–109 mm (n = 200; Pyle

1997). Tail length of Bicknell's 60–75 mm (n = 127; VINS), of Gray-cheeked 63–79 mm (n = 185; Pyle 1997). Majority of Gray-cheeked Thrushes have wings >95 mm in length (Ouellet 1993); 85% of Bicknell's have wings <95 mm (VINS). Birds with wing lengths 94–98 mm (usually young female *C. m. minimus* and adult male Bicknell's) are not safely identifiable. As befits a longer distance migrant, Gray-cheeked Thrush shows more pointed wing morphology (Phillips 1991, Pyle 1997). Difference in length between primaries (P) 8 and 6 is 3–7 mm for Bicknell's and 5–10 mm for Gray-cheeked; P8 is 24–29 mm longer than P1 in Bicknell's; 27-35 mm longer in Gray-cheeked (Pyle 1997). Ratio of primary:tertial length may be useful in separating the two species: ≤1:1 in Bicknell's, ≥1:1 in Gray-cheeked (Lane and Jaramillo 2000).

Subtle but clear distinctions in song help separate Bicknell's and Gray-cheeked thrushes. Primary difference is constant or slightly rising inflection at end of Bicknell's song, whereas Gray-cheeked song falls to lower frequencies towards the end (Ouellet 1993). This difference consistent across breeding range of both species and detectable in field. Nocturnal flight calls of the two species also differ subtly (see Ball 1952, Evans 1994), these perhaps only safely distinguished by spectrographic examination of recordings.

Identification from other North American *Catharus* is less difficult, but requires care. Hermit Thrush (*C. guttatus*) is much brighter rufous on upper tail-coverts and tail, showing far more contrast than Bicknell's. Hermit also has more extensively and discretely spotted breast with a whiter ground color. Swainson's Thrush (*C. ustulatus*) has pale lores more or less connected to a broad buffy eye-ring broken narrowly before the eye, a warm buff wash on face and breast and, particularly in boreal-eastern populations (*swainsoni* group), colder olive-brown upperparts. Bicknell's Thrushes that are more olivaceous on back tend to show noticeable contrast with reddish highlights in tail and wings. Pacific Swainson's Thrush (*ustulatus* group) shows rufescent color in tail that contrasts with back, which itself is a warmer brown than in boreal-eastern (*swainsoni* group) birds, but buffy facial pattern invariably distinguishes all individuals of this species from Bicknell's Thrush. Boreal-eastern populations of Veery (*C. fuscescens*) more richly and uniformly reddish brown above, less heavily spotted on breast; spots, if discrete, sparse and small. Populations breeding in Newfoundland, central Appalachian, and the West, e.g., Rocky Mtn. region, duller and less rufescent (or tawny) above and evince sharper breast spotting; these differ from Bicknell's Thrush in having more uniformly colored upperparts, sparsely and finely spotted breast, orange-pink base of lower mandible, and greater contrast of flanks with upperparts (gray versus brown).

Males and females indistinguishable in field. Individuals in Basic I plumage often separable from adults through first full summer by retention of buffy-tipped Juvenal feathers in greater and median wing-coverts, occasionally scapulars and mantle. No appreciable seasonal changes in plumage after completion of Definitive Prebasic molt.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Occupies a restricted and highly fragmented breeding range. Breeds north to sw. Quebec in Réserve La Verendrye, se. Quebec along northern shore of St. Lawrence River and Gaspé Peninsula (Ouellet 1993, 1996), Magdalen Is., Quebec (probably extirpated; Ouellet 1996, D. McNair pers. comm.), nw. and n.-central New Brunswick (Erskine 1992, Nixon 1996), and Cape Breton I., Nova Scotia, including the small, outlying St. Paul and Scaterie Is. (Erskine 1992, D. Busby pers. comm.). Breeds south to Catskill Mtns. of se. New York State (Atwood et al. 1996, Peterson 1988), Green Mtns. of s. Vermont (Kibbe 1985, Atwood et al. 1996), White Mtns. of central New Hampshire (Richards 1994, Atwood et al. 1996), mountains of w. and central Maine (Adamus 1987, Atwood et al. 1996), s.-coastal New Brunswick (possibly extirpated; Erskine 1992, Christie 1993), and sw.-coastal Nova Scotia (probably extirpated; Erskine 1992, D. Busby pers. comm.). Possible but unconfirmed local and sporadic breeding in n.-coastal Maine (Atwood et al. 1996, Rimmer and McFarland 1996).

Winter range. Figure 1. Confined to Greater Antilles. Specimen and field-survey data indicate bulk of wintering population in Dominican Republic (Wetmore and Swales 1931; Ouellet 1993; Rimmer et al. 1997, 1999), where widely distributed and locally common from sea level to 2,220 m (Rimmer et al. 1999). Few records from Haiti; restricted to higher elevations, mainly in southwest (Massif de la Hotte) and east (Massif La Visite; Wetmore and Swales 1931; Woods and Ottenwalder 1983, 1986). Uncommon and local in Jamaica, mainly in Blue Mtns. from 1,200 to 2,225 m elevation (R. and A. Sutton unpubl.; VINS). Rare winter resident in e. and se. Puerto Rico, in Luquillo Mtns. at 450–720 m elevation and Sierra de Cayey at 720 m (Arendt 1992, J. Wunderle unpubl.). Recorded in e. Cuba at 1,600–1,960 m in Sierra Maestra (Rompré et al. 2000, Y. Aubry and G. Rompré pers. comm.); two Oct specimens from w. Cuba (Havana) in 1960s (Garrido and Garcia Montaña 1975) probably

represent transients. No confirmed winter records elsewhere.

OUTSIDE THE AMERICAS

Owing to difficulty of sight identification of Bicknell's and Gray-cheeked thrush, none of 43 "Gray-cheeked Thrush" records from Britain and Ireland has been conclusively identified as Bicknell's (Knox 1996). A specimen from Bardsey, Gwynedd, Britain on 10 Oct 1961 was identified by Charles Vaurie as *bicknelli* (Clafton 1963), but the bird had a 100-mm wing and a dull lower mandible more consistent with Gray-cheeked (Knox 1996). A well-photographed bird on Isles of Scilly on 20 Oct 1986 appeared to be Bicknell's (Curson 1994), but could be extreme example of nominate Gray-cheeked (Knox 1996). Most records of the 2 species from Isles of Scilly, all between 22 Sep and 26 Nov, majority in second half of Oct (Curson 1994). A small number of "Gray-cheeked Thrush" records also from France, Germany, Norway, Italy, and Iceland (Curson 1994).

HISTORICAL CHANGES

Local extirpations documented during twentieth century, but no clear evidence of rangewide declines. Few quantitative data to assess population changes. Historic breeding populations disappeared on Mt. Greylock, MA (10 pairs in 1950s, 0 in 1973; Veit and Petersen 1993); Magdalen Is., Quebec (Ouellet 1996, D. McNair pers. comm.); Seal and Mud Is., Nova Scotia (Wallace 1939, Erskine 1992, D. Busby pers. comm.); Cape Forchu, sw. Nova Scotia (J. Marshall pers. comm.); Fundy National Park, New Brunswick (Christie 1993); and Grand Manan I., New Brunswick (B. Dalzell pers. comm.). Further range contraction in Canadian Maritime provinces suggested by mid-1990s surveys showing fewer occupied sites than during 1986–1991 Breeding Bird Atlas (D. Busby pers. comm.) survey period. Species' presence, however, confirmed on 63 of 73 historic (pre-1992) U.S. breeding sites surveyed in 1992–1995 (Atwood et al. 1996), suggesting no large-scale changes in recent distribution. Recently discovered occupancy of second-growth habitats in industrial forestry landscapes in Quebec, New Brunswick, and Nova Scotia (Ouellet 1993, 1996; Holmes and Nixon 1997; D. Busby pers. comm.) may indicate either a shift in habitat use or population increases (Ouellet 1993, 1996), but more likely reflects species' specialization on disturbed habitats.

Changes on wintering grounds not well documented but likely due to extensive habitat loss and degradation throughout Greater Antilles, including montane forests currently preferred by Bicknell's Thrush; <1.5% of forest cover remains in Haiti and about 10% in Dominican Republic (Stattersfield et al. 1998). Jamaica has lost 75% of its original forest and Cuba 80-85% (Stattersfield et al. 1998). Of 14 identifiable historic (pre-1991) sites of occurrence in Dominican Republic, Bicknell's Thrush located at 7 of 11 surveyed in 1995-1997; several reported historic sites severely degraded to point of being unrecognizable or unsuitable for species' continued occupancy (Rimmer et al. 1999).

FOSSIL HISTORY

No known records. There are, however, late-Pleistocene fossils of *Catharus* sp. from cave deposits in Virginia that could apply to *bicknelli* (Guilday et al. 1977) and additional unidentified *Catharus* fossil records cited in Wetmore 1962.

SYSTEMATICS

GEOGRAPHIC VARIATION

Possible latitudinal variation, both in size and dorsal coloration, but rigorous study needed (Todd 1963, Ouellet 1993). Todd (1963) proposed the possibility of a tawnier brown montane subspecies in New York State and New England, and a colder olive-brown subspecies in the Canadian Maritime Provinces and se. Quebec. He further suggested that the brown versus olive color polymorphism seen in n. Vermont by Wallace (1939) represents contact between these forms. It is now unclear if the trend from brown birds in south to olive birds in north represents a true cline or if the two forms are intermixed throughout the range (see Appearance: molts and plumages, below). It should be clarified whether this is true polymorphism, or only the separation of extremes in normal variation in dorsal color.

SUBSPECIES

None recognized. See Geographic variation, above.

RELATED SPECIES

Belongs to a species group with other Nearctic spotted *Catharus* thrushes, including Swainson's, Hermit, Gray-cheeked, and Veery; especially closely related to the latter two. Percent nucleotide divergence in mitochondrial DNA nonprotein coding control region (396 base pairs sequence) is 2.2% to Veery and 2.3% to Gray-cheeked Thrush (WGE). Relationships among these species are so close as to make specifying sister taxa uncertain. Bicknell's Thrush and Veery probably arose from within a Gray-cheeked-like ancestor. Based on control region-molecular clocks derived from Zink and Blackwell (1998) and Freeland and Boag (1999) for

passerines, this split probably occurred in the mid-Pleistocene era (about 500,000 to 850,000 yr ago). This is also suggested by the 1.7% divergence estimated by G. Seutin for a restriction fragment analysis of the entire mitochondrial genome of Gray-cheeked and Bicknell's thrushes (cited in Ouellet 1993). Relationships of Nearctic *Catharus* to Neotropical *Catharus* and Wood Thrush (*Hylocichla mustelina*) yet to be worked out, although it seems likely Wood Thrush is a *Catharus* (Winker and Rappole 1988).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

A nocturnal, long-distance migrant; routes and timing poorly documented owing to difficulty of distinguishing Bicknell's and Gray-cheeked thrushes in the field. Examination of hand-held birds only reliable means of separating migrants of the two species. Analysis of specimen and banding data, using wing-chord as identification criterion (<94 mm = Bicknell's, >98 mm = Gray-cheeked), suggests elliptical southern portion of migratory route between North American breeding grounds and Greater Antillean winter range. Most southbound migrants may depart East Coast from mid-Atlantic states or Carolinas on overwater flight to Greater Antilles; fall records scarce south of Virginia. Northward passage appears to be more concentrated through Southeast, as spring specimens from Florida, Georgia, both Carolinas, and Virginia outnumber fall records nearly 2:1. Entire migration in both directions concentrated east of Appalachian Mtns.

TIMING AND ROUTES OF MIGRATION

Spring. No information on departure from Greater Antillean wintering grounds; probably late Apr, as birds still present in Dominican Republic second week of Apr (J. Faaborg unpubl.). No verifiable U.S. records prior to May. Based on identification of specimens (n = 2; Wallace 1939) and nocturnal flight calls (n = 8 birds; Evans 1994) in e.-central Florida, migrants pass northward first half of May; earliest specimen record 3 May in Brevard Co. (Wallace 1939). No records from Florida's west coast or other Gulf Coast states. Only one reliable spring record from Georgia, a male collected on McQueen's I., Chatham Co., 8 May 1949 (Georgia Museum Natural History specimen data). Three verifiable spring specimens from S. Carolina: two near Charleston 10 and 15 May, one inland at Chester 6 May (Charleston Museum specimen data). Spring migrants of Bicknell's/Gray-cheeked thrush complex in N. Carolina recorded 24 Apr to 30 May, with 2 unsubstantiated Mar reports; 50% of birds pass in 15-d period mid-May (Lee 1995). Only Bicknell's specimen considered authentic, taken near Southport, Brunswick Co., 12 May 1939 (Lee 1995), although 3 additional specimens reported by Wallace (1939) collected 5–18 May. Three specimen records Virginia coastal plain 17–21 May (Wallace 1939).

Bulk of confirmed (on basis of wing length) spring migrants recorded between Maryland and New England. Two specimens from Washington, D.C. on 16 and 27 May; two from Laurel, MD, both 14 May (Wallace 1939). Ten Bicknell's Thrushes banded at two e. Maryland sites 18-31 May (B. Ross and J. Weske unpubl.). At Island Beach State Park, NJ, only 3 of 43 identified Bicknell's Thrushes banded 1964–1999 captured in spring, 18-26 May (G. and E. Mahler, R. McKinney, R. Yunick unpubl.). At a Queen's Co. banding station in w. Long I., NY, species made up 24% of spring transients of Bicknell's/Gray-cheeked thrush complex (n = 24 Bicknell's, 76 Gray-cheeked) banded from 1932 to 1939; earliest date 11 May, latest 27 May (Beals and Nichols 1940). Farther east in Suffolk Co., Long I., NY, Bicknell's Thrush comprised 24% of identified spring migrants (n = 4 Bicknell's, 17 Gray-cheeked) banded in 1959–1974, all on single date 28 May 1967 (Lanyon et al. 1970, W. Lanyon unpubl.).

In New England, 5 verifiable (wing-chord ≤93 mm) spring specimens in coastal Connecticut 15–27 May, 4 in e. Massachusetts 20 May–11 Jun, the latter record of an exceptionally late female (Wallace 1939). At a coastal banding site in se. Massachusetts, 18% of new captures of Bicknell's/Gray-cheeked thrush complex in 1966–1996 referable to Bicknell's (n = 17); earliest date 23 May, latest date 6 Jun, mean date 29 May ± 4.1 d SD (Manomet Observatory for Conservation Sciences [MOCS] unpubl.). On Appledore I. off s. Maine coast, 4 captures of Bicknell's among 44 individuals of the species complex banded in 1983–1999, 18 May–1 Jun (S. Morris unpubl.). Earliest recorded occurrence on high-elevation breeding grounds in n.-central Vermont 16 May, well established in Green Mtns. by 25 May in most years (VINS). Reported to return to n. White Mtns. 25–30 May (Wallace 1939).

West of Appalachian Mtns., no identifiable Bicknell's among 94 individuals of Bicknell's/Gray-cheeked thrush complex banded in springs of 1961–1994 in sw. Pennsylvania (Powdermill Nature Reserve [PNR] unpubl.). Possible vagrancy indicated by spring captures of 5 apparent Bicknell's among 371 individuals of both species banded on n. Lake Erie shore at Long Point, Ontario in 1962–1998 and 6 of 102 captures at Prince Edward Point on northeast shore of Lake Ontario in 1975–1989

(Long Point Bird Observatory [LPBO] unpubl.). At Braddock Bay on south shore of Lake Ontario, 2 identifiable Bicknell's among 50 individuals of species complex banded in springs of 1986-1999 (E. Brooks unpubl.). Possibility of misidentifications of similar *Catharus* species and erroneous wing-length measurements must be considered in evaluating all banding records of apparent Bicknell's Thrush.

Fall. Migrants identified on basis of nocturnal flight calls passing over n. Gaspé Peninsula in late Sep 1948 (Ball 1952, Evans 1994). Latest record on Mt. Mansfield, VT, 3 Oct; one presumed local hatch-year (HY) bird banded 29 Aug 1996 was recaptured 30 Sep (VINS). Six birds reported from Whiteface Mt., an Adirondacks breeding site, 26 Sep 1948 (Carleton 1999). Few reliable records from northern part of migratory range, as migrants appear to move rapidly southeastward. No confirmed Bicknell's among 21 "Gray-cheeked Thrushes" banded at a central Vermont site 1981–2000 (VINS). On the east slope of Adirondack Mtns. at 730 m elevation, individual HY Bicknell's banded on 9 Sep 1992 and 24 Sep 1994, respectively (W. Lanyon unpubl.). In Canadian Maritime Provinces, 1 of 7 "Gray-cheeked Thrushes" banded on Kent I., New Brunswick, a Bicknell's by wing length, a HY bird on 5 Oct 1980 (J. Cherry and P. Cannell unpubl.). Similarly, at Atlantic Bird Observatory off sw. Nova Scotia, 1 of 7 individuals of the two species banded in 1996–1998 had a wing length consistent with Bicknell's, this a HY bird on 14 Sep 1998 (T. Fitzgerald unpubl.).

In New England, majority of fall records from coastal or near-coastal locations. Seven identified specimens from Massachusetts 26 Sep–16 Oct, 9 from Connecticut 21 Sep–12 Oct (Wallace 1939). On se. Massachusetts coast, 19 of 214 banded fall migrants (9%) of Bicknell's/Gray-cheeked thrush complex identifiable as Bicknell's by wing length; earliest date 22 Sep, latest 20 Oct, mean date 6 Oct ± 6.9 d SD (MOCS unpubl.).

Fall transients appear to concentrate at coastal sites between Long I., NY, and Virginia. At w. Long I. banding station, Bicknell's Thrush constituted 42% of identified fall migrants of the two species (n = 117 Bicknell's, 278 Gray-cheeked); earliest date 7 Sep, latest date 8 Nov, 66% of captures 21 Sep–5 Oct (Beals and Nichols 1940). At Huntington, Suffolk Co., Long I., Bicknell's Thrush constituted 16% of identified fall migrants of both species (n = 17 Bicknell's, 109 Gray-cheeked); early date 9 Sep, late date 24 Oct, mean passage date 5 Oct ± 8.6 d SD (Lanyon et al. 1970, W. Lanyon unpubl.). At Island Beach State Park in e. New Jersey, 40 identifiable Bicknell's banded 11 Sep–20 Oct in 1964–1999 (G. and E. Mahler, R. McKinney, R. Yunick unpubl.). At Cape May, NJ, 2 of 11 individuals of Bicknell's/Gray-cheeked thrush complex banded in 1990 and 1991 identifiable as Bicknell's, both HY birds captured on 7 Oct 1990 (T. Leukering unpubl.). At Sandy Spring, MD, 7 Bicknell's banded 1975–1984, between 20 Sep–19 Oct (J. Weske unpubl.). At another e. Maryland site, 7 Bicknell's banded 1979–1994 over a similar range of dates, 21 Sep–13 Oct (B. Ross unpubl.). On Shenandoah River in e. Virginia, 3 identifiable Bicknell's banded among 53 individuals of the species complex in 1976–1994, all HY birds 12 Sep–18 Oct (W. Oberman unpubl.). Among fall migrants of Bicknell's/Gray-cheeked thrush complex (n = 947) at a coastal Virginia banding site (Kiptopeke), Bicknell's Thrush accounted for 30% of individuals captured over 4 yr (1968, 1969, 1971, 1980; Wilson and Watts 1997). Median autumn capture dates over same 4 yr: 4–7 Oct, differing significantly from Gray-cheeked Thrush in only one year (1968; 7 Oct and 2 Oct, respectively; Wilson and Watts 1997). Range of passage dates at this site narrower for Bicknell's than for Gray-cheeked Thrush; none captured during first half of Sep, none after third week of Oct (Wilson and Watts 1997). One Kiptopeke bird captured on 26 Sep 1999 originally banded at Appledore I. off s. Maine coast on 18 May 1998 (B. Wilson pers. comm.).

Reliable fall records relatively scarce south of Virginia, suggesting offshore flight from mid-Atlantic to Greater Antilles. Two records support such an overwater flight: a specimen collected on Bermuda on the exceptionally late date of 23 Nov 1957 (American Museum of Natural History specimen data, *fide* J. Marshall) and a migrant banded on New Providence I., Bahamas, 16 Oct 1993 (G. Seutin unpubl.). On mainland, only one reliable record for N. Carolina, a specimen collected on 27 Sep 1900 in Raleigh (Wallace 1939). Within the Bicknell's/Gray-cheeked thrush complex, 75% of fall migrants in N. Carolina occur during a 20-d period late Sep–early Oct, with earliest record 30 Aug and latest 29 Oct (Lee 1995). In S. Carolina, only a single fall record, a HY specimen collected south of Charleston 13 Oct 1993 (Charleston Museum specimen data). Two identifiable Georgia specimens, both from Atlanta area, 7 Oct 1915 (Wallace 1939) and 21 Sep 1970 (Georgia Museum of Natural History specimen data). At three Georgia banding sites, one identifiable Bicknell's among 22 individuals of Bicknell's/Gray-cheeked complex in 1984–1999, banded at Butler I., 26 Oct 1996 (D. Cohrs and G. Schmalz unpubl.). In Florida, only three reliable fall records: 1 Bicknell's among 31 birds of both species banded in Tallahassee 1967–1998 (HY bird on 23 Sep 1979; P. Homann unpubl.); another among 41 birds of the two species banded near Orlando 1995–1998 (HY on 13 Oct 1997; P. Small et al. unpubl.); single fall Florida specimen near Apalachicola 23 Sep 1967

(Tall Timbers Research Station specimen data). No other reliable fall record from any Gulf Coast states.

As in spring, birds identifiable as Bicknell's Thrush on basis of wing length captured at fall banding sites well west of breeding range and main migration path. At Long Point, Ontario, 1% of all Bicknell's/Gray-cheeked thrushes (n = 55 of 4,102) banded 1963-1998 referable to Bicknell's; dates ranged from 31 Aug–6 Oct (LPBO unpubl.). At Prince Edward Point, Ontario, 9 of 265 (3%) individuals of the species complex banded 1975–1989 identifiable as Bicknell's; dates 15 Sep–7 Oct (LPBO unpubl.). At Braddock Bay, NY, 1% of banded birds of both species referable to Bicknell's, two HY individuals on 16 Sep 1988 and 26 Sep 1990 (E. Brooks unpubl.). In Finger Lakes region of New York, 1 Bicknell's banded among 32 birds of the two species in 1987–1999 (15 Sep 1999; J. Gregoire unpubl.). Farther south, 18 identifiable Bicknell's among 1,441 new bandings of Bicknell's/Gray-cheeked thrush in sw. Pennsylvania 1961-1994; early date 22 Sep, late date 12 Oct (PNR unpubl.). At fall banding site in Allegheny Mtns. of W. Virginia, 3 apparent Bicknell's among 74 individuals of the species complex banded 1991–1999, 9 Sep-5 Oct (Allegheny Front Migration Observatory unpubl.).

Winter residents on territories in Dominican Republic in early Nov; earliest date 5 Nov (VINS).

MIGRATORY BEHAVIOR

Little information. Stopover lengths not well documented, but few transients appear to linger at stopover sites. No evidence of spring stopovers. Mean minimum autumn stopover on se. Massachusetts coast 2.9 d ± 2.1 SD (range 1–7, n = 8 of 19 birds; MOCS unpubl.). Mean stopover of banded Bicknell's Thrushes (n = 10 of 24 birds) in w. Long I., NY, 1.3 d, maximum stopover 2 d (Beals and Nichols 1940). No recaptures of banded fall migrants at another Long I. site (n = 17 Bicknell's; W. Lanyon pers. comm.), at Kiptopeke, VA, in 1997-2000 (n = 9 Bicknell's; B. Johnson unpubl.), or in sw. Pennsylvania (n = 18 Bicknell's; PNR unpubl.). Possible premigratory movements in e. Dominican Republic suggested by mist-net captures of 6 individuals 10–11 Apr 1974; none captured at same site 7–9 Jan 1975 (J. Faaborg unpubl.). This might, however, simply indicate food-based habitat shift in response to late-winter dry season.

Age ratios strongly skewed towards hatch-year (HY) birds throughout migratory range. Of 152 known-age birds banded at 18 e. North America sites, 90% were immature. Only 3 mid-Atlantic banding stations with fall adult ratios >20% (Kalbfleisch on Long I., NY [29% after-hatch-year individuals, AHY, n = 5; W. Lanyon unpubl.], Sandy Spring, MD [29%; n = 2; J. Weske unpubl.], and Kiptopeke, VA [22%; n = 2; B. Johnson unpubl.]). Small sample sizes obscure possible differences in timing between age classes.

CONTROL AND PHYSIOLOGY

Little information. Some evidence for premigratory fat deposition. On Mt. Mansfield, VT, of 8 birds (2 known breeding adults, 6 presumed local immatures) examined 2–44 d after initial captures in fall (Aug–Sep), 5 gained 0.7–10.2% (mean 5.3%) of original body mass, 1 remained at same mass, and 2 lost 1% and 6%, respectively, of original mass (uncorrected for time of day; VINS). Only 1 HY bird had detectable subcutaneous fat.

Few data on fat or mass changes of migrants. On se. Massachusetts coast, mean mass of transients at initial capture 29.9 g ± 4.5 SD in fall (n = 20), 32.9 g ± 3.9 SD in spring (n =17); fall migrants (n = 8) gained average of 2.9 g ± 4.7 SD during stopovers (range –0.2–10.2; MOCS unpubl.). In sw. Pennsylvania, mean mass of 17 fall migrants 30.8 g ± 2.7 SD (PNR unpubl.). At Kiptopeke, VA, mean mass of AHY birds (n = 2) 29.2 g ± 3.4 SD, of HY birds (n = 7) 27.6 g ± 1.6 SD; AHY birds with higher average fat scores than HYs (B. Johnson unpubl.).

HABITAT

BREEDING RANGE

In U.S., a habitat specialist restricted to montane forests dominated by balsam fir (*Abies balsamea*), with lesser amounts of spruce (red [*Picea rubens*] and black [*P. mariana*]), white birch (*Betula papyrifera* var. *cordifolia*), mountain ash (*Sorbus* sp.), and other hardwood species. At southern extent of range in Catskill Mtns., generally breeds above 1,100 m elevation; minimum elevations at which species occurs decrease by 85 m/1° latitude northward, with individuals recorded as low as 750 m on several Maine peaks (VINS). Lowest nest in Vermont documented at 1,006 m (VINS). Often associated with recently disturbed areas undergoing vigorous succession, characterized by standing dead conifers and dense regrowth of balsam fir (Wallace 1939, VINS). Highest densities typically found in chronically disturbed (high winds, heavy winter ice accumulation) stands of dense, stunted fir on exposed ridgelines or along edges of human-created openings (e.g., ski trails), or in regenerating "fir waves" (*cf.* Sprugel 1976; Marchand 1984, 1995; VINS). In the White Mtns. of New Hampshire, Sabo (1980) found Bicknell's Thrush at a mean elevation of 1,290 m in exposed mid- to upper slopes dominated by conifers (75% of foliage volume) with mean canopy height of 4.8 m.

In Canada, occupies montane fir forests in s. Quebec and New Brunswick up to 1,178 m elevation

(Ouellet 1993, Rompré et al. 1997, Connolly 2000, Nixon et al. in press, D. Busby pers. comm.), coastal maritime spruce-fir forests in New Brunswick and Nova Scotia (Wallace 1939, Erskine 1992, D. Busby pers. comm.), and regenerating stands of mixed forest following forest fires or clear cutting in Quebec and New Brunswick, generally >450 m (Ouellet 1993, Nixon 1996, Nixon et al. in press).

In Quebec montane forests, occupied sites had significantly higher components of balsam fir than unoccupied sites (19,920 stems/ha versus 7,240 stems/ha; Connolly 2000); fir made up 71.1%, 75.1%, and 88.5% of all stems recorded at 3 discrete geographic study areas (Rompré et al. 1997). Spruce and hardwoods species significantly less abundant on occupied than unoccupied sites (Connolly 2000). Mean total stem density varied from 43.7 to 106.3/m^2 on occupied sites, and trees <2.5 cm diameter at 20 cm height above ground were the dominant size class (Rompré et al. 1997). Occupied sites had a lower percentage of herbaceous ground cover, higher percentage of moss ground cover, more dead fallen trees, more snags and stumps, and higher overall tree density (stems >2.5 cm diameter) than unoccupied sites (Connolly 2000). Mean canopy heights of occupied habitats ranged from to 5.4 m in Parc de la Gaspésie, to 7.5 m in ZEC des Martres, to 14.1 m on Mont-Mégantic (Rompré et al. 1997).

In predominantly industrial forest landscape of Central Highlands of New Brunswick, Bicknell's Thrush found at 457–760 m elevation, but most (67%) >600 m (Nixon 1996, Nixon et al. in press). Most occupied sites in second-growth, regenerating forest following large-scale disturbance by clear-cutting or fire. These "non-traditional" habitats (Ouellet 1993) dominated by deciduous species; 89% of occupied sites with higher densities of deciduous stems than coniferous stems, 63% of these with twice as many deciduous as coniferous stems (Nixon et al. in press). White birch dominant tree species on occupied sites, followed by balsam fir and cherry (*Prunus* sp.). Stem densities on regeneration sites high (47% of sites >40,000 stems/ha, 74% sites >20,000 stems/ha), but similar between occupied and unoccupied sites (Nixon et al. in press). Most (>70%) trees on occupied sites had diameters ≤2.5 cm, but in 5–10 cm size class, balsam fir significantly more abundant than on unoccupied sites. Mean canopy height on occupied regeneration sites 4.4 m; most harvested or planted 10–12 yr earlier (range 5–17 yr; Nixon et al. in press).

On Cape Breton I., Nova Scotia, most (78%) birds found in unmanaged "traditional" fir-dominated habitat, 22% in areas of regenerating industrial forest (D. Busby pers. comm.). Over all habitat types occupied by Bicknell's Thrush on Cape Breton, 54% with >70% coniferous cover, 30% classified as "mixed," 15% with >70% deciduous cover (D. Busby pers. comm.). Mean canopy height <5 m on 46% of occupied Cape Breton sites.

SPRING AND FALL MIGRATION

Little information. Reported to be habitat generalist; " . . . migrants usually . . . in shady lanes, along well-vegetated beaches, and in denser woodlots, occasionally emerging into more open orchards and gardens" (Wallace 1939: 259). In coastal Virginia, regularly captured in mist-nets in upland shrub and dune scrub forest dominated by loblolly pine (*Pinus taeda*), various oak species (*Quercus* sp.), wax myrtle (*Myrica cerifera*), and early successional, oldfield habitats (Wilson and Watts 1997). Little evidence that montane forests preferentially selected by migrants (e.g., Rimmer and McFarland 2000; but see Wallace 1939: 259–260).

WINTER RANGE

Current preferred winter habitat mesic to wet broadleaf montane forests in Dominican Republic (Rimmer et al. 1999), Haiti (Wetmore and Swales 1931; Woods and Ottenwalder 1983, 1986), Cuba (Rompré et al. 2000, Y. Aubry and G. Rompré pers. comm.), Jamaica (R. and A. Sutton pers. comm., VINS), and Puerto Rico (J. Wunderle unpubl.). In Dominican Republic, found at all elevations from sea level to 2,200 m, although 62% of occupied sites in forests >1,000 m elevation (Rimmer et al. 1999). Majority (75%) of occupied sites ($n = 24$) in broadleaf-dominated forests ("cloud/montane broadleaf forest" and "submontane broadleaf rainforest"; Tolentino and Peña 1998) at all elevations, 19% in mixed broadleaf-pine forests, and 6% in pine-dominated forests. Primary, wet and/or mesic forests constituted 78% of all occupied sites; only 6% of occupied sites in predominantly dry forests (Rimmer et al. 1999). Use of regenerating secondary forests (22% of occupied sites) in Dominican Republic may indicate winter habitat flexibility or recent shift from preferred primary broadleaf forest habitat, much of which has been lost or degraded.

In Cuba's Parque Nacional Turquino, found in ridgeline forest ("bosque nublado" and "matoral subalpino"), characterized by steep slopes and dense, broadleaf vegetation with few or no pines (Y. Aubry and G. Rompré pers. comm.). In Parc Nacional Macaya in Haiti, occurs in wet montane rain forest and cloud forest (Woods and Ottenwalder 1983). In Jamaica's Blue Mtns., inhabits montane forests, including "upper montane rain forest over shale," "high altitude scrub forest over shale," and "modified upper montane rain forest" (R. and A. Sutton pers. comm.). These habitats, considered to be "highest quality" available, char-

acterized by undisturbed, mature broadleaf trees with relatively open understory and few invasive exotic plant species (R. and A. Sutton pers. comm.). Most occupied sites in Jamaica featured *Podocarpus urbani*. In e. and se. Puerto Rico, found in "lower montane wet forest," characterized by a human-modified, heterogeneous mix of native secondary forest, shrubby edges and fields, dense fern and bamboo thickets, and overgrown plantations (Wunderle 1995, J. M. Wunderle pers. comm.).

In Dominican Republic, some evidence for sexual habitat segregation, or segregation of sexes by geographic area (VINS). In Sierra de Bahoruco on Haitian border, in predominantly undisturbed broadleaf montane forests, 19 of 23 birds mist-netted in Nov 1998 and Jan 2000 were males. At a smaller, more recently disturbed montane forest site in Cordillera Septentrional in northcentral part of country, 9 of 11 birds captured in Jan 2000 were female. At a similar site 23 km to east, 4 females and 3 males captured in Jan 2000. These results preliminary and may be an artifact of small sample sizes or habitat disturbance from human activities and/or 1998 hurricane; warrant more intensive investigation.

FOOD HABITS

FEEDING

Main foods taken. Insects and other arthropods during breeding season; beetles (Coleoptera) and ants (Formicidae) constitute bulk of food volume. Regularly takes wild fruits during migration. Forages primarily for arthropods during winter, but may feed regularly on fruits.

Microhabitat for foraging. During breeding season, generally feeds on or close to ground, but may glean foliage or branches of both coniferous and deciduous trees; sometimes fly-catches from exposed perches (Wallace 1939, VINS). Considered predominantly a ground forager in interior forest habitat by Dilger (1956a). Nestling diet samples suggested that majority of prey delivered were taken above ground (A. Strong unpubl.). No information during migration. Little information from wintering grounds, but reported in dense vine tangles within a few meters of forest floor, but not actually on ground, in the Dominican Republic; 1 record of 3 birds in canopy of an aril-producing tree (R. Greenberg pers. comm.).

Food capture and consumption. Reported to be a "versatile" feeder, moving rapidly by swift hops or short flights on ground below trees or among low branches (Wallace 1939, VINS). Often searches methodically for insects, pausing and peering; may foliage-glean in outer branches; some aerial pursuit of insect prey (Wallace 1939, VINS). "Sally-strikes" and foot-scratching under litter surface recorded in Vermont (A. Strong unpubl., VINS). In winter, recorded hover-gleaning at foliage for arthropods (R. Greenberg pers. comm.).

DIET

Major food items. Invertebrates during breeding season, primarily ants, beetles and lepidopteran larvae. Stomach contents of adults collected on Mt. Mansfield, VT (n = 5), and Slide Mtn., New York State (n = 2) in late Jun and early Jul contained an average of 34% beetles (range 1–95%) and 29% ants (range 0–55%); one bird contained 90% chrysomelid beetles (Wallace 1939). Animal matter constituted nearly 100% of these samples, but 2 birds showed small amounts of unidentified plant matter (Wallace 1939). Lepidopteran and other larvae constituted bulk of food delivered to nestlings in Vermont, but beetles and adult Hymenoptera important nestling prey items (Wallace 1939; A. Strong unpubl.).

Quantitative analysis. Wallace (1939) reported average stomach analyses from 7 breeding adults from the Green and Catskill Mtns.: 34% beetles (Coleoptera, dominated by Chrysomelidae, Elateridae, Cerambycidae, Carabidae, and Staphylinidae), 29% ants (Hymenoptera: Formicidae), 12% Diptera (dominated by Tipulidae), and 9% holometabolous larvae (dominated by Lepidoptera). Less than 5% of the diet was made up of each of Gastropoda, Phalangida, Aranidae, Hemiptera, Homoptera, Neuroptera, Tricoptera, Lepidoptera, and other Hymenoptera.

Ants were not found in any of 4 Vermont nestlings sampled immediately after being fed (A. Strong unpubl.). All 4 chicks had been fed coleopterans (mean 41.3% ± 34.4 SD of total diet, including Chrysomelidae, Elateridae, Cephaloidae, Cantharidae), while the esophagi of 3 contained larvae (mean 49.3% ± 15.8 SD of their total diet, including Diprionidae, Neuroptera, Geometridae, and Bibionidae). Dipterans were found in the diets of 2 nestlings (one with 17% Tipulidae, the other with 12% Chironimidae), each of which had also been fed homopterans (9% Cicadellidae, 6% *Cinara* sp. [an exotic aphid that attacks fir]). One nestling had been fed a slug (Gastropoda), one a mite (Acarina), one a spider, and one an adult conifer sawfly (Diprionidae; A. Strong unpubl.). Size of prey delivered to nestlings averaged 10.72 mm ± 5.11 SD in length (range 3.6 mm [aphid]-25.1 mm [larvae], n = 41); mean length of larvae 13.63 mm ± 5.14 SD (range 5.6-25.1 mm, n = 20) and of Coleoptera 9.32 mm ± 3.07 SD (range 5.6-14.6 mm, n = 10; A. Strong unpubl.).

On Mt. Mansfield, VT, three 7-d-old nestlings contained Lepidoptera larvae, one probable metallic

wood-boring beetle (Buprestidae) larvae, a grasshopper (*Melanoplus* sp.) nymph, and several unidentified beetles and ants (Wallace 1939). Stomach of a depredated 11-d-old fledgling just out of the nest contained 1 cerambycid beetle, a small snail shell, a green Lepidoptera larvae, chitinous remains of unidentified beetles and fragments of various Hymenoptera (Wallace 1939).

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

Resting oxygen consumption at thermoneutrality 3.26 $cm^3 O_2/g \times h \pm 0.05$ SE ($n = 4$ adults from Mt. Moosilaukee, NH; Holmes and Sawyer 1975). At temperatures below thermoneutrality, metabolic rate increased linearly with decreasing ambient temperature, but at a lower rate than in 4 sympatric thrush species, suggesting adaptation to colder summer temperatures of subalpine zone (Holmes and Sawyer 1975).

DRINKING, PELLET-CASTING, AND DEFECATION

No information.

SOUNDS

VOCALIZATIONS

Development. Little information. One captive-reared juvenile on Mt. Mansfield, VT, acquired all characteristic call notes during first summer, but developed only rudimentary song, beginning at 15 d, that lacked typical phrasing and precise tonal quality (Wallace 1939). Same captive bird, exposed to wild males the following summer, learned to imitate their songs "with perfection, but usually reverted soon after to his off-tune, winter song" (Wallace 1939: 317).

Vocal array. CALL NOTES. Most characteristic call note during breeding season is harsh, penetrating, downward slurred whistle, the *Beer* Call (Fig. 2A), variously rendered as *beer, veer, peert, queep*, or *quee-a* (Brewster 1883, Langille 1884, Ball 1952, Dilger 1956b). Highly variable in intensity and pitch, given by both sexes. Mean high frequency 5.8 kHz, mean low frequency 3.2 kHz ($n = 29$ recordings; Ouellet 1993), mean duration 3,052 ms ($n = 25$ recordings, Ouellet 1993). Variants include less piercing, lower-pitched notes, e.g., inquisitive *pe-irt* (Wallace 1939).

Several additional calls used in situations of alarm and aggression. A rolling, wrenlike chatter, or Growl Call, *crr-rr-rr*, given by agitated adults (Fig. 2B; Wallace 1939, VINS); also heard in captive-reared juvenile (Wallace 1939). Soft, low-pitched *chook-chook* or *chuck-chuck* given by both sexes, especially near nest (Wallace 1939, VINS). Adults tending nest or fledglings also give soft, whining, high-pitched whistle *weee*, similar to that of American Robin (*Turdus migratorius*; VINS). Fledglings give thin, nasal or metallic *cheer* calls, difficult to locate, often when parents away foraging (VINS).

Variety of call notes described by Wallace (1939) at nest, including several exchange calls and various chirps and warbles by female during nest-building, incubating, and brooding.

Nocturnal flight calls of migrants, distinguishable from those of Gray-cheeked Thrush, recorded in e.-central Florida (Evans 1994) and described from Gaspé Peninsula as *cree-e-e* (Ball 1952). These calls characterized by tone with bandwidth of 0.5–1.0 kHz and duration of 150-280 ms, rising sharply within 10–20 ms from initial frequency of 1.5–2.0 kHz to 4.8–5.8 kHz, then descending uniformly at 6–8 Hz/ms (Evans 1994). Initial rising section of lower amplitude than latter descending portion and often inaudible to human ear. Frequency domain and shape parameters similar to those of diurnal calls recorded on Mt. Mansfield, VT (Evans 1994).

SONG. Delivered primarily by male, but females occasionally sing on nest during incubation, hatching, and brooding (Wallace 1939, VINS), as well as during activities away from nest (VINS). Song composed of 4 measurable phrases (see Fig. 2C), quantitatively described below by Ouellet (1993) from 32 individual recordings across breeding range. Part I consists of 3–4 introductory notes generally audible to humans only from distances ≤10-12 m. Part II mean duration 0.77 ms ± 0.04 SE, mean high frequency 7.2 kHz ± 0.16 SE, mean low frequency 3.2 kHz ± 0.17 SE, mean amplitude (difference between highest and lowest frequencies) 3.8 kHz ± 0.21 SE. Mean duration of Part III 0.56 ms ± 0.04 SE, mean high frequency 6.4 kHz ± 0.15 SE, mean low frequency 2.9 kHz ± 0.07 SE, mean amplitude 3.7 kHz ± 0.15 SE. Part IV mean duration 0.61 ms ± 0.04 SE, mean high frequency 6.0 kHz ± 0.84 SE, mean low frequency 2.9 kHz ± 0.11 SE, mean amplitude 3.1 kHz ± 0.13 SE.

Qualitative rendering of typical male song *chook-chook, wee-o, wee-o, wee-o-ti-t-ter-ee* (Wallace 1939). Introductory (2–3) low plucking notes "hurriedly followed by two to four, usually three, high-pitched, vibrant, ringing phrases that slur downward . . . Usually on the third of these phrases, there is an emphatic break which is accompanied by both rise in pitch and increased intensity . . . This climax phrase, consisting of several merged notes, is held for an instant, then runs imperceptibly into the closing notes, which are unemphasized" (Wallace 1939: 308-309). Pitch of final phrase constant or rising, whereas that of Gray-cheeked Thrush drops (Ouellet 1993).

Songs variable within populations, sometimes delivered in abbreviated form (Wallace 1939, VINS). Full songs regularly given in flight, most often at dusk, presumably by males (see Behavior: locomotion, below). Female song on nest described as "very low, whisperingly thin, and hoarse" (Wallace 1939). Males heard to give Whisper Songs next to females before copulations, occasionally in winter (VINS).

Geographic variation. Individual variation in song quality confounds interpretation of geographic variation; no consistent differences or regional dialects apparent (J. Marshall pers. comm.). Call notes reported to be similar across breeding range (J. Marshall pers. comm.), but sonographic analysis reveals up to 10 quantitatively distinct call types/bird (Ball 2000).

Phenology. Vocalizes regularly throughout winter. Sporadic calls throughout day, but most vocalizing confined to 15–20 min periods at dawn and dusk; typical *Beer* Call is perceptibly quieter and less intense than on breeding grounds (VINS). Subdued, partial and full songs occasionally heard (VINS).

Songs seldom heard within first week after arrival on breeding grounds, frequency of calling gradually increases during first 1–2 wk after return (VINS). Within 2 wk after arrival (early Jun in Vermont), songs and calls given frequently throughout day (Rimmer et al. 1996). Singing reaches peak in mid-Jun, declines sharply by late Jun and becomes more restricted to dawn and dusk (Rimmer et al. 1996). During incubation and hatching periods, dawn and dusk chorus involves fewer birds, vocal bouts shorter than during mating period (Ball 2000). Vocal activity increases during week after young fledge (Ball 2000).

In Quebec, song activity peaks earlier (5–30 Jun) than calling activity (30 Jun–23 Jul; Ball 2000). Extent of vocal activity in Jul varies among years (Wallace 1939, VINS), may be influenced primarily by frequency of renesting attempts (see Demography and populations: population regulation, below). Very little vocalizing during period of Prebasic molt and fledgling independence in Aug, but a marked resurgence of calling, with intermittent singing, occurs early to mid-Sep (Wallace 1939, VINS). Dusk flight songs occasionally given during this time.

Daily pattern. During breeding season, calls and songs may start as early as 1 h before sunrise. Vocalizing concentrated at dawn and dusk, although spread throughout day during peak of mating activities, generally lowest during early to mid-afternoon (Wallace 1939, VINS). Dawn and dusk bouts consist of both calling and singing, which often climax in brief period of only 5–10 min (VINS). In Quebec, dawn song peak earlier (04:00–05:00) than dawn peak of calling (06:00); dusk peak for both songs and calls similar (21:00; Ball 2000). Dusk bouts typically more vigorous than dawn bouts but cease abruptly with onset of darkness, although vocalizations occasionally given in full darkness at all hours of night (Wallace 1939, Ball 2000, VINS).

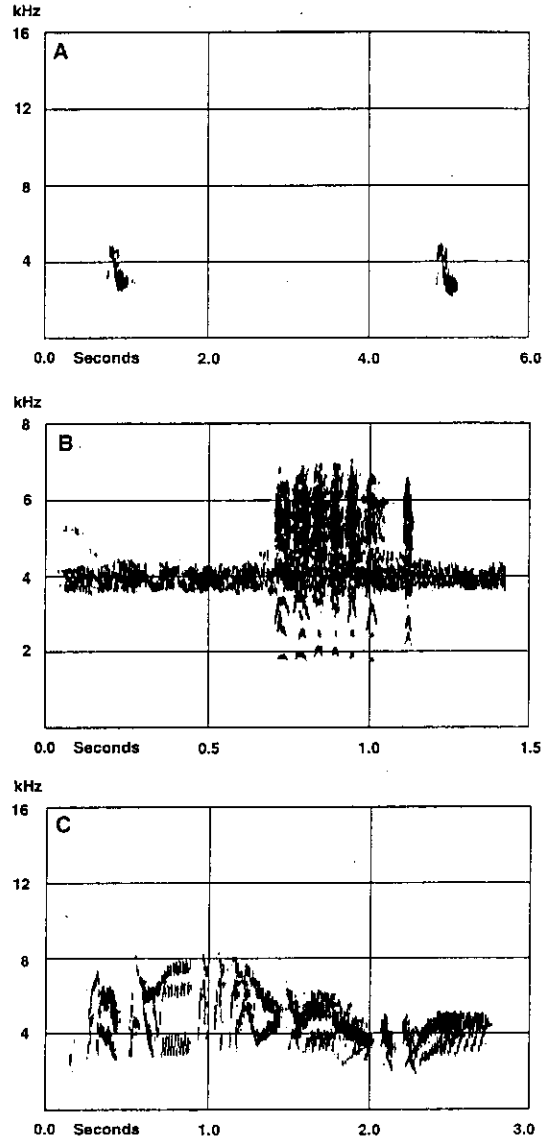

Figure 2. Vocalizations of Bicknell's Thrush. A. Characteristic diurnal call note (*Beer* Call; BLB no. 17542, recorded 19 Jun 1989, Whiteface Mtn., NY). B. Chatter or Growl Call note (Library of Natural Sounds, Laboratory of Ornithology, Cornell University, no. C. Advertising song (BLB no. 17543, recorded 29 Jun 1989, Gaspé Peninsula, Quebec). Prepared by staff of Borror Laboratory of Bioacoustics (BLB), The Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph (with effective frequency resolution of 300 Hz [A and C] and 150 Hz [B] and a 200-point FFT transform size).

still need

No clear evidence of weather effects on vocal activity, as songs and calls given during all but most severe weather conditions in early and mid-Jun (Rimmer et al. 1996). High winds single most limiting

condition on vocal behavior in Vermont. Frequency of singing in Quebec higher during dry, warm weather than in cold, wet conditions (M. Ball unpubl.).

Places of vocalizing. Male song often delivered from exposed perches, usually on dead snags or tops of live trees. May also be given from well-concealed perches in dense vegetation. During mating period, male often sings vigorously near female or prospective nest site (Wallace 1939, VINS). Females known to sing while on nest (Wallace 1939), and from concealed song perches (documented through radiotelemetry) away from nest (VINS).

Repertoire and delivery of songs. Little information, not well studied. Extensive inter- and intra-individual variation in song quality obscures differentiation of male song types. Statistical analysis of sonograms from 18 males throughout breeding range, however, indicates mean repertoire size of 2.4 song types ± 1.21 SD (range 1–6, based on differences in number, shape, frequency, and duration of syllables; M. Ball unpubl.). Song types appear not to be shared among individuals or across breeding range; song types sung serially within an individual song bout, which may contain 4 to as many as 175 songs (Ball 2000). Individuals probably convey their identity through distinct song types; not known whether particular song types used to communicate other information. Song-switching rates higher during dawn and dusk choruses than at other times of day, suggesting that individuals switch song types in relation to social context (Ball 2000).

Mean repertoire size of statistically identifiable call types (all variants of *Beer* Call) across breeding range 3.5 ± 2.54 SD (range 1–10, n = 23 presumed males; M. Ball unpubl.). Mean call repertoire of birds from Gaspesie, Quebec 5.5 ± 2.59 SD (range 1–10, n = 10), that of birds from elsewhere in breeding range 1.9 ± 0.86 SD (range 1–4, n = 13; M. Ball unpubl.). In Vermont, 5–10% males have repeated song elements or other anomalies (distinguishable to human ear) that allow consistent, accurate individual identification (VINS).

Little information on rates of delivery. Rarely, up to 15–20 songs/min given by males for several minutes, typically when females absent from nest (VINS).

Social context and presumed functions. Male song presumed to serve primarily for mate-attraction, although counter-singing suggests function in male-male communication, may be especially strident, accelerated (speed approx. 2 times), and frequent (exceeding 15 songs/min) when soliciting females in the presence of other males and during mate-guarding. Penetrating, counter *Beer* Calls often given between or among neighboring males, appear to be primary means of indicating location. Less intense versions of these calls also exchanged by neighboring birds on wintering grounds, may function in territorial defense. Rolling/staccato Growl Call often used in close male-male aggressive encounters, between neighboring birds in winter, or by male or female in response to perceived threats near nest (VINS). Whisper or sub-song is a quiet version of full song, given by males in close proximity (<5 m) to female; may function to attract female while avoiding detection by nearby males; often precedes copulations. Female known to give sub-song while eggs hatching on nest (Wallace 1939, VINS). Stridency, speed, and rate of sub-song appear to vary inversely to proximity of other males. Close range observation via radiotelemetry suggests that females occasionally sing away from nest.

NONVOCAL SOUNDS

None known.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Little information. Hopping appears to be primary mode of terrestrial locomotion; long, springing hops associated with relatively short femur and long tarsometatarsus may be adaptation for foraging in dense microhabitats (Dilger 1956a).

Flight. In montane forests, occasionally hawks insects with short sallies from perch (Wallace 1939, VINS). Flight songs common at dusk during peak mating period, less common at dawn (Wallace 1939, Dilger 1956b, VINS). Typically consist of 10- to 15-s flights 25–75 m above ground, often in large circles >100 m in diameter (Wallace 1939, VINS). Some straight-line flights up- or down-slope up to 0.5 km in distance (Wallace 1939, VINS). Birds tend to rise rapidly from perches before circling and to drop abruptly back after completing flight songs (Dilger 1956b). Dusk flight song heard on one occasion in Sierra de Bahoruco, Dominican Republic, on 7 Nov 1998, occasionally given at dusk during fall pre-migratory period (VINS).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Adults on breeding grounds observed preening and bathing; older nestlings preen, head-scratch, stretch, and flap wings (Wallace 1939, VINS).

Sleeping, roosting, sunbathing. Nocturnal roost locations of breeding males vary from night to night. Females roost on nest during incubation and brooding periods. In montane forests of Dominican Republic, radio-tagged wintering birds moved 150–500 m from diurnal home ranges in broadleaf forests to nocturnal roost sites in adjacent pine forests. Most roost sites in canopy of pine forests 10–20 m above ground; some evidence of loosely communal roosting. Individual

birds roosted in same general locations of pine forest each night, but one bird that typically roosted in pines remained on daytime territory in broadleaf forest for an entire night and following day, returned to pines the next evening. Movements to and from roost sites occurred at dusk and dawn, respectively.

Daily time budget. Not well documented. Vocal activities concentrated at dawn and dusk on both breeding and winter grounds.

AGONISTIC BEHAVIOR

Physical interactions. Chases common on breeding grounds, especially during mating period, but physical attacks appear to be rare. Both male-male and male-female chases observed.

Communicative interactions. Aggressive postures described by Dilger (1956b) include Upward and Horizontal Stretch. Other hostile displays include Bill-Gaping, Crest-Raising, Wing- and Tail-Flicking, and Foot-Quivering (Dilger 1956b). *Beer* Call frequently elicits aggressive response, especially among males (Dilger 1956b, VINS, WGE). Adults with older nestlings or fledglings may aggressively scold human intruders, giving loud, harsh *peert* calls with bill opened wide and crest-feathers raised; occasionally may fly directly at intruder, veering abruptly <1 m away (Wallace 1939, VINS).

SPACING

Territoriality. See Demography and populations: range, below. On breeding grounds males not territorial in classic sense. Shortly after arrival, males begin to call and sing from song-posts throughout home range but show little physical defense of these areas. Identification of individuals using radio-telemetry and color-band resights verifies that several males often call and sing from same area within one hour. Females apparently territorial, often overtly aggressive to conspecifics during nest-building and egg-laying periods. In montane broadleaf forests of Dominican Republic, maintains discrete territories that are largely non-overlapping and appear to be defended, primarily by vocalizations. Older birds more sedentary than first-winter birds, some of which adopt mobile, "floating" strategy.

Individual distance. No information.

SEXUAL BEHAVIOR

Mating system and sex ratio. Mating system unusual and not easily categorized; may be most similar to that of Smith's Longspur (*Calcarius pictus*), which has been termed female-defense polygynandry (Briskie 1993), in that both males and females mate with multiple partners, multiple paternity is common, and >1 male often feeds nestlings. In Vermont, >75% of broods sired by multiple males; some males with offspring in 2 nests in the same breeding season. Of 13 broods in 1998 and 1999, 10 with ≥2 sires, 3 with single father (VINS).

Overall, 4-yr mean male:female ratio on 3 Vermont study plots 1.8:1.0 (annual range 1.4–2.8:1.0; VINS). Cause of male-biased sex ratio not known, may relate to ratio at hatching, differential natal dispersal patterns, events on wintering grounds (e.g., differential male and survival due to winter habitat segregation); needs investigation.

Pair bond. No specific information. Extremely difficult to assess, given dynamic nature of mating associations.

Courtship displays. Males pursue females in rapid flights through dense thickets, with crest erect and bill gaping, often singing (Wallace 1939). Up to 3 males observed around female on ground singing Whisper Songs, apparently competing for copulations; male may droop and then rapidly flutter wings before copulating (VINS). Male observed to resume foraging shortly after copulation. Dusk flight songs during mating period assumed to have courtship function.

Extra-pair copulations. Apparent rarity or absence of traditional pair bonds obscures terminology. Multiple paternity of most broods indicates that females regularly copulate with ≥2 males during fertile period.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. See Spacing: territoriality, above. During migration, most often solitary or in groups of 2–3 individuals.

Play. No information.

Nonpredatory interspecific interactions. Agonistic encounters with Swainson's Thrush occasionally observed on breeding grounds, including chases and displacement from song-posts (Able and Noon 1976; VINS). This species and Hermit Thrush attracted to playbacks of Bicknell's Thrush vocalizations and may react aggressively to song broadcasts (VINS, WGE). American Robin and White-throated Sparrow (*Zonotrichia albicollis*) observed to displace Bicknell's Thrush from song-posts (VINS).

PREDATION

Kinds of predators. Few documented predators of adults. Remains of 2 radio-tagged females found in or below active Sharp-shinned Hawk (*Accipiter striatus*) nest in mid-elevation red spruce forest up to 2 km from known home ranges on Mt. Mansfield, VT (VINS). Five other dead, radio-tagged adults found on hardwoods forest floor probably depredated by Sharp-shinned Hawks; 2 of these recovered at plucking-posts of this species. Radio-tagged female with dependent fledglings found cached underneath rotting log; tooth marks in skull suggested depredation by long-tailed weasel (*Mustela frenata*; VINS). Occasional mobbing and chasing of Northern Saw-whet

Owl (*Aegolius acadicus*) suggests that this species may depredate adults or free-flying young (VINS).

Of 7 radio-tagged fledglings known to have died, all taken by predators. One found at Sharp-shinned Hawk plucking-post, others apparently killed by mammals. Juveniles probably more susceptible to mammalian predation than adults, due to less developed flight skills and conspicuous begging behavior.

Red squirrel (*Tamiasciurus hudsonicus*) only confirmed predator of eggs and nestlings (Wallace 1939, VINS). Other suspected or likely nest predators include Blue Jay (*Cyanocitta cristata*), Common Raven (*Corvus corax*), eastern chipmunk (*Tamias striatus*), boreal red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), and weasel (*Mustela* sp.; Wallace 1939, VINS). Other potential predators observed in breeding habitat include red fox (*Vulpes fulva*), coyote (*Canis latrans*) and raccoon (*Procyon lotor*). Possible predators in winter include Sharp-shinned Hawk, Ridgway's Hawk (*Buteo ridgwayi*), mongoose (*Herpestes auropunctatus*), and rats (*Rattus* sp.).

Response to predators. Agitated *Beer* Calls by nesting adults often given in response to approach of potential predators, including humans, especially during nestling stage (VINS). Growl Call may also be used. Mobbing of red squirrel, Northern Saw-whet Owl, and Blue Jay occasionally observed (VINS). One incubating female flushed silently at approach of red squirrel, did not vocalize or remain visibly close by while squirrel ate eggs in nest (VINS).

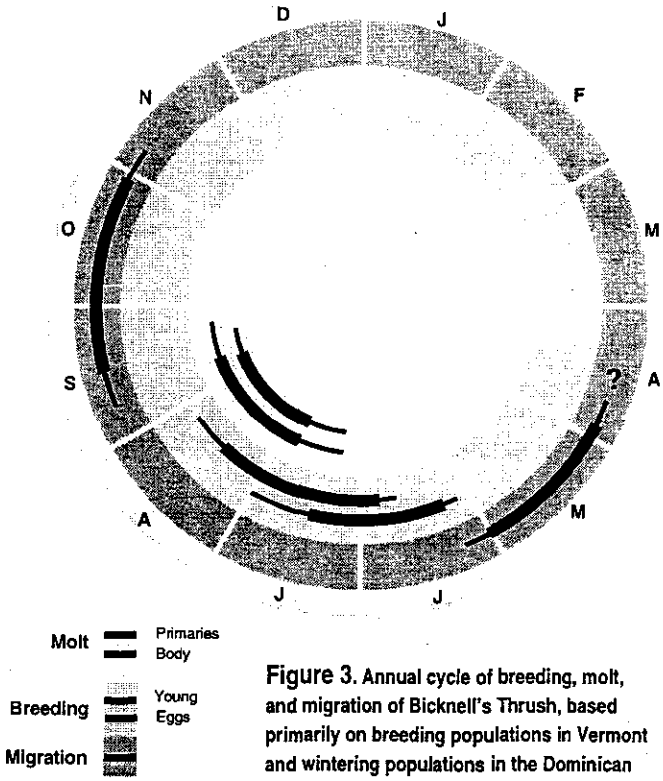

Figure 3. Annual cycle of breeding, molt, and migration of Bicknell's Thrush, based primarily on breeding populations in Vermont and wintering populations in the Dominican Republic. Thick lines show peak activity; thin lines, off-peak.

BREEDING

PHENOLOGY

Pair formation. Little information. Earliest known arrival date of breeding male in Vermont 16 May, of female 23 May (VINS). Breeding males arrive significantly earlier than females (mean difference 1.7 d, 95% Confidence Interval [CI] = 3.2–0.3). Mating activities probably begin shortly after female arrival, as evidenced by frequent singing and calling throughout day in late May and early Jun (Rimmer et al. 1996). Mating associations are dynamic and probably tied to stage of individual females' fertile periods, likely influenced by availability of other mating opportunities and chick-feeding by males.

Nest-building. Earliest confirmed nest construction date in Vermont 1 Jun (VINS); other extrapolated nest-initiation dates of 2–4 Jun (Wallace 1939). Reported nest with 3 eggs on Seal I., Nova Scotia, 3 Jun 1901 (Reed 1904) suggests late May construction and is exceptionally early, as eggs laid in 3 other Seal I. nests were 13–14 Jun (Tufts 1909).

First brood per season. See Figure 3. In Vermont, 71% of 89 clutches initiated in first 3 wk of Jun; later clutches probably represent renesting attempts. Clutch initiation dates: Vermont, 7 Jun–14 Jul (n = 89; Wallace 1939, VINS); New Hampshire, 21 Jun–14 Jul (n = 5; Wallace 1939, Richards 1994); Massachusetts, 18 Jun (n = 1; Veit and Petersen 1993); Quebec, 6 Jun–20 Jul (n = 7; Wallace 1939, Y. Aubry unpubl.); Nova Scotia, 3-14 Jun (n = 4; Wallace 1939, Tufts 1962). Known hatching dates 23 Jun–29 Jul (70% by 6 Jul) in Vermont (n = 68; Wallace 1939, VINS), 26 Jun–14 Jul in Quebec (n = 6 nests; Y. Aubry unpubl.). Known fledging dates 3 Jul–3 Aug (70% by 14 Jul) in Vermont (n = 53; Wallace 1939, VINS), 8–24 Jul in Quebec (n = 6 nests; Y. Aubry unpubl.). Young stay in nest 9–13 d (average 11.4 ± 1.3 SD, n = 17; Wallace 1939, VINS).

Second brood per season. Second brood rare, one confirmed instance in Vermont. Female that fledged 2 chicks on 2 Jul initiated second clutch on 7 Jul, built nest while feeding fledglings and continued feeding during egg-laying (VINS). Renesting attempts after early-season failures common. Mean interval between loss of first nest and initiation of second clutch in Vermont 6.8 d (range 5–12, n = 5). One female renested successfully on third attempt, requiring only 2 d from loss of second clutch to initiation of third (VINS).

NEST SITE

Selection process. Little information. Probably selected solely by female. Females build nests 17–

1,344 m apart in successive years (mean 182.9 m ± 267.8 SD, n = 26; VINS). No statistical difference between distances for females of failed versus successful previous year's nest, although large movements tend to follow failures. One older female moved 1,344 m and another 540 m after failing the prior year; these distances more than twice those between any other successive year's nests. One female in 2000 nested 1,715 m away from nest she built in 1998 as yearling bird. Renesting attempts averaged 52.7 m ± 28.5 SD from first nest (range 19-87, n = 7; VINS).

Microhabitat. Usually located in dense stands of young to mid-successional fir or "krummholz," uncommonly in more mature, open forests (Wallace 1939, VINS). Often found in dense regrowth along natural or artificially created edges. On 2 ski areas in Green Mtns. of Vermont, nests averaged 10.8 m ± 8.97 SD from ski-trail edge (range 0–33, n = 26; VINS).

On nest-centered 5-m radius plots (n = 103) in Vermont, mean densities of large woody stems (<8.0 cm diameter at 10 cm above ground) 163.4 ± 107.34 SD (VINS). Balsam fir accounted for 67% of all live woody stems <8.0 cm diameter within 5 m of nests, followed by white birch (11.7%), dead stems (9%), mountain ash (6.1%), mountain-holly (*Nemopanthus mucronata*; 1.9%), and red spruce (1.1%); 11 other species each accounted for <1%. Leaf litter depth ranged from 1.5 to 21.5 cm (mean 5.1 ± 2.9, n = 74). On nest-centered 11.3-m radius plots (n = 103), mean density of live trees 8–23 cm dbh (diameter at breast height) was 33.4 ± 18.7 SD (range 5–89), mean density of dead standing trees 8–23 cm dbh 11.9 ± 8.2 SD (range 0–34). Mean densities of live trees >23 cm dbh was 3.25 ± 4.95 SD (range 0–30), of standing dead trees >23 cm dbh 2.3 ± 2.9 SD (range 0–22). Canopy dominated by balsam fir at 81 of 103 nests (79%), balsam fir and white birch codominant at 9 nests, mix of balsam fir and mountain ash at 5 nests, white birch dominant at 4 nests, mix of several species at 2 nests, balsam fir and red spruce codominant at 1 nest, red spruce at 1 nest. Mean canopy height within 11.3 m of nests ranged from 1.2 to 17.9 m (mean 5.4 ± 2.9 SD, n = 103). Slope ranged from 0° to 46° (mean 18.7° ± 10.4 SD, n = 101).

Site characteristics. Vermont nests typically built at base of 1–4 horizontal branches against trunk of small tree (70%; n = 105), occasionally up to 3 m from trunk on horizontal branches of larger trees (VINS). Support branches average 1 cm diameter (range 0.1–5.25, n = 93). Some nests supported between two closely spaced trees (23%; n = 105). One nest inside cavity of balsam-fir snag, another perched on shelf created by broken snag. Most nests (103 of 118; 87%) in balsam fir, but also in red spruce (n = 10), paper birch (*Betula papyrifera*; n = 3), and dead standing fir (n = 2; Wallace 1939, VINS). Average nest tree height 3.2 m ± 1.55 SD (range 0–11, n = 102) and mean dbh 5.7 cm ± 5.24 SD (range 1–31.5, n = 102). Nest orientation in relation to trunk averaged 161° (n = 27 in southeastern quadrant, 22 in southwestern quadrant, 15 in northwestern quadrant, 13 in northeastern quadrant). Of 118 Vermont nests, mean height above ground 2.05 m ± 1.18 SD (range 0.46–10 m; Wallace 1939, VINS). Mean vegetation concealment in 25-cm diameter circle around 98 nests, estimated from 1 m away, was 74.7% ± 24 SD overhead, 62.7% ± 27.4 SD to north, 64.9% ± 29.3 SD to south, 63.8% ± 27.4 SD to east, and 67% ± 27.1 SD to west. Mean nest height of 8 Quebec nests 1.5 m ± 0.34 SD (range 1.0–2.0), 7 in balsam fir, 1 in a paper birch (Y. Aubry unpubl.).

NEST

Construction process. Only females observed constructing nests (Wallace 1939, VINS). One nest built in 11 d (Wallace 1939), one in 9 d (VINS). One renest built in 2 d (VINS). May exceptionally prolong construction or abandon nest if interrupted while building (Wallace 1939, VINS). Interval between nest-building visits about 2 min; same as time spent arranging material from each load (Wallace 1939). Foundation built first, followed by walls, interior cavity, and lining (Wallace 1939).

Structure and composition matter. Bulky, cup-shaped nest built primarily of twigs and moss. Exterior shell of most nests in montane forests of Vermont constructed of twigs of balsam fir, occasionally of red spruce and paper birch, profusely interwoven with strands of moss (primarily *Pleurozium schreberi*, often lesser amounts *Sphagnum* spp.; Wallace 1939, VINS). Proportions of twigs and moss vary; some nests reported to be almost entirely constructed of moss (Wallace 1939). Other materials found in nest walls include grasses, sedges, stalks of herbaceous flowering plants or ferns, dry leaves, bark strips, hair, and lichen (Wallace 1939, VINS). Interior layer of wall consists of decayed vegetation, such as leaf mold. Inner lining of Vermont nests invariably composed of threadlike, black rhizomorphs of horsehair fungus (*Marasimius androsaceous*; McFarland and Rimmer 1996); some nests may also be lined with fine stems of grasses or sedges (Wallace 1939, VINS). One nest on ski area contained pieces of nylon rope woven in cup (VINS).

Dimensions. Mean minimum-maximum outside diameter of 20 Mt. Mansfield, VT, nests in 1930s, 11.5 × 12.8 cm (range 10.3–14.1); inside diameter 6.3 × 7.2 cm (range 5.8–8.7); outside height 8.6 cm (range 7.1–9.6); inside depth 4.6 cm (range 3.8–6.4; Wallace 1939). Average outside diameter of 79 nests from Vermont in 1992–2000, 11.3 cm ± 1.8 SD (range 5–16); inside diameter 7.1 cm ± 1.3 SD (range 5.3–12); outside height 8.1 cm ± 1.9 SD (range 1.6–14); inside depth 4.4 cm ± 0.9 SD (range 2–6.5; VINS).

Microclimate. No information.

Maintenance or reuse of nests. Not known to reuse old nests; builds new nest when renesting. One female reused exact nest site in tree for 2 yr in Vermont. Female often pokes and probes rapidly at bottom of nest during nestling stage (VINS).

Nonbreeding nests. None reported.

EGGS

Shape. Subelliptical.

Size. Twenty-nine eggs from 8 clutches on Mt. Mansfield, VT, in 1935 had mean length of 21.9 mm (range 21.0–23.0) and mean breadth of 16.6 mm (range 16.0–17.5; Wallace 1939). Ten eggs from Vermont in late 1990s had mean length of 22.38 mm ± 0.78 SD (range 20.48–23.6) and 8 eggs had mean breadth of 16.29 mm ± 1.64 SD (range 12.36–17.5; VINS).

Mass. No information.

Color. Bluish green with variable amounts light brown speckling. Spots typically concentrated around larger end but may be uniformly distributed over egg, ranging in appearance from very small dots to larger, irregular blotches. Eggs of olive-phased birds reported to be nearly plain, those of brown-phased birds more heavily blotched (Wallace 1939). Individual clutches may contain both lightly and heavily spotted eggs (Wallace 1939, VINS).

Surface texture. Smooth, semiglossy.

Eggshell thickness. No information.

Clutch size. First clutches invariably 3–4 eggs. Of 13 Mt. Mansfield, VT, nests examined in 1935, 7 contained 3 eggs, 6 contained 4 (Wallace 1939). Of 59 known or probable first-clutch nests examined on Mt. Mansfield and Stratton Mtn., VT, mean clutch size 3.6 ± 0.49 SD (range 3-4; VINS). Three Nova Scotia clutches from 1907 each with 3 eggs (Tufts 1962), two 1999 nests from Gaspé Peninsula in Quebec each with 4 eggs, 3 Gaspé nests in 2000 each with 3 eggs (Y. Aubry unpubl.). Nests initiated earlier in season tend to have 4 eggs, later nests 3 (Wallace 1939, VINS). Mean clutch size of 13 known second attempts 3.1 ± 0.28 SD (range 2–4; VINS). One known third attempt contained 3 eggs.

Egg-laying. Little information. Eggs laid at 1-d intervals, usually in early morning. One observation of an egg laid at noon (Wallace 1939). For first nests, laying begins several days after nest completion. For renests, laying may begin before nest completely constructed; building continued during and after eggs laid in one documented second-brood nest (VINS). Prior to and during egg-laying, males active and vocal in nest area. Females often aggressive toward conspecific intruders. Intraspecific nest parasitism at one Quebec nest documented on basis of genetic analyses (G. Seutin pers. comm.).

INCUBATION

Onset of broodiness and incubation. By female alone, usually beginning with penultimate egg (Wallace 1939, VINS).

Incubation patch. Developed only by female; single median abdominal patch. In Vermont, earliest date of fully developed patch 9 Jun and latest 31 Jul (VINS).

Incubation period. In Vermont, incubation period to nearest day, 9–14 d (average 12 ± 1.6 SD, n = 8; Wallace 1939, VINS). Eggs in 1 Quebec nest hatched 13–14 d after incubation began (Y. Aubry unpubl.).

Parental behavior. Female alert and watchful but restless on nest, frequently shifting position, rolling and inspecting eggs, picking at nest bottom, preening, and taking insects within reach (Wallace 1939, VINS). Most females remain tightly on nest, flushing only at close range (Wallace 1939, VINS). Female may leave nest to feed as early as predawn, frequently leaves during day, some birds at 5–10 min intervals; few remain off nest >15 min, but one bird left clutch unattended for >1 h (Wallace 1939, VINS). Females reported to sing during all stages of incubation, including hatching, at 4 Mt. Mansfield nests (Wallace 1939). At one Stratton Mtn. nest, female sang muted song on nest as eggs began to hatch (VINS). Males occasionally visit nests and sing or call nearby during incubation, but are not known to feed incubating females (see Parental care: feeding, below; Wallace 1939, VINS).

Hardiness of eggs against temperature stress; effect of egg neglect. No information.

HATCHING

Preliminary events. Female reported to become increasingly agitated during 24 h before hatching, frequently inspecting and picking at eggs, in one case even bringing an insect and prodding at eggs with it (Wallace 1939).

Shell-breaking and emergence. Eggs pipped in circle around widest part of egg, break into 2 parts (Wallace 1939). Chicks generally hatch within 24 h of each other (Wallace 1939, VINS). Hatching of individual chicks may take up to 12 h (Wallace 1939).

Parental assistance and disposal of eggshells. Female may assist emerging chick by tugging vigorously at egg (Wallace 1939). Eggshells invariably removed and deposited away from nest (Wallace 1939, VINS), not known to be eaten.

YOUNG BIRDS

Condition at hatching. Altricial and nidicolous. Skin with flushed, pale reddish appearance; margin of bill whitish yellow, interior of mouth bright orange (Wallace 1939). Body mass of one nestling immediately after hatching 1.7 g (Wallace 1939).

Growth and development. See Table 1 for measurements. Combined average daily rate of mass gain for

Table 1. Mass (g) and body measurements (mm) of nestling Bicknell's Thrush from Green Mtns., VT. Day 1 is hatching day. Data shown as mean (*n*) for Wallace 1939 (A) and mean ± SD (*n*) for VINS (B).

Age (d)	Mass	Wing length	Tarsus length	Source
1	2.5 (3)		8 (3)	A
2	3.6 (4)	7.8 (3)	10.1 (6)	A
3	6.47 (9)	9.5 (9)	11.8 (9)	A
4	9.8 (9)	12.1 (9)	14.9 (9)	A
5	12.9 (9) 15.5 ± 2.83 (2)	16.5 (9)	18.2 (9)	A B
6	15.7 (6) 18.5 ± 3.3 (5)	21.7 (6)	21.2 (6)	A B
7	17.2 (5) 15.4 ± 0.87 (5)	25.8 (8)	22.8 (8) 22.6 (1)	A B
8	20.7 (5) 20.6 ± 2.11 (11)	31.6 (8)	25.8 (8)	A B
9	22.9 ± 1.15 (4)	35.6 (5)	26.9 (5)	A B
10	21.8 (3)	41.7 (8)	28.9 (8)	A
11	Slight increase (3) 23.7 ± 1.47 (3)	44.8(3)	30 (3)	A B
12	24.8 (1)			A

3–9 nestlings on Mt. Mansfield, VT, 2.6 g ± 0.9 SD (range 1.2–3.5) between ages 1–8 d, total increase of little more than 1 g between ages 8–11 d (Wallace 1939). Mean wing length increased 4.6 mm/d ± 1.4 SD (range 1.8–6.1) between days 2-11, mean tarsus length 2.2 mm/d ± 0.8 SD (range 1.1–3.3; Wallace 1939). Tail-feathers erupted on day 7, grew average of 3.1 mm/d ± 1.6 SD between days 8–11 (Wallace 1939). Four clutches on Mt. Mansfield measured at mid-nestling stage (5–8 d old) and just before fledging gained 0.3–2.1 g/d (average 1.3 ± 0.6 g, n = 10; VINS). Chicks sometimes audible up to 15 m from nest from about day 5 to fledging. Late in nestling period, young preen, stretch, and beat wings. Just before fledging, may perch on nest rim, walk and hop around nest and onto nest support branches. Young leave nest with body mass nearly that of adult's (Wallace 1939, VINS).

PARENTAL CARE

Brooding. Only by female. Time spent brooding declines with nestling age, sharply after day 1. Mean brooding periods 20.2 min on 1-d-old chicks (range 4.6–42.3, n = 14 brooding events), 7.6 min on 2-d-old chicks (range 0.3-18.5, n = 28 brooding events), 7.5 min on 3-d-old chicks (range 0.2-17.2, n = 45 brooding events), 6.9 min on 5-d-old chicks (range 0.7–23.7, n = 40 brooding events), 3.3 min on 7-d-old chicks (range 0.2–10.3, n = 12 brooding events; VINS).

Feeding. Both sexes feed chicks. Male occasionally delivers food to brooding female, who feeds nestlings or may eat it herself, especially when nestlings are very young (Wallace 1939, VINS). Male and female may feed young simultaneously (Wallace 1939, VINS). First food deliveries of day may be brought by male in near darkness of predawn, before female has left nest from night's brooding (Wallace 1939). At 25 Vermont nests observed by videography, one female fed at each nest, with 2 provisioning males most common (60%), followed by 1 male (20%), 3 males (16%), and 4 males (4%; VINS). Four males documented to feed at >1 nest within single breeding season, 3 feeding 2 broods simultaneously (nests 186–443 m apart). One male simultaneously provisioned

at two nests 443 m apart, shared feeding of nestlings at first nest, was sole male feeder at second nest. First nest fledged 3 d after second nest hatched; male then left care of fledglings to the other male and fed second brood at nearly twice the rate as he had fed young at first nest. Individual female, total male, and total adult provisioning rates did not differ between nests with single and multiple male feeders. Some males did not feed at nests in which they sired young, and some males fed at nests in which they sired no young. Male feeding rates increased with nestling age until day 7–8 and then decreased until fledging. Multiple male feeders also reported at nests in Gaspé Peninsula, Quebec, with 3 males attending 2 different nests in 2000 (Y. Aubry unpubl.).

Nest sanitation. Unhatched eggs often removed within several days of others hatching. Chicks that die at early age are removed. In one case, an 8-d-old chick died and was crushed into nest cup bottom by surviving siblings. Young produce fecal sacs, usually subsequent to food deliveries. Adults typically wait after feeding young, peering at raised and protruding cloaca, which is oriented towards outside of nest, until fecal sac emerges. Adults eat up to 3 fecal sacs/visit, especially when chicks young. No more than one uneaten fecal sac carried away each feeding trip. Few fecal sacs eaten and none carried away during first day of nestling life. With nestlings 2–7 d old, adults eat 0.7 to 1.9 fecal sacs/h and carry away 0.05–0.36 sacs/h. By day 7, eating:disposal ratio nearly 1:1; from day 8 to fledging ratio steadily increases to 1:2, as fewer and fewer fecal sacs produced. From 8–12 d, adults eat 0.23-0.3 fecal sacs/h and carry away 0.6–1.1 sacs/h. Chicks usually leave excrement in nest cup and on rim when fledging. (VINS).

COOPERATIVE BREEDING

Not documented.

BROOD PARASITISM

Interspecific not known to occur; little or no overlap in breeding habitat with Brown-headed Cowbird (*Molothrus ater*).

FLEDGLING STAGE

Departure from nest. Nestlings fledge 9–13 d after hatching (average 11.4 d ± 1.3 SD, n = 17 known to exact day; Wallace 1939, VINS). In 3 Quebec nests, fledging 12–14 d after hatching (Y. Aubry unpubl.). Tarsus, toes, and bill are adult length, but wings only half-grown and tail about one-fifth grown at fledging (Wallace 1939, VINS). Young at nearly adult weight when leaving nest (Wallace 1939, VINS).

Growth. Little information. One Vermont fledgling captured 30 d after leaving nest increased mass from 22.1 g to 25.8 g (VINS). One nestling retained in captivity grew wings and tail about 3 mm/d until adult size achieved (Wallace 1939).

Association with parents or other young. Little information, but fledglings may remain with adults up to 14 d after leaving nest. Adults often split brood. One known case of 2 males splitting brood, apparently emancipating female. In another case, female and one of 2 male feeders split brood; second male continued to feed nestlings in another nest. Movements of family groups not well documented, but adults with dependent fledglings found up to 280 m away from known nest sites. (VINS)

Ability to get around, feed, and care for self. No information.

IMMATURE STAGE

Little information. Movements and habitat use during postfledging period of independence poorly known. Of 11 Vermont fledglings radio-tagged in 2000, 7 known to have been depredated (mean survival 8.1 d ± 6.6 SD after fledging, range 1–19), 2 disappeared after 8 and 19 d, respectively, and 2 survived until transmitter batteries expired (40 and 31 d, respectively). Of these latter 2 birds, one remained within 275 m of its natal nest site in montane fir forest, while the other moved nearly 1 km downslope after about 10 d to hardwood-dominated forest at elevations 700–900 m, and remained there. One free-flying juvenile banded on 25 Jul stayed within 100-m radius of banding location in stunted fir forest at 1,150–1,175 m elevation until 22 Aug, then disappeared (VINS).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Breeds at approximately 1 yr old and annually thereafter. Of known-age female breeders at 85 Vermont nests in 1994–1999, older (≥2-yr-old) females outnumbered yearling females 73 to 12 (85.9% to 14.1%). Of 25 Vermont males with known paternity at 1998 and 1999 nests, only 2 (8%) were yearling birds, while this age-class constituted about 25% of entire male study population. Highly irregular settlement patterns further suggest that some yearling males fail to mate (VINS).

Clutch. See Breeding: eggs, above. Mean clutch size in Vermont 3.6 ± 0.49 SD (range 3–4, n = 59; VINS).

Annual and lifetime reproductive success. In Vermont, annual reproductive success among males skewed but generally low. Of 21 males with known paternity at nests in 1998 and 1999, 13 (62%) sired only 1 chick, 4 (19%) sired 2 chicks, 3 (14%) sired 3 chicks, and 1 (5%) sired 4 chicks; these are minimum estimates (VINS).

Annual Mayfield daily survival rate of nests (probability of nest surviving 1 d without failure) on Stratton Mtn., VT: 0.98 ± 0.014 SE (n = 39 nests), and on Mt. Mansfield, VT: 0.96 ± 0.007 SE (n = 56 nests). Daily survival rates of Vermont nests strikingly biennial in response to balsam fir cone production and red squirrel population cycles. From 1994 to 2000, fall cone crops very high in even-numbered years, resulting in high red squirrel populations during following springs and summers, with consequent low productivity for Bicknell's Thrush because of nest depredation. In odd-numbered years, fall cone production invariably lower, spring and summer squirrel populations reduced, and thrush nesting success markedly higher (VINS).

Average number of young fledged/nest in Vermont: Stratton Mtn. 2.1 ± 1.37 SD (range 0–4, n = 30); Mt. Mansfield 1.5 ± 1.59 SD (range 0–4, n = 46).

Number of broods normally reared per season. Only one brood normally reared; one documented second brood (see Breeding: phenology, above).

Proportion of total females that rear at least one brood to nest-leaving. Percentage of females that raise one brood to independence each year in Vermont: Stratton Mtn. 1997 = 85.7%, 1998 = 88.8%, 1999 = 0%, 2000 = 90.9%; Mt. Mansfield 1999 = 62.5%, 2000 = 62.5% (VINS).

LIFE SPAN AND SURVIVORSHIP

Longevity record for banded male 8 yr, for female 7 yr. Annual survival rate of older birds captured on Vermont breeding grounds, based on Cormack-Jolly-Seber model (Lebreton et al. 1992, Cooch and White 1998, White and Burnham 1999, Bertram et al. 2000), was not dependent on time or sex on 4 study plots. To account for uncertainty in model selection, range of mean parameter estimates averaged over all 16 models in the candidate set for each study plot, weighted by Akaike model weights, and most parsimonious model used (Burnham and Anderson 1998, Bertram et al. 2000). Annual survivorship on Mt. Mansfield ridgeline in 1992–1999: 54.7% ± 6.5% SE with mean parameter estimates for all models ranging from 54% to 55.8%; Mt. Mansfield east slope in 1995-1999: 74.8% ±8.6% SE, mean estimates 71.9–79.1%; Stratton Mtn. ski-area plot 1997–1999: 73.9% ± 10.1% SE, mean estimates 75.6–88.3%; Stratton Mtn. natural plot 1997–1999: 94.6% ± 28.4 SE, mean estimates 86.1–94%. No difference in survivorship between Stratton Mtn. ski area and natural area plots. Survival rate of juveniles poorly known because of apparent natal dispersal; only 3 of 115 (2.6 %) nestlings and dependent fledglings and 9 of 62 (14.5 %) independent juveniles banded in Vermont 1992–1998 documented to return to breeding site. Two nestlings that returned were females from the same nest. On Mt. Mansfield in 2000, only 2 of 11 (18.2%) radio-tagged fledglings known to have survived beyond 30 d. Annual survival rate of wintering individuals captured at montane broadleaf forest site in Sierra de Bahoruco, Dominican Republic, based on Cormack-Jolly-Seber model estimates, was not time dependent in 1994–1999: 72.9% ± 14.3% SE, with mean parameter estimates for all models ranging from 68.4% to 79.7% (VINS).

DISEASE AND BODY PARASITES

Diseases. No information.

Body parasites. Unidentified *Mallophaga* found on remiges of 36 of 90 (40%) adults examined in Vermont during 2000 and on primaries of 15 of 46 (33%) birds examined in Dominican Republic 1996–2000 (VINS). Nymphs of 4 individual *Ixodes scapularis* ticks removed from base of bill and around eyelids of 2 adult Bicknell's Thrushes (1 male, 1 female) on Stratton Mtn., VT, in late May 1999; these presumably acquired during northward migration in U.S. (VINS). Unidentified ticks found on 3 of 46 (7%) birds examined in Dominican Republic. Nestlings reported parasitized by blow flies (*Protocalliphora* sp.) at 1 Vermont nest (Wallace 1939), but no instances of this parasitism noted at 85 Vermont nests in 1990s.

CAUSES OF MORTALITY

Exposure. Some nestling deaths attributable to severe weather, e.g., >2-d periods of cold (3–5°C), wet conditions, often with heavy rain and high winds (VINS).

Predation. See Behavior: predation, above.

Competition with other species. Not known.

RANGE

Initial dispersal from natal site. Little information. See Breeding: immature stage, above. One Vermont juvenile captured in mist-net 507 m from nest site 30 d after fledging (VINS). No documentation of dispersal away from natal site, but assumed due to very low natal philopatry of banded juveniles in Vermont.

Fidelity to breeding site and winter home range. See Breeding: nest site, above. Both older males and females of all ages site-faithful on breeding grounds, as indicated by mist-net recaptures at same sites over successive years. Between-winter philopatry documented in broadleaf forest in Sierra de Bahoruco, Dominican Republic, with 14 of 27 banded individuals recaptured between winters (mean distance between captures 95.4 m ± 92.6 SD, range 0–260 m; VINS).

Male banded on Mt. Mansfield, VT, on 16 Jun 1995 recaptured in mist-net in Sierra de Bahoruco of Dominican Republic <6 mo later, on 2 Dec 1995. This individual occupied same breeding home range during 1996 and 1997 summers and was strongly suspected, although not confirmed, to reoccupy same winter territory in 1996/1997 (Rimmer and McFarland

in press). High variance in feather deuterium values from small study areas in Sierra de Bahoruco, Dominican Republic, compared to more uniform values in discrete areas of breeding range, suggests mixing of breeding populations in winter (Hobson et al. in press).

Dispersal from breeding sites. Only 1 documented long-distance breeding dispersal of yearling male on Equinox Mtn., VT, that was captured 17.2 km distant 2 yr later on Stratton Mtn., VT. High variance in feather deuterium values of yearling birds within breeding populations suggests high natal dispersal and/or considerable movement among montane habitat patches (Hobson et al. in press). This is also supported by estimates of gene flow among 4 ne. U.S. mountain ranges derived from mitochondrial DNA control region sequence data (WGE).

Home range. On breeding grounds, males range more widely than females. Using 95% fixed-kernel estimates from radio-tracking data on Stratton Mtn., VT, males averaged 4.53 ha ± 2.17 SD, while females averaged 2.33 ha ± 1.01 SD. Individual male home ranges overlap extensively with those of 2–7 other males, often intersecting near nest sites. Males had 1–4 known nest sites within home range. Female home ranges generally overlap little. During inclement weather early in breeding season on Mt. Mansfield, VT, some males descend to midelevation transitional forest, some females move to south-facing slopes. Winter home range sizes poorly known, but evidence from mapping vocalizations in broadleaf forests of Sierra de Bahoruco, Dominican Republic, suggests 0.5–2 ha (VINS).

POPULATION STATUS

Numbers. Breeding densities difficult to ascertain because of unusual mating system, rugged terrain, and dense habitat. One of the most rare, range-restricted breeding species in e. North America. Based on amount of potential breeding habitat from remote-sensing data, mean home range area in Vermont, and dual assumptions of nonoverlapping home ranges and saturated habitat, estimated rangewide breeding population of 25,000–50,000 individuals (VINS). Estimates of effective population size derived from mitochondrial DNA control region genealogies, with methods derived from coalescence theory, are comparable (WGE). More than 90% of birds believed to breed within U.S, only an estimated 2,000–2,500 pairs breeding in Canada (Nixon 1999). In U.S., Adirondack Mtns. contain largest area of montane forest breeding habitat, followed in descending order by White Mtns. of New Hampshire, mountains of w. and central Maine; Green and Taconic Mtns. of Vermont, and Catskill Mtns. of New York State (Atwood et al. 1996, VINS).

Trends. See Distribution: historical changes, above. Little information from any part of range, due to lack of adequate baseline data on population levels. Virtually unsampled by Breeding Bird Survey. Point-count data collected annually at 68 ne. U.S. montane forest sites beginning in early 1990s; trend information not yet available. Anecdotal evidence of recent breeding-population declines on several small Vermont peaks (VINS). Capture rates of migrant "Gray-cheeked" Thrushes (n = 3,252, included known Bicknell's and Gray-cheeked) in coastal Virginia declined significantly from 1968 to 1995 (Wilson and Watts 1997).

POPULATION REGULATION

Few data. Apparent biennial cycle of balsam-fir cone crops in montane forests of Vermont correlates to elevated predator populations and depressed reproductive success of Bicknell's Thrush in summers following high cone crops. Recruitment in Vermont, as measured by annual number of yearling individuals captured, correlated to previous year's breeding productivity.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. No information.

Pesticides and other contaminants/toxins. Little information. Blood and feather mercury (Hg) levels examined in 18 adults from 5 breeding sites across ne. U.S. in 1999 and 2000. Mean blood Hg 0.192 ppm ± 0.188 SD (range 0.038–0.795, n = 14); no consistent age, sex, or geographic differences. Mean feather Hg levels, indicating chronic body burden, 0.739 ppm ± 0.429 SD (range 0.171-1.61, n = 18), highest in 2 older males from Whiteface Mtn. in Adirondacks, 1.561 and 1.61 ppm, respectively. Among known-aged birds on Mt. Mansfield, VT, significantly higher feather Hg levels in older birds (mean 0.924 ppm ± 0.26 SD; males 0.801 ± 0.203 SD [n = 4], females 1.170 ± 0.175 SD [n = 2]) than in yearling birds (mean 0.434 ppm ± 0.118 SD, n = 3 males). Mercury toxicity thresholds not known in this or other terrestrial insectivorous bird species.

Collisions with stationary/moving structures or objects. No documented cases of mortality from collisions with TV towers, but several migrants that may be Bicknell's Thrush recovered below towers in Leon Co., FL (Tall Timbers Research Station specimen data; n = 5) and in downtown Atlanta, GA (Georgia Museum of Natural History [GMNH] specimen data; n = 2). One record of a fall migrant killed by striking a building in Atlanta (GMNH specimen data).

Degradation of habitat. Well-documented decline of high-elevation forests in ne. U.S. during 1960s and 1970s (Johnson and Siccama 1983, Eager and Adams 1992). Red spruce dieback especially pronounced, but mortality of balsam fir also extensive and wide-

spread (Miller-Weeks and Smoronk 1993), although most of this from naturally occurring fir waves. Atmospheric deposition of acidic ions from industrial sulfur and nitrogen oxides strongly, although not conclusively, implicated as a causal factor in red spruce decline (Johnson et al. 1992, NAPAP 1992). Increased winter-freezing injury of spruce, possibly mediated through reductions in calcium reserves, may be directly linked to high levels of acidic deposition (DeHayes et al. 1999). Despite declining trends in atmospheric sulfate concentrations resulting from mandates of 1990 Clean Air Act amendments, acidity of precipitation in ne. North America does not appear to be decreasing (Scherbatskoy et al. 1999).

Heavy metal toxicity from airborne pollutants also implicated as contributing cause of high-elevation forest decline in ne. U.S., particularly in Adirondack and Green Mtns. (Gawel et al. 1996). Several recent studies, however, indicate that lead concentrations in the forest floor are rapidly decreasing (Friedland et al. 1992, Miller and Friedland 1994, Wang and Benoit 1997). Little information on other heavy metals in montane forests.

Atmospheric deposition of airborne mercury 2–5 times higher in montane forests of Mt. Mansfield, VT, than in surrounding low-elevation areas (Lawson 1999). Methylation rates and possible uptake in terrestrial food chain of montane forests unknown.

Global climate change may exert profound, long-term impacts on balsam-fir forests. The average global surface temperature could rise 1.6–6.3°F (0.9–3.5°C) by 2100, with significant regional variation (EPA 2000). A modeling effort using USDA Forest Service Forest Inventory Data, numerous environmental variables, and equilibrium climate variables provided by five Global Circulation Models (assuming doubling of atmospheric carbon dioxide) predicts an average reduction of 96% in area occupied by balsam fir in e. U.S. (Iverson et al. 1999, Prasad and Iverson 1999).

Recreational and commercial development in montane forests contribute to increased habitat fragmentation and loss, but cumulative effects poorly known. In Vermont, 13 mountains >915 m in elevation are developed for recreational skiing; many of these offer mountain-biking programs during summer. Ski area development pressures similar in New Hampshire and Maine, less so in Catskill and Adirondack Mtns. of New York State.

Proliferation of telecommunications towers on mountaintops of ne. U.S., also development of wind-power generation facilities, may further fragment montane breeding habitat and introduce disturbance from construction and servicing activities.

Industrial forestry practices in Canada, such as clear-cutting and pre-commercial thinning, may cause adverse, short-term impacts on Bicknell's Thrush breeding habitat, but effects unknown.

Disturbance at nest and roost sites. Incubation and brooding females vary in tolerance to disturbance near nest. Qualitative observations suggest that birds nesting in areas of high or moderate human activity may become habituated to nearby disturbance. Females in areas of undisturbed habitat and low human activity much more prone to flush from nests (VINS).

Direct human/research impacts. Little evidence. Of 108 Vermont nests monitored from 1992 to 2000, 3 abandonments in early egg stage may have resulted from discovery and/or subsequent visits by researchers (VINS).

MANAGEMENT

Little specific information. Vegetation management of montane forest breeding sites developed for recreational skiing can enhance habitat for Bicknell's Thrush, or minimize possible adverse impacts. Maintenance of low fir-spruce thickets in 3–7 m wide bands of gradually increasing height along ski-trail edges can provide nesting and foraging sites. Maintaining forested "islands" of maximum size between ski trails, minimizing width of trails, and maximizing connectivity of habitat in developed areas may increase suitability. Vegetation management or construction at breeding sites should be conducted outside nesting season. In industrial forests of Canada, harvesting operations should be scheduled to ensure a continuous supply of regenerating (5–15 yr old) clear cuts across the landscape (Nixon et al. in press).

APPEARANCE

MOLTS AND PLUMAGES

The following is based on Dwight 1900, Wallace 1939, 1949, Ouellet 1993, Curson 1994, Pyle 1997, Lane and Jaramillo 2000, and personal observations of authors. Sexes known or assumed to be similar in all plumages, unless otherwise noted.

Hatchlings. Natal down dark gray or blackish, visible at hatching only in cephalic, dorsal, and humeral tracts. Remigial quills emerge from skin at 2–3 d, feather tips from quills at 6–7 d.

Juvenal plumage. Acquired by complete Prejuvenal (postnatal) molt.

Upperparts, including lesser and median wing-coverts, olive-brown to brown (sepia or raw umber), most feathers with prominent buffy subterminal spots or shaft streaks, these markings darker and more diffuse on rump and upper tail-coverts. Greater wing-coverts brownish, variably tipped with narrower, buffy shaft-streaks. Remiges brownish, rectrices brownish to chestnut-brown. Chin and throat whitish, unstreaked or with few faint dusky streaks. Breast and sides whitish to buffy-white, feathers darker buff

towards tip with dusky terminal bar, giving scaled appearance. Remainder of underparts dull whitish with buffy tinge, under tail-coverts more strongly tinged buffy to buffy-brown. Moderately distinct buffy eye-ring, slightly thicker posteriorly.

Basic I plumage. Prebasic I molt partial; includes all feathers except remiges, rectrices, and primary-coverts. Usually includes some to all median-coverts and 0–4 inner greater-coverts (Pyle 1997, VINS). Occurs late Jul–mid-Sep on breeding grounds (Fig. 3).

Basic I plumage similar to Definitive Basic, but often with variable numbers of retained buff-tipped Juvenal feathers in median and greater wing-coverts, occasionally in scapulars and mantle. Retained Juvenal rectrices significantly more pointed than those of Definitive Basic birds (Collier and Wallace 1989, VINS), P10 is 0–6 mm in length (4–10 mm in Definitive plumages; Pyle 1997).

No documented Prealternate I molt. Worn spring aspect of Basic I plumage similar to Definitive Alternate plumage, but remiges and rectrices may have browner appearance than those of Definitive-plumaged birds (Wallace 1939). Close inspection may reveal moderate wear of distal flight feathers.

Definitive Basic plumage. Definitive Prebasic molt complete, early Jul through Sep on breeding grounds (Fig. 3). In Vermont, birds in very early stages of remigial molt (≤3 primaries shed; n = 8) captured from 4 Jul to 1 Aug (VINS). Latest individuals in active flight-feather molt examined in mid-Sep (latest 13 Sep). Mean calculated molt-duration of 4 males examined both early and late in same molt cycle was 50.5 d ± 4.9 SD (range 47–59 d). Birds in midmolt stages typically had 4–5 primaries growing simultaneously (none >5) and all 12 rectrices. Yearling males tended to initiate molt slightly earlier than older birds of both sexes. One male examined in molt in 3 consecutive years was calculated to begin 23 Jul as yearling, 29 Jul and 30 Jul in following 2 yr. Weight changes of 5 males recaptured 24–43 d apart in same molt cycle varied from –1.0 g to 3.0 g (mean 0.8 g ± 1.5 SD). Nearly all captures of molting birds (n = 14 of 17) in same area occupied during breeding season.

Contour-feather molt begins shortly after shedding of P1, usually in spinal and ventral tracts, and terminates in capital tract shortly after remigial molt is complete.

No evidence for Definitive Prealternate molt. Worn spring aspect of Definitive Basic plumage nearly indistinguishable from that in fall; slightly more olive (versus grayer) dorsal coloration reported by Wallace (1939) to be acquired through wear.

Upperparts (head, nape, mantle, wing-coverts, upper tail-coverts) vary from olive-brown to brownish (sepia or raw umber), typically contrasting with brighter, chestnut-tinged tail; this contrast may be less evident when tail- and wing-feathers worn and duller, or contrast may be slight in birds with warmest brown back color. Degree of chestnut tinge in tail and of contrast with dorsal coloration varies. Although Wallace (1939) suggested clinal dichromatism in dorsal coloration, with northern birds tending to be olive and southern birds brown, much geographic intergradation exists, even within breeding sites (VINS, WGE). Wings brownish to olive-brown, remiges often showing slight chestnut tone, especially on outer webs and bases of primaries, giving perceptibly warmer effect than rest of upperparts (except tail). Chin and throat unstreaked off-white to buff, males tending more towards buff. Lores and postocular crescent dull gray. Double malar stripes dusky, lower stripe more prominent. Breast off-white with buffy wash, with prominent, wedge-shaped dusky (blackish) spots; these become more diffuse, more rectangular in shape, and paler (brownish) on sides and lower breast, less extensive and bold overall than on Hermit Thrush. Belly off-white, flanks usually show grayish or dusky brownish wash.

BARE PARTS

Bill and gape. Upper mandible and distal half to one-third of lower mandible blackish gray, proximal half to two-thirds of lower mandible bright pale yellowish to orange-yellow. Entire lower mandible may be suffused with pale yellowish flesh in juveniles.

Iris. Dark brown in all ages.

Legs and feet. Light purplish flesh to purplish flesh, some individuals with darker brownish wash on tarsi. Toes invariably darker than tarsi. Soles of feet vary from flesh to dull pale yellow. Legs grayish in juveniles, especially on leading edge, grayish flesh on hind edge; soles of feet pale yellow.

MEASUREMENTS

LINEAR

See Appendix.

MASS

See Appendix. Also see Migration: control and physiology, above. Mass of some females during breeding season may reflect addition of egg in oviduct (VINS).

PRIORITIES FOR FUTURE RESEARCH

Many aspects of the breeding and wintering ecology, demography, and behavior of Bicknell's Thrush remain poorly known. A lack of baseline population data and logistical difficulties hinder attempts to clarify this species' conservation status. A standard-

ized, regionwide monitoring program, currently in its early stages, is needed to determine breeding-population trends and distributional changes. Similar efforts are warranted on the wintering grounds, where limiting factors may be most severe. Development of accurate methods to census populations and estimate densities are needed in both areas. Accurate calculations of total population size, based on GIS projections of occupied habitats and spatially explicit density estimates, are needed throughout the breeding range. A formal conservation assessment is needed to assess the possibility that Bicknell's Thrush may qualify for federal Endangered or Threatened listing, in both the U.S. and Canada.

Many landscape-level questions about the species' ecology and population dynamics require focused research. Information is needed on reproductive success, demographics, and site persistence in habitat patches of different size and isolation; on the existence of source/sink population dynamics; on patterns of natal dispersal and breeding recruitment; and on levels of population interchange among habitat patches. The apparent male-biased breeding sex ratio requires rangewide investigation; its causes and demographic/ecological correlates must be determined. Accurate estimates of breeding population density in different habitat types across the species' range are needed. Detailed understanding of habitat use, breeding status and success, demography, site persistence, and effects of silvicultural practices (e.g., pre-commercial thinning) in regenerating industrial forests of Maritime Canada is needed to guide management. The species' status in regenerating clear-cuts in both montane and low-elevation forests in Maine should be investigated. Distributional status in coastal maritime forests of Canada needs clarification, as does possible existence of contact/hybrid zone with Gray-cheeked Thrush along north shore of Gulf of St. Lawrence. The possibility that Bicknell's Thrush may occur in unglaciated areas of southeastern Newfoundland should be investigated.

Research is needed on potential effects of food availability and its temporal-spatial variability on breeding system structure and reproductive success; relative diets of adults, nestlings, and fledglings; postfledging dispersal and habitat use; postbreeding movements and habitat use of adults; effects of human activities (e.g., recreational development, telecommunications towers) on spacing patterns and reproductive success.

In winter, distribution and habitat use of Bicknell's Thrush in Cuba and Haiti, and to lesser extent Jamaica, need to be better understood. Protected status of core wintering areas must be carefully assessed, and needs for further protection specifically identified. Occupancy of primary versus second-growth winter habitats needs study, as does existence of possible sexual habitat segregation. Demographic studies are needed to investigate microhabitat use, overwinter survival and site persistence by age and sex, between-winter site fidelity and survivorship. Spacing patterns and movements of age and sex classes throughout winter need further study, as do possible seasonal shifts in diet and body condition.

Stopover ecology is virtually unknown. Studies of banded, transient individuals are needed to determine stopover lengths, physiological condition, diet, and habitat use. A thorough study (currently underway by VINS, summary in Migration: timing and routes, above) of available banding and specimen data would help establish migratory routes and timing, and might identify specific geographic areas of importance to stopover migrants. Establishment of standardized criteria for field and in-hand identification would facilitate determination of distribution and migration patterns.

Additional research is needed on song and call repertoire, degree of sharing across breeding range and among neighbors, recognition of "types" by birds themselves, responses of Bicknell's Thrush to Gray-cheeked Thrush vocalizations, and vice versa, across the breeding range.

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Appendix. Linear measurements (mm) and mass (g) of Bicknell's Thrush. Regional and winter data from mist-netted birds (VINS, WGE), breeding-range data from specimens (Ouellet 1993). Data shown as mean ± SD (range, *n*).

	AHY males	AHY females	HY individuals[1]	AHY sex unknown	HY sex unknown
Bill length					
Exposed culmen					
Breeding range	12.71 ± 0.76 (10.6–16.7, 73)	12.56 ± 0.52 (11.8–13.7, 19)			
S. Vermont	12.6 ± 0.81 (11–14.2, 36)	13.0 ± 1.49 (11.1–17.9, 17)			
N. Vermont	12.8 ± 1.16 (8.9–14.9, 40)	12.2 ± 1.13 (8.9–13.2, 13)			
Mt. Mansfield, VT			11.3 ± 0.61 (9.9–12.3, 27)		
Dominican Republic				12.7 ± 0.68 (11.8–15.1, 33)	12.6 ± 0.86 (11.1–13.7, 12)
Culmen from nares					
Breeding range	9.09 ± 0.41 (8.1–10.2, 73)	9.1 ± 0.42 (8–9.9, 19)			
Catskills, NY	9.2 ± 0.4 (8.3–9.7, 12)				
Adirondacks, NY	9.2 ± 0.44 (8.5–10, 17)				
S. Vermont	9.3 ± 0.54 (7.6–10.5, 42)	9.5 ± 0.67 (8.4–10.9, 18)			
N. Vermont	9.4 ± 0.61 (8–10.3, 40)	9.1 ± 0.43 (8.6–10.2, 14)			
White Mtns., NH	9.2 ± 0.32 (8.5–9.6, 11)				
Mt. Mansfield, VT			8.4 ± 1.06 (7–12.9, 27)		
Dominican Republic				9.4 ± 0.6 (8.4–10.9, 33)	9.7 ± 1.55 (8.4–14.1, 11)
Culmen depth					
S. Vermont	4.0 ± 0.21 (3.5–4.3, 37)	4.2 ± 0.2 (3.8–4.5, 17)			
N. Vermont	4.1± 0.35 (3.6–4.9, 33)	4.0 ± 0.44 (3.3–4.9, 10)			
Mt. Mansfield, VT			3.8 ± 0.18 (3.7–4, 3)		
Dominican Republic				3.9 ± 0.15 (3.7–4.3, 33)	4.0 ± 0.37 (3.6–5, 11)
Culmen width					
S. Vermont	4.2 ± 0.37 (3.6–5.1, 37)	4.3 ± 0.53 (3.5–5.5, 17)			
N. Vermont	4.4 ± 0.49 (3.6–5.5, 37)	4.4 ± 0.42 (3.9–5.2, 11)			
Mt. Manfield, VT			4.1 ± 0.31 (4–5, 27)		
Dominican Republic				4.1 ± 0.24 (3.6–4.8, 33)	4.2 ± 0.23 (4–4.7, 11)
Wing length					
Unflattened wing-chord					
Breeding range	92.92 ± 2.73 (84.8–98.8, 74)	87.78 ± 3.87 (81.7–95.2, 19)			
Catskills, NY	91.9 ± 2.42 (88–96, 32)	86.9 ± 2.46 (82.5–88, 5)			
Adirondacks, NY	93.9 ± 1.96 (91–97, 17)				
S. Vermont	91.0 ± 2.75 (85.5–97, 60)	87.8 ± 2.04 (83.5–91, 25)			
N. Vermont	91.8 ± 2.94 (84.5–100, 134)	87.4 ± 2.24 (83.5-93, 56)			
White Mtns., NH	93 ± 2.73 (86.5–96, 12)				
Mt. Mansfield, VT			88.7 ± 2.87 (82–95, 61)		
Dominican Republic				92.1 ± 3.5 (85–100, 66)	89.1 ± 2.32 (84.5–94.5, 41)
Tail length					
Breeding range	68.73 ± 2.79 (62.1–77.6, 74)	65.57 ± 2.61 (61.6–70.6, 19)			
Catskills, NY	69 ± 3.41 (64–75, 12)				
Adirondacks, NY	70.6 ± 2.53 (65.5–74, 17)				
S. Vermont	66.8 ± 2.66 (62–73, 37)	62.4 ± 2.97 (54–67, 18)			
N. Vermont	67.2 ± 3.94 (60.7–74.5, 37)	63.9 ± 3.0 (60.4–68.3, 10)			
White Mtns., NH	68.9 ± 3.26 (62–73, 11)				
Mt. Manfield, VT			62.6 ± 3.04 (57–69, 23)		
Dominican Republic				68.3 ± 3.09 (63.1–73.5, 30)	64.4 ± 2.77 (60.5–58.8, 10)

Tarsus length[2]					
Breeding range	29.24 ± 0.69 (27.5–30.7, 72)	28.89 ± 0.5 (28.1–29.7, 17)			
Catskills, NY	28.6 ± 1.02 (27–30.1, 12)				
S. Vermont	33.0 ± 0.93 (31–34.9, 37)	31.8 ± 0.83 (30.1–33.1, 17)			
N. Vermont	32.7 ± 1.37 (28.3–34.7, 40)	32.1 ± 1.88 (28.2–34.5, 13)			
Mt. Manfield, VT			29.3 ± 1.73 (26.6–34.2, 28)		
Dominican Republic				32.9 ± 1.32 (29.9–35.3, 31)	32.6 ± 1.1 (30–34, 11)
Mass[3]					
Breeding range	28.18 ± 2.02 (20.5–33.0, 38)	31.97 ± 4.27 (28.7–36.8, 3)			
Catskills, NY	27.7 ± 1.85 (24.3–31.9, 33)	27.8 ± 1.97 (24.6–29.5, 5)			
Adirondacks, NY	27.8 ± 1.32 (26–30, 17)				
S. Vermont	27.5 ± 1.95 (21–32.4, 62)	26.8 ± 2.65 (22.3–34.5, 26)			
N. Vermont	27.5 ± 1.54 (24–31.9, 118)	28.1 ± 3.51 (23–37, 45)			
White Mtns., NH		28.3 ± 1.54 (24.9–30.8, 12)			
Mt. Mansfield, VT			26.9 ± 1.44 (24.1–30.2, 62)		
Dominican Republic[4]				27.2 ± 1.76 (23.8–30.6, 60)	26.8 ± 1.86 (22.1–30.6, 41)

[1]Late summer/fall hatch-year individuals.
[2]Regional and winter data reported using "field" tarsus (distance from lateral condyle to third scale; VINS).
[3]Mass of some females during breeding season may reflect addition of egg in oviduct (VINS).
[4]Individuals in Sierra de Bahoruco, broadleaf forest captured in Nov and recaptured in Mar had changes in mass ranging from −1.4 to 2.0 g (0.13 ± 1.18, $n = 7$).

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