



Long-term demographic changes in a Bicknell's Thrush population

Report to the Nuttall Ornithological Club for 2016-17

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Abstract:

Bicknell's Thrush is a species of the highest conservation concern and is the target of ongoing, multi-national conservation planning under the auspices of the International Bicknell's Thrush Conservation Group. Although many aspects of the ecology of this species are well-understood, numerous information gaps persist that hinder the design and implementation of effective conservation practices and policies. In particular, we lack a clear understanding of the factors that limit population growth of Bicknell's Thrush, which in turn limits our ability to target conservation actions efficiently. In this study, we directly addressed this problem by testing a series of hypotheses about causes of variation in Bicknell's Thrush apparent survival. We used banding data from atop Mt. Mansfield, Vermont (2001-2015), and compared Cormack-Jolly-Seber models using an information theoretical approach and a four-step model-selection procedure. Our 15 year dataset included unique capture histories for 178 Bicknell's Thrush, most of whom (59%) were captured in only one year of our study. Bicknell's Thrush survival and recapture probability did not vary between sexes or age groups. Apparent survival averaged 0.61 between 2001 and 2015, from a low of 0.51 (95% CI: 0.35, 0.68) to a high of 0.71 (95% CI: 0.48, 0.86). Contrary to our hypotheses, apparent survival was higher after a mast year (0.71, 95% CI: 0.58, 0.81) than after a non-mast year (0.50, 95% CI: 0.41, 0.60). Balsam fir cone production in Eastern Northern America is partially driven by warm growing seasons in the year prior to masting. These weather conditions may also be favorable to Bicknell's Thrush (e.g., by increasing insect abundance), with the result being higher apparent survival. Apparent survival was negatively affected by drought conditions on the wintering grounds ($\text{SOI } \beta = -0.32$, 95% CI: -0.72, 0.08) which are

known to influence insect biomass. Our results suggest that a suite of weather conditions influence Bicknell's Thrush apparent survival, given that an index of weather (SOI) was selected over rain data. We hypothesized that tropical storms create favorable habitat disturbance on the wintering grounds, and the number of tropical storms and hurricanes passing near Hispaniola (July through December) was positively related to apparent survival ($\beta=0.30$, 95% CI: -0.11, 0.71). Covariates presenting deforestation levels and rainfall on the wintering grounds and Swainson's Thrush (a potential competitor) relative abundance on the breeding grounds were not selected as informative. The results of this research have provided insight into the relative importance of factors operating during the winter, including rainfall-driven variation in winter habitat quality and deforestation, and during the breeding season, including competition with an invading competitor and annual cycles of nest predation.

Introduction

Bicknell's Thrush is a rare, range-restricted songbird, breeding only in high-elevation fir (*Abies balsamea*) forests of the northeastern United States (U.S.) and southeastern Canada and wintering in wet, broadleaf forests in Haiti and the Dominican Republic (Townsend et al. 2015). With a narrow distribution, a small global population size thought to consist of no more than 120,000 individuals (Hill and Lloyd 2017), well-documented threats to its breeding and wintering habitat (IBTCG 2017), and some evidence of recent population declines (Ralston et al. 2015), Bicknell's Thrush is a species of high conservation concern. It is currently listed as Threatened under Canada's Species at Risk Act (COSEWIC 2009), is identified as Vulnerable by the IUCN (Birdlife International 2016), and is being reviewed for listing under the U.S. Endangered Species Act (77 FR 48934).

Recognized as a distinct species only since 1995 (Monroe et al. 1995), no long-term demographic studies of Bicknell's Thrush have yet been conducted. However, given current and forecast threats - loss of habitat and altered interspecific interactions due to climate change, deforestation on the wintering grounds, and incompatible forestry practices on the breeding grounds, in particular - and evidence of population declines, a better understanding of long-term trends in vital rates is key to ongoing efforts to craft a conservation strategy. Analyses that describe patterns of change in demography will yield insight into the factors that may limit population growth in the species, in turn allowing for a more effective targeting of conservation actions. The Conservation Action Plan for Bicknell's Thrush (IBTCG 2017) identifies numerous actions on the breeding and wintering grounds that may help stem population declines and promote recovery of the species, yet at present the empirical data needed to prioritize among these actions are lacking. As a consequence, it remains unclear whether, for example, limited resources are best invested in reducing deforestation on the wintering grounds or increasing the amount of suitable breeding habitat. Delivering effective and efficient conservation depends on knowing when, where, and by which factors populations are limited (Marra et al. 2015).

Vermont Center for Ecostudies (VCE) has maintained a long-term demographic study (1992-present) of Bicknell's Thrush, and other mountain birds, on Mount Mansfield, Vermont, in the core of the species' breeding range, and is thus uniquely well-positioned to address this critical information gap. By following the fate of individually marked birds over time, we can estimate

key demographic parameters, including local abundance, survival, and recruitment, or the number of new individuals added to the population each year. We can also identify correlates of temporal variation in these parameters. Identifying correlates of change in vital rates offers insight into the factors that may limit population growth and contribute to population declines.

Here, we outline a series of hypotheses about the factors that limit survival of Bicknell's Thrush. We define survival as the probability that an individual survives from one breeding season to the next and returns to the population. Our study design does not allow us to separate mortality from permanent emigration (i.e., a marked bird that fails to return may have either died or chosen to permanently relocate to a different area), and thus we estimate "apparent" rather than true survival (Lebreton et al. 1992), although the effect on population growth is the same. We focus on putatively important factors operating on the breeding and wintering grounds; although mortality during migration may have important effects on survival (Newton 2007, 2008), we lack important pieces of information about Bicknell's Thrush migration (e.g., location of key stopover areas) that would allow us to include this part of the species' life cycle in our models. In particular, we addressed the following hypotheses about variation in survival:

Increased relative abundance of Swainson's Thrush (*C. ustulatus*) is associated with reduced survival of Bicknell's Thrush. Swainson's Thrush is a putative competitor of Bicknell's Thrush, historically limited to lower elevations (Able and Noon 1976) but apparently becoming increasingly common at elevations formerly occupied only by Bicknell's Thrush (VCE, unpubl. data). Swainson's Thrush may be able to directly exclude Bicknell's Thrush from areas of overlap via agonistic interactions (Freeman and Montgomery 2015) or may reduce fitness of individuals in areas of sympatry via competition for shared resources. In either case, we predict that increased relative abundance of Swainson's Thrush will be associated with decreased apparent survival (via territory abandonment or displacement) of Bicknell's Thrush.

Increased drought stress on wintering grounds is associated with reduced survival of Bicknell's Thrush. Winter rainfall is correlated with overwinter survival in some Nearctic-Neotropical migrants that winter in the Greater Antilles, presumably via effects of moisture on food abundance (Silleet et al. 2000, Wilson et al. 2011). Whether this is also true of Bicknell's Thrush is unclear, as the wet, montane forests that they inhabit on Hispaniola may be well-buffered against occasional drought (e.g., Wolfe et al. 2015). The El Niño Southern Oscillation (ENSO) is a key driver of winter rainfall in the Caribbean, and relatively dry years occur in the Caribbean during ENSO events followed by a relatively wet year after an ENSO event (Curtis and Adler 2000, Anthony Chen and Taylor 2002). We predict that the dry El Niño years will yield lower survival of Bicknell's Thrush (e.g., Silleet et al. 2000). However, ENSO is not the sole driver of variation in rainfall patterns on the wintering grounds of Bicknell's Thrush. The Normalized Difference Vegetation Index (NDVI) is a remotely sensed measure of the greenness of Earth's landscape, and can be used to quantify temporal and spatial variation in drought stress independently of ENSO. We predict lower survival of Bicknell's Thrush during years when the NDVI in wintering areas is low, indicating a relatively "brown" landscape (e.g., Wilson et al. 2011). If precipitation-driven variation in winter habitat quality is a limiting factor, we predicted a positive relationship between adult survival and winter rainfall on Hispaniola and negative

relationships between adult survival and two indices of winter precipitation over the entire Caribbean.

Loss of forest cover on the wintering grounds is associated with reduced survival of Bicknell's Thrush. Deforestation on the wintering grounds is believed to be a primary threat to Bicknell's Thrush, but empirical evidence for a relationship between rates of forest loss and population growth is lacking (IBTCG 2017). In large part, the inability to test this hypothesis has been a consequence of the difficulty of obtaining accurate measures of change in forest cover; however, annual estimates of gain and loss of forest cover are now available at fine spatial scales for the entire planet (Hansen et al. 2013). Assuming that the inability to locate and procure a territory in suitable wintering habitat results in mortality of individuals, we predict a negative relationship between survival and the amount of forest loss within suitable wintering areas on Hispaniola.

Biennial mastings by balsam fir produces a trophic cascade that leads to reduced survival of Bicknell's Thrush. Balsam fir generally cannot sequester enough carbon during the short growing seasons, which are characteristic of northeastern mountains to reproduce every year. Instead, balsam fir across the region produce cones every other year, which appears to initiate a trophic cascade that may directly reduce apparent survival of Bicknell's Thrush. Red squirrels (*Sciurus vulgaris*) respond to the mass production of fir cones by moving upslope into fir forests and by increasing their reproductive output, such that the abundance of red squirrels in high-elevation forests increases dramatically, albeit temporarily. Increased abundance of red squirrels leads to substantially elevated rates of nest predation on Bicknell's Thrush, and this effect seems synchronous across the breeding range (K.P. McFarland, in prep.). As a consequence, we predict lower survival in the year following the production of a cone crop.

Tropical storm frequency is related to survival of Bicknell's Thrush. Bicknell's Thrush populations are subjected to tropical storms, during migration and the wintering grounds, which can result in severe habitat destruction and indirect and direct adult mortality (Wunderle et al. 1992, Wiley and Wunderle 1993, Newton 2007, Dionne et al. 2008). However, Bicknell's Thrush inhabit highly disturbed habitat year-round (McFarland et al. 2013, Townsend et al. 2015), and tropical storms in the previous year could conceivably improve habitat for Bicknell's Thrush in the following year. Therefore, tropical storm frequency during and immediately after migration (when birds may be recovering from migratory flights, October through December for Bicknell's Thrush) could result in direct mortality of birds, whereas storm frequency from July through December of the previous year may be more predictive of habitat conditions in the current year. We predicted that the frequency of tropical storms passing near Hispaniola would have both negative and positive effects on Bicknell's Thrush survival.

Methods: capture and banding

We have collected capture-recapture data on the ridgeline of Mount Mansfield (44.5274°N, 72.8152°W) annually since 1992. In this study, however, we used banding data (May through

July) from 2001 to 2015, because we only had complete covariate coverage over that timeframe. The study area comprises approximately 9 ha of balsam fir forest at elevations of 1,160 - 1,190 m. Absolute effort has varied from year-to-year, but at a minimum we conducted weekly banding sessions between June and September of each year, using 12-18 nylon mist nets (12 x 2.5-m and 6 x 2.5-m, 36-mm mesh) placed at sites primarily on the Amherst, Lakeview, and Long Trail hiking trails. Nets were generally opened from late afternoon until dusk and from dawn until early afternoon on the following morning. Bicknell's Thrushes were captured both passively and through the use of vocal lures (recorded playbacks), while other species were passively captured. Each individual was fitted with a uniquely-numbered U.S. Geological Survey (USGS) leg band. We sexed individuals according to Pyle (1997), and placed all birds into one of two "age" categories: *first year captures* and *after first year captures*. All birds were placed in the first year captures category during their initial capture year. In all subsequent years, these birds were considered as after first year captures. We adopted this approach over concern about the repeatability of multiple banders correctly ageing birds in the second year of their life through subtle plumage characteristics.

Methods: covariates

We constructed a series of covariates to help us explain variation in survival and recapture probability. All covariates were grand mean centered and scaled by 1.0 SD. Most of our wintering ground covariates were exclusively from Hispaniola; where the majority of Bicknell's Thrush are hypothesized to overwinter (McFarland et al. 2013).

NET.HOURS: recapture probability covariate representing the number of net hours (1 12-m net open for 1 hour) during May-July each year to account for the annual variation in capture effort. We predicted that net hours in year t would be positively associated with recapture probability in year t .

MAST: apparent survival covariate representing mast year status (1=mast year) in year t . Masting data were collected annually by VCE staff on Mount Mansfield and Stratton Mountain (43.0905°N, 72.9280°W), Vermont. In mast year, fir trees produce large numbers of cones, and we predicted lower survival (from year t to $t+1$) following mast years in year t .

FOREST.LOSS: apparent survival covariate representing the area of annual forest lost within the boundaries of predicted Bicknell's Thrush habitat on Hispaniola (McFarland et al. 2013). The amount of annual forest loss (ha) for Hispaniola were calculated using the Google Earth Engine environment and data high resolution Global Forest Cover (Hansen et al. 2013). The Hansen et al. (2013) dataset is available annually and considers forest cover to be land covered by vegetation >5 tall. We predicted that apparent survival from year t to $t+1$ would be negatively affected by the amount of forest loss in calendar year t .

NDVI: apparent survival covariate of the estimated NDVI within the predicted winter distribution of Bicknell's Thrush (McFarland et al. 2013) from 1 December through 31 March each year. Using the Google Earth Engine, we processed Global MODIS (MOD13Q1; https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1) vegetation indices collated over a 16-d periods at a 250-m resolution. We predicted that NDVI from Dec

(year t) through March (year t_{+1}) would be negatively related to apparent survival from year t to year t_{+1} .

Rainfall: apparent survival covariate of the mean rainfall over portions of the Bicknell's Thrush winter range on Hispaniola (McFarland et al. 2013). McFarland et al. (2013) used MaxEnt (Phillips et al. 2006) to quantify the probability of use by Bicknell's Thrush in Caribbean forests, and they used a probability of ≥ 0.25 as the cut off value to distinguish habitat from non-habitat within a $\sim 1 \text{ km}^2$ pixel. In our analysis, we used monthly rainfall totals from the Climate Hazards Group Infrared Precipitation with Stations (CHIRPS 2.0; Funk et al. 2014) (ftp://ftp.chg.ucsb.edu/pub/org/chg/products/CHIRPS-2.0/camer-carib_monthly/tifs/) from all pixels on Hispaniola with predicted MaxEnt values of ≥ 0.25 . We created two rainfall covariates representing fall and winter rainfall (September through March) and just March rainfall; both of which have been positively linked to survival in migratory bird populations (Peach et al. 1991, Rockwell et al. 2012). We predicted that fall and winter rainfall totals from September (year t) through March (year t_{+1}) (**CHIRPS.FW**) and just March (year t_{+1}) (**CHIRPS.M**) would both be positively related to apparent survival from year t to year t_{+1} .

SOI: apparent survival covariate created from the Southern Oscillation Index (SOI): mean from September (year t) through March (year t_{+1}). Negative SOI values indicate the warm phase (i.e., El Nino) of ENSO, or warmer-than-average sea surface temps in the tropical Pacific Ocean which generally translates into fewer storms and less rainfall in tropical Atlantic. Therefore, we predicted that SOI from September (year t) through March (year t_{+1}) would be negatively related to apparent survival from year t to year t_{+1} .

Tropical storm intensity: We used tropical storm path data from the National Hurricane Center (National Oceanic and Atmospheric Administration; <http://www.nhc.noaa.gov/data/>) to determine the number of tropical storms that passed within 250 km of the center of Hispaniola. We only counted storms that were of tropical storm strength or greater (i.e., we excluded tropical depressions and waves) when they passed near (≤ 250 km) Hispaniola. We predicted that Bicknell's Thrush apparent survival (year t to year t_{+1}) would be negatively affected by tropical storm frequency from October through December (year t) (**STORM.t**), but positively affected by past tropical storm frequency from July through December (year t_{-1}) (**STORM.T-1**).

N.SWTH: apparent survival covariate of the number of uniquely captured Swainson's Thrush from May through July each year. We predicted that Bicknell's Thrush apparent survival (from year t to t_{+1}) would be negatively related to the number of uniquely captured Swainson's Thrush in year t_{+1} .

Methods: model comparison

To test our hypotheses, we used our banding data (May through July) from 2001 to 2015, because we had complete covariate coverage over that timeframe. We constructed Cormack-Jolly-Seber models in program MARK (Cormack 1964, Jolly 1965, Seber 1965, White and Burnham 1999) to investigate annual variation in apparent survivorship of adult Bicknell's Thrush. Nestlings and hatch-year birds were not included in our analysis.

The winter precipitation covariates (NDVI, CHIRPS, and SOI) were not strongly correlated ($r < 0.3$). We assessed over-dispersion by calculating the quasi-likelihood parameter ($c\text{-hat}$) within MARK, which suggested moderate over-dispersion ($c\text{-hat} = 1.66$) in our dataset. Therefore, we used the quasi-likelihood Akaike's information criterion corrected for small sample size (QAICc) to compare models (Anderson et al. 1994). We drew inference from all models included in the model confidence set ($\Delta\text{QAICc} < 2.0$). For nested models (identical models except for one additional parameter), we excluded the model with one additional parameter if it fell with 2 QAICc units of the simpler model (Arnold 2010).

We used a 4-step model selection procedure starting with a model where survival and recapture probability varied (independently) with time. At each step, we built upon the parsimonious model from the previous step. In the first step, we compared models where recaptured probability varied with the number of net hours or sex. In the second step, we modeled survival (including interaction terms) as a function of time, age, and sex. In the third step, we included time-varying survival covariates for Swainson's Thrush relative abundance, winter drought conditions and rainfall, deforestation, mast year status, and tropical storm severity. In the fourth and final step, we combined models in the confidence set.

Preliminary Results & Discussion

Our 15 year dataset includes unique capture histories for 178 Bicknell's Thrush, most of whom (59%) were captured in only one year of our study. Four models were included in the confidence set, and Bicknell's Thrush survival and recapture probability did not vary between sexes or age groups. Recapture probability was 0.52 across all years, but it varied annually from 0.39 (95% CI: 0.23, 0.59) to 0.68 (95% CI: 0.43, 0.85) (Figure 1). As we predicted, recapture probability was positively influenced by the number of net hours (NET.HOURS) each season (median = 601, min-max = 158-1541) (Figure 2). Approximately 750 net hours would be needed to have a 50% probability of recapturing a Bicknell's on Mount Mansfield. These recapture rates are likely influenced by the rough terrain and dense vegetation on Mount Mansfield, which prevents us from setting up nets off of already established hiking trails (e.g., the Long Trail). It is quite likely that the curve in Figure 1 would be substantially steeper if we were able to distribute nets evenly throughout a circular- or rectangular-shaped study area, but this is not physically possible atop Mt. Mansfield.

Figure 1. Annual recapture probability (with 95% confidence intervals) of Bicknell's Thrush atop Mt. Mansfield from 2002 to 2015.

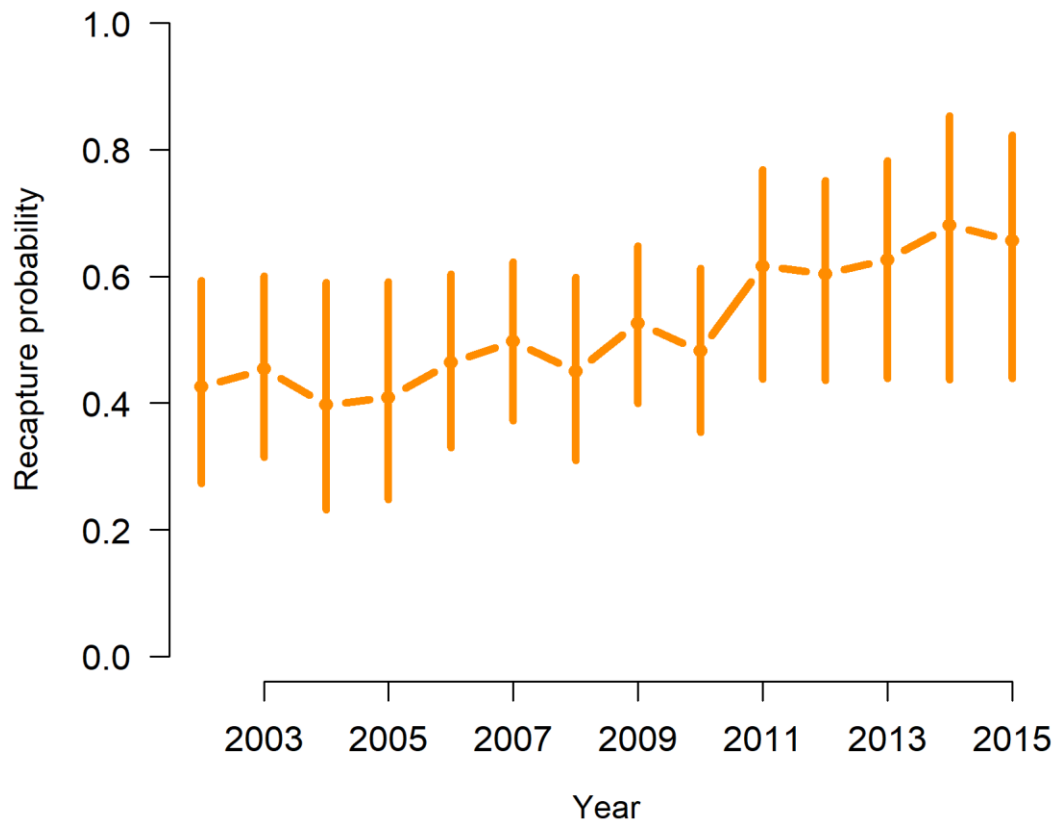
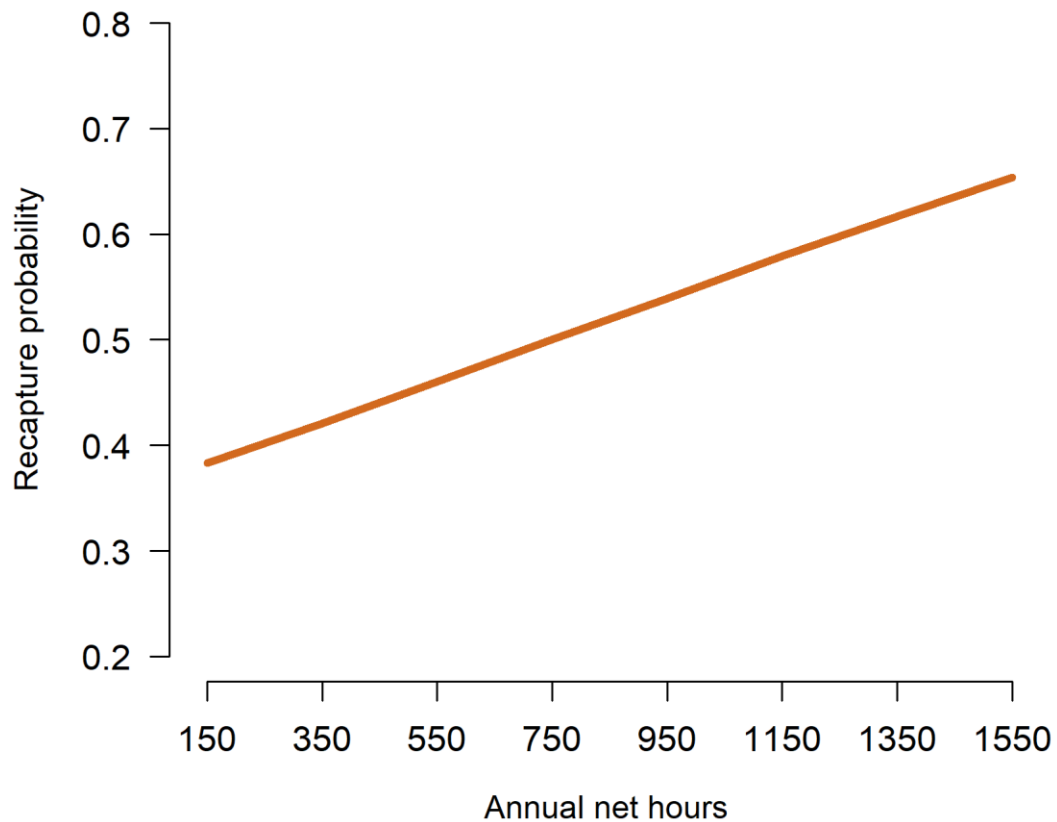
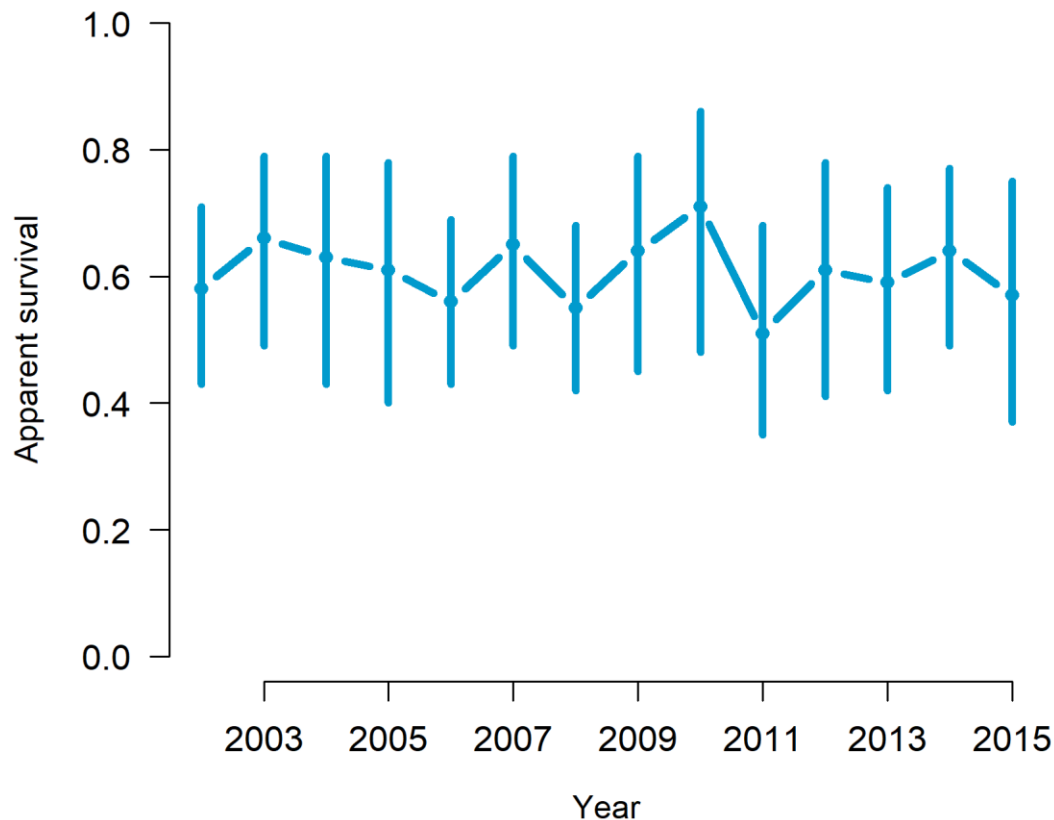


Figure 2. Annual recapture probability of Bicknell's Thrush (across all years) positively increases with netting effort (1 net hour = 1 12-m net open for 1 hour).



Apparent survival of Bicknell's Thrush averaged 0.61 between 2001 and 2015, from a low of 0.51 (95% CI: 0.35, 0.68) to a high of 0.71 (95% CI: 0.48, 0.86) (Figure 3).

Figure 3. Apparent annual survival estimates (with 95% confidence intervals, estimated from all models in the confidence set) of Bicknell's Thrush from Mount Mansfield, Vermont.



Surprisingly, Bicknell's Thrush apparent survival was related to mast year status (MAST $\beta=0.86$, 95% CI: -0.12, 1.85), and survival was higher after a mast year (0.71, 95% CI: 0.58, 0.81) than after a non-mast year (0.50, 95% CI: 0.41, 0.60). Red squirrel populations increase following mast years (Gurnell 1983) with negative repercussions for Bicknell's Thrush populations. In one study, daily nest survival rates were negatively correlated ($r=-0.76$) with red squirrel abundance and nest success significantly decreased following mast years (McFarland and Rimmer 2002). However, balsam fir cone production in Eastern Northern America is partially driven by warm growing seasons in the year prior to masting (Messaoud et al. 2007). These weather conditions may also be favorable to Bicknell's Thrush (e.g., by increasing insect abundance), with the result being higher apparent survival.

As we predicted, Bicknell's Thrush apparent survival was negatively affected by drought conditions on the wintering grounds (SOI $\beta=-0.32$, 95% CI: -0.72, 0.08). Winter precipitation is thought to influence insect biomass, which in turn influences apparent survival, muscle and overall body mass, and spring migration timing (Sillett et al. 2000, Studds and Marra 2005, Wilson et al. 2011, Cooper et al. 2015). However, local habitat conditions can mediate the effects

of drought on bird populations. For example, in Costa Rica White-collared Manakin (*Manacus candei*) ENSO conditions strongly influence apparent survival of birds in young forests, but not mature forests (Wolfe et al. 2015). CHIRPS.FW rainfall data over the same time period was moderately correlated with SOI values ($r = 0.39$, $p = 0.17$), but CHIRPS.FW was not selected during our model selection procedure. Our results suggest that a suite of weather conditions influence Bicknell's Thrush apparent survival, given that an index of weather (SOI) was selected over rain data.

The number of tropical storms and hurricanes passing near Hispaniola (July through December) ranged from 0 to 4 in a given year, and STORM.T-1 was positively related to apparent survival ($\beta=0.30$, 95% CI: -0.11, 0.71), and also moderately correlated with CHIRPS.FW ($r = 0.63$, $p = 0.02$). Unfortunately, we are unable to directly measure habitat creation and destruction on the Bicknell's Thrush wintering grounds, therefore, STORM.T-1 is likely an index to many covariates including weather and habitat disturbance.

The results of this research have provided insight into the relative importance of factors operating during the winter, including rainfall-driven variation in winter habitat quality and deforestation, and during the breeding season, including competition with an invading competitor and annual cycles of nest predation. Future research into the population dynamics of Bicknell's Thrush would benefit from a direct measure of insect availability and abundance and habitat disturbance and conditions on the wintering grounds.

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