Research Paper

Apparent survival of a range-restricted montane forest bird species is influenced by weather throughout the annual cycle

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ABSTRACT. To conserve small and fragmented populations, we need an understanding of their population dynamics. With a global population estimate of < 120,000, Bicknell's Thrush (*Catharus bicknelli*) is considered one of the Nearctic-Neotropical migrants at greatest risk of extinction. This range-restricted songbird breeds in high-elevation fir (*Abies balsamea*) forests of the northeastern United States and eastern Canada, and primarily overwinters in forests of the Dominican Republic. The Conservation Action Plan for Bicknell's Thrush identifies numerous actions that may help stem population declines and promote recovery of the species, yet the empirical data needed to prioritize among these actions are lacking. We fit Cormack-Jolly-Seber models with mark-recapture data to test a series of hypotheses about the factors that limit apparent survival in 178 adult Bicknell''s Thrush (50 females and 128 males) captured on the breeding grounds in Vermont (June-July, 2001-2015). We focused on putatively important factors from throughout their annual cycle: cyclical population dynamics of nest predators, and weather effects on food abundance on the breeding and wintering grounds. Apparent survival of Bicknell's Thrush was relatively stable (mean $\Phi = 0.61$, 95% CI: 0.54, 0.68) over our 15-year study, and most strongly associated with fir mast production. Apparent survival was higher following years during which fir trees produced large mast crops (mean $\Phi = 0.67$, 95% CI: 0.55, 0.79), compared to following nonmast years ($\Phi = 0.56 \pm 0.06$, 95% CI: 0.43, 0.68). These results are likely driven by the reduced red squirrel density and increased nesting success and site fidelity of adult thrushes following nonmast years. Apparent survival of Bicknell's Thrush was also associated with relatively wet conditions on the wintering grounds in Hispaniola as assessed via the El Niño-Southern Oscillation (ENSO) precipitation index (ESPI). These relatively wet December-March periods are likely linked to greater primary productivity and the local availability of fruits and arthropods consumed by Bicknell's Thrush. Our research provides the most comprehensive examination of potentially limiting factors on Bicknell's Thrush populations to date and suggests future avenues of research exploring the relationship between food availability, survival, and climate change induced reductions in rainfall for the Greater Antilles.

La survie apparente d'une espèce d'oiseau forestier de montagne à répartition restreinte est influencée par le temps au cours de son cycle annuel

RÉSUMÉ. Il est important de comprendre la dynamique des petites populations fragmentées si on veut conserver leur population. La Grive de Bicknell (*Catharus bicknelli*), dont la population mondiale est estimée à < 120 000, est considérée comme l'une des espèces migratrices néarctiques-néotropicales les plus à risque d'extinction. Cet oiseau chanteur à répartition restreinte niche dans les sapinières (*Abies balsamea*) de haute altitude dans le nord-est des États-Unis et l'est du Canada, et hiverne principalement dans les forêts de la République dominicaine. Le plan d'action destiné à la conservation de la Grive de Bicknell liste de nombreuses activités qui pourraient contribuer à freiner les baisses de population et promouvoir le rétablissement de l'espèce, mais les données empiriques nécessaires pour établir quelles activités sont prioritaires sont manquantes. Au moyen de données de marquage-recapture, nous avons conçu des modèles de Cormack-Jolly-Seber pour tester une série d'hypothèses quant aux facteurs qui pourraient limiter la survie apparente de 178 Grives de Bicknell adultes (50 femelles et 128 mâles) capturées sur des sites de nidification au Vermont (juin et juillet, 2001-2015). Nous nous sommes concentrés sur les facteurs supposément importants dans l'ensemble du cycle annuel : dynamique de population cyclique des prédateurs de nids et effets du temps sur la quantité de nourriture aux sites de nidification et d'hivernage. La survie apparente des grives a été relativement stable (Φ moyenne = 0,61; IC à 95 % = 0,54 et 0,68) durant les 15 années de l'étude et a été le plus fortement associée avec la production de cônes par les sapins. La survie apparente a été le plus élevée à la suite d'années de forte production de cônes (Φ moyenne = 0,67; IC à 95 % = 0,55 et 0,79), comparativement à la survie à la suite d'années sans production de cônes ($\Phi = 0,56 \pm 0,06$; IC à 95 % = 0,43 et 0,68). Ces résultats sont certainement influencés par la densité réduite d'écureuils roux, le meilleur succès de nidification et la fidélité plus grande des adultes au site suivant les années sans production de cônes. La survie apparente de la Grive de Bicknell était aussi associée avec des conditions relativement humides sur les aires d'hivernage sur l'île d'Hispaniola, telles qu'établies par l'indice de précipitation (ESPI) El Niño-oscillation australe (ENSO). Ces périodes relativement humides en décembre-mars sont vraisemblablement liées à une plus grande productivité primaire et à la disponibilité locale de fruits et d'arthropodes consommés par la Grive de Bicknell. Notre recherche représente l'examen le plus complet des facteurs limitant possiblement les populations de Grives de Bicknell jusqu'à maintenant, et propose des axes de recherche explorant la relation entre la disponibilité de nourriture, la survie et la diminution des précipitations induite par les changements climatiques pour les Grandes Antilles.

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INTRODUCTION

The population dynamics of migratory birds are shaped by environmental processes occurring throughout their annual cycle (Sillett et al. 2000). In particular, weather patterns have been linked to variation in adult survival in birds at every stage of the annual cycle (Newton 1998). Although severe episodic weather can directly kill adult birds (Roberts 1907*a*, *b*, Smith and Webster 1955, Newton 2007), the effects of weather on adult survival are thought to be largely mediated through changes in food availability and foraging opportunities (Smith 1982, Newton 1998) that operate throughout the year in different locations. For example, annual apparent survival of adult Sedge Warblers (*Acrocephalus schoenobaenus*) is strongly influenced by drought conditions on the African nonbreeding grounds; during droughts, seasonal wetland habitat acreage diminishes, competition for food supplies intensifies, and adult apparent survival declines (Peach et al. 1991, Baillie and Peach 1992). Similarly, winter precipitation is thought to be an important driver of Nearctic-Neotropical migratory bird populations, with relatively dry winters associated with lower apparent survival, delayed spring migration, and subsequently reduced breeding output (Ryel 1981, Sillett et al. 2000, Studds and Marra 2011, Rockwell et al. 2012).

In much of the tropical and subtropical regions of the Western Hemisphere, storm frequency and rainfall patterns (especially during the Caribbean winter dry season) are strongly influenced by El Niño-Southern Oscillation (ENSO) via changes in ocean temperatures and wind intensity and direction (Curtis and Adler 2000, Giannini et al. 2000, 2001, Bell and Chelliah 2006). Relatively wet ENSO periods are associated with substantial increases in arthropods (e.g., aerial insects and spiders), primary productivity, and rates of flowering and fruiting in plant communities (Polis 1997, Polis et al. 1998, Holmgren et al. 2001). These wet periods are also associated with improved overall body condition and survival in Nearctic-Neotropical migrants that overwinter in the Caribbean (Sillett et al. 2000, Strong and Sherry 2000). The apparent survival (and fecundity) of Black-throated Blue Warblers (*Setophaga caerulescens*), for example, is lower following relatively dry winters in Jamaica (Sillett et al. 2000). Insect prey biomass also broadly declines over the winter in the Caribbean, so that spring migrants are food limited and in relatively poorer condition than at the start of the winter (Marra and Holberton 1998, Strong and Sherry 2000), which could increase mortality during migration (Owen and Black 1989, Morrison et al. 2007).

Similarly, the normalized difference vegetation index (NDVI) is often investigated as a measure of annual variation in winter habitat quality. The NDVI is a remotely sensed indicator of vegetation "greenness" and density that has a well-established relationship to net primary productivity (Pettorelli et al. 2005). Favorable environmental conditions and increased abundance, survival, and body condition in migratory bird species have been positively correlated with NDVI values from the nonbreeding grounds (Møller 1989, Szép 1995, Peach et al. 2001, Saino et al.

2004). For these bird species, NDVI is likely a predictor of food availability because insect species richness and abundance are often positively correlated with NDVI (Gordo 2007, Lassau and Hochuli 2008, Jepsen et al. 2009).

Bicknell's Thrush (*Catharus bicknelli*) is a rare, range-restricted songbird, breeding only in high-elevation fir (*Abies balsamea*) forests of the northeastern United States and southeastern Canada and wintering predominantly in wet, broadleaf primary forests of the Dominican Republic (Townsend et al. 2015). With a recent global population estimate of < 120,000, Bicknell's Thrush likely have one of the smallest population sizes of any regularly occurring migratory songbird species within the contiguous U.S. and Canada (Hill and Lloyd 2017), and is considered one of the Nearctic-Neotropical migrants at greatest risk of extinction and thus of highest continental conservation concern (Rich et al. 2004, Wells 2007, Townsend et al. 2015). In the northeastern U.S., 95% of the breeding population is found above 805 m elevation in naturally fragmented "sky islands" of montane fir forest (Hill and Lloyd 2017). Similarly, on the nonbreeding grounds in the Dominican Republic, most of the occupied habitat is remote, montane forest that is naturally and anthropogenically fragmented (McFarland et al. 2013, 2018).

Recognized as a distinct species from the Gray-cheeked Thrush (*Catharus minimus*) only since 1995 (Monroe et al. 1995), no long-term demographic studies of Bicknell's Thrush have yet been conducted. However, the reproductive output of Bicknell's Thrush is known to vary with the cone cycle of balsam fir: the dominant tree species within Bicknell's Thrush breeding habitat (McFarland and Rimmer 2002, Townsend et al. 2015). Balsam firs generally produce cones every other year, and this resource pulse appears to drive changes in populations of red squirrel (*Tamiasciurus hudsonicus*), a key predator on the nests of Bicknell's Thrush and other montane bird species (Gurnell 1983, McFarland and Rimmer 2002, Strong et al. 2004). In mast years, balsam fir cones form in late spring and mature in August and early September (Frank 1990). Red squirrels move upslope into fir forests during mast years and store mature cones in middens during autumn, and the size of these middens is directly related to overwinter squirrel survival (Smith 1968, Rusch and Reeder 1978, McFarland and Rimmer 2002). The presence of this cached food source enables squirrels to persist within the fir forests into the following spring, which leads to substantially elevated rates of nest predation on Bicknell's Thrush (McFarland and Rimmer 2002, Townsend et al. 2015). In contrast, when mature fir cones are not present during the autumn and subsequent spring, red squirrels likely emigrate downslope to mixed hardwood stands and may be entirely absent from fir forests during the breeding period of Bicknell's Thrush in June and July (McFarland and Rimmer 2002, Townsend et al. 2015). It is conceivable that the altitudinal migration of red squirrels, and subsequent changes to the predation risk of nests and adults, directly influences the interannual site fidelity and true survival of Bicknell's Thrush (Jason M. Hill and Kent P. McFarland, *personal observations*).

Fig. 1. Hypothesized links between environmental covariates and the apparent survival of Bicknell's Thrush between primary periods (June-July) in year$_t$ and year$_t$+1. For example, we predicted that Bicknell's Thrush site fidelity decisions (and therefore, apparent survival) would be influenced by the presence of red squirrels and mature fir cones during the autumn premigration period (August-early October). Previous research has consistently documented reduced nesting success for Bicknell's Thrush in the summer following an autumn with many mature fir cones and red squirrels. Red squirrels, a common nest predator of montane birds, are generally absent from Bicknell's Thrush breeding habitat following winters without mature cones to sustain them.
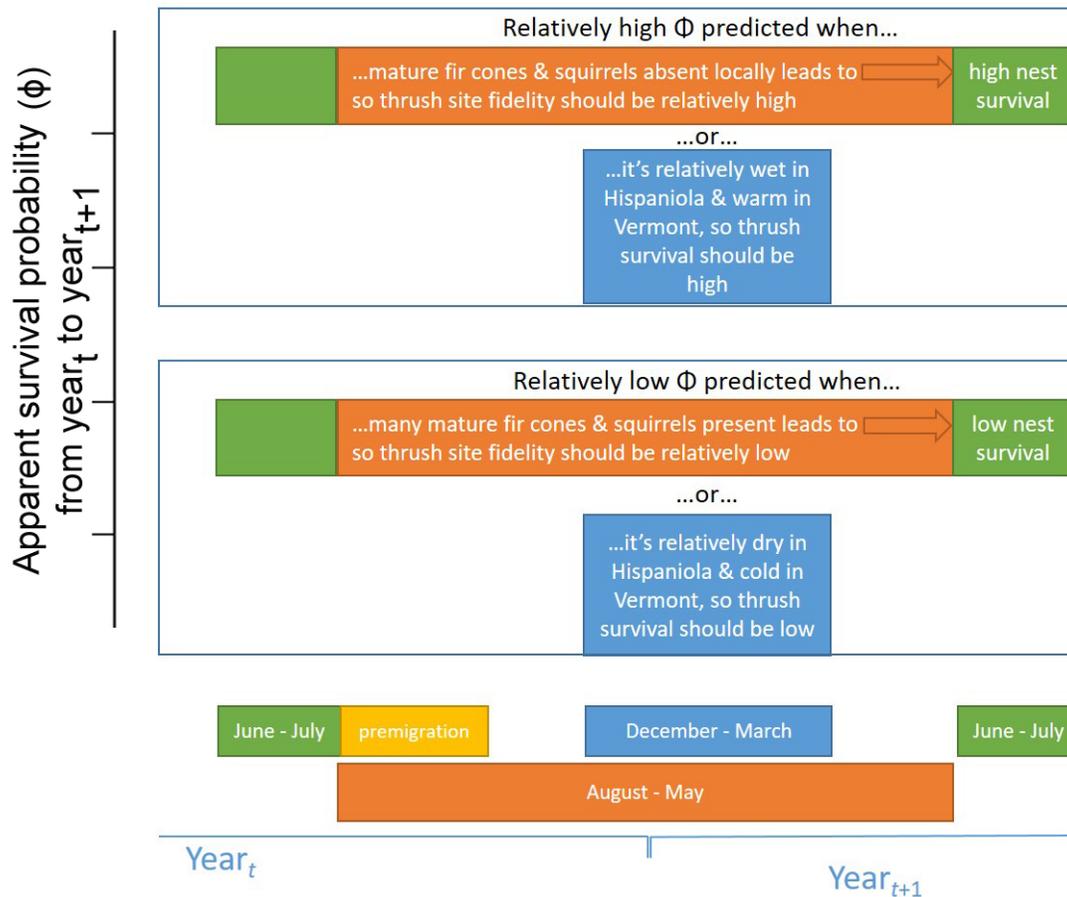
A better understanding of long-term trends in vital rates is key to ongoing efforts to craft a conservation strategy given current and forecasted threats to the species, which include loss of habitat and altered interspecific interactions due to climate change, deforestation on the wintering grounds, and incompatible forestry practices (e.g., precommercial thinning) on the breeding grounds (Lloyd and McFarland 2017). 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 (Lloyd and McFarland 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).

We take advantage of a long-term demographic monitoring project of one breeding population of Bicknell's Thrush in Vermont to test a series of hypotheses about the factors that limit survival and thus potentially influence rates of population growth (Fig. 1). We focused on putatively important factors operating on the breeding and wintering grounds, including the cyclical population dynamics of a nest predator (red squirrel, *Sciurus vulgaris*), and weather effects on food abundance on the breeding and wintering grounds (Table 1). Each of these factors has been proposed as potentially limiting population size of migratory songbirds in general, or Bicknell's Thrush in particular.

Table 1. Environmental covariates and their associated hypotheses used to model the apparent survival of Bicknell's Thrush.

Covariate description	Measurement period and location	Hypothesized relationship to Bicknell's Thrush apparent survival
Fir mast status	September-May; Mt. Mansfield, Vermont	Negative. Mature fir cones in autumn reliably predict relatively high abundance of red squirrel (a nest predator) and lower local nesting success during the next breeding season. We predicted that thrush would exhibit lower site fidelity (year$_t$ to year$_{t+1}$) in areas with mature cones present in autumn of year$_t$.
ENSO precipitation index (ESPI): a remotely-sensed measurement of atmospheric circulation and precipitation patterns	December-March; Global index	Positive. Positive ESPI values generally indicate above-normal winter temperatures and precipitation for the northern Caribbean and is associated with increased food availability.
CHIRPS (Climate Hazards Group InfraRed Precipitation): daily precipitation data	December-March; Dominican Republic	Positive. December through March is typically the driest period of the year for much of the Caribbean. Wetter conditions on the wintering grounds are associated with increased food availability.
Mean monthly winter temperature in Vermont	December-March; Mt. Mansfield, Vermont	Positive. We predicted that warmer winters in Vermont would result in greater spring insect abundance when thrush return from the wintering grounds and result in greater site fidelity.
Normalized difference vegetation index (NDVI): remotely sensed indicator of vegetation greenness	December-March; Dominican Republic	Positive. Positive NDVI values are associated with relatively green vegetation, a proxy of food availability. Favorable environmental conditions and increased abundance, survival, and body condition in migratory bird species have been positively correlated with NDVI values from the nonbreeding grounds.

METHODS

Study site

Mt. Mansfield (44°32′38.21″ N, 72°48′51.52″ W, 1338 m) is the tallest peak in Vermont and has been a site for investigation into montane forest bird ecology for > 30 years. Vegetation is dominated by balsam fir, with interspersed red spruce (*Picea rubra*), heart-leafed paper birch (*Betula cordifolia*) and mountain ash (*Sorbus* spp.). Like other montane forests throughout the range of Bicknell's Thrush, the dense vegetation is stunted by chronic exposure to high winds and heavy winter ice loads (Richardson et al. 2004; McFarland, Lambert, Rimmer, et al., *unpublished data*).

Bicknell's Thrush capture, mark, and recapture

Adult thrush were passively captured in an array of static mist nets (44°31′42.53″ N, 72°48′56.39″ W, ~1170 m) below the summit of Mt. Mansfield in an area of ~25 ha; net locations did not change between years. We strived to open nets a minimum of 1-2 days every week in June and July from 2001 through 2015 (i.e., 14 annual survival periods, and 15 primary capture-mark-recapture periods); annual differences in field crew size and net closures because of rain and high winds resulted in substantial variation in net hours (one 12-m net open for one hour) across years (range = 158.4 to 1541.0 net hours). We outfitted each thrush with a uniquely numbered USGS aluminum leg band and sexed adult thrushes according to Pyle (1997).

Modeling survival, hypotheses, and choice of covariates

We fit Cormack-Jolly-Seber (CJS) models within program MARK to estimate the probabilities of apparent annual survival (Φ, probability of remaining alive and remaining within the study area) and recapture (ρ) from our live-encounter banding records; as is standard for CJS models, adult thrushes newly captured in

2015 (the last primary period) were not included in our modeling effort (Cormack 1964, Jolly 1965, Seber 1965, White and Burnham 1999). Goodness-of-fit tests, including for overdispersion, conducted with the R package R2ucare (Gimenez et al. 2018, R Core Team 2019), suggested that our data were appropriate for CJS models (Pradel et al. 2005). We considered total net hours (a measure of netting effort) across June and July (2002-2015) as our only covariate modeling recapture probability. The remaining covariates represented processes, during the breeding and wintering periods that we hypothesized to affect Bicknell's Thrush apparent survival (Table 1). Although mortality during migration likely has important effects on survival (Newton 2006), we lack important pieces of information about Bicknell's Thrush migration (e.g., location of key stopover areas) that would allow us to include covariates (e.g., severity of weather during migration) describing this part of the species' life cycle in our models. We measured Pearson's correlation between all nonbinary covariates prior to our model selection procedure; all correlation coefficients were less than an absolute value of 0.52.

We predicted higher male apparent survival because male Bicknell's Thrush tend to be physically larger and have longer lifespans than females (Townsend et al. 2015). A previous examination of Bicknell's Thrush banding data noted relatively low site fidelity for adults initially captured in their second year (i.e., SY birds; McFarland, *unpublished data*). However, we did not have estimates of age (or individual covariates describing bird condition) for all thrushes in our dataset. We predicted, therefore, that site fidelity (a component of apparent survival) would be lowest for birds following their initial capture.

The balsam fir cone cycle is highly synchronous among mountains in the Northeast and is best described by a boom and bust pattern: in "mast years" > 75% of firs typically produce cones whereas < 1% of firs produce cones in nonmast years (McFarland and Rimmer 2002). Since 1994, we have annually collected fir mast data within our study area on Mt. Mansfield using visual surveys

conducted June-September (McFarland and Rimmer 2002; McFarland, *unpublished data*). Mature cones in autumn of year$_t$ predict relatively low reproductive success at that location in the breeding season of year$_{t+1}$ (McFarland and Rimmer 2002). It is conceivable, therefore, that Bicknell's Thrush use the presence of mature cones during August and September (prior to autumn migration in early October) to gauge the probability of breeding success at that location in the following year (sensu Danchin et al. 2004, Thomson et al. 2006, Townsend et al. 2015). Alternatively, nesting failures in year$_t$ may increase survival rate by reducing parental investment costs (Santos and Nakagawa 2012).

We examined the effects of weather on apparent survival of Bicknell's Thrush in multiple ways. We estimated mean monthly temperature (°C) for the winter (December-March) between primary periods on Mt. Mansfield because relatively warm winters in Vermont may be associated with increased availability and abundance of invertebrate prey (Bowles et al. 2002) when thrush return in May (Townsend et al. 2015). Birds returning to areas of relatively low food density may be more likely to permanently emigrate away from their former breeding sites (Tye 1992). We acquired global summary of the month (GSOM) climate data from the Mt. Mansfield National Oceanic and Atmospheric Administration (NOAA) Station (station ID: GHCND:USC00435416; 44°31′29.31″ N, 72°48′55.42″ W, 1204 m; https://www.ncdc.noaa.gov/cdo-web/datasets).

To model the effect of ENSO on avian apparent survival, we used the ENSO precipitation index (ESPI): a remotely-sensed measurement of atmospheric circulation and precipitation patterns. Positive ESPI values are associated with the El Niño (warm) phase of the ENSO cycle and generally indicate above-normal winter temperatures and precipitation for the northern Caribbean (Giannini et al. 2000, 2001, National Weather Service 2018). We calculated mean monthly ESPI values for the winter (December-March) between primary periods.

We obtained NDVI data from within the Google Earth Engine and accessed MOD13Q1 NDVI data, which is calculated every 16 days at 250-meter resolution (Carroll et al. 2017). The NDVI ranges from -1 to 1, and typical vegetation values range from 0 (sparse and relatively brown vegetation) to 1 (dense and relatively green vegetation); negative values are typically associated with water features (Carroll et al. 2017). We calculated mean monthly NDVI values from December through March across the predicted Bicknell's Thrush range within the Dominican Republic (McFarland et al. 2013).

We also directly estimated winter precipitation within the winter range of Bicknell's Thrush in the Dominican Republic (McFarland et al. 2013). We used CHIRPS (Climate Hazards Group InfraRed Precipitation) daily precipitation data from the Climate Hazards Group within ArcGIS (ESRI 2018). Climate Hazards Group InfraRed Precipitation is a global rainfall dataset, from 1981 to present, which combines satellite imagery with weather station data to predict daily rainfall at 0.05° x 0.05° spatial resolution (Funk et al. 2014, 2015). We calculated the mean monthly rainfall from December through March between each primary period; this four-month period corresponds with the driest period of the year for much of the Caribbean (Faaborg et al. 1984, Studds and Marra 2011). We included covariates for both

ESPI and CHIRPS in our candidate models because they were weakly and nonsignificantly correlated (r = 0.35, P = 0.23) and assessed climate at different scales.

Model selection with MARK

We used a hierarchical modeling approach to identify the parsimonious structure and covariates of Φ and ρ using Akaike's information criterion corrected for small sample size (AICc; Sugiura 1978, Burnham and Anderson 2002, Hill and Diefenbach 2013, 2014). We started with a general model in which apparent survival and recapture probabilities varied by sex and time (i.e., Φ(sex + time), ρ(sex + time)). We selected the parsimonious recapture structure from four candidate models (constant, time-varying, constant by sex, and time-varying by sex). We then added the net hours covariates to the parsimonious p structure and retained it if it improved (i.e., lowered the AICc of) the model. We then identified the parsimonious survival structure from four candidate models (constant, time-varying, constant by capture cohort, and constant by sex). The resulting model was used to assess the explanatory power of the remaining apparent survival covariates.

Assessing the effect of mast production and climatic covariates on apparent survival

We assessed the relative importance of our five environmental covariates on apparent survival by calculating the R^2_Dev statistic (Skalski 1996, Grosbois et al. 2008). The R^2_Dev statistic measures the proportion of variation in survival explained by the addition of a covariate compared to models with constant and year-varying survival. The recapture structure was kept the same among the models used to calculate the R^2_Dev statistic (Santisteban et al. 2012). From the parsimonious model without apparent survival covariates, we added a single environmental covariate. We considered each covariate biologically informative if it explained > 20% of the temporal variation in apparent survival (Grosbois et al. 2008). We calculated model-averaged estimates ± unconditional SE (Powell 2007) from the parsimonious model without covariates and any model with a biologically informative covariate.

RESULTS

From 2001 through 2014, we captured 178 (50 female and 128 male) adult Bicknell's Thrush on Mt. Mansfield, Vermont; the mean recapture rate was 0.69 between 2002 and 2015, and 59% of adult thrush (*n* = 105) were never recaptured. The number of net hours (median = 601.00 net hours, interquartile range or IQR = 415.38-1191.81) increased substantially over the years, and recapture probability (p̄ = 0.52, SE = 0.05, 95% CI: 0.42, 0.61) increased with the number of net hours (β = 0.38, SE = 0.20, 95% CI: -0.00, 0.76). Recapture probability was lowest in 2004 (ρ = 0.40), the year with fewest net hours (158.38), and it was highest in 2014 (ρ = 0.67), the year with the greatest netting effort (1541.00 net hours). Models including sex-specific or time-variant probabilities of apparent survival and recapture were not well supported (Table 2).

Contrary to our expectations, NDVI, winter rainfall, and Vermont winter temperatures were not biologically informative predictors of Bicknell's Thrush annual apparent survival (Table 3; Φ̄ = 0.61 ± 0.03, 95% CI: 0.54, 0.68). Our model selection process indicated that fir mast status and the ENSO precipitation index

Table 2. Model selection results examining variation in annual apparent survival (Φ) and detection probability (ρ) of adult Bicknell's Thrush captured in Vermont from 2001 to 2015. Models with K parameters were compared by differences in their Akaike's information criterion corrected for small sample sizes (ΔAICc) and are listed with their Akaike weight (w_i).

Model[†]	ΔAICc	w_i	K	Deviance
Φ(mast year status), ρ(net hours)	0.00	0.31	4	221.77
Φ(ESPI), ρ(net hours)	0.06	0.30	4	221.83
Φ(CHIRPS), ρ(net hours)	1.77	0.13	4	223.54
Φ(mean winter temperature on Mt. Mansfield), ρ(net hours)	2.39	0.09	4	224.15
Φ(.), ρ(net hours)	3.22	0.06	3	227.04
Φ(NDVI), ρ(net hours)	3.66	0.05	4	225.42
Φ(Age[./.]), ρ(net hours)	4.13	0.04	4	225.90
Φ(sex), ρ(net hours)	5.28	0.02	4	227.04
Φ(time), ρ(net hours)	12.92	< 0.01	16	208.79
Φ(sex + time), ρ(net hours)	15.16	< 0.01	17	208.77
Φ(sex + time), ρ(.)	22.60	< 0.01	16	218.46
Φ(sex + time), ρ(sex)	24.55	< 0.01	17	218.15
Φ(sex + time), ρ(time)	36.56	< 0.01	29	201.60
Φ(sex + time), ρ(sex + time)	39.04	<0.01	30	201.57

[†]Abbreviations: (.) = constant; ESPI = El Niño-Southern Oscillation precipitation index; CHIPRS = Climate Hazards Group InfraRed Precipitation daily precipitation data; NDVI = normalized difference vegetation index; Age[./.] = constant survival by capture cohort.

Table 3. The proportion of variation in apparent survival explained by the addition of each environmental covariate (R^2_Dev). We considered a covariate biologically informative if it explained > 20% of the temporal variation in apparent survival.

Covariate	R^2_Dev
Fir mast status	0.29
ENSO precipitation index (ESPI)	0.29
Climate Hazards Group InfraRed Precipitation (CHIRPS)	0.19
Mean monthly winter temperature in Vermont	0.16
Normalized difference vegetation index (NDVI)	0.09

(ESPI) both explained 29% of the temporal variation in apparent survival. Contrary to our hypothesis, however, apparent survival was greater (β = 0.86 ± 0.39, 95% CI: 0.10, 1.63) following mast years (Φ = 0.67 ± 0.06, 95% CI: 0.55, 0.79) compared to after nonmast years (Φ = 0.56 ± 0.06, 95% CI: 0.43, 0.68). Annual apparent survival was also higher when conditions were relatively wet on the nonbreeding grounds, but only as measured via ESPI (β = 0.55 ± 0.26, 95% CI: 0.04, 1.05) and not local rainfall (CHIRPS, β = 0.03 ± 0.02, 95% CI: -0.004, 0.07) or NDVI (β = -0.002 ± 0.002, 95% CI: -0.007, 0.001). Annual variation in NDVI within predicted habitat for Bicknell's Thrush was muted, ranging from a low of 0.71 in 2000 to a high of 0.78 in 2014 and 2015 (median = 0.77, IQR: 0.77-0.78; Fig. 2). In our dataset, Vermont winter temperatures (β = 0.27 ± 0.16, 95% CI: -0.04, 0.58) was not strongly or significantly correlated with the El Niño-Southern Oscillation precipitation index (r = -0.20, P = 0.50).

DISCUSSION

Our research provides the most comprehensive examination of the effects of weather and other potentially limiting factors on Bicknell's Thrush demographics to date, and our analysis yielded insight into the factors driving variation in annual apparent

Fig. 2. Model-averaged annual apparent survival estimates (with 95% confidence intervals in purple) of adult Bicknell's Thrush captured and recaptured in Vermont from 2001 to 2015 with annual ESPI values (panel A). Both mast year status and ESPI were biologically informative covariates describing nearly 30% of the temporal variation in apparent survival. An "M" above the X-axis of panel A, indicates that mature fir cones were present in our study area from September (year$_t$) through the subsequent breeding season (year$_t$+1); 2002 was the first mast year within our study period, for example. The CHIRPS mean monthly rainfall (panel B), mean winter temperature in our Vermont study area (panel C), and the mean monthly NDVI (panel D) were not biologically informative apparent survival covariates. Note: ESPI = ENSO precipitation index; CHIRPS = Climate Hazards Group InfraRed Precipitation; NDVI = Vegetation greenness.
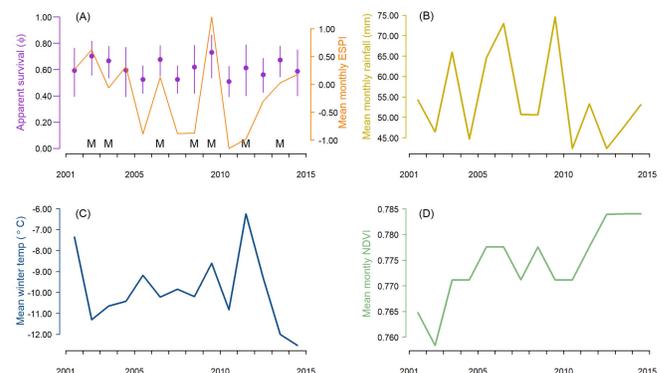
survival of this species. Bicknell's Thrush apparent survival was relatively stable (median Φ = 0.61, IQR: 0.56-0.66) over our 15-year study, which mirrors the stable population trends of this species in Vermont (Hill and Lloyd 2017). These apparent survival

estimates were remarkably similar to mean apparent survival estimates (0.56-0.75) reported for five other North American thrush (Turdidae species) species (Powell et al. 2000, Gardali et al. 2003, DeSante and Saracco 2009, Evans et al. 2011). In our study, Bicknell's Thrush' apparent survival was parsimoniously predicted by variation in seasonal resource pulses, namely masting by balsam fir.

Resource pulses, such as periodic mast production, are a common feature of many terrestrial ecosystems. In temperate and boreal forests, mast may play a keystone role in structuring community dynamics through interactions across trophic levels (Ostfeld and Keesing 2000). There is a predictable link between mast abundance and apparent survival in birds when mast is directly consumed by the birds. For example, spring temperature is negatively associated with serotinous Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) cone availability in the Rocky Mountains; as spring temperatures have increased, the resulting decline in cone production has likely driven declines in adult survival and a 60% decline in the population of South Hills Crossbills (*Loxia curvirostra* complex) over a five-year period (Santisteban et al. 2012). However, pulsed resources often initiate far-reaching cascades of direct and indirect effects that permeate through food webs and exert pronounced population effects as well; these effects have been documented among songbird and rodent populations in a variety of forest communities including temperate deciduous forests dominated by oak (*Quercus* spp.; McShea 2000, Schmidt and Ostfeld 2003, Clotfelter et al. 2007), southern beech (*Nothofagus* spp.; King 1983, White and King 2006), sugar maple (*Acer saccharum*; Fiola et al. 2017), European hornbeam (*Carpinus betulus*; Jędrzejewska and Jędrzejewska 1999), and boreal and montane fir forests (Messaoud et al. 2007, Townsend et al. 2015).

Masting, a primary resource pulse, is often followed by a secondary pulse that emerges as mast-consuming small mammal populations increase in response to abundant seeds. Tertiary resource pulses may subsequently result as predators respond to increases in their rodent or avian prey base (Dunn 1977, Jędrzejewska and Jędrzejewska 1999, McShea 2000, Fiola et al. 2017) as is likely the case for Bicknell's Thrush (McFarland and Rimmer 2002, this study). Cascading secondary and tertiary resource pulses can substantially affect songbird populations through decreased productivity (McFarland and Rimmer 2002, Schmidt and Ostfeld 2003, Fiola et al. 2017) and reduced juvenile and adult survivorship (Schmidt 2003).

In our study, fir mast indirectly influenced adult Bicknell's Thrush apparent survival (likely site fidelity, specifically), which was ~11% higher following mast years than nonmast years. These results do not support our hypothesis that the presence of mature cones in the autumn of mast years influences site fidelity in Bicknell's Thrush. Given our results, adult Bicknell's Thrush site fidelity may be more strongly influenced by prior nesting success as opposed to future predation risk. Indeed, prior nesting success is a reliable predictor of site fidelity for many species, including Prothonotary Warbler (*Protonotaria citrea*), Bobolink (*Dolichonyx oryzivorus*), Brown Thrasher (*Toxostoma rufum*), and American Robin (*Turdus migratorius*; Blancher and Robertson 1985, Bollinger and Gavin 1989, Haas 1998, Hoover 2003). Following mast years, red squirrel relative abundance is typically high

throughout the fir zone, because > 75% of fir trees produce mast during mast years; this allows red squirrels to build large middens, resulting in higher overwinter survival and a subsequent decrease in songbird reproductive success in the following spring (Smith 1968, Rusch and Reeder 1978, McFarland and Rimmer 2002; Mountain Birdwatch 2.0 https://knb.ecoinformatics.org/view/doi:10.5063/F1XW4H49). Therefore, Bicknell's Thrush may simply be unable to mitigate the risk of nest predation by red squirrels by emigrating elsewhere.

Vegetation greenness (NDVI) within predicted winter habitat in the Dominican Republic, which we expected would reflect increased food availability (Wilson et al. 2011), was not an important covariate of apparent survival in Bicknell's Thrush. This lack of a relationship is likely in part a consequence of the low interannual variability of NDVI estimates within Bicknell's Thrush winter habitat. In addition, the positive relationship between NDVI and rainfall, presumably the mechanism linking NDVI to increased food availability and increased survival of birds, disappears when annual precipitation exceeds ~1200 mm (Nicholson et al. 1990). Above this level, additional rainfall produces only minimal gains in NDVI. Nearly all of the areas considered potential winter habitat for Bicknell's Thrush in the Dominican Republic receive > 1300 mm of precipitation annually (Izzo et al. 2010), suggesting that NDVI is likely a poor indicator of interannual variation in weather conditions that might influence the survival of Bicknell's Thrush by regulating food availability.

Indeed, when examining variation in rainfall via a more direct index, EPSI, we found that Bicknell's Thrush apparent survival increased during relatively wet winters on the wintering grounds. Thus our results are in keeping with other research that has demonstrated a positive relationship between rainfall and apparent survival of migratory birds (Peach et al. 1991, Sillett et al. 2000, Rockwell et al. 2017). The presumed mechanism underlying this relationship is that food availability is lower for migrants during dry years, leaving them in poorer condition and at greater risk of mortality during the nonbreeding season or spring migration (Strong and Sherry 2000, Marra and Holmes 2001, Smith et al. 2010). For Bicknell's Thrush, this would imply a positive relationship between precipitation and the availability of either fruit or insects (Townsend et al. 2012).

Although rainfall clearly plays a key role in seasonal patterns of abundance for many species (Wolda 1978) and contributes to spatial variation in insect abundance and diversity (Janzen and Schoener 1968), correlations between interannual variation in precipitation and insect abundance are rarely documented (but see Hawkins and Holyoak 1998). Indeed, most of the evidence for moisture as a driver of food availability for migrant birds comes from comparisons among habitats (e.g., Smith et al. 2010) or within seasons (e.g., Strong and Sherry 2000). Similarly, long-term patterns in fruit production by tropical trees and shrubs are poorly known, but are not consistently linked to variation in rainfall (Polansky and Boesch 2013). Thus, although our results demonstrate a positive effect of winter rainfall on Bicknell's Thrush apparent survival, we suggest that the underlying mechanism is uncertain. Future work might profitably focus on quantifying the influence of interannual variation in rainfall on fruit production and insect abundance within the winter range of Bicknell's Thrush.

Our understanding of Bicknell's Thrush population dynamics would likely be improved by measuring the factors (e.g., food availability and habitat quality) that directly affect Bicknell's Thrush survival and site fidelity, especially during the nonbreeding period. Improved knowledge of migratory connectivity patterns and local habitat use outside of the breeding grounds would also potentially allow researchers to use covariates of finer spatial resolutions than the regional (e.g., CHIRPS rainfall data) and global (e.g., ESPI) covariates used in our study. With the majority of Bicknell's Thrush overwintering in the Dominican Republic, it will be critically important to understand how this species is affected by the conversion of forest to agricultural field, likely the primary driver of forest loss within the nonbreeding range of Bicknell's Thrush (McFarland et al. 2013, Curtis et al. 2018). Between 2000 and 2016, cloud forest and moist broadleaf forest in the Dominican Republic, likely the two most important types of forest on the wintering grounds for Bicknell's Thrush (McFarland et al. 2013), declined by 5.9% and 8.9%, respectively (Lloyd and Leon, *unpublished data*). Deforestation on the nonbreeding grounds has been linked to declines of Wood Thrush (*Hylocichla mustelina*) in Central America (Taylor and Stutchbury 2016) and Golden-winged Warblers (*Vermivora chrysoptera*) in northern South America (Kramer et al. 2018), but our annual apparent survival estimates are likely too imprecise to detect any comparable trend in apparent survival. With Haiti's primary forests now almost completely vanished (Hedges et al. 2018), conservation of remaining broadleaf forests in the Dominican Republic take on additional significance for Bicknell's Thrush.

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