



EL NIÑO–SOUTHERN OSCILLATION INFLUENCES ANNUAL SURVIVAL OF A MIGRATORY SONGBIRD AT A REGIONAL SCALE

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ABSTRACT.—Global climate cycles have been shown to influence demographic rates of birds at local scales, but few analyses have examined these effects at larger, regional scales. We examined the relationship of broad-scale climate indices to apparent survival of a subspecies of Swainson's Thrush (*Catharus ustulatus*) across a large portion of the subspecies' breeding range along the Pacific slope of North America. We developed 69 *a priori* Cormack-Jolly-Seber models to examine effects of El Niño–Southern Oscillation (ENSO), North Atlantic Oscillation, Pacific Decadal Oscillation, latitude, region, and residency status on survival. The most parsimonious model included an ENSO effect, a regional effect, and a residency effect on survival. The ENSO had a positive effect on survival probability, and the effect was consistent across the entire portion of the breeding range examined. Additional analyses of *a posteriori* models provided strong support for an effect of dry-season precipitation along the spring migration route in western Mexico on annual survival. Our results suggest that survival of this Neotropical migrant is strongly influenced by ENSO-related weather changes during one or more periods of its annual cycle. Because many western Neotropical migrants migrate through and winter in the same general geographic area as Swainson's Thrushes, it is possible that other such species are similarly influenced by ENSO. If, as some climate models predict, annual variation in ENSO increases, Swainson's Thrush may suffer greater variation in annual survival. Directly associating climate with key demographic parameters provides a powerful approach to predicting a species' response to climate change. Received 6 February 2012, accepted 4 July 2012.

Key words: *Catharus ustulatus*, Cormack-Jolly-Seber, MAPS program, migration, precipitation, residency, survival, Swainson's Thrush.

La Oscilación del Sur-El Niño Afecta la Supervivencia Anual de un Ave Canora Migratoria a Escala Regional

RESUMEN.—Se ha demostrado que los ciclos climáticos globales influyen las tasas demográficas de las aves a escalas locales, pero pocos análisis han examinado estos efectos a escalas regionales. Examinamos la relación entre índices climáticos a gran escala y la supervivencia aparente de una subespecie de *Catharus ustulatus* a través de una porción grande del área de reproducción a lo largo de la costa pacífica de Norte América. Desarrollamos 69 modelos Cormack-Jolly-Seber *a priori* para examinar los efectos de la Oscilación del Sur-El Niño (ENSO), la oscilación del Atlántico Norte, la oscilación decenal del Pacífico, la latitud, la región y el estado de residencia en la supervivencia de las aves. El modelo más parsimonioso incluyó un efecto de la ENSO, un efecto regional y un efecto de la residencia sobre la supervivencia. La ENSO tuvo un efecto positivo en la probabilidad de supervivencia, y el efecto fue consistente a través de toda la porción examinada del área de reproducción. Análisis adicionales de modelos *a posteriori* dieron un fuerte sustento para un efecto de la precipitación en la temporada seca a lo largo de la ruta migratoria de primavera en el occidente de México sobre la supervivencia anual. Nuestros resultados sugieren que la supervivencia de este migrante neotropical se ve fuertemente influenciada por cambios climáticos relacionados con la ENSO durante uno o más periodos de su ciclo anual. Dado que muchas especies de migrantes neotropicales occidentales usan las mismas áreas de migración e invernada que *C. ustulatus*, es posible que tales especies se vean influenciadas por la ENSO de manera similar. Si la variación anual en la ENSO se incrementa, como predicen algunos modelos climáticos, *C. ustulatus* podría sufrir una mayor variación en la supervivencia anual. La asociación directa del clima con parámetros demográficos clave representa un enfoque poderoso para predecir la respuesta de una especie al cambio climático.

GLOBAL CLIMATE CYCLES affect regional and local weather patterns and may be important drivers of avian demographic rates and population dynamics (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005). The direction and magnitude of climate effects

on demography and population dynamics often appear to be related to precipitation patterns, which can affect primary productivity and resource availability (Polis et al. 1997, Wright et al. 1999, Holmgren et al. 2001, Gordo and Sanz 2010) and the body condition

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and phenology of migratory birds (Hüppop and Hüppop 2003, Wolfe and Ralph 2009). However, effects of climate cycles on migratory species may be complicated by differing climatic conditions across their breeding, migrating, and wintering ranges. Therefore, broad-scale studies that link demography and climate are needed to better understand the effects of climate both across the range and throughout the life cycle of migratory species.

Three major global climate cycles may affect demographic rates and population dynamics of migratory landbirds in western North America: El Niño–Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), and Pacific Decadal Oscillation (PDO). The ENSO, a coupled ocean–atmospheric cycle, has a strong influence on precipitation patterns that varies dramatically among regions (Kurtzman and Scalón 2007, Tourigny and Jones 2009). Warm-phase, or El Niño, events are associated with drier conditions in the Pacific Northwest and southern Central America and increased precipitation in California and Mexico, especially western Mexico (Caso et al. 2007, Kurtzman and Scalón 2007, Miller and Goodrich 2007, Tourigny and Jones 2009). These effects are approximately reversed during cold-phase, or La Niña, events.

The NAO affects weather predominantly in the temperate regions of North America and Europe. The effects of NAO on regional climate along the west coast of North America have been less studied than those of ENSO. The NAO is associated with milder winters in the Pacific Northwest.

In contrast to ENSO or NAO, the PDO generally oscillates over a period of decades. However, PDO is positively correlated with ENSO, and its effects on western North American weather patterns appear to depend on ENSO conditions. Generally, warm-phase PDO events amplify the effects of El Niños, and cold-phase PDO events amplify the effects of La Niñas (Kurtzman and Scanlon 2007, Miller and Goodrich 2007).

Adult survival can be a key demographic driver of avian population dynamics in Neotropical migrant species (Noon and Sauer 1992, Woodworth 1999, DeSante et al. 2001, Saracco et al. 2008). Few studies have examined links between survival rates of Neotropical migratory birds and climate cycles, and, to our knowledge, none have been conducted on species that breed in western North America. Studies of local breeding or wintering populations have found associations between ENSO and adult survival, reproduction, and body condition (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005, Wolfe and Ralph 2009), but the broad-scale effects of ENSO on avian population dynamics remain unknown. Previous studies have also found associations between NAO and avian reproduction and phenology (Nott et al. 2002, Hüppop and Hüppop 2003), but these studies have only examined breeding-range effects of NAO during or just prior to the breeding season. The effects of NAO on avian survival remain unstudied. The effects of PDO on migratory bird populations have not been studied, but because PDO tends to amplify the effects of ENSO, it may enhance or mediate the effects of ENSO, depending on its phase.

Here, we examine effects of climate cycles on adult annual apparent survival rates of the Pacific slope subspecies of Swainson's Thrush (*Catharus ustulatus ustulatus*; American Ornithologists' Union [AOU] 1957). This subspecies provides an ideal study organism for understanding broad-scale climate effects on survival because (1) it is abundant in appropriate habitat across its breeding range, (2) it is readily captured in ground-level mist nets

across its breeding range in numbers sufficient for survival-rate estimation from capture–recapture models (DeSante and Kaschube 2009), and (3) its breeding, migrating, and wintering ranges cover a broad latitudinal gradient over which climate-cycle influences on weather patterns vary greatly. Our objectives were to (1) examine effects of climate cycles on adult survival of Swainson's Thrush across a broad portion of its western breeding range, and (2) identify links between climate cycles and regional weather patterns to suggest hypotheses for the mechanisms by which climate cycles may affect demographic rates. Understanding the links between climate, regional weather patterns, and demography will allow the identification of regions where a species' demography will be most vulnerable to climate change.

METHODS

We used mark–recapture data collected at Monitoring Avian Productivity and Survivorship (MAPS) stations (DeSante et al. 2004) within the breeding range of the Pacific slope subspecies of Swainson's Thrush in Washington, Oregon, and California during 1992–2006 (Online Supplement, Appendices S1 and S2; see Acknowledgments). This subspecies breeds in riparian and wet coniferous forests from Southeast Alaska to California and winters from Mexico to Costa Rica (Ruegg and Smith 2002). We included data from 25,516 captures of 10,870 individual adult birds from 56 stations at which the species was considered a usual (>50% of the years during which the station was operated) breeder, and stations which were in operation for ≥ 4 years (Fig. 1). We chose to restrict our analyses to the Pacific slope subspecies because genetic and band-recovery data indicate that this subspecies migrates and winters in different locations than the other subspecies (*C. u. incana*, *C. u. swainsonii*, and *C. u. clarescens*; AOU 1957, Ruegg and Smith 2002). Birds were aged according to criteria in Pyle (1997) and banded with uniquely numbered bands provided by the U.S. Geological Survey's Bird Banding Laboratory.

We limited our analysis to captures of adult (after-hatching-year) birds, and used Cormack–Jolly–Seber (CJS) models to estimate annual adult apparent survival probability between breeding seasons, hereafter referred to as “adult survival,” the complement of which is death and permanent emigration. Recapture rates of juvenile birds were dramatically lower than adult recaptures, and high postnatal dispersal makes it difficult to interpret variation in apparent survival of juveniles. Therefore, we did not examine variation in juvenile apparent survival. We developed an *a priori* set of candidate models to estimate adult survival with covariates for climate indices, space, time, and residency as well as null models.

An unknown proportion of birds captured at MAPS stations are transient individuals moving through the area as migrants, floaters, or birds that establish territories in nearby areas. Incorporating these individuals into capture–recapture models can result in underestimates of survival. We used “transient” CJS models to minimize this bias (Nott and DeSante 2002, Hines et al. 2003), which classifies a bird as a resident if it is captured more than once, at least 6 days apart, during its first year of capture. We included this residency effect in all models because of its strong support in previous survival analyses of MAPS data and to increase precision of survival estimates of resident adults (DeSante and Kaschube 2009).

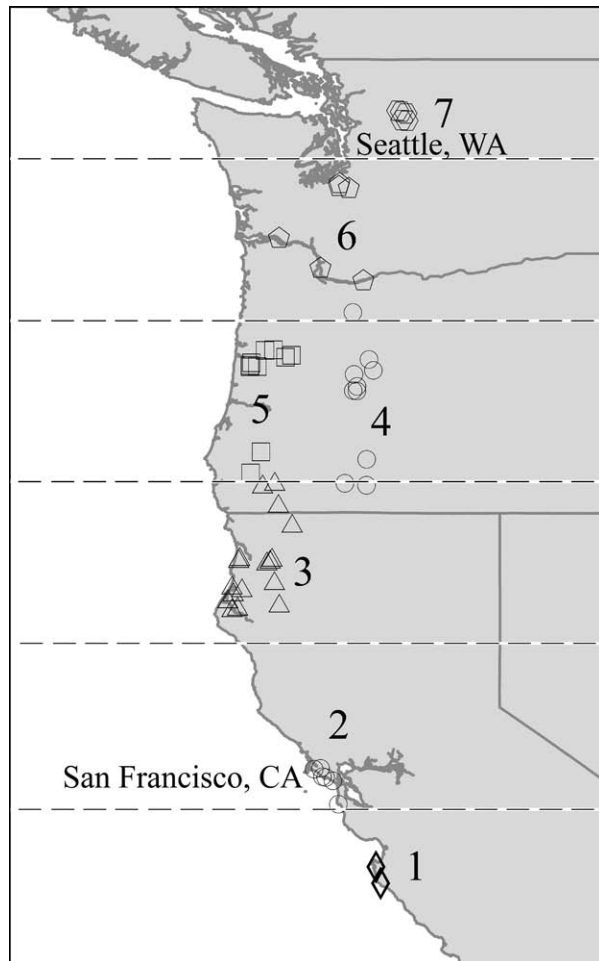


FIG. 1. Monitoring Avian Productivity and Survivorship (MAPS) banding stations from which Swainson's Thrush captures were used in this analysis. Regions used in models estimating survival and recapture probabilities are numbered. Dashed lines indicate 2.5° latitude intervals within which regions were established.

To examine the effects of climate indices on annual survival, we included covariates of ENSO, NAO, and PDO in our models. We used the El Niño–Southern Oscillation Precipitation Index (ESPI) to index ENSO patterns because, unlike traditional Southern Oscillation Index (SOI) or sea surface temperature (SST) anomaly indices, ESPI values contain information from both atmospheric pressure (SOI) and SST. Values of ESPI, NAO, and PDO indices were obtained from the National Oceanic and Atmospheric Administration (NOAA) (NOAA Climate Prediction Center 2010). Several studies of the ecological effects of climate cycles have used the annual mean of the index (i.e., January–December; Sillett et al. 2000, Wolfe and Ralph 2009). However, we used averaged climate indices from July to April. This 10-month average includes the typical peak of ENSO (October–December) and NAO (December–March) and is strongly correlated with precipitation anomalies that are typically associated with these climate indices (Hüppop and Hüppop 2003, Tourigny and Jones 2009). Climate effects on herbivores and insectivores may also lag by a year (Bullock and Solis-Magallanes 1990, Polis et al. 1997, Holmgren

et al. 2001). Therefore, we included models that allowed survival to vary according to climate indices from the previous year in our candidate model set. The effects of ENSO can be altered under a warm or cold PDO regime. Because PDO exerts its primary influence through ENSO (Kurtzman and Scanlon 2007, Miller and Godrich 2007), PDO was not considered alone in a model but always with ESPI. Because of the degree of collinearity between ESPI and PDO and the fact that ENSO exhibits a more pronounced effect on weather in western North America than PDO, we used residuals of PDO–ESPI regression in models with ESPI instead of the actual PDO values (Graham 2003).

To examine geographic variation in survival, we considered regional (reg) and latitudinal (lat) effects in our models. Banding stations were assigned to regions based on 2.5° latitudinal bands and broad elevational differences (<615 m vs. >615 m) within bands. Stations on the border of a latitudinal band were placed in the adjacent region with stations of similar elevation ($n = 3$). These criteria resulted in seven regions (Fig. 1). We also included models that allowed survival to vary by a station-specific latitudinal covariate.

In addition to estimating survival probability, CJS models provide estimates of the nuisance parameter, recapture probability (p). We compared a model of constant recapture probability to one that incorporated a station-specific covariate (mean number of captures per adult per year). This covariate has been used successfully to model site-specific variation in capture rate (Julliard 2004, Saracco et al. 2008). Because MAPS utilizes a constant-effort design and previous analyses of MAPS data for Swainson's Thrush have shown little evidence of temporal variation in recapture probability (DeSante and Kaschube 2009), we did not consider models allowing for time-varying recapture probability.

Our *a priori* model set was created by first considering the following temporal effects on survival: time-dependent survival (t ; i.e., an independent survival rate for each year), climate covariates (ESPI, NAO, or ESPI–PDO) that allowed survival to vary over time but constrained survival to covary with annual climate cycle values, and no effect of time (time-constant survival). For each of these temporal survival models, we also considered the following spatial effects: banding station latitude (lat), region (reg), or no spatial variation. Only biologically relevant two-way interactions were included in candidate models. These included (1) latitude \times climate, region \times climate, latitude \times time, and region \times time to examine whether climate or year affects survival differently among regions–latitudes; and (2) latitude \times residency status and region \times residency status to examine whether probability of residency varied spatially. All combinations of temporal, spatial, and two-way interactions, plus null models, resulted in a set of 69 candidate models (Online Supplement, Appendix S3; see Acknowledgments).

A goodness-of-fit test was conducted on the most general model using the median \hat{c} method in Program MARK. The estimated value of \hat{c} ($\hat{c} = 1.455$; 95% confidence interval [CI]: 1.435–1.476) suggested that there was overdispersion in this model. As a result, we adjusted Akaike's information criterion (AIC_c) using the median \hat{c} and compared models using $QAIC_c$ (Burnham and Anderson 1998). Model selection results and parameter estimates were computed with MARK as executed by R (R Development Core Team 2010) using the RMark package (Laake and Rexstad 2010). The 95% confidence intervals of the standardized regression coefficients for climate variables of the top-performing model were examined to assess whether they included zero, and beta values were

reported on the link (logit) scale. Model-averaged parameter estimates were calculated using MARK (White and Burnham 1999).

The first-interval survival for birds of unknown residency status is the product of the probability of the bird being a resident and first-interval resident survival (Hines et al. 2003). The probability of a newly marked adult bird of unknown residency status being a resident bird (τ) was calculated by dividing our time-constant estimate of first-interval survival for birds of unknown residency status by our estimate of time-constant survival for resident birds. The probability of any newly marked adult bird being a resident was calculated by dividing the total number of resident birds (sum of birds of known residency status with those of unknown residency status multiplied by τ) by the total number of birds captured in a given region.

To examine the possible mechanisms behind effects of climate cycles on Swainson's Thrush survival, we conducted an additional CJS analysis of the effects of climate-cycle-related precipitation on Swainson's Thrush survival. This analysis was identical to the analysis above, except using region- and time-specific precipitation indices as climate covariates instead of climate cycles. The ENSO exhibited significant influence on survival (see below), so we looked for spatial and temporal patterns in precipitation associated with ENSO over the annual cycle of Swainson's Thrush (Fig. 2). El Niño events were associated with decreased rainy-season precipitation (May–November) in southern Mexico and Central America (WETWIN) and increased

dry-season precipitation (November–May) in northwestern Mexico and southern California (SPRMIG) (Caso et al. 2007, Tourigny and Jones 2009). We incorporated the precipitation data from these two regions into our analysis because they represented rainy-season precipitation on the winter grounds and dry-season precipitation during spring migration of our focal species. To be thorough, we also included two periods of precipitation not associated with ENSO but that might influence Swainson's Thrush survival: the North American Monsoon (NAM) from June to October in northwestern Mexico and southern California (NAMMIG), and precipitation on the winter grounds prior to spring migration from December to April (LATEWIN). In all, precipitation indices from four distinct regions–seasons were calculated and included in the analysis (Fig. 3). No interactions among the four precipitation indices were included in this analysis because its objective was to identify the time and region in which precipitation most influenced Swainson's Thrush survival. Thus, 51 total candidate models were considered in this precipitation analysis (Online Supplement, Appendix S4; see Acknowledgments). We used precipitation data from the Global Precipitation Climatology Project (GPCP; NOAA Earth System Research Laboratory 2010) to examine these patterns because it was standardized and is available for the entire range of Swainson's Thrush. To calculate each of the four precipitation indices, we used the average of the standardized GPCP values for

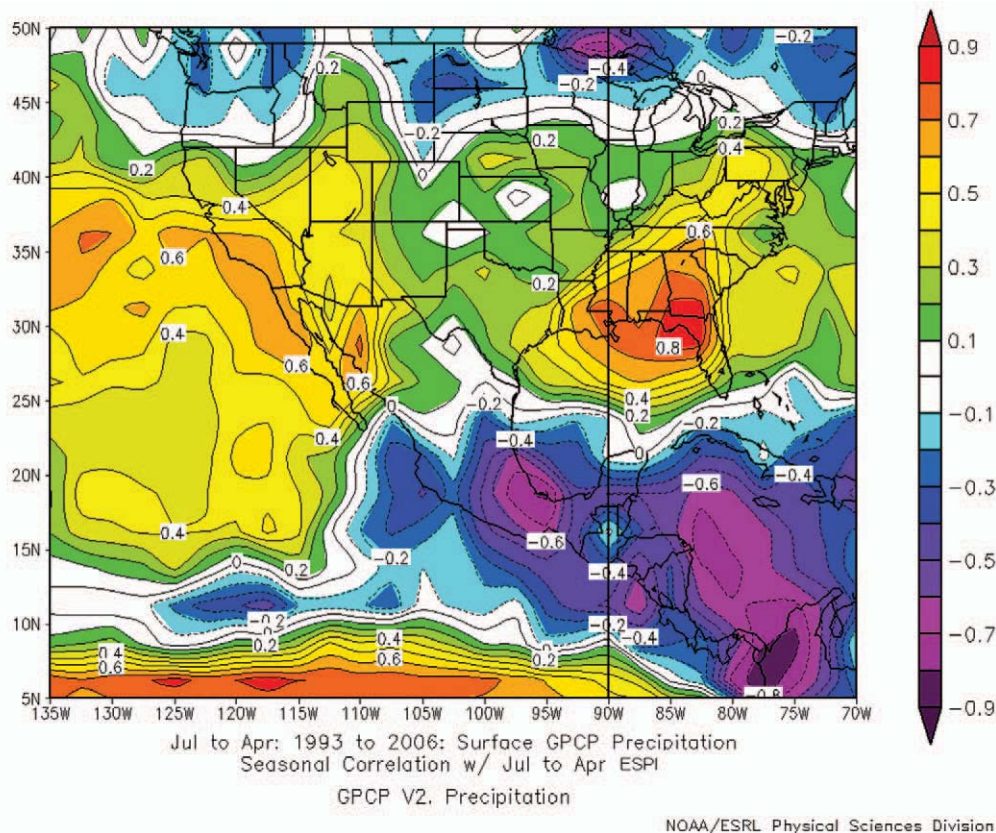


FIG. 2. Correlation coefficients (r) between ESPI (1992–1993 to 2005–2006) and concurrent mean Global Precipitation Climatology Project (GPCP) precipitation from July to April. The relationship is considered significant with 95% confidence when $r > 0.567$ or $r < -0.567$. (Images provided by the NOAA/ESRL Physical Sciences Division, Boulder, Colorado, from their website at www.esrl.noaa.gov/psd/)

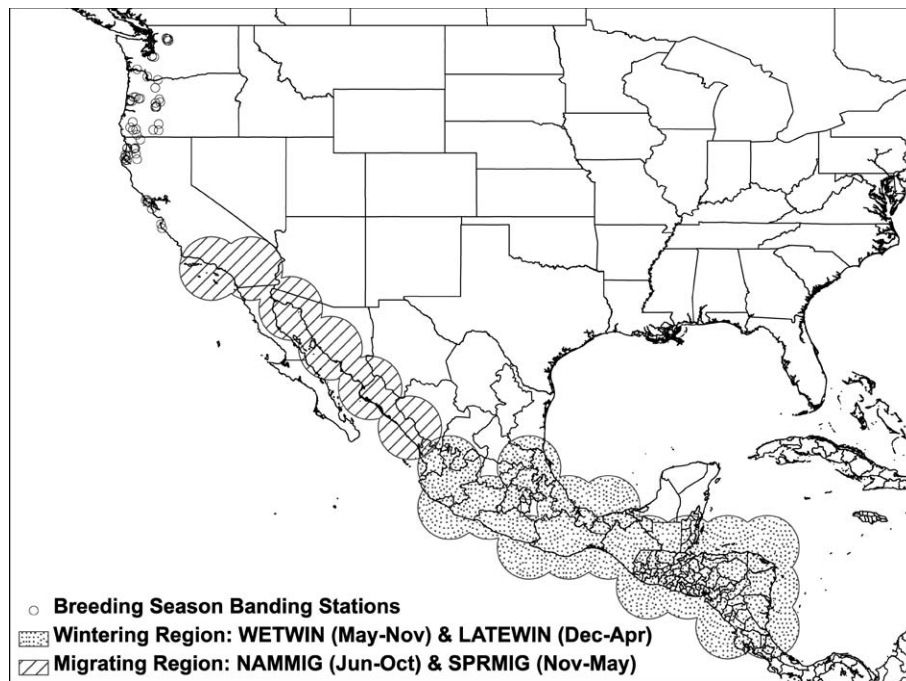


FIG. 3. Map of North and Central America showing wintering and migrating regions for a *posteriori* precipitation analysis of Swainson's Thrush annual apparent survival and breeding-season banding stations used in survival analyses.

each $2.5 \times 2.5^\circ$ latitude–longitude GPCP grid square in a region over its respective months to ensure that the values were representative of annual variation across the entire region and were not dominated by regions that received the most precipitation. Given the significant influence of ENSO on Swainson's Thrush survival (see below), we predicted that a model incorporating one of the two ENSO-related precipitation anomalies would be selected. Because these precipitation models were developed after examining climate-cycle effects on survival, we considered them *a posteriori* explanations and present the results as hypotheses in need of further examination.

RESULTS

The most parsimonious CJS model included the following effects on survival: ESPI during the survival period, region, residency status, and an interaction between region and residency status (Table 1). The top model was 44× more supported than the nested model that did not incorporate ESPI; ESPI exhibited a significantly positive effect on variation in adult annual survival (Table 2 and Fig. 4) and received 85.9% of cumulative model selection weight. By contrast, effects of NAO and PDO on survival were not well supported ($w_{\text{NAO}} = 0.12$, $w_{\text{PDO}} = 0.20$). The model-averaged difference in survival between the strongest El Niño and La Niña years during the course of our study ranged from 5.0% (in region 5) to 8.8% (in region 1). The model-averaged variation in ESPI effect among regions is primarily the result of the third-ranked model, which included an interaction term between ESPI and region (Table 1).

Although there was spatial heterogeneity in survival, no clear latitudinal pattern was observed (Fig. 5). Standardized model

coefficients for the residency indicator variable in the survival model and for the station-specific capture covariate in the recapture probability model both differed from zero (95% CIs did not include zero), which suggests their importance. The probability of a newly marked adult bird being a resident generally increased with latitude (Fig. 5). Our southernmost region had dramatically lower survival than the other regions. However, removing data from this region did not change the order of the top models or alter the parameter estimates significantly, so we present only results that included all regions.

The analysis of the *a posteriori* precipitation model set provided strong support for an effect of dry-season precipitation along the spring migration route on Swainson's Thrush survival (Table 3). The top model ($w_i = 0.73$) included the effect of winter and spring rains along the spring migration route, region, residency, and the region \times residency interaction on survival. In this top-ranked model, the confidence interval of the beta coefficient for dry-season precipitation along the migration route did not overlap zero (Table 4).

DISCUSSION

The only climate cycle that was strongly associated with the annual survival of Swainson's Thrushes was ENSO, which had a strong positive effect across much of their Pacific slope breeding range. Though recruitment is generally considered the most important factor driving population dynamics of short-lived species like Swainson's Thrush (Noon and Sauer 1992, Johnson and Geupel 1996), differences in survival of the magnitude we observed would also have a substantial effect (Noon and Sauer

TABLE 1. Top 12 models (of 69 candidate models from climate-cycle analysis) of annual apparent survival (ϕ) and recapture probability (p) of adult Swainson's Thrushes captured at MAPS banding stations in the western United States, 1992–2006. Models are ranked according to difference in quasi-Akaike's information criterion (ΔQAIC_c) and reported with model weight (w_i) and the number of estimated parameters (k).

Model ^a	k	ΔQAIC_c	w_i
$\phi_{\text{ESPI} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	0.0000	0.5341
$\phi_{\text{ESPI} + \text{PDO} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	18	2.0036	0.1961
$\phi_{\text{ESPI} + \text{reg} + \text{res} + \text{ESPI} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	23	2.9274	0.1236
$\phi_{\text{NAO} + \text{reg} + \text{res} + \text{NAO} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	23	4.7260	0.0503
$\phi_{\text{NAO} + \text{reg} + \text{res} + \text{NAO} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	4.7395	0.0499
$\phi_{\text{NAO} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	23	7.0786	0.0155
$\phi_{\text{NAO} + \text{reg} + \text{res} + \text{NAO} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	16	7.5774	0.0121
$\phi_{\text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	9.3601	0.0050
$\phi_{\text{ESPI} + \text{PDO} + \text{reg} + \text{res} + \text{ESPI} \times \text{reg} + \text{PDO} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	30	9.3851	0.0049
$\phi_{\text{ESPI} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	9.5622	0.0045
$\phi_{\text{ESPI} + \text{PDO} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	18	11.5672	0.0016
$\phi_{\text{t} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	29	11.7046	0.0015

^aDescription of covariates: ESPI = El Niño–Southern Oscillation Precipitation Index (July–April), ESPIp = El Niño–Southern Oscillation Precipitation Index of previous year, PDO = Pacific Decadal Oscillation index (July–April), PDOp = Pacific Decadal Oscillation index of previous year, NAO = North Atlantic Oscillation index (July–April), NAOp = North Atlantic Oscillation index of previous year, reg = regions (defined by latitude and altitude; $n = 7$), lat = latitude of station, res = residency status, t = time (year), and cap = banding-station-specific mean captures per adult per year.

1992, Woodworth 1999, DeSante et al. 2001, Saracco et al. 2008). In addition, Nott et al. (2002) found that breeding productivity of Swainson's Thrushes at MAPS stations in Oregon and Washington was weakly positively correlated ($r = 0.66$, $P = 0.182$) with ENSO. Thus, ENSO may have a positive effect on both Swainson's Thrush survival and productivity, in which case it would have a substantial influence on the species' population dynamics along the Pacific slope of North America.

The positive effect of ENSO on Swainson's Thrush survival that we observed was opposite to the effect of ENSO on survival of Black-throated Blue Warblers (*Setophaga caerulescens*) in Jamaica and Yellow Warblers (*S. petechia*) in Manitoba (Sillert et al. 2000, Mazerolle et al. 2005). However, these species have different breeding and wintering ranges, as well as migratory pathways, than the Pacific slope subspecies of Swainson's Thrush. El Niño causes drought conditions in the Caribbean and South America, where Black-throated Blue Warblers and some Yellow Warblers overwinter, and most likely decreases food supply prior to spring migration (Sillert et al. 2000, Tourigny and Jones 2009). By contrast, El Niño may increase food supplies in wintering ranges and migratory routes of Swainson's Thrushes (see below). Thus, it appears that El Niño cycles may influence survival of eastern and western North American migrants in opposite directions, but more species need to be examined before general conclusions can be made.

The lack of regional variation in ENSO effects on survival was somewhat surprising given that ENSO effects on weather patterns are highly variable across the regions considered (Caso et al. 2007, Tourigny and Jones 2009; Fig. 2). This lack of regional variation in ENSO effects suggests that broad-scale climate indices influence population dynamics on a scale that may be much larger than local or regional "hot spots" (Post et al. 2009). However, the third-ranked

TABLE 2. Parameter estimates (on logit-link scale), standard errors (SE), and lower and upper 95% confidence interval limits (CI) from top-ranked model, $\phi_{\text{ESPI} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$ estimating annual apparent survival (ϕ) and recapture probability (p) of adult Swainson's Thrushes captured at MAPS banding stations in the western United States, 1992–2006. Estimates for continuous covariates (ϕ : $\hat{\beta}_{\text{ESPI}}$ and p : $\hat{\beta}_{\text{cap}}$) represent standardized coefficients. See Figure 1 for regional distinctions and Table 1 for descriptions of model covariates. The estimate for the effect of ENSO on survival is in bold.

Parameter	Estimate	SE	Lower CI	Upper CI
ϕ : $\hat{\beta}_0$	-3.3788	0.2208	-3.8115	-2.9460
ϕ : $\hat{\beta}_{\text{ESPI}}$	0.0828	0.0269	0.0301	0.1356
ϕ : $\hat{\beta}_{\text{reg}2}$	2.3047	0.2435	1.8274	2.7820
ϕ : $\hat{\beta}_{\text{reg}3}$	2.1545	0.2362	1.6915	2.6175
ϕ : $\hat{\beta}_{\text{reg}4}$	2.4057	0.2519	1.9120	2.8993
ϕ : $\hat{\beta}_{\text{reg}5}$	2.5815	0.2328	2.1252	3.0378
ϕ : $\hat{\beta}_{\text{reg}6}$	2.6038	0.2568	2.1005	3.1070
ϕ : $\hat{\beta}_{\text{reg}7}$	2.7199	0.2479	2.2340	3.2057
ϕ : $\hat{\beta}_{\text{res}}$	3.3565	0.2952	2.7779	3.9351
ϕ : $\hat{\beta}_{\text{reg}2 \times \text{res}}$	-1.8696	0.3272	-2.5109	-1.2284
ϕ : $\hat{\beta}_{\text{reg}3 \times \text{res}}$	-1.7688	0.3165	-2.3892	-1.1484
ϕ : $\hat{\beta}_{\text{reg}4 \times \text{res}}$	-1.9663	0.3354	-2.6236	-1.3091
ϕ : $\hat{\beta}_{\text{reg}5 \times \text{res}}$	-2.0873	0.3111	-2.6969	-1.4776
ϕ : $\hat{\beta}_{\text{reg}6 \times \text{res}}$	-2.1525	0.3399	-2.8186	-1.4863
ϕ : $\hat{\beta}_{\text{reg}7 \times \text{res}}$	-2.3248	0.3297	-2.9710	-1.6786
p : $\hat{\beta}_0$	0.3818	0.0489	0.2860	0.4776
p : $\hat{\beta}_{\text{cap}}$	0.4632	0.0651	0.3357	0.5907

model included an interaction between ENSO and region and, although it had relatively little support ($w_i = 0.12$), it suggests that ENSO's effect on survival may vary slightly by region. Therefore, further examinations of regional differences in the effects of ENSO on demographic rates are warranted in this and other species.

Annual survival and residency probability were notably low in region 1 (Fig. 5). These banding stations are located along relatively major coastal river systems in central California (Big Sur and Carmel) that are heavily used as stopover sites during migration, thus accounting for the low residency of Swainson's Thrushes captured there. The cause of the anomalously low adult survival probability from these two stations is not clear, but removing data from this outlying region did not alter the findings of our study. If nonresident migrating individuals are captured in multiple years or remain at these stopover sites for >6 days within a year and, thus, are classified as residents, survival estimates from transient models will be biased low. A few studies have found that migrants regularly return to stopover sites, but stopover fidelity varies widely among species and may not be the usual case for long-distance migrants (Cantos and Telleria 1994, Catry et al. 2004). On the other hand, Swainson's Thrush populations in the Sierra Nevada and southern California have declined dramatically in recent years (to the point where

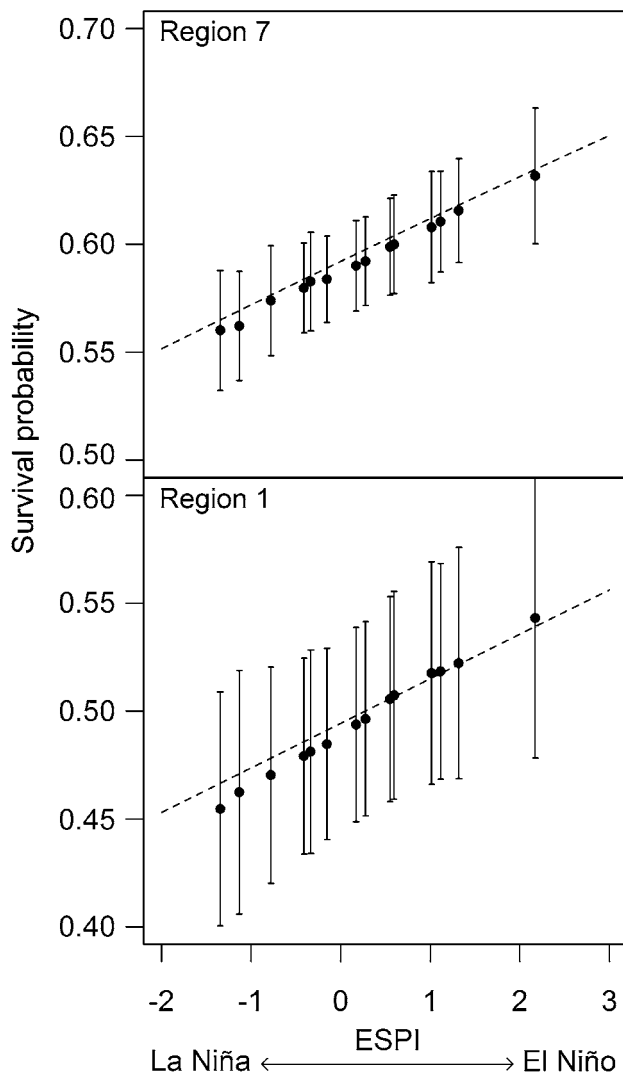


FIG. 4. Model-averaged annual apparent survival (\pm SE) of resident adult Swainson's Thrushes, from regions 1 and 7, in relation to the El Niño–Southern Oscillation Precipitation Index (ESPI), 1992–1993 to 2005–2006. Dashed lines indicate the estimated magnitude of the ESPI effect on survival from the top-ranked model; the slope of the relationship was the same for the other regions, but the intercept varied among regions.

they are rarely captured at MAPS stations in those areas), and it has been suggested that their declines resulted from low overwintering survival (Marshall 1988). Perhaps the low apparent survival of our region-1 birds is not an artifact associated with migration stop-over sites and is part of the same phenomenon that caused declines in southern California and Sierran populations. Clearly, detailed information on migratory connectivity is needed.

Like other climatological analyses of ENSO's effect on precipitation in North and Central America, we found that ENSO was negatively associated with July–April rainy-season precipitation anomalies in southern Mexico and Central America (Rauscher et al. 2008, Tourigny and Jones 2009) and positively associated with dry-season precipitation anomalies in southern California and western Mexico (Caso et al. 2007, Tourigny and Jones 2009; Fig. 2). Both of

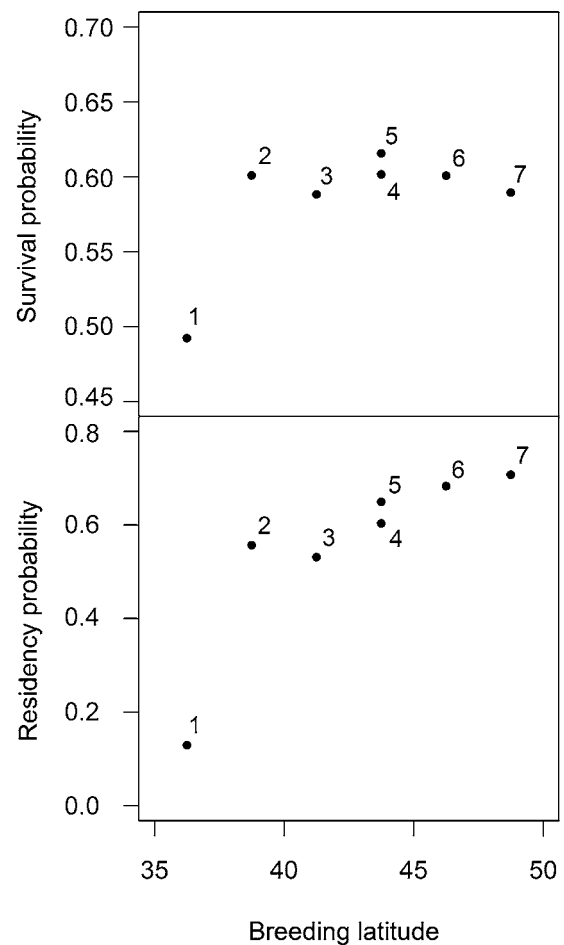


FIG. 5. Time-constant probability of annual apparent survival and residency for Swainson's Thrush in relation to breeding latitude (latitudinal midpoint of the region's latitudinal band) for the seven regions we considered. Regions are identified in Figure 1.

these anomalies may produce conditions that increase survival of Swainson's Thrushes. Most of the forests in southern Mexico and Central America are light-limited, and El Niño-related drying in the rainy season has been shown to enhance primary productivity, fruit production, and lepidopteran abundance in this region (Wright et al. 1999, Van Bael et al. 2004), likely increasing food availability for Swainson's Thrushes on their wintering grounds. In addition, El Niño-associated increases in winter and spring dry-season precipitation in the water-limited tropical deciduous forests of western Mexico likely lead to increased food availability for Swainson's Thrushes during their northern migration. Increased precipitation in western Mexico is associated with increased plant productivity, and with greater fruit and insect abundance up to 6 months later (Bullock and Solis-Magallanes 1990, Polis et al. 1997, Mandujano 2006). In addition, warm, southerly winds associated with incoming low-pressure systems, which are favorable to spring migration, have also been associated with El Niño events (Finley and Raphael 2007). Our *a posteriori* precipitation analysis clearly supported the effect of dry-season precipitation along the spring migration route on Swainson's Thrush survival and provided little support for a

TABLE 3. Top 8 models (of 51 candidate models from a *posteriori* precipitation analysis) of annual apparent survival (ϕ) and recapture probability (p) of adult Swainson's Thrushes captured at MAPS banding stations in the western United States, 1992–2006. Models are ranked according to difference in quasi-Akaike's information criterion (ΔQAIC_c) and reported with model weight (w_i) and the number of estimated parameters (k).

Model ^a	k	ΔQAIC_c	w_i
$\phi_{\text{SPRMIG} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	0.0000	0.7332
$\phi_{\text{SPRMIG} + \text{reg} + \text{res} + \text{SPRMIG} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	23	2.8023	0.1806
$\phi_{\text{WETWIN} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	5.1780	0.0551
$\phi_{\text{reg} \times \text{res}' P_{\text{cap}}$	16	8.0111	0.0134
$\phi_{\text{LATEWIN} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	9.1031	0.0077
$\phi_{\text{NAMMIG} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	17	9.9869	0.0050
$\phi_{\text{LATEWIN} + \text{reg} + \text{res} + \text{LATEWIN} \times \text{reg} + \text{reg} \times \text{res}' P_{\text{cap}}$	23	11.3817	0.0025
$\phi_{\text{t} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}}$	29	12.1383	0.0017

^aDescription of covariates: SPRMIG = dry-season spring-migration precipitation index (November–May), WETWIN = rainy-season winter-range precipitation index (May–November), LATEWIN = late-winter precipitation index (i.e., prior to spring migration departure) on the winter range (December–April), NAMMIG = North American Monsoon precipitation index on the migration route (June–October), reg = regions (defined by latitude and altitude; $n = 7$), lat = latitude of station, res = residency status, t = time (year), and cap = banding-station-specific mean captures per adult per year.

winter-range precipitation effect. Because these analyses were not part of our *a priori* model set, the conclusion that winter–spring precipitation along the spring migration route is the major driver of the effect of ENSO on survival of Swainson's Thrushes should be treated as a hypothesis in need of further confirmation. Studies of the relationship between ENSO cycles and resource availability at stopover sites in western Mexico and wintering sites in Central America could provide insights into the mechanisms that drive the survival pattern we observed.

Identifying associations between regional climate patterns and demographic parameters is crucial to understanding the effects of climate change on Neotropical migrants. Recent climate-change models predict that ENSO extremes will become more intense with greater annual variation (Paeth et al. 2008), possibly causing greater fluctuations in Swainson's Thrush populations. In addition, increased stochasticity in productivity and survival can have negative effects on populations beyond those predicted by deterministic population models (Boyce et al. 2006). Our approach provides a method to test hypotheses about the location and timing of mechanisms that influence annual survival, and we encourage their implementation in studies of other migratory species. Directly associating climate with key demographic parameters provides a powerful approach to predicting a species' response to climate change. Furthermore, the implication of our results that population dynamics of western migratory bird species may oscillate synchronously and depend on ENSO-driven precipitation anomalies during spring migration is a novel hypothesis that deserves further investigation.

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TABLE 4. Parameter estimates (on logit-link scale), standard errors (SE), and lower and upper 95% confidence interval (CI) limits from the top-ranked model, $\phi_{\text{SPRMIG} + \text{reg} + \text{res} + \text{reg} \times \text{res}' P_{\text{cap}'}$ estimating annual apparent survival (ϕ) and recapture probability (p) of adult Swainson's Thrushes captured at MAPS banding stations in the western United States, 1992–2006. Estimates for continuous covariates (ϕ : $\hat{\beta}_{\text{SPRMIG}}$ and p : $\hat{\beta}_{\text{cap}'}$) represent standardized coefficients. See Figure 1 for regional distinctions and Table 3 for descriptions of model covariates. The estimate for the effect of dry-season spring-migration precipitation on survival is in bold.

Parameter	Estimate	SE	Lower CI	Upper CI
ϕ : $\hat{\beta}_0$	-3.3888	0.2207	-3.8213	-2.9562
ϕ : $\hat{\beta}_{\text{SPRMIG}}$	0.0959	0.0305	0.0361	0.1557
ϕ : $\hat{\beta}_{\text{reg}2}$	2.3201	0.2434	1.8430	2.7972
ϕ : $\hat{\beta}_{\text{reg}3}$	2.1683	0.2362	1.7054	2.6312
ϕ : $\hat{\beta}_{\text{reg}4}$	2.4176	0.2518	1.9240	2.9112
ϕ : $\hat{\beta}_{\text{reg}5}$	2.5965	0.2327	2.1403	3.0526
ϕ : $\hat{\beta}_{\text{reg}6}$	2.6169	0.2568	2.1135	3.1203
ϕ : $\hat{\beta}_{\text{reg}7}$	2.7290	0.2478	2.2432	3.2148
ϕ : $\hat{\beta}_{\text{res}}$	3.3724	0.2953	2.7936	3.9512
ϕ : $\hat{\beta}_{\text{reg}2 \times \text{res}}$	-1.8824	0.3272	-2.5238	-1.2410
ϕ : $\hat{\beta}_{\text{reg}3 \times \text{res}}$	-1.7835	0.3166	-2.4040	-1.1629
ϕ : $\hat{\beta}_{\text{reg}4 \times \text{res}}$	-1.9782	0.3355	-2.6357	-1.3207
ϕ : $\hat{\beta}_{\text{reg}5 \times \text{res}}$	-2.0985	0.3112	-2.7084	-1.4886
ϕ : $\hat{\beta}_{\text{reg}6 \times \text{res}}$	-2.1672	0.3400	-2.8337	-1.5008
ϕ : $\hat{\beta}_{\text{reg}7 \times \text{res}}$	-2.3330	0.3298	-2.9794	-1.6865
p : $\hat{\beta}_0$	0.3808	0.0489	0.2850	0.4766
p : $\hat{\beta}_{\text{cap}'}$	0.4643	0.0651	0.3368	0.5919

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