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CORRELATIONS BETWEEN EL NIÑO–SOUTHERN OSCILLATION AND CHANGES IN NEARCTIC–NEOTROPIC MIGRANT CONDITION IN CENTRAL AMERICA

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ABSTRACT.—Climatic changes induced by the El Niño–Southern Oscillation (ENSO) commonly influence biological systems; however, climatic variability and multitrophic interactions within tropical latitudes remain poorly understood. We examined relationships between migrant condition and ENSO during spring migration in Costa Rica. Our study is based on correlating an ENSO index with body-condition metrics of six Nearctic–Neotropic migrant bird species during stopover in Costa Rica over a 10-year period. This study is the first to report correlations between El Niño and changes in condition of multiple migrant species. The condition of one insectivore improved, whereas two frugivores experienced reduced condition during El Niño. Our detected correlations suggest that the ENSO cycle may influence changes in migrant mass; such interactions may ultimately affect demographics of certain frugivorous and insectivorous migrant species. Potential future management considerations are discussed in light of global climate change and our findings. *Received 27 January 2008, accepted 28 April 2009.*

Key words: condition index, Costa Rica, El Niño–Southern Oscillation, ENSO, spring migration.

Correlaciones entre la Oscilación del Sur El Niño y Cambios en la Condición de Aves Migratorias Neártico-Neotropicales en América Central

RESUMEN.—Los sistemas biológicos son comúnmente influenciados por los cambios climáticos inducidos por la Oscilación del Sur El Niño. Sin embargo, aún se sabe poco sobre las variaciones climáticas y las interacciones multitróficas en latitudes tropicales. Examinamos las relaciones entre la condición migratoria y El Niño durante la migración de primavera en Costa Rica. Nuestro estudio se basa en la correlación de un índice de El Niño con medidas de la condición corporal de seis especies de aves migratorias neártico-neotropicales durante las paradas en Costa Rica durante un periodo de 10 años. Este estudio es el primero en reportar una correlación entre El Niño y cambios en la condición corporal de múltiples especies migratorias. La condición de una especie insectívora mejoró, mientras que la de dos especies frugívoras presentó una reducción durante El Niño. La correlación detectada sugiere que el ciclo de El Niño puede influenciar la masa corporal de las aves migratorias, y que estas interacciones pueden afectar en última instancia la demografía de ciertas especies migratorias frugívoras e insectívoras. Se discuten consideraciones futuras para el manejo en el contexto de cambio climático global y de nuestros hallazgos.

LITTLE IS KNOWN about relationships between El Niño and biological systems in the Neotropics, in part because of the difficulties inherent in assessing the influence of climatic variation on food webs and their component trophic cascades. Several studies have shown that the combination of La Niña and El Niño, collectively referred to as the "El Niño–Southern Oscillation" (ENSO) cycle, may influence survivorship of tropical vertebrate species. Wright et al. (1999) showed that ENSO-induced fruit shortages may influence frugivorous mammal populations in Panama. Work in the Caribbean indicated that El Niño-induced dry seasons may have negatively affected overwintering survivorship of Black-throated Blue Warblers (*Dendroica caerulescens*), perhaps as a result of reduced food availability (Sillet et al. 2000). The potential influence of ENSO on condition of migrating landbirds in Central America has not been studied.

While in Central America, Nearctic–Neotropic migrants (hereafter "migrants") rely on stopover sites that are rich in resources conducive to fat acquisition or refueling in order to successfully complete their semiannual migrations (Leu and Thompson 2002). Stopover duration has been linked to both the migrant's energetic condition upon arrival at a site (Bairlein 1985,

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Biebach et al. 1986, Moore and Kerlinger 1987, Schaub and Jenni 2001, Bayly 2006) and availability of resources at that site (Russell et al. 1994, Schaub and Jenni 2001). Climatic variability and ENSO may strongly influence availability of resources necessary for successful completion of migration.

Migrants that rely heavily on insects for refueling during stopover may not be strongly affected by ENSO. Typically, insects are a less stochastic resource than fruit throughout climatic cycles, in that arthropods are one trophic level removed from fruiting plants and are thus buffered from climatic fluctuations (Terborgh and Faaborg 1980, Terborgh and Winter 1983, Levey and Stiles 1992). Also, in the tropics, insects are less seasonal than fruit because many insects rely on foliage, which is abundant year-round in lowland tropical rainforests. By contrast, migrants that are largely reliant on fruit for refueling may be affected by ENSO-induced fruit depressions.

For example, in parts of Central America, certain ENSO phases are thought to be responsible for wet seasons that can synchronize fruit masting events. Alternatively, dry seasons associated with other phases of ENSO can result in fruit shortages (Wright et al. 1999, Williamson and Ickes 2002). Because of the proximity of the Caribbean and the pronounced El Niño-induced "dry zone" in the Gulf of Mexico, Ropelewski and Halpert (1987) suggested that a dry period is associated with an El Niño event in northeastern Costa Rica, our study region. We used an ENSO metric in association with bird capture data to formulate the central question of the present study: Does migrant condition change in response to ENSO?

Methods

Monitoring stations were located near the village of Tortuguero on the northeast coast of Costa Rica in Limon Province (83°31′7″W, 10°33′51″N). Tortuguero is dominated by lowland, wet, broadleaf tropical forest (Holdridge 1987) that is broken by canals and rivers that flow east into the Caribbean Sea. The area receives an average rainfall of >5,000 mm per year, which makes it one of the wettest regions in the country. Most of the forest lands surrounding the village are protected by the 19,211-ha Tortuguero National Park and Barra del Colorado National Wildlife Refuge. Our monitoring stations were located in second-growth tropical forest and coastal scrub that occurs between forest and coast; some stations were located in a narrow scrub zone between forest and sand beach, whereas others were bordered by either river or canal (Ralph et al. 2005).

Tortuguero's wet season begins from mid- to late April and continues through January. The wet season is interrupted by a short dry season, usually in September. The long dry season tends to occur from February to March, but even during this period precipitation is common (Janzen 1983).

Since 1995, five to nine banding stations located near the village of Tortuguero have been operating 10–15 mist nets annually from mid-January to November. One "central" station was run at least five times every 10 days, and the other "satellite" stations were run at least once every 10 days (March–May). Protocols for capturing and processing birds were described in Ralph et al. (1993).

Detecting potential relationships between changes in migrant condition and ENSO depends on the ability to detect changes in migrant fat and muscle mass. Layers of fat deposition, visible on captured birds, have been used to quantify the quality of stopover sites (Moore and Kerlinger 1987; Dunn 2000, 2002). The amount of fat carried by individual passerine migrants accounts for most variation in body mass; when standardized for body size, mass is a crude predictor of an individual's fat and muscle content (Connell et al. 1960; Odum 1960; Rogers and Odum 1964, 1966; Winker 1995; Morris and Glasgow 2001). Winker (1995) used this relationship to calculate a "condition index" that we employed here. Condition indices were created for each species during spring migration using the following formula: condition index = mass*100/wing chord. Recent studies have generated condition indices based on residuals from an ordinary least-squares (OLS) linear regression of body mass against a linear measure of size (i.e., wing chord; Green 2001). Use of residuals for analysis was considered unsatisfactory for the present study because of frequently unsatisfied assumptions associated with OLS residual analyses as they pertain to condition indices (see Green 2001).

Study species were chosen on the basis of historically high capture rates and the diversity of dietary guilds they represent. Diets of predominantly insectivorous birds (Eastern Wood-Pewee [*Contopus virens*], Canada Warbler [*Wilsonia canadensis*], Prothonotary Warbler [*Protonotaria citrea*], and Northern Waterthrush [*Seiurus noveboracensis*]) and predominantly frugivorous birds ("Traill's" Flycatcher [*Empidonax alnorum/traillii*] and Swainson's Thrush [*Catharus ustulatus*]) during spring migration were based on published accounts (Barlow 1980, Morton 1980, Willis 1980, Blake and Loiselle 1992, Lefebvre et al. 1992, Levey and Stiles 1992, Rappole et al. 1993, Poulin and Lefebvre 1996, Parrish 1997, J. D. Wolfe pers. obs.). Two major problems were encountered during this review: (1) much of the available literature concerning resources used during spring migration was incomplete, contradictory, or both (see Levey and Stiles 1992, Poulin and Lefebvre 1996, Parrish 2000); and (2) all the migrant species we analyzed show some form of dietary plasticity (Morton 1980, Blake and Loiselle 1992, Lefebvre et al. 1992, Levey and Stiles 1992). As a consequence, our dietary categorizations are based on resources documented to be the most commonly used during spring migration and overwintering periods in tropical latitudes.

We calculated an average condition index for each of the target species if five or more individuals were captured during each spring migration (April–May) in the years 1996–2005 (Table 1). A single cross-validation goodness-of-fit test was conducted for each species during the year of highest capture (e.g., Swainson's Thrush in 2003, Traill's Flycatcher in 2001, etc.; see Table 1). This cross-validation goodness-of-fit test was performed by omitting five randomly selected individuals from the developmental data set and then using the remainder to generate 95% confidence intervals (CIs). Goodness-of-fit was determined by calculating the percentage of omitted individuals that fell within the 95% CIs (Stauffer 2007). Fully 87% (26 of 30) of the randomly selected omitted samples fell within the 95% CIs derived from the subsample data set, validating reasonably good fit for smaller sample sizes.

For the years 1996–2005, average Southern Oscillation index (SOI) values were derived from monthly index data available through the National Oceanic and Atmospheric Administration's Climate Prediction Center. The SOI was used to measure the strength of ENSO in Central America, as has been done in previous climate studies (Ropelewski and Halpert 1996, Sillet et al. 2000). A strong positive value indicates La Niña conditions, and a strong negative value indicates El Niño conditions (or dry-season

Table 1. Total number of individuals captured for each species during the spring migrations of 1996–2005 in Tortuguero, Costa Rica.

Year	Swainson's Thrush	Traill's Flycatcher	Eastern Wood-Pewee	Canada Warbler	Prothonotary Warbler	Northern Waterthrush
1996	28	9	2	7	12	43
1997	40	7	17	23	5	38
1998	38	12	19	15	5	43
1999	17	5	1	12	21	46
2000	30	9	12	6	3	57
2001	22	32	9	3	17	50
2002	34	25	34	3	13	85
2003	45	7	24	9	3	41
2004	30	5	13	7	39	21
2005	25	16	24	4	8	43

conditions; Ropelewski and Halpert 1987). Average condition index values were evaluated in relation to the annual mean SOI using linear regressions in the program MINITAB; because of the exploratory nature of the study, significance is defined as $P < 0.1$.

Results

Our analysis of 1,273 total migrant captures over 10 spring migratory events (1996–2005) indicated differential correlations between migrant dietary guilds and ENSO. Traill's Flycatchers had lower condition indices during El Niño years and higher ones during La Niña years (Fig. 1); this pattern was reflected in a positive correlation between SOI and condition index (adj. $r^2 = 0.88$, df = 6, $P = 0.001$). Swainson's Thrushes had lower condition indices during El Niño and higher ones during La Niña years (Fig. 2), as reflected by a positive correlation between condition index and SOI (adj. $r^2 = 0.26$, df = 9, $P = 0.074$). Mass changes of the Eastern Wood-Pewee, an insectivore, during El Niño were opposite to that of the frugivorous Swainson's Thrush and Traill's Flycatcher. Eastern Wood-Pewee had high condition indices during El Niño and low indices during La Niña years (Fig. 3); there was a negative correlation between condition index and SOI (adj. $r^2 = 0.39$, df = 7, $P = 0.06$). Lastly, there was no detectable correlation between El Niño and condition index in Canada Warblers (adj. $r^2 = 0.14$, df = 6, $P = 0.22$), Prothonotary Warblers (adj. $r^2 = 0.0$, df = 8, $P = 0.611$), or Northern Waterthrushes (adj. $r^2 = 0.0$, df = 9, $P = 0.388$).

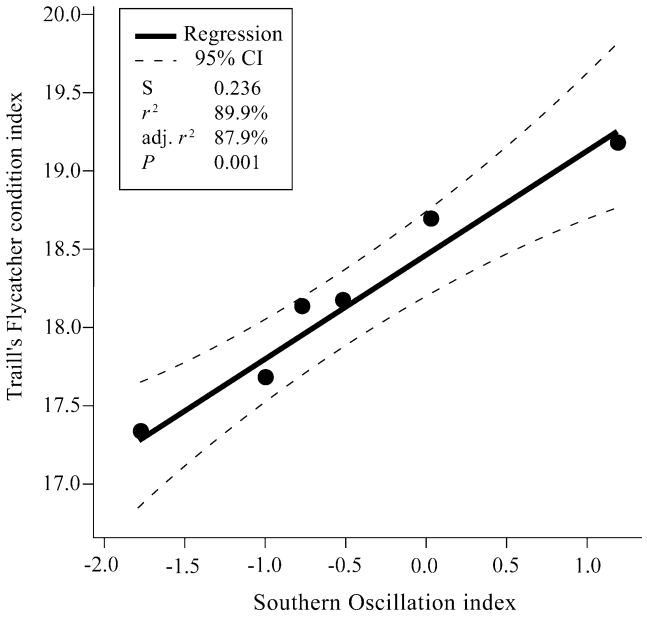

Fig. 1. Linear regression between the condition index of Traill's Flycatcher, a predominantly frugivorous migrant, and the Southern Oscillation index (SOI) (regression equation: condition index = 18.49 + 0.6914 SOI).

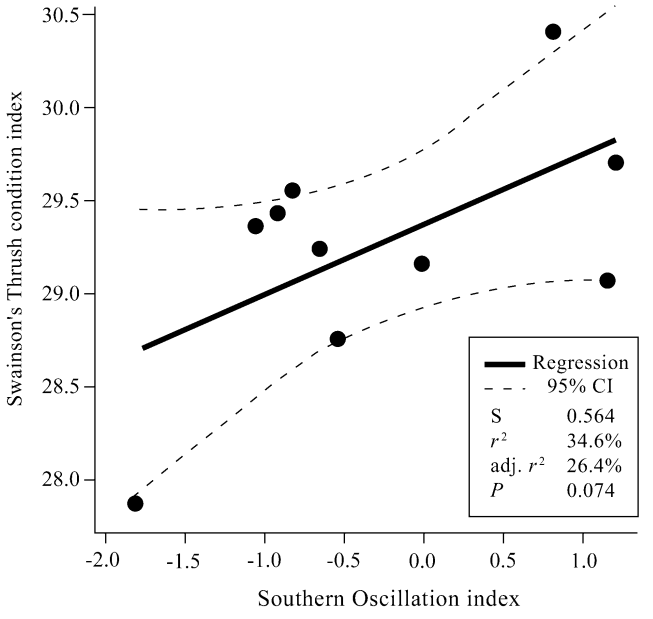

Fig. 2. Linear regression between the condition index of Swainson's Thrush, a predominantly frugivorous migrant, and the Southern Oscillation index (SOI) (regression equation: condition index = 29.36 + 0.3815 SOI).

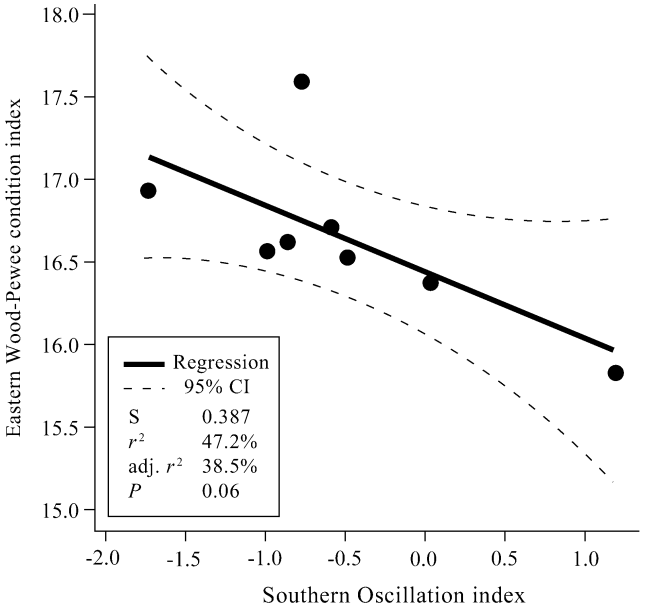

Fig. 3. Linear regression between the condition index of Eastern Wood-Pewee, a predominantly insectivorous migrant that commonly captures aerial insects, and the Southern Oscillation index (SOI) (regression equation: condition index = 16.43 − 0.3942 SOI).

Discussion

Our findings indicate that spring migrant condition was often correlated with ENSO and may have varied by foraging guild. Despite the breadth of our data set and the unique nature of our results, there are potential problems with the metrics we used.

Condition indices remain a popular, yet crude, measure of migrant mass corrected for body size. Several potential biological occurrences may have influenced our results: degree of migrant water retention, changes in migrant gut mass and content, population or sex differences in wing chord, and population or sex differences in the timing of migratory passage can all potentially alter condition indices. However, our results coupled with the robust nature of our data set (1996–2005) lend credence to the validity of the detected trends.

Swainson's Thrushes and Traill's Flycatchers, both frugivorous in spring migration (Levey and Stiles 1992, J. D. Wolfe pers. obs.), exhibited lower condition indices during El Niño events. Given synchronous responses of fruiting plants to heavy precipitation (Wright et al. 1999, Williamson and Ickes 2002), during El Niño-induced dry periods, fruit abundance may be insufficient to facilitate refueling in migrant frugivores.

Eastern Wood-Pewees, in contrast to frugivores and other insectivores, exhibited a positive correlation between condition index and El Niño. This result was unexpected, given that insectivores are thought to rely on resources that are, in contrast to fruit, buffered from climatic fluctuations and, thus, less variable (Terborgh and Faaborg 1980, Terborgh and Winter 1983, Levey and Stiles 1992). We believe that the positive correlation in condition index of Eastern Wood-Pewees can be attributed to an increase in spatial concentration and abundance of aerial insects around moisture refugia during El Niño (Janzen 1973).

In contrast to Eastern Wood-Pewee, Northern Waterthrush and Prothonotary Warbler (skulking insectivores) and Canada Warbler (a skulking–sallying insectivore) had no detectable correlation between condition and El Niño. The lack of correlation may be explained by their foraging behavior and dietary plasticity. Prothonotary Warblers, Canada Warblers, and, to a lesser extent, Northern Waterthrushes all feed primarily on predominantly sessile, plant-associated insects (Lack and Lack 1972, Post 1978, Morton 1980, Lefebvre et al. 1992, Parrish 1997). The dietary plasticity of these three species, which rarely augment their diets with fruit while in Central America, along with the plant-associated insect communities included in their diets, may buffer them from climatic variability and subsequent trophic cascades (Levey and Stiles 1992).

In summary, two predominantly frugivorous migrants responded negatively to El Niño, an insectivore that relies on aerial insects responded positively to El Niño, and three insectivores that feed on foliage-dependent insect communities showed no correlation with El Niño. However, the preliminary and exploratory nature of our study necessitates future research pertaining to climatically induced trophic cascades during migration in tropical latitudes.

Three facets of the natural history of migrant passerines must be taken into account when judging the importance of our findings: (1) many migrants include fruit in their diet while in tropical latitudes (Levey and Stiles 1992); (2) populations of some migratory species are declining (Robbins et al. 1989, Askins et al. 1990, Ballard et al. 2003, Rich et al. 2004); and (3) survivorship during migration may be the limiting demographic factor for some species (Moore et al. 1993, Butler 2000, Moore and Aborn 2000, Sillet and Holmes 2002, Newton 2006). These findings and our results, coupled with recent climate models that predict exacerbated ENSO cycles in response to climate change (Timmermann et al. 1999), suggest that declining populations of migratory birds may face greater variability in stopover resources in the near future. Subjection to warming trends and subsequent fruit shortages may further limit the potential recovery of some migratory species.

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