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Abstract

Annual survivorship in migratory birds is a product of survival across the different periods of the annual cycle (i.e., breeding, wintering, and migration), and may vary substantially among these periods. Determining which periods have the highest mortality, and thus are potentially limiting a population, is important especially for species of conservation concern. To estimate survival probabilities of the willow flycatcher (*Empidonax traillii*) in each of the different periods, we combined demographic data from a 10-year breeding season study with that from a 5-year wintering grounds study. Estimates of annual apparent survival for breeding and wintering periods were nearly identical (65-66%), as were estimates of monthly apparent survival for both breeding and wintering stationary periods (98-99%). Because flycatchers spend at least half the year on the wintering grounds, overall apparent survivorship was lower (88%) on the wintering grounds than on the breeding grounds (97%). The migratory period had the highest mortality rate, accounting for 62% of the estimated annual mortality even though it comprises only one quarter or less of the annual cycle. The migratory period in the willow flycatcher and many other neotropical migrants is poorly understood, and further research is needed to identify sources of mortality during this crucial period.

The phases of the annual cycle (e.g., breeding, wintering, and migration) for a migratory species are commonly treated as distinct periods. Yet, population dynamics in migratory birds are determined by the totality of factors experienced during all phases of the annual cycle across the entire geographic area occupied during migration and stationary periods (Runge and Marra 2005, Norris and Taylor 2006). Moreover, there is a growing recognition of the interconnectedness of the different phases, via carry-over effects, where the circumstances an individual experience in one period can have consequences in subsequent periods (Webster et al. 2002, Harrison et al. 2011, Marra et al. 2015a). For example, population declines in red knot (*Calidris canutus rufa*) on the breeding grounds in eastern North America have been quantitatively linked to reduction in prey at an important stopover site (Baker et al. 2004, McGowan et al. 2011), highlighting the importance of understanding population dynamics for migratory species across all phases of the annual cycle.

Annual survivorship, a key component of population demographics, is the product of survival in each phase of the annual cycle. Survival rates can vary among the periods of the annual cycle, and only by understanding survivorship throughout the annual cycle can we begin to assess where population limitation is occurring (Newton 2004). Yet, most estimates of survivorship in migratory passerines are for 12-month annual periods, which average survival probabilities across different periods of the year. Moreover, the majority of annual survivorship estimates are based on breeding ground studies (Marra et al. 2015a), while the estimates of winter survival are few (but see Conway et al. 1995, Sillett and Holmes 2002, Dugger et al. 2004, Blackburn and Cresswell 2016, Marra et al. 2015b), despite the fact that migrants spend the majority of their annual cycle on their wintering grounds. Only one published study to date has estimated survival during the migratory period for a small passerine (Sillett and Holmes 2002), even though the migratory period is considered a time of high mortality (Newton 2006).

In this study, we partitioned survivorship across the annual cycle of the willow flycatcher (*Empidonax traillii*), a long-distance Neotropical migrant breeding across much of the contiguous U.S. and southern Canada, and wintering from central Mexico to northern South America (Sedgwick 2000). We accomplished this by combining data from a 10-year demographic study on breeding southwestern willow flycatchers (*E. t. extimus*)(Paxton et al. 2007) with a 5-year wintering demography study of willow flycatchers in Costa Rica (Koronkiewicz et al. 2006). By linking survival rates estimated from breeding and wintering populations with strong migratory connectivity (Webster et al. 2002), we can estimate survival for each period in the annual cycle (Sillett and Holmes 2002). Although the individuals tracked from our two studies were different, we have evidence for strong connectivity between the southwestern subspecies and Costa Rica's northern Pacific lowlands where our wintering study was conducted based on molecular genetics, morphological characteristics, and direct linkages between study areas (Paxton et al. 2007, Koronkiewicz et al. 2006). Our objectives were to: (1) estimate annual survival based on return-rates of banded birds on the breeding grounds and compare these to published estimates of annual survival based on return-rates of banded birds on the wintering grounds; (2) estimate within-season survival for both breeding and wintering birds; and (3) combine survival estimates from the breeding and wintering seasons to estimate survival during the migratory period.

Methods

Study sites

We derived estimates of apparent survival from the breeding grounds based on a long-term (1996-2005) demographic study at two sites in central Arizona, USA (Paxton et al. 2007): Roosevelt Lake (33º39'N, 110º58'W) and San Pedro/Gila River confluence (32º59'N, 110º46'W). Both sites are located within the core breeding range of the southwestern willow flycatcher (Unitt 1987), and hosted some of the largest known breeding populations during that time period. Each site was composed of multiple riparian woodland patches of Sonoran Desert riparian forest (Brown 1980), surrounded by arid, non-breeding habitat, and fairly isolated from other known breeding locations. Willow flycatchers are highly territorial and vocal, have high site fidelity (Sedgwick 2004), and extensive surveys allowed us to detect breeding flycatchers with high certainty across each site. The breeding ground study began each year in late April, and extended to early August, which matches the arrival and departure dates of breeding flycatchers.

The wintering ground study was conducted from 1998-2003 at two sites in northwest Costa Rica (Koronkiewicz et al. 2006): Chomes (10º05'N, 85º05'W) and Bolson (10º20'N, 85º25'W). Both study sites were freshwater seasonal wetlands within tropical dry forest (Holdridge 1967), and supported two of the largest wintering populations detected in Costa Rica (Lynn et al. 2003). This region of Costa Rica is heavily deforested, with most land converted to agriculture use (sugarcane fields and livestock grazing), and thus these seasonal wetlands are fairly isolated within the greater landscape. Wintering willow flycatchers are vocal and territorial (Sogge et al. 2007), have between-year return rates higher than observed on the breeding grounds (68% and 55% in winter and breeding, respectively), and most returning birds occupied the same approximate territory location from year to year (Koronkiewicz et al. 2006). On the wintering grounds, flycatchers begin arriving as early as mid-September and begin departing by April, while our research was consistently conducted in mid-winter (December/January) and late-winter (March/April), with occasional early-winter visits.

Banding and monitoring.

Flycatchers were captured using mist nets both passively and via target-netting techniques (Sogge et al. 2001), and each individual received a unique color combination from an anodized aluminum numerical bird band and another color band (Koronkiewicz et al. 2005). All individuals on the breeding ground were aged based on plumage (i.e., hatch-year, second-year, after-hatch year), while on the wintering grounds hatch-year and after-hatch year birds could not be distinguished because juvenile plumage was molted prior to or upon arrival to the wintering grounds. However, over 70% of the birds on the wintering grounds in a given year were returning adults (Koronkiewicz et al. 2006). Overall, we captured and banded 74% (range: 68-88%) and 78% (range: 47-100%) of detected flycatchers in a given year at the breeding and wintering sites, respectively. Banded flycatchers were detected via color-band resighting and occasional recaptures, with locations recorded via GPS or onto high-resolution aerial photographs. Banding and resighting efforts were constant across years on both the breeding and wintering grounds during their respective study periods.

Survivorship analysis

For both the breeding and wintering populations, we used Program MARK (White and Burnham 1999) to estimate apparent annual and within-season survival rates (Φ) and detection probabilities (*p*) of adults. AICc model selection (Burnham and Anderson 2002) suggested that of multiple factors evaluated influencing Φ and *p* (e.g., year, sex, site), annual variation was the most parsimonious source of variation in apparent survival for the breeding population (AICc Wi = 1.0)(Paxton et al. 2007), while average apparent survival followed by yearly variation were the strongest models for the wintering population (AICc Wi = 0.60)(Koronkiewicz et al. 2006).

We estimated annual apparent survival probabilities (i.e., survivorship across a 12-month period) from 1999-2003 separately for the breeding and wintering populations. Encounter histories from before and after this time period were included in the breeding season analysis to allow for accurate estimates of both Φ and p for the first and last years of this period. Estimates of wintering annual survival were obtained from Koronkiewicz et al. (2006).

Next, we calculated within-season survival rates, i.e., estimates of survival during the breeding and wintering stationary periods, separately for the two studies. We estimated within-season survival on the breeding grounds by grouping all resighting and recapture encounters of banded flycatchers throughout the breeding season into two equal periods: May 1 to June 15th and June 16th to early-August. The average interval between these periods, 1-month, was used to estimate the average survival rate in a 1-month period. We estimated monthly winter survival from the 3-month interval between the mid-winter (December/January) and late-winter (March/April) research periods. Seasonal estimates of apparent survival for the 3-month average breeding period and the 6-month average wintering period were obtained by raising their within-season monthly estimates to the third and sixth power, respectively.

Between-season survival estimates, which are calculated separately for the breeding and wintering data, are needed to estimate survivorship during the migratory period. Between-season survival is calculated as the product of survival from all other periods; for example, between-season survival for the breeding population is the product of survival rates during the migration and wintering periods. Average between-season survival estimates for each period were derived by dividing their average annual survival rates by their respective average within-season survival rates; e.g., for breeding grounds:

$$\Phi_{\text{between-season (non-breeding)}} = \Phi_{\text{annual (breeding)}} / \Phi_{\text{within-season (breeding)}}$$

To estimate survival rates during the migratory periods, we combined the mean survival probability from both the breeding and wintering studies (Sillett and Holmes 2002). Separately, between-season survivorship from both stationary periods were divided by the within-season survival rates of the opposite stationary period to estimate survivorship during the migratory period; e.g., for breeding grounds:

$$\Phi_{\text{spring and fall migration survivorship}} = \Phi_{\text{between-season (non-breeding)}} / \Phi_{\text{within-season (wintering)}}$$

The estimates for survivorship during migration are for both spring and fall migration combined, which are each estimated to be 3-months long on average. To estimate survival probabilities separately for the spring and fall migratory periods we assumed equal survival rates and took the square-root of the migratory period estimate, and the cubed-root of the migratory period survival estimate to obtain monthly migration survival rates.

Estimates of variance (SE) and 95% confidence intervals for annual and within-season survival estimates were calculated by Program MARK. Estimates of variance in survival for the between-season and migratory period were calculated using the delta method (Sillett and Holmes 2002), with a 95% confidence interval approximated by $\Phi \pm 1.96*SE$. All parameter estimates are presented as percentages with 95% confidence intervals in parentheses.

Results

Breeding season survivorship

Annual apparent survival probabilities on the breeding grounds averaged 66% (64-68%) with all years combined, and ranged from 56-73% among years (Table S1). Within-season estimates of monthly survival during this period were high, averaging 99% (96-100%; Table S2). Survival across the entire breeding season, assuming a 3-month average time period, was 97% (88-99%; Table S2). Using the average annual and within-season estimates, average between-season survival (i.e., survival across fall migration, winter, and spring migration) was 68% (64-73%; Table 1).

Winter season survivorship

Annual apparent survivorship estimates on the wintering grounds averaged 65% (59-70%)(Koronkiewicz et al. 2006), almost identical to that on the breeding ground during the same time period (1999 to 2003; Table S1). Yearly variation in annual estimates (54-72%) was also similar to yearly variation in breeding ground estimates. Within-season monthly survival rates averaged 98% (95-99%), with a mean seasonal estimate of 88% (77-94%), assuming a 6-month average wintering period (Table S2). Between-season survival rates for the wintering grounds was 74% (69-79%; Table 1).

Migratory season survivorship

Using the between-season survivorship estimates from the breeding and wintering grounds, and their opposite stationary period's within-season survival rates, our estimate of apparent survival for the entire migratory period was 77-78% (Table 1). Assuming equal mortality between the fall and spring migrations, we estimated 88% survival each for the spring and fall migration, and a monthly survival rate of 92% (Table 1).

Discussion

Our results indicate that willow flycatcher survival is highest during the breeding period, followed by winter, and lowest during the migratory periods. Spring and fall migration, making up only one quarter of the flycatchers' annual cycle, accounted for 62% of flycatchers' annual mortality (Figure 1). In contrast, the stationary periods (i.e., breeding and wintering), totaling 9 months of the annual cycle, accounted for only 9% and 29% of the flycatchers' estimated annual mortality, respectively. While the estimates of survival across the annual cycle were derived from studies of two different populations, the linkage between the two populations is strong, providing confidence in survival estimates throughout the annual cycle. Our breeding ground study was within the core range of the southwestern subspecies, at two of the largest known breeding sites, and analysis of molecular genetics and morphology both indicate strong connectivity between the southwestern subspecies and the Pacific lowlands of Costa Rica where our wintering study was conducted (Paxton et al. 2011). Despite the fact that the southwestern subspecies only constitutes approximately 0.2% of the estimated 3.2 million willow flycatchers (Rich et al. 2004), and the species winters over a large area from central Mexico to South America, we documented direct linkage between our breeding and wintering study sites via 2 individuals banded in the southwestern subspecies' range that were recaptured in Costa Rica (Koronkiewicz and Sogge 2001). One of these individuals was detected for multiple consecutive seasons at both the wintering site (Koronkiewicz et al. 2006) and breeding site (Paxton et al. 2007) examined in this study. Finally, strong site fidelity, high quality habitat, and similar annual estimates of survival on both the breeding and wintering sites lends support that the populations are facing similar mortality pressures.

This study is only the second effort to partition mortality throughout the annual cycle of a long-distance migratory passerine. Our results are consistent with Sillett and Holmes (2002) study of black-throated blue warblers (*Dendroica caerulescens*) which also found that the greatest amount of mortality occurred during the migratory time period (87-89% total annual mortality), although their estimate was higher than our estimate of 62% total annual mortality in flycatchers. Overall, we estimated lower survivorship in the stationary periods and higher survivorship in the migration period than black-throated blue warblers, but our 95% confidence intervals encompassed the average survival estimates for the warbler (this study: Table 1, Sillett and Holmes 2002: Figure 1), suggesting that mean seasonal estimates of survivorship are not statistically different between the species. Mortality during migration may be directly related to events encountered during migration (e.g., degradation or loss of suitable habitat, unpredictable weather, navigation errors)(Moore et al. 1995, Newton 2010, Diehl et al. 2014), or indirectly associated with conditions experienced during the stationary periods via carry-over effects that increase the likelihood of mortality during migration (Paxton et al. 2014, Marra and Holmes 2001), or most likely a combination of both factors. However, understanding the patterns that shape mortality throughout the annual cycle for small passerines is limited by challenges in following individuals throughout their annual cycle, as evidenced by the paucity of research on survival probabilities across the annual cycle of passerines (Newton 2006). While recent developments in tracking small birds (e.g., geolocators) can help identify migratory pathways (Stutchbury et al. 2009, Delmore et al. 2012, Bairlein et al. 2012) they cannot illuminate where mortality occurs because of the need to re-capture individuals to retrieve stored data. Until methods are developed to follow individuals throughout their annual cycle, innovative methods such as employed in this paper are needed to estimate mortality rates in migrants, especially during the migratory period.

The agreement between our study and Sillett and Holmes (2002) that migration is a period of high mortality is consistent with the general consensus that migrants face considerable challenges during migration (Moore et al. 1995, Newton 2006). If pressures increase in any one phase of the annual cycle, for example from continuing habitat loss, rising predation levels, or disruptive changes in climate, the high cost of migration may no longer be counterbalanced by productivity and survivorship during the stationary periods (but see Rakhimberdiev et al. 2015). In fact, a number of migratory species are experiencing higher population declines than resident birds (Sauer and Link 2011, Sanderson et al. 2006), suggesting for some species that the cost of migration is potentially overwhelming potential benefits. However, to determine the ecological drivers that shape mortality throughout the annual cycle more studies are needed across diverse taxa with varying migration distances and routes, habitat requirements, and foraging strategies. For example, southwestern willow flycatchers and black-throated blue warblers both migrate relatively short distances between their breeding and wintering grounds, and comparisons with species that migrate longer distances (e.g. breed at more northern latitudes in the boreal forest of North America or winter further south in South America) may reveal higher rates of mortality during migration associated with longer migration distances (*sensu* Alerstam and Lindstrom 1990, see also Lok et al. 2015). Moreover, mortality during migration may not be evenly distributed between fall and spring migration if migration routes and ecological conditions differ between seasons. For larger species such as raptors, which can be tracked for multiple years with satellite transmitters, Klaassen et al. (2014) found that the rate of mortality was six times higher during migration than the stationary periods, but there was substantially higher mortality during spring migration associated with crossing the Sahara desert. Similarly, Eurasian spoonbills (*Platalea leucorodia leucorodia*) migrating long distances across the Sahara desert had higher mortality during spring migration than populations migrating shorter distances that did not cross an ecological barrier (Lok et al. 2015).

Compared to the monthly survival rate during migration (92%), the stationary periods have relatively low mortality risk (99% and 98% monthly survival rates in breeding and wintering, respectively). These results are consistent with other studies that also found low mortality during the winter period (Conway et al. 1995, Klaassen et al. 2014, Blackburn and Cresswell 2016). We believe our survival estimates during the breeding and non-breeding stationary periods are robust, given the length of each study (10 and 5 years, respectively), the relatively large number of birds tracked (yearly average of 257 and 38 individuals, respectively), and high detection rate (average 78% and 95%, respectively)(Koronkiewicz et al. 2006, Paxton et al. 2007). Birds on the breeding grounds were monitored from the first arrivals to the end of the breeding season, while the winter study period typically started subsequent to the arrival of the first wintering birds; nonetheless, an average of 77% of the non-breeding birds were banded in a given year, with 97% year-to-year territory fidelity, resulting in our estimates being derived from a group of individuals with long-term persistence and high detectability. However, the high rates of survival we documented for these periods may not be the same in breeding or wintering areas that are of lower quality than our study sites (Marra and Holmes 2001, Marra et al. 2015b). Given that some of the birds monitored at our study sites may have migrated to wintering or breeding habitats of lower-quality, some of the mortality we attributed to the migratory period may have been due to reduced survival in lower-quality stationary sites (Leyrer et al. 2013, Rakhimberdiev et al. 2015). Additionally, our partitioning of survivorship across the annual cycle was based on estimates averaged across years, and did not consider the observed variation among years. This variation among annual survival rates across years is likely driven by differential survival in either breeding, wintering, or migratory periods, but annual fluctuations in survival for these periods are not necessarily linked.

Understanding patterns of survival across the entire annual cycle is especially important for migratory species with declining or threatened populations, such as the endangered southwestern willow flycatcher. Southwestern willow flycatchers are believed to be primarily limited by breeding habitat (Marshall 2000, USFWS 2002), and possibly by wintering habitat (Lynn et al. 2003), but we lack information on possible limitations along migration routes. Conservation efforts aimed only at breeding and wintering sites may not help alleviate population declines if high rates of mortality during migration cannot be compensated by increased productivity or survivorship during the stationary periods. Moreover, increasing pressures on the availability of suitable stop-over habitat during migration may continue to suppress breeding populations, delaying or hindering recovery efforts. Unless we understand the factors that influence mortality throughout the annual cycle of migratory passerines we will be unable to enact effective conservation plans for these species (Moore et al. 1995, Newton 2004).

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manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table Legend

Table 1. Average (1999-2003) seasonal and monthly estimates of annual, within-season, and between-season survival rates on the breeding and wintering grounds of the willow flycatcher, and estimates of survival rates during the migratory period (spring and fall combined).

	Seasonal estimate (%)		Monthly estimate (%)	
Period	Survivorship	95% C.I.	Survivorship	95% C.I.
Breeding grounds				
Annual	66	64-69	97	96-97
Within-season	97	89-99	99	96-100
Between-season	68	64-73	96	95-97
Wintering grounds				
Annual	65	59-71	96	96-97
Within-season	88	77-94	98	96-99
Between-season	74	69-79	95	94-96
Migration				
Breeding-based	78	64-92	92	86-97
Wintering-based	77	66-89	92	87-96

Figure legend

Figure 1. Estimated seasonal and monthly rates of mortality on the breeding, wintering, and migratory periods of willow flycatchers.