

Short communication

Apparent survival and return rate of breeders in the southern temperate White-rumped Swallow *Tachycineta leucorrhoa*

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Life-histories and demographic parameters of southern temperate bird species have been little studied. We estimated return rates between years and sexes, and adult apparent survival and recapture probabilities with mark–recapture data on White-rumped Swallows and found a lower return rate of unsuccessful females. There was little support for influences of sex or year on survival rates. The estimates were equivalent to the lowest value reported for a northern congener, in contrast to the prediction of geographical variation under life-history theory.

Keywords: mark–recapture, nesting success, *Tachycineta bicolor*, *Tachycineta leucorrhoa*.

Site fidelity, the tendency to return to a previously occupied location (Switzer 1993), may confer a number of benefits, especially for migratory species, including an increased knowledge of the location of key resources (Rappole & Jones 2002), improved chances of maintaining a breeding territory and securing a mate (Shields 1984, Pärt 1994), and reduced predation risk by minimizing the exposure to unfamiliar environments (Shutler & Clark 2003). However, individuals showing site fidelity may also incur costs of inbreeding (Walter *et al.* 1988) or lower reproductive success if habitat quality declines (Greenwood *et al.* 1978). Dispersers may find richer resources, leave behind predators and parasites, or find fewer competitors and better or genetically unrelated mates (Clobert *et al.* 2001). High site fidelity is reflected in high return rates of surviving birds

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(the proportion of captured individuals that return to the site and are captured again during the subsequent season), but as the return rate is the product of survival and detection probability (Martin *et al.* 1995), low return rates do not necessarily imply low site fidelity.

Adult survival is a key life-history trait known as a trade-off with reproductive effort in numerous northern temperate and subtropical species (Ghalambor & Martin 2001, Martin 2002), yet few studies have found the predicted inverse relationship between survival and reproductive effort (Murphy *et al.* 2000, Bijleveld & Mullers 2009). Many subtropical passerine species exhibit higher adult survival compared with northern species (Ghalambor & Martin 2001, Martin 2002), but for many other subtropical and southern temperate species this pattern of higher survival rates has yet to be confirmed. In general, there have been relatively few investigations of putative factors influencing survival in southern temperate passerines.

We used mark–recapture methods to estimate apparent (local) survival rates of the White-rumped Swallow *Tachycineta leucorrhoa*, a southern temperate species whose distribution ranges from southern Brazil, Paraguay, Uruguay and northern Argentina south to La Pampa and Buenos Aires (Ridgely & Tudor 1989).

Our main objective was to estimate apparent survival (ϕ) and recapture (P) rates in relation to sex and year, enabling us to compare apparent survival rates with those of north-temperate Tree Swallows *Tachycineta bicolor*. We also assessed whether return rates of male and female swallows were higher following a previously successful breeding attempt.

METHODS

Study area and field methods

The study was carried out in a flat farming landscape at the Instituto Tecnológico de Chascomús, Buenos Aires Province, Argentina (35°64'S, 58°01'W), from 2002 to 2008. The average temperature across the breeding seasons analysed (September to December, 2002–2007, SMN 2008) was 16.2 ± 0.5 °C (\pm sd) and the average cumulative rainfall was 356 ± 130 mm (\pm sd). White-rumped Swallows are small, migratory and secondary cavity-nesting passerines that have used a nestbox system to breed since 2002 (Massoni *et al.* 2007). During the nesting period (October–December) birds were trapped at the nestbox as described in Massoni *et al.* (2007). Some nesting attempts failed (due to females deserting after capture, hatching failure, poor weather or nestling mortality), reducing the number of males captured. Adults and nestlings were fitted with an individually numbered metal ring, all nests were checked every 1–2 days and the number of fledglings was recorded. Annual return rate was defined as the proportion of

banded adults in the year t that were known to return in the year $t + 1$. A nest was considered successful if at least one nestling fledged.

Statistical analysis

Using contingency tables we compared return rates between years and sexes, and between previously successful and unsuccessful adults (STATISTICA 6.0; Statsoft Inc., Tulsa, OK, USA). When estimating adult return rates, individuals banded as nestlings were added to the dataset on the first year they were recaptured breeding in the study area. Adults that abandoned after human interference were excluded from the analyses for both sexes.

Adult survival analysis

Using models for live encounter data we corrected for the probability of encounter (P) and obtained estimates of apparent survival (φ), the product of true survival probability and site fidelity. We estimated adult apparent survival (φ) and recapture (P) rates using Cormack–Jolly–Seber (CJS) open-population capture–recapture models as available in Program MARK 5.1 (White & Burnham 1999), following maximum-likelihood procedures and notation described by Lebreton *et al.* (1992). During 2002–2004, the number of nesting attempts was rather small and we did not capture males because they are more sensitive to capture and handling (our pers. obs.). Therefore, our dataset included 7 years with female captures (2002–2008) and 4 years with male captures (2005–2008). We used MARK linear modelling capabilities to code models that accounted for the lack of data on male capture histories by fixing male survival and recapture rate estimates to 0 for years prior to 2005 (Dugger *et al.* 2006). This procedure allowed us to use all encounter histories instead of using only the last 4 years of the study.

We tested whether the general model ($\varphi_{(r,s)} P_{(r,s)}$) fitted the data and assumptions underlying the CJS. We used the Median \hat{c} method (variance inflation factor) to estimate a value of c derived from a logistic regression analysis (Cooch & White 2006). We used this estimated \hat{c} value to correct AIC_c into $QAIC_c$. A set of 16 models alternating constancy and time and sex effects for φ and P were developed: $\varphi_{(r,s)} P_{(r,s)}$, $\varphi_{(r,s)} P_{(t)}$, $\varphi_{(r,s)} P_{(s)}$, $\varphi_{(r,s)} P_{(.)}$, $\varphi_{(t)} P_{(r,s)}$, $\varphi_{(s)} P_{(r,s)}$, $\varphi_{(.)} P_{(r,s)}$, $\varphi_{(t)} P_{(s)}$, $\varphi_{(s)} P_{(t)}$, $\varphi_{(t)} P_{(t)}$, $\varphi_{(s)} P_{(t)}$, $\varphi_{(s)} P_{(s)}$, $\varphi_{(s)} P_{(.)}$, $\varphi_{(t)} P_{(.)}$, $\varphi_{(.)} P_{(s)}$, $\varphi_{(.)} P_{(.)}$. Akaike's Information Criterion (AIC) weighted for sample size (AIC_c) and overdispersion ($QAIC_c$) was used in model selection (Anderson *et al.* 2000). Models with the lowest $QAIC_c$ values were retained as the best compromise between high proportion of deviance explained and low number of parameters in the model. The mean adult life-expectancy was calculated using the equation $1 - \ln^{-1}(\varphi)$ (Stenhouse & Robertson 2005). Reported values are percentages and estimated values \pm se.

RESULTS

Return rates and nesting success

During the study we performed 497 capture events; nest failures caused by human disturbance were excluded (11% of all the nests initiated in the colony) and our dataset was composed of 161 females and 69 males. Return rates did not differ between years (females: $\chi^2_3 = 4.0$, $P = 0.5$, $n = 161$; males: $\chi^2_2 = 0.7$, $P = 0.6$, $n = 69$), and 43.5% of females and 42% of males were recaptured in the subsequent year ($\chi^2_1 = 0.04$, $P = 0.84$). Overall, the return rate was 43% (including both sexes).

The return rates of females after a successful vs. an unsuccessful nesting attempt differed significantly. The proportion of females returning to the study site was higher after a successful nesting event (59% of successful females and 24.7% of unsuccessful females returned the next year, $\chi^2_1 = 19.3$, $P < 0.001$, $n = 161$). We found no effect of previous nesting success on the males' return rate (42.6% of all the successful males and 40% of unsuccessful males returned the next year, $\chi^2_1 = 0.03$, $P = 0.85$, $n = 69$). Also, to avoid underestimation of the return rate of birds that failed, we evaluated the return of unsuccessful birds not only in the first consecutive year after failure, but also in all the following years analysed, i.e. whether a bird that failed a nesting attempt was ever seen again ($t \geq 1$). Only one female that failed in 2004 returned again to the colony in 2007, i.e. one female of the 75.3% of unsuccessful females that did not return the first year after the failure.

Model selection and estimates

Only one model was within the two $\Delta QAIC_c$ units from the top model ($\varphi_{(.)} P_{(.)}$), suggesting an effect of sex on adult apparent survival and a constant recapture probability (Table 1). The third ranked model had less support

Table 1. Results of Cormack–Jolly–Seber mark–recapture models executed in the program MARK arranged by $\Delta QAIC_c$ values including constant (.) and time- (t) and sex-varying (s) apparent survival and recapture probability in White-rumped Swallows. Differences in $QAIC_c$ values from the top model ($\Delta QAIC_c$), Akaike's model weights (w_i), number of parameters (k), and deviance are shown. Fully parameterized model: $\varphi_{(r,s)} P_{(r,s)}$, $\Delta QAIC_c > 15.5$ and $w < 0.0001$.

Model	$\Delta QAIC_c$	w_i	k	Deviance
$\varphi_{(.)} P_{(.)}$	0.00	0.42	2	28.66
$\varphi_{(s)} P_{(.)} \varphi_{(s)} P_{(.)}$	1.76	0.17	3	28.39
$\varphi_{(.)} P_{(s)}$	2.04	0.15	3	28.66
$\varphi_{(.)} P_{(r,s)}$	3.47	0.07	6	23.87
$\varphi_{(s)} P_{(s)}$	3.75	0.06	4	28.31
$\varphi_{(.)} P_{(t)}$	4.02	0.05	5	26.51

($\Delta\text{QAIC}_c > 2$) and suggested weak differences in recapture probabilities for males and females. The rest of the models almost doubled the ΔQAIC_c , suggesting they had little support (Table 1).

The estimate of apparent adult survival and recapture probability under the best model ($\varphi_{(.)}$ $P_{(.)}$) for all years and sexes combined was 0.409 ± 0.033 and 0.902 ± 0.052 , respectively (Table 2). We also used model-averaging based on the six models with $w \geq 0.05$ to estimate parameters (Table 2); the estimated apparent survival was 0.405 ± 0.038 for females and 0.416 ± 0.049 for males. The model-averaged estimates of recapture probability were between 0.880 and 0.916 for females, and between 0.893 and 0.914 for males (Table 2).

DISCUSSION

Return rates and nesting success

Overall, the return rate of White-rumped Swallows in Chascomús was 43% (including both sexes), a value that falls within the range reported for Tree Swallows by Custer *et al.* (2007) of 40–50%. As the return rate of a species is the product of the apparent (local) survival rate and the detection probability, we cannot speculate on the similarities (or lack of) between these congeners.

When comparing the return rates of females and males after a successful vs. an unsuccessful nesting attempt, we found only a lower apparent return rate of unsuccessful females and this relationship remained unchanged if we considered the return after more than 1 year after failure. Our results are similar to those reported for Tree Swallows and other bird species, where females typically disperse following reproductive failure (Greenwood & Harvey 1982, Clark & Shutler 1999, Winkler *et al.* 2004, but see Shutler & Clark 2003). Also,

like Tree Swallows, White-rumped Swallows have an extremely high number of extra-pair young (Ferretti 2010) and male breeding success is probably underestimated. Because females returned more often after successful breeding, we suggest that females are actively coming back to the site, i.e. exhibiting experience-based choices to return (Bollinger & Gavin 1989) instead of merely reducing risk by not dispersing to a potentially lower quality breeding site. Another explanation for the low return rate of unsuccessful females (compared with males) is that they may suffer higher mortality than males, as females work significantly harder when raising offspring (i.e. higher number of feeding visits, see Bulit *et al.* 2008). However, the most important causes of failure in Chascomús were hatching failure and mortality of very young nestlings, and females that failed at those stages would probably not incur higher costs when compared with males, as males aggressively defended the vicinity of the nestbox during incubation (our pers. obs.); therefore, higher dispersal rates of unsuccessful females at Chascomús are more likely to be due to dispersion after failure. If poor quality females are more likely to fail and also are more likely to have higher mortality, intrinsic quality differences among individuals might explain the difference in return rates between successful and unsuccessful females (low quality hypothesis, Coulson 1968, but see Haas 1998).

Model selection and estimates

The overall estimate of apparent adult survival, $\varphi_{(.)}$, of White-rumped Swallows in Chascomús for all years and sexes combined was 0.409 (Table 2). Although one of the models including sex differences in apparent survival was partially supported, the model-averaged estimates of female (0.405) and male (0.416) apparent survival were

Table 2. Estimates of apparent survival (φ) and recapture probability (P) from the top models in program MARK.

Model	Parameter	Year	Estimate \pm se	95% CI		Lifespan		
				Lower	Upper			
$\varphi_{(.)}$ $P_{(.)}$	φ		0.409 \pm 0.033	0.346	0.475	2.12		
	P		0.902 \pm 0.052	0.744	0.967			
Model-averaging	φ females		0.405 \pm 0.038	0.334	0.481	2.11		
	φ males		0.416 \pm 0.049	0.325	0.513	2.14		
	P females		2003	0.899 \pm 0.187	0.136	0.998		
			2004	0.916 \pm 0.065	0.676	0.983		
			2005	0.888 \pm 0.091	0.568	0.980		
			2006	0.891 \pm 0.083	0.606	0.977		
			2007	0.912 \pm 0.064	0.685	0.980		
			2008	0.909 \pm 0.083	0.584	0.986		
		P males		2006	0.903 \pm 0.082	0.596	0.983	
				2007	0.893 \pm 0.09	0.569	0.982	
			2008	0.914 \pm 0.076	0.614	0.986		

contained within a 95% confidence interval of the overall estimate (Table 2). This could suggest a weak influence of sex on apparent adult survival, or that our sample size is not big enough to show different apparent survival rates between sexes. The 1% difference between the apparent survival rates of males and females could lead to a biased sex ratio in this population, although the difference seems to be small. As the sex ratio of this colony has not yet been described, we cannot establish a link between these two relevant parameters of the biology of the species. If the lower return rate of unsuccessful females is a consequence of a higher dispersal probability instead of a higher mortality (as discussed above), then the relatively smaller apparent survival of females could be underestimated. Under this scenario, the real year-to-year survival of females and males would be more similar and closest to the apparent male survival (0.416).

As none of the partially supported models detected annual variation in apparent survival rates we also modelled female survival using only the larger and longer sample of female recaptures; again, we did not detect annual survival differences when considering only females ($\varphi_{(t)} P_{(c)} \Delta\text{QAIC}_c > 7.5$). The apparent survival estimates for Tree Swallows considering only the studies that used a similar methodology, varied between 40–48% (Custer *et al.* 2007), 42% (Robertson & Rendell 1990) and 51% (Shutler & Clark 2003). In this study, all the models including sex and time effects on recapture probabilities had little support, suggesting weak differences for males and females, and between years, on recapture probabilities. Also, the entire model-averaged range of estimates was within the interval derived from the most supported model with constant recapture probabilities (0.902).

The life expectancy of White-rumped Swallows is 2.12 years for this breeding colony, 2.11 for females and 2.14 for males, compared with 2.7 years for Tree Swallows (Custer *et al.* 2007). Although these values seem quite similar, they could imply a lower life expectancy for White-rumped Swallows (close to 2 years on average vs. 3 years for Tree Swallows) and, as both species breed annually, almost one additional breeding season for the northern species. As is frequently pointed out, survival rates might be underestimated due to permanent emigration, i.e. dispersion to other areas. The difference reported here on life expectancy between these two species could be due to a real survival difference or to a different dispersal pattern. However, with the available data on the southern species we have no way to discriminate between these two mechanisms.

According to life-history theory and empirical studies, adult survival of Neotropical species (species inhabiting South and Central America) is higher than that of northern temperate species (Stearns 1976, Roff 2002, Martin 2004). Our estimates of apparent survival are similar to the lowest value reported for Tree Swallows and this relatively low adult survival is expected to be accompanied

by a greater reproductive effort of the southern species (Skutch 1985, Martin 1996). The nestling feeding rates of White-rumped Swallows are twice those of the northern species (Bulit *et al.* 2008); therefore, a higher investment in parental feeding rates might be related to their relatively low apparent survival. Martin *et al.* (2000) also reported feeding rates in Argentina that were nearly twice the rates in Arizona. As an alternative explanation, Stearns (1992) suggested that adult survival might evolve along other physiological, behavioral or life-history traits shared with their congeners. As Martin (1996) pointed out, more studies between phylogenetic and ecologically similar northern and southern temperate species are needed to deepen our understanding of avian life-history evolution. The genus *Tachycineta* represents an excellent opportunity to discriminate between these two competing hypothesis because it could provide comparative data on survival estimates of different, but phylogenetically related, species across the western hemisphere with different environments, trade-offs and life-history parameters. If, in spite of the mentioned differences, adult survival rates are similar across the continent, the phylogenetic inertia would be more important. This study contributes to reducing the knowledge gap and shows a lack of differences in survival between two closely related northern and southern temperate species.

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