Survival rates of hirundines in relation to British and African rainfall

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The BTO's Retrapping Adults for Survival scheme is designed to monitor survival rates of species of conservation concern that are monitored relatively poorly by other forms of ringing. Here we present temporal trends in survival rates for three hirundine species, Barn Swallow *Hirundo rustica,* House Martin *Delichon urbicum* and Sand Martin *Riparia riparia*. Estimates of apparent survival rate were similar to those found in previous studies and were correlated with rainfall on the African wintering grounds, but not with rainfall in Britain, suggesting that overwinter food resources may be more limiting.

There is currently concern over the population status of Palaearctic–African migrants in Europe, as most of these species have shown consistent population declines over the last 30 years; particularly amongst species inhabiting open, dry habitats in Africa (Sanderson *et al* 2006). At a European scale both Sand Martin *Riparia riparia* and Barn Swallow *Hirundo rustica* declined in numbers between 1970 and 1990 but not subsequently, whereas House Martin *Delichon urbicum* numbers showed no change between 1970 and 1990, but have since shown a significant decline (Sanderson *et al* 2006). In England, Swallow numbers have fluctuated markedly over the last 30 years (Robinson *et al.* 2003), while declines have been observed recently in numbers of Sand Martin (1997–2004) and House Martin (1984–94) (Baillie *et al* 2007).

All three species are widely distributed in Britain but they winter in different parts of Africa (Cramp 1988). They all share a broadly similar ecology; in particular they feed on aerial invertebrates on both the breeding and non-breeding grounds. The abundance of these is well known to be positively related to rainfall (*eg* Wolda 1978, Frampton *et al* 2000). This relationship is likely to be strong in arid areas, such as the Sahel, where many British migrants pass through on migration or spend the winter (Wernham *et al* 2002). Consequently, one might expect rainfall to have a significant effect on annual survival rates, as has already been demonstrated for Sand Martin (*eg* Cowley & Siriwardena 2005) and for a number of other migrant species, such as warblers (*eg* Peach *et al* 1991, Szép 1995, Sherry & Holmes 1996).

The British Trust for Ornithology's (BTO) Retrapping Adults for Survival (RAS) scheme was started in 1998 to monitor the survival rates of species of conservation concern that are not well monitored by other forms of ringing. For most small-bodied long-distance migrants, the recovery rates from general ringing are too low to provide precise estimates of survival rates, and many species do not occur in the habitats covered by the Constant Effort Sites ringing programme (CES, Peach *et al* 1996), where retrapping of live birds increases the precision of the survival estimates considerably. A number of species monitored by RAS are migrants: in particular, RAS projects are operated for all three common hirundine species in Britain. Although large numbers of hirundines are ringed each year in Britain, most of these are caught at autumn migration roosts, which may comprise birds originating over a wide area, including continental Europe (*eg* Crick *et al* 1977). RAS aims to focus efforts on ringing species at breeding colonies, thus providing information on adult birds of known origin from which to estimate survival rates. Here we present initial results from the RAS scheme describing adult survival rates in the three hirundine species, and explore the influence of rainfall on the breeding or wintering grounds in determining patterns of annual adult survival.

METHODS

The BTO's Retrapping Adults for Survival scheme began formally in 1998, but many ringers had essentially been following RAS methodology for some years previously, and we include these data where possible (for Sand Martin enough sites had data back to 1990, for House Martin back to 1994). RAS ringers operate within a defined study area, usually a continuous area of suitable breeding habitat often set within a wider matrix of less suitable or unsuitable habitat. The aim each breeding season is to ring, retrap or resight each adult breeding bird (*ie* all breeding pairs) on the site. RAS ringers are actively encouraged to operate their project annually for a minimum of five years, preferably longer. Sites may appear and disappear from the time series, although missing years within a time series are unusual.

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For these analyses we considered projects with five or more years of data, of which there were 11: four sites each for Sand Martin and Swallow and three sites for House Martin (Fig 1). A number of additional projects contribute data to the RAS scheme for these species, but had not at the time of these analyses completed five years' operation; in the future these sites will contribute, and strengthen the scope of monitoring.

Survival rate estimation

Apparent adult survival rates were estimated using the program MARK 4.3, based on the standard Cormack–Jolly–Seber (CJS) model (Lebreton *et al* 1992, White & Burnham 1999). Because each study is restricted to a relatively limited area (though this often encompasses the majority of the suitable breeding habitat in the area), true survival rates cannot be estimated, as any permanent emigration from the breeding area will be confounded with mortality. However, for most short-lived passerines at least, fidelity to a breeding site is high, with relatively limited movement between seasons (Paradis e*t al* 1996).
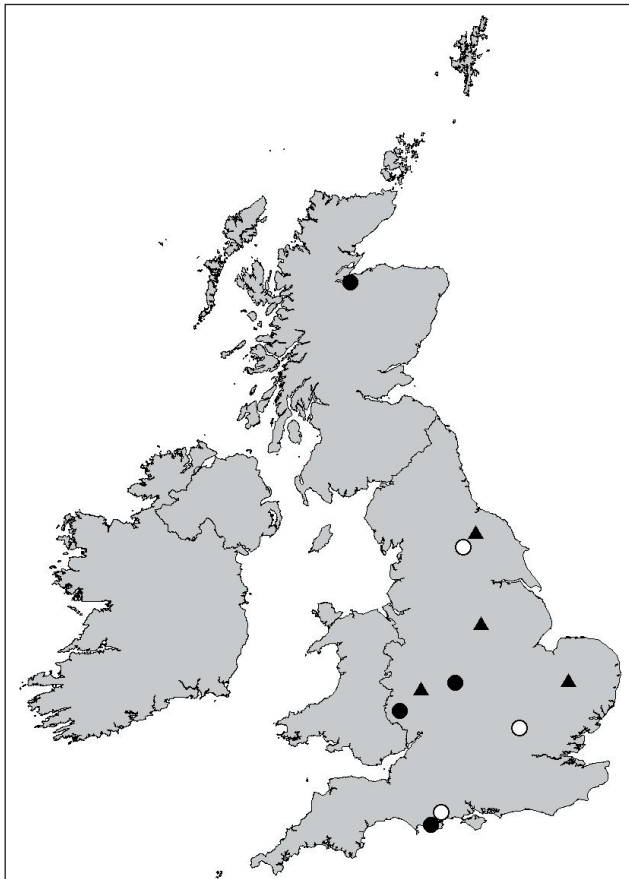

Figure 1. Location of RAS projects contributing to the analyses. Open circles are House Martin sites, closed circles Sand Martin sites and triangles Swallow sites.

Before formal modelling, we tested the goodness-of-fit of the CJS model to the recapture histories from each site using the 'Release' tests provided in MARK (Burnham *et al* 1987). This showed that the basic CJS model provided an acceptable fit for each species, with the overdispersion parameter ($\hat{c}$) less than 1.2 in each case. In particular, there were few problems of transience, where birds are caught fewer times than expected, because RAS ringers focus on particular breeding populations.

In referring to the models fitted, we follow a similar notation to that used by Lebreton *et al* (1992). In particular, we fitted models (separately for each species) where survival (ϕ) and recapture (p) probabilities vary between sites (denoted s) and year (t). Variation between years, in either survival or recapture, may occur independently between sites (s*t), or similarly (in parallel) across sites (s+t), in which case the annual variation is the same across sites, but the mean survival differs. If a site was not operated in a given year, the recapture probability was fixed at zero for that year (most often at the start or end of the time series for a site to match up years with the other sites).

Survival rates were modelled initially as site- and time-specific (model s*t). We then constructed a model with a site-specific intercept and annual deviations from this intercept in parallel across sites (model s+t), to estimate the average survival rate across all sites. This model is the one of most interest, as it provides the annual pattern of variation in survival, taking into account differences in survival between sites (perhaps because of habitat quality, for instance). To test whether survival rates differed between years (individually) we compared a model with annual time variation (s+t for Sand Martin and Swallow or s*t for House Martin, see below) with a model in which survival varied linearly with time, either in parallel or differently between sites, as appropriate.

We used Akaike's Information Criterion (AIC) to select between the different survival/recapture-rate models and likelihood ratio (χ^2) tests to assess the significance of differences between particular models. The AIC provides a relative measure of model fit allowing for the number of parameters used. A lower value indicates a more parsimonious model (better fit for the number of parameters used), and a difference in value of at least 2 signifies a substantially more parsimonious model.

Rainfall data

Summer rainfall data were obtained by extracting monthly totals for June, July and August from the England & Wales precipitation index (Wigley & Jones 1987) and calculating minimum, mean and maximum monthly rainfall for each year. For winter rainfall, we used the CRU_TS_2.1 gridded monthly rainfall data set (Mitchell & Jones 2005) and extracted data relevant to the wintering range of each

species (based on information in Wernham *et al* 2002). For Sand Martin, which winters in the western Sahel, we took an area bounded by (in the southwest) 5°N 15°W and (northeast) 17°N 0°W and for House Martin, which winters farther east, the area 5°N 0°W to 17°N 15°E was delimited. For each of these areas we extracted rainfall data for each month of the wet season (May to September) and calculated the mean, minimum and maximum monthly rainfall for each year. Because British Swallows winter in southern Africa, we also calculated mean, minimum and maximum monthly rainfall for October to December (the rainy season) for the area 35°S 15°W to 25°S 35°W (from information in Wernham *et al* 2002).

Unfortunately, winter rainfall figures were available only for the period 1990–2002, so we could not fit these relationships directly in MARK (using all the survival data). Instead, we simply regressed survival on rainfall; weighting each point (annual survival estimate) by the inverse of its

Table 1. Models of adult survival rates fitted for three hirundine species. Models test for differences in survival rates (P, first three lines) or recapture rates (*P*, final two lines) due to variation between sites (s) or year (t). Numbers are used in the text to refer to particular models; see the text for full details of each model. For each species we also indicate the total numbers of adult birds caught and years the sites were operated, in aggregate.

	n	No of parameters	AIC	Residual deviance
House Martin	1,528 / 29			
1. $\phi_t\,p_{s*t}$		40	90.6	201.5
2. $\phi_{s+t}\,p_{s*t}$		42	89.9	196.6
3. $\phi_{s*t}\,p_{s*t}$		55	87.2	166.2
4. $\phi_{s*t}\,p_s$		32	95.4	223.0
5. $\phi_{s*t}\,p_{s*t}$		55	87.2	166.2
Sand Martin	12,607 / 45			
1. $\phi_t\,p_{s*t}$		58	301.5	411.8
2. $\phi_{s+t}\,p_{s*t}$		61	305.6	409.7
3. $\phi_{s*t}\,p_{s*t}$		83	345.2	404.9
4. $\phi_{s*t}\,p_s$		47	380.2	512.5
5. $\phi_{s*t}\,p_{s*t}$		83	345.2	404.9
Barn Swallow	1079 / 24			
1. $\phi_t\,p_s$		11	7.5	134.5
2. $\phi_{s+t}\,p_s$		14	2.7	123.6
3. $\phi_{s*t}\,p_s$		27	18.3	112.2
4. $\phi_{s*t}\,p_s$		27	18.3	112.2
5. $\phi_{s*t}\,p_{s*t}$		44	22.4	79.9

variance to account for the fact that survival in some years was estimated more precisely than in others.

RESULTS

For Sand Martin and House Martin, AIC indicated that trapping effort varied over time on each site (comparing model 5 [$\phi_{s*t}\,p_{s*t}$] with model 4 [$\phi_{s*t}\,p_s$], Table 1). For Swallow there was less evidence for differences in effort between years so we used a simpler model that assumed a constant recapture probability across years. Average apparent survival rates between years for adults of the three species were broadly similar (House Martin ϕ = 0.367 ± 0.053, Sand Martin ϕ = 0.303 ± 0.014; Barn Swallow ϕ = 0.404 ± 0.028), survival being averaged across time from model 2.

For Sand Martin there was no evidence of differences between sites in annual variation in survival rates (model 1 [ϕ_t] had the lowest AIC), while for Swallow average survival rate varied between sites, but the pattern of variation between years was similar across sites (model 2 [ϕ_{s+t}], Table 1). For House Martin the situation was more complex, with AIC indicating the most parsimonious model contained both site- and time-specific variation (model 3 [ϕ_{s*t}]). However, the actual pattern in survival rates through time at each of the sites was broadly similar (Fig 2), with differences apparent mostly between the northern and two southern sites. Indeed, a model with survival rates similar at the two northern sites (but with site-specific intercept) and different at the southern site was markedly more parsimonious (AIC = 82.1).

For both Swallow and Sand Martin, there was significant annual variation in survival rates (Swallow: χ^2 = 11.0, p = 0.05, Sand Martin χ^2 = 24.6, P < 0.02). However, for House
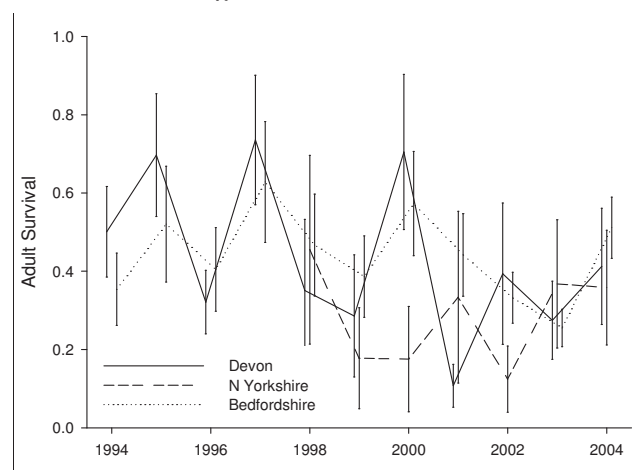

Figure 2. Adult survival at three RAS sites for House Martin from model $\phi_{s*t}\,p_{s*t}$. Lines link annual estimates, and bars indicate ± 1 standard error.

Martin, a simple linear trend provided a sufficient fit to the data (AIC = 82.0); over the period observed, survival declined significantly (slope = -0.086 ± 0.029, $\chi^2 = 7.82$, $P = 0.02$). There appears to be little similarity in the annual pattern of variation in survival between the three species (Fig 3), which suggests that variables on the wintering grounds may be more important in determining annual variation in survival than those on the breeding grounds. Indeed, there was no apparent relationship with summer rainfall in Britain (monthly mean, minima or maxima) for any of the three species (all $R^2 < 0.05$). However, for each species, rainfall in either western (House and Sand Martin) or southern (Swallow) Africa was correlated with annual variation in survival (all $R^2 \geq 0.50$). For Sand Martin, minimum monthly rainfall was the best predictor, for House Martin maximum monthly rainfall, and for Swallow mean monthly rainfall, in the wintering area appropriate for each species (Fig 4).

DISCUSSION

Given their similar ecology, it is perhaps not surprising that the three species have similar overall apparent survival rates, although there seems to be little correspondence between the three species in year-to-year variation in survival. The differences in average survival rate between species may be attributable to differences in return rates between the species. Swallows are known to be highly site faithful (Turner 2006), martins perhaps less so (Cramp 1988). The estimates of survival are similar to those of previous mark–recapture studies, *eg* for Sand Martin ϕ_{ad} = 0.289–0.312 (Cowley & Siriwardena 2005) and for Swallow ϕ_{ad} = 0.356–0.372 (Møller & Szép 2005). These estimates of return rates are surprisingly close to the
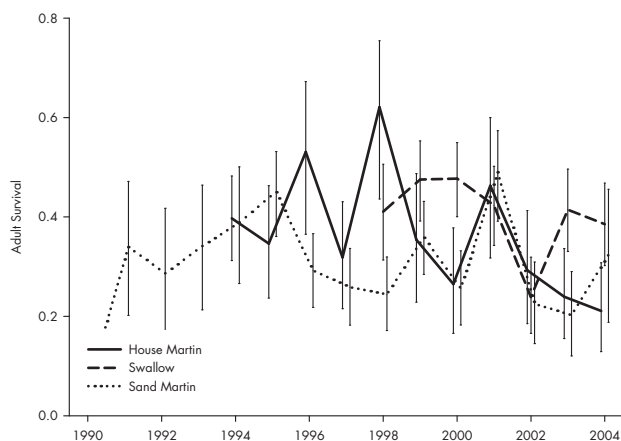

Figure 3. Adult survival at RAS sites for three species of hirundine from model $\phi_{s+t}p_{s*t}$ for each species. Lines link annual estimates, and bars indicate ± 1 standard error.
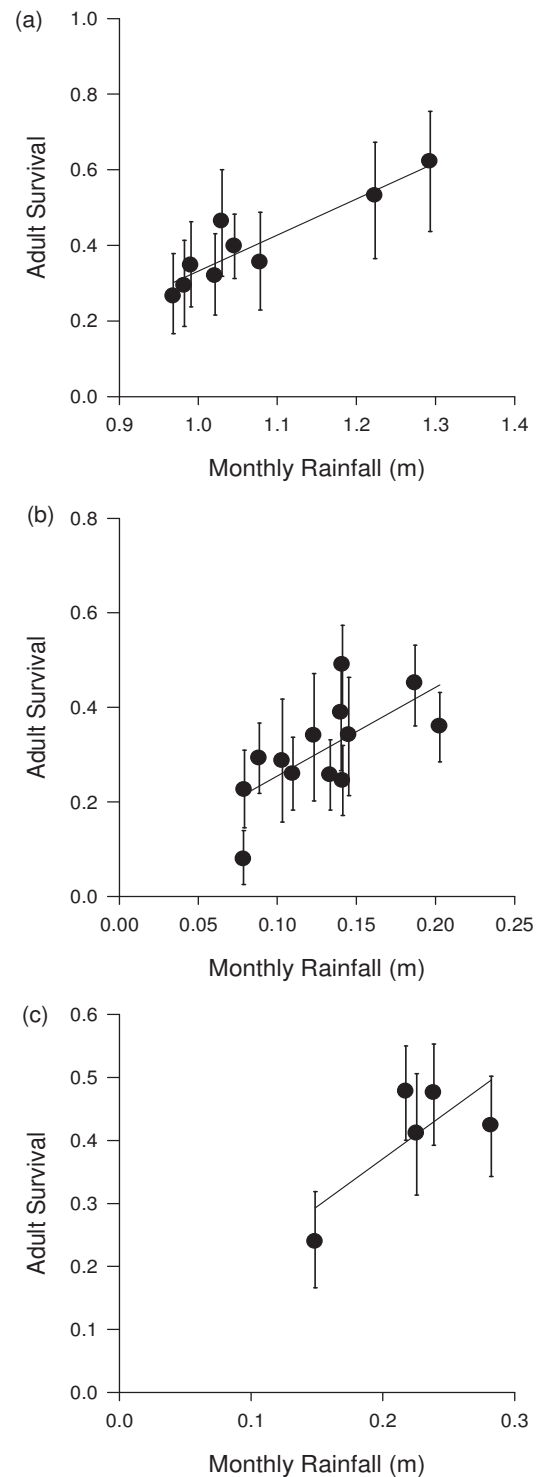

Figure 4. Relationships between adult survival of hirundines and rainfall on the wintering grounds. Each point represents a year, and bars ± 1 standard error. (a) House Martin and maximum monthly rainfall during the wet season; slope of best-fit line = 0.97 ± 0.16, R^2 = 0.84, $P < 0.001$. (b) Sand Martin and minimum monthly rainfall during the wet season; slope of best-fit line = 2.01 ± 0.61, R^2 = 0.50, $P < 0.01$. (c) Swallow and mean monthly rainfall during the early austral summer; slope of best-fit line = 1.50 ± 0.80, R^2 = 0.54, $P = 0.15$.

estimates of survival derived from the recovery of dead birds in Britain: 0.379 for Swallow (Siriwardena *et al* 1998), 0.354 for Sand Martin and 0.366 for House Martin (both Dobson 1990); these figures for martins were derived using now-utdated methods, however, so may be underestimates. Ring-recovery estimates of survival are likely to be closer to the 'true' survival rate because, being based upon national populations, they are much less affected by immigration and emigration than are mark–recapture estimates. The close agreement between the recapture and recovery estimates suggests that hirundines are highly site faithful, *ie* emigration is limited. Supporting this, Paradis *et al* (1996) found that mean breeding dispersal was only 0.6 km for House Martin and for Swallow and 1.2 km for Sand Martin; hence, for these species at least, mark–recapture studies may come close to monitoring 'true' survival.

There was some evidence of a decline in survival for House Martin but, because this does not correspond with a period of major population decline, the significance of this result for the national population is unclear. Survival rates of migratory birds may be influenced by factors on the breeding or non-breeding grounds, during the journey between them, or (most probably) by a combination of these. It has been demonstrated previously that rainfall on both the breeding and non-breeding grounds affects the survival of Palaearctic hirundine species, particularly Sand Martins, and other species, such as warblers, probably through impacts on vegetation and the availability of insect prey (Peach *et al* 1991; Szép 1995; Cowley & Siriwardena 2005). Sand Martins spend the northern winter in generally arid areas, whereas House Martins winter in wetter areas farther east (although the core wintering areas for these species are imprecisely known). In arid areas, a certain minimum threshold precipitation is required to promote vegetation growth, and hence insect abundance. Consequently it may be that, during periods of water stress, vegetation growth is slowed sufficiently to affect the insect abundance of the subsequent months. In moister areas with a higher water table, water will not be as limiting, so even in times of relatively low rainfall, food resources may still be common (Poulin *et al* 1992). Although rainfall is an important variable in determining survival for both species, the way this is manifested seems to differ between climatic regions. That rainfall in Britain is not correlated with survival may suggest that in temperate climes food abundance is less limiting or, perhaps more likely, that the determinants of insect abundance are rather more complex.

These results show, at least for these species, that the RAS scheme provides a useful way of monitoring survival rates, that these are broadly comparable across sites within species and that they correlate with environmental factors. As the scheme develops, with more sites and longer runs of data, it will be interesting to see whether survival rates really

are comparable across the country, or whether regional variation can be detected. The estimation of survival rates was made more difficult by the fact that recapture rates varied between years within a site, and thus required several parameters to account for what is, in effect, a nuisance variable. In developing RAS further, one would ideally want to encourage ringing of a greater number of birds and a more constant effort between years in ringing and recapturing birds (which may be practically difficult). Whilst RAS ringers are encouraged to record the number of hours they spend on fieldwork each year, insufficient data were available to include in these analyses, in part because we used data from before the formal start of RAS. Preliminary analyses, restricted to those sites where such data were available suggested that recapture rates were positively correlated with recorded effort, and that using this information could greatly increase the precision with which survival rates could be estimated.

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