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Survival rates in West African savanna birds

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Despite widespread interest in life histories and the comparison of parameters between tropical and temperate regions, there are still relatively few multispecies studies assessing annual survival in Afrotropical species. We used data from systematic mist-netting of savanna birds in Nigeria, between 2001 and 2008, to estimate survival for 40 Afrotropical bird species. Best-supported models were those incorporating constant survival (27 of 40) or the effects of transience (13 of 40). Survival ranged from 0.269 to 0.948 (mean \pm SE = 0.64 ± 0.02), varied within and between families, and showed a positive relationship with mass in passerines. Survival was highest in the insectivorous Malaconotidae (0.79 ± 0.13) and lowest in the granivorous Estrildinae (0.51 ± 0.04). This pattern was also evident in a comparison of survival between guilds (highest in insectivores and lowest in granivores) suggesting that these species encounter seasonal starvation risks or exhibit a seasonal response to water availability, i.e. emigration from the study area leading to reduced site fidelity and lower apparent survival. Our estimates of adult survival are higher than those previously obtained from this site, comparable with those from other Afrotropical studies (i.e. >0.60) and higher than those from temperate zones (0.53 ± 0.01 , $n = 79$).

Keywords: survival, tropical savanna species, West Africa

Introduction

Increasing emphasis on analysis of life history variation over the past 30 years (Martin 1987, Ghalambor and Martin 2001, Stutchbury and Morton 2008) has resulted in a growing need for robust estimates of life history parameters. Although much of the grounding for this work started with the assessments and investigations of Moreau in the Palaearctic/Afrotropical system (Moreau 1944, Lack 1948, 1954, 1968), most of the emphasis in recent years has focused on the Nearctic/Neotropical system (Karr et al. 1990, Johnston et al. 1997, Francis et al. 1999, Parker et al. 2006, Blake and Loiselle 2008). In consequence, much of the recent generation of empirical data relating to life history parameters (particularly survival estimation) and the difference between tropical and temperate systems has shown a bias towards the Neotropics. In contrast, there is a comparative dearth of such data for Afrotropical species. Dowsett (Dowsett and Dowsett-Lemaire 1984, Dowsett 1985) and other authors (e.g. Woodall 1975) produced useful estimates in the 1970s and 1980s, however these employed statistical techniques (e.g. life table and return rates) that failed to account for emigration. The development of mark–recapture modelling approaches (Pollock et al. 1990, Lebreton et al. 1992, Pradel 1993) and software such as SURGE (Lebreton et al. 1992), RELEASE (Burnham et al. 1987), U-CARE (Choquet et al. 2009) and,

particularly, MARK (White and Burnham 1999), provided an array of useful and user-friendly tools for modelling survival. In addition, this software also allowed for the inclusion of group (age and sex), time-dependence and other effects as well as incorporating means of assessing emigration, transience and trap-shyness/dependence. Whilst this has resulted in much improved methods for developing robust estimates of survival for all species, these tools have been used in relatively few multispecies studies of Afrotropical birds (Peach et al. 2001, McGregor et al. 2007).

Previous studies have provided valuable estimates of annual adult survival for a variety of Afrotropical species but have also highlighted considerable range and variability between species and sites (e.g. Nigeria, range: 0.19–0.96; McGregor et al. 2007). Some species (e.g. *Colius striatus*) had much lower annual survival rates than for north temperate species. Similar variability, both among species within sites and between species across sites, has been identified in other studies in tropical areas (range: 0.32–0.80; Blake and Loiselle 2008). This degree of variability suggests that methodological approaches (Clobert and Lebreton 1991, Sandercock et al. 2000) and site-specific differences (e.g. in predator densities, flocking tendency and food availability) (Martin and Li 1992, Jullien and Clobert 2000, Bennett and Owens 2002) may play important roles

in influencing the extent of variation in survival estimates. Clearly, survival rates need to be assessed across many sites and ecological situations in Africa before any generalisations can be made.

In this paper, we use an extended sequence of mark–recapture data to build on the work undertaken by McGregor et al. (2007) in Nigeria. We adopt a modified modelling approach to derive survival estimates for a range of Afrotropical landbirds. Our aim in doing this was fourfold. First, this study formed part of a longer-running project examining the life histories of tropical species with the aim of assessing trade-offs between life history parameters. To achieve this it was important to derive estimates of survival that were as robust, precise and as biologically meaningful as possible. Second, we wanted to explore whether the general hypothesis of high survival across tropical species holds true and, further, to examine whether phylogenetic or guild-specific effects result in differences in survival between families and guilds. Third, we wanted to identify whether the passerine species here exhibited a relationship between survival and body mass. Finally, we wanted to assess how our estimates compared with those derived in other studies in tropical Africa and make comparisons with estimates of mean survival for temperate passerines.

Materials and methods

Study area

The study was conducted within the 300 ha Amurum Forest Reserve (AFR) on the Jos Plateau, Nigeria (09°52' N, 08°58' E). The AFR lies within the Southern Guinea zone (Keay 1949) and is comprised predominantly of Guinea savanna scrub with patches of relict gallery forest and inselbergs. The reserve is surrounded on all sides by heavily degraded subsistence farmland. Fuel-wood collection by local villagers, regular uncontrolled burning, harvesting of grass for thatch and the encroachment of farming and cattle grazing have resulted in a degraded savanna habitat in the reserve.

The altitude of the Plateau (c. 1 270 m) results in more rainfall than locations at similar latitudes within Nigeria and consequently has a relatively shorter dry season. The climate of the study area is strongly seasonal, characterised by a dry season occurring between November and April. Mean daily minimum and maximum temperatures and monthly rainfall are lower at this time (14.2 °C and 33.2 °C; 7.4 mm) than during the 6–7 months of the wet season (22.9 °C and 36.7 °C; 196 mm) (data from Elgood et al. 1994). Mean annual rainfall over the course of the study was estimated as 1 332 mm from monthly rainfall summaries from Jos Airport (located approximately 26 km from AFR).

Collection of data

Up to 270 m of four-panel mist nets were used between 06:00 and 10:30 at five locations across the reserve between 2002 and 2008. One of these sites was operated as a constant effort site that was used for a 14-day period on two occasions each year – just prior to, and immediately after, the dry season. Net locations were initially selected in order to maximise number of individuals caught and species variation. To aid in this, nets were erected in a variety of

habitats (grassland, scrub, gallery forest and inselberg edges) across AFR. Net locations remained constant after initial selection and, from 2006, we attempted to ensure that visits were made to each of the locations (except the CES) in each season (i.e. early rains, late rains, early dry and late dry). Capture periods (i.e. consecutive number of days in which the nets were opened) ranged between 10 and 20 d and were operated throughout the year between August and April. The average interval between capture periods was 108 d, although this also includes the lengthy periods between May and August each year when no captures were made. Excluding this period, the mean interval between periods was 76 d with a mean of nine capture days each month.

Intensive mist-net captures over prolonged periods will inevitably result in some trap shyness in local bird populations and a consequent reduction in catches over time (Elder 1985). Given that we visited each location at least four times each year, with usually at least two months interval between each visit, we consider this unlikely to have been a significant issue. All captured birds were fitted with uniquely numbered metal rings and aged and sexed where possible. Morphometric measurements were taken (maximum wing-chord to 1 mm [Svensson 1992] and mass to 0.1 g) to assist ageing, sexing and allow later assessment of any relationship of mass with survival. Mass data for the species used in this study are available in Cox et al. (2011). Determination of the age of individuals was generally straightforward for most species. Certain species (e.g. some Cisticolidae) occasionally proved problematical to age with confidence; such individuals were excluded from all analyses.

Survival analysis

A total of 14 524 captures of 10 950 individuals of 161 Afrotropical species were made between November 2001 and December 2008 at AFR. Evidence suggests that juvenile and immature birds often exhibit higher levels of transience, which can lead to a negative bias to survival estimates (Clobert and Pradel 1993, Johnston et al. 1997). To reduce this effect we included only those individuals displaying full adult plumage. This resulted in there being 3 712 recaptures of 2 355 individuals of 102 species available for use in this study. Too few recaptures of individuals were made of most species to estimate apparent adult survival in all species. We, therefore, selected the 36 passerine and four non-passerine species for which there were >5 retrapped individuals for analysis of survival (mean number of recaptured individuals of selected species \pm SE = 39 ± 6.3).

Analysis of survival was performed using the general methods of capture–mark–recapture modelling outlined by Lebreton et al. (1992) and Burnham and Anderson (2002). Data were analysed, and parameter estimates developed, using the program MARK (White and Burnham 1999). Where possible we used standard Cormack–Jolly–Seber time-dependent models (i.e. ϕp_t , where ϕ is the probability that an animal alive at time i is alive at time $i + 1$, and p is the probability that an animal at risk of capture at time i is captured at $i + 1$, t indicates time-dependence) as starting models. Assessments of the suitability of these as starting models were first made using goodness-of-fit tests. We

used the median \hat{c} technique within MARK to derive the variance inflation factor (\hat{c}) and assess the extent of lack of fit (i.e. heterogeneity or over- or under-dispersion) of the model to the data. Ten replicates were used for each of 10 design points between bounds for \hat{c} of 1–3. Providing $1 < \hat{c} < 3$, the model was considered acceptable and the likelihood of the general and nested reduced-parameter models was corrected using MARK's 'c-hat adjustment function'. For under-dispersed models (i.e. where $\hat{c} < 1$) we followed the generally accepted convention of adjusting \hat{c} to unity (providing $\hat{c} > 0.5$). Where fit of the general model was inadequate ($\hat{c} > 3$), progressively less parameterised models were tested in order to find a suitable starting model.

McGregor et al. (2007) used models that allowed for the inclusion of data from resightings (Barker 1999) to generate their estimates. Although this method further reduces the impact of any trap shyness, the combined effects of the longer duration of our study and the additional parameters inherent in the Barker models led to over-parameterisation of models and consequent difficulties in obtaining reasonable values of \hat{c} . We therefore reverted to more standard mark-recapture models.

Heterogeneity in survival models can often be the result of transience (i.e. an individual moving away from the study area after initial capture effectively resulting in a probability of recapture of zero) or trap-dependence (i.e. the probability of an individual being caught being dependent on its previous history of capture) within the sample of marked individuals. To assess this, we used the program U-CARE (Pradel 1993, Choquet et al. 2005) to assess goodness-of-fit tests 3.SR and 2.Ct (see Burnham et al. (1987) and Lebreton et al. (1992) for further details of these tests) on all starting models. These tests check assumptions relating to fates of individuals and, where they proved significant (and indicative of transience or trap-dependence), a less parameterised time-since-marking (TSM) model (Pradel et al. 1997, Sandercock 2006) was used as the starting model (providing $1 < \hat{c} < 3$). TSM models (i.e. $\phi_{a2-t|t} p_{a2-t|t}$, where $a2$ indicates a different estimation of the parameter between the first and all subsequent occasions) enable the partitioning of survival and recapture probabilities between first and subsequent capture occasions. This allows for differential assessment of survival and recapture rates between these two periods and assessment of the extent of such effects.

Model selection was performed using information theoretic methods (Akaike information criterion; AIC) (Akaike 1985, White and Burnham 1999). Models corrected for overdispersion (using the relevant \hat{c} value) have their AIC statistics automatically adjusted within MARK. These quasi-likelihood adjusted QAIC_c values are generated following an adjustment to the likelihood term and it is these, rather than the original AIC_c values that are used for model selection (after Lebreton et al. 1992 and Burnham and Anderson 1998). The QAIC_c values are reported here for all adjusted models.

Sparseness of data for certain species, combined with high variance, often led to parameter estimates of, or approaching, 0 or 1. In such cases, confidence intervals were recalculated using Profile Likelihood methods within the program MARK. Species for which this was not possible were excluded from the analyses.

Given that duration of intervals between capture periods was generally unequal, these were converted to relative annual intervals, i.e. the duration of the interval (d)/365.25, to produce annual survival rates.

MARK was unable to generate biologically reasonable parameter estimates for certain species when using time-dependence (i.e. $\phi > 0.99$ with SE of zero). These models were removed from the candidate model set in such instances and model averaging performed with the remaining, less parameterised, models. Although this resulted in lower averaged values for ϕ , in most cases the parameter estimates produced were within 10% of those obtained from the best-supported model. In 17 of 37 species this was greater than the estimate derived from the single model. Overall, ϕ for the mean weighted-average model was 0.011 (2%) less than the mean from the single models (0.627 vs 0.638; Table 1).

Annual estimates of survival for both the best-supported model identified by MARK and a composite from those models with more than 5% support (using the 'weighted model averaging' procedure) are reported here. All model outputs and parameter estimates reported here incorporate the adjustment made using the relevant \hat{c} value.

We used published data (Martin and Li 1992, Peach et al. 2001, McGregor et al. 2007, Blake and Loiselle 2008) to enable cursory comparisons of estimated survival rates between our study and those obtained for temperate species. Only those data for species known to be resident or short-distance migrants were included (i.e. long-distance migrants were excluded). When comparing survival estimates across regions we used estimates based on mist net capture-mark-recapture studies wherever possible. For some species this was not possible since the only available survival estimates had been derived by other means (e.g. comparative analysis of ringing recoveries (dead birds) and recaptures (e.g. Farner 1945); recoveries (e.g. Dobson 1990) or using other models (e.g. Brownie; Baillie and McCulloch 1993), or Jolly-Seber; Boano and Cucco 1991). As a result, some of our comparisons may have been affected by the relatively low survival estimates obtained when using life-table approaches (i.e. through failure to account for capture of all surviving individuals). To reduce this effect we selected only those estimates derived from studies with large sample sizes or few methodological issues.

We used data from Elgood et al. (1994) to identify foraging guilds in Nigerian species. Standard analysis of variance (ANOVA) and t -tests were used to compare means in most cases. All ANOVAs fitted assumptions of normal distribution on examination of residuals. Levene's tests were used to assess equality of variances before comparison of means and, where unequal variances were detected between samples, we used the robust test, i.e. the Welch statistic. All statistical testing was performed using SPSS 17 (SPSS, Inc., Chicago, USA).

Results

Survival analysis

Limitations of the data sets required that the starting model for most species be less parameterised than one

Table 1: Capture statistics, starting models used to determine goodness-of-fit of the model set in MARK, and variance inflation factor (\hat{c}) used to adjust parameter estimates. Species names follow the African Bird Club List of African Birds (<http://www.africanbirdclub.org>). Transient status (T) was identified over residence (R) by a >50% change in capture rate between wet and dry periods

Species	No. individuals captured (I)	Number of recaptures	No. individuals recaptured (R)	Return rate (I/R)	Starting model ^a	Migratory status	\hat{c}
Columbidae							
<i>Turtur abyssinicus</i>	68	44	20	0.294	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.922
Coliidae							
<i>Colius striatus</i>	223	95	51	0.229	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.97
Lybiidae							
<i>Pogoniulus chrysoconus</i>	186	134	45	0.242	$\phi_c p_{a2-cl/c}$	T	0.97
<i>Lybius vieilloti</i>	36	33	16	0.444	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.024
Pycnonotidae							
<i>Pycnonotus barbatus</i>	311	111	68	0.219	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.013
<i>Chlorocichla flavicollis</i>	34	24	14	0.424	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.922
Cisticolidae							
<i>Camaroptera brachyura</i>	137	168	53	0.387	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.462
<i>Cisticola guinea</i>	30	29	12	0.400	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.649
<i>Cisticola aberrans</i>	57	28	16	0.281	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.002
<i>Cisticola cantans</i>	39	26	12	0.308	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.886
Sylviidae							
<i>Melocichla mentalis</i>	24	17	11	0.458	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.375
<i>Eremomela pusilla</i>	33	21	13	0.394	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	1.154
<i>Sylvietta brachyura</i>	32	31	18	0.563	$\phi_{a2-cl/c} p_{a2-cl/c}$		1.154
Muscicapidae							
<i>Cossypha niveicapilla</i>	80	75	27	0.338	$\phi_c p_{a2-cl/c}$	T	1.172
<i>Cercomela familiaris</i>	45	37	15	0.333	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.433
<i>Myrmecocichla cinnameiventris</i>	41	11	7	0.171	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	2.65
Turdidae							
<i>Turdus pelios</i>	190	87	55	0.289	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	1.059
Platysteiridae							
<i>Platysteira cyanea</i>	51	53	24	0.471	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.078
Zosteropidae							
<i>Zosterops senegalensis</i>	152	55	31	0.204	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.285
Nectariniidae							
<i>Cyanomitra verticalis</i>	87	80	34	0.391	$\phi_c p_{a2-cl/c}$	R	1.325
<i>Chalcomitra senegalensis</i>	202	62	39	0.193	$\phi_c p_t$	T	1.024
<i>Cinnyris venustus</i>	206	42	25	0.122	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.694
Malaconotidae							
<i>Malaconotus sulfureopectus</i>	25	14	12	0.480	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.614
<i>Tchagra senegalus</i>	41	24	15	0.366	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.972
Emberizidae							
<i>Emberiza tahapisi</i>	226	31	16	0.071	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	1.014
Passeridae							
<i>Sporopipes frontalis</i>	62	41	19	0.307	$\phi_{a2-cl/c} p_t$	R	1.843
Ploceinae							
<i>Ploceus luteolus</i>	45	26	17	0.378	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.839
<i>Ploceus cucullatus</i>	301	34	27	0.090	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	0.97
<i>Ploceus nigricollis</i>	116	63	41	0.353	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.006
<i>Ploceus vitellinus</i>	205	76	45	0.220	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	1.107
<i>Euplectes hordeaceus</i>	165	47	27	0.164	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.845
<i>Euplectes franciscanus</i>	1252	360	200	0.160	$\phi_t p_t$	T	0.922
Estrildinae							
<i>Estrilda caerulea</i>	378	326	144	0.381	$\phi_t p_t$	T	1.171
<i>Estrilda troglodytes</i>	136	24	14	0.103	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.953
<i>Uraeginthus bengalus</i>	498	226	104	0.209	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.899
<i>Lagonosticta rufopicta</i>	62	38	21	0.339	$\phi_{a2-cl/c} p_{a2-cl/c}$	R	1.015
<i>Lagonosticta senegala</i>	400	137	88	0.220	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	1.141
<i>Lagonosticta sanguinodorsalis</i>	305	300	109	0.357	$\phi_t p_t$	R	1.072
<i>Lagonosticta rara</i>	34	26	14	0.412	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	1.259
<i>Spermestes cucullata</i>	424	43	27	0.064	$\phi_{a2-cl/c} p_{a2-cl/c}$	T	0.807

^a ϕ = Apparent annual survival probability; p = recapture probability; t = time dependence; c = constancy; $a2-/-$ = TSM model with two 'age' groups, i.e. difference in rate between first and subsequent intervals

incorporating full time-dependence. As a result, it was not possible to identify annual differences in survival or to relate any potential differences to annual climate variability. For 36 of 40 species tested, a model incorporating a TSM factor proved the most suitable starting model (Table 1). A fully time-dependent starting model (i.e. $\phi_t p_t$) was appropriate only in the three species having the most recaptures (*Euplectes franciscanus*, $N = 200$; *Estrilda caerulescens*, $N = 144$; *Lagonosticta sanguinodorsalis*, $N = 109$). A time-dependent element was used in starting models in the recapture component for a further three species. Modelling of survival for all remaining species was developed from a TSM starting model except for *Pogoniulus chrysoconus*, *Cossypha niveicapilla*, *Cyanomitra verticalis* and *Cinnyris venustus* (all of which instead used constant survival probability and a two-stage component in recapture probability (i.e. $\phi_c p_{a2-c/c}$)).

Significant values for test 3.SR (i.e. $p < 0.05$) identified the likelihood of transience in only three of the 40 species (*Pycnonotus barbatus*, *C. venustus* and *Uraeginthus bengalus*). TSM models were used as the starting models for these species.

Minor over- or under-dispersion was indicated in the starting models for most of the study species (Table 1); however, the variance inflation factor (\hat{c}) was < 1.9 (range: 0.375–1.843, mean \pm SE = 1.06 ± 0.061) for 39 of the 40 species tested. Although the value of \hat{c} for *Myrmecocichla cinnamomeiventris* exceeded this ($\hat{c} = 2.65$), it was still within the boundaries of acceptable limits (i.e. $0 < \hat{c} < 3$) and was, therefore, retained within the analyses.

For most species, the observed encounter histories were best described by models incorporating constant survival and recapture probabilities ($\phi_c p_c$) (27 of 40; Table 2). All remaining species (except *Turdus pelios*, *E. franciscanus*, *E. caerulescens* and *L. sanguinodorsalis*) were best modelled using a TSM approach in either the survival or recapture probability. Most species showed similar support under the QAIC_c for both the constant model and the recapture TSM ($\phi_c p_{a2-c/c}$) and differences in QAIC_c values for these differed by < 2 in most cases. Four species (*Cossypha niveicapilla*, *Sylvietta brachyura*, *Sporopipes frontalis* and *Ploceus nigricollis*) had 2–4 times more support (using Akaike weights) for the TSM recapture model than for full constancy. Few species were best modelled using time-dependence in either survival or recapture and those that were tended to be species with the largest data sets (e.g. *Chalcomitra senegalensis* and *E. caerulescens*).

Survival estimates

Annual survival ranged from 0.269 to 0.948 (mean \pm SE = 0.64 ± 0.02) across the 40 species assessed (Table 2). Survival was also positively correlated with mass in the 36 passerine species assessed here (Pearson $r_{36} = 0.59$, $p < 0.001$). Survival within families was very variable for all except the Ploceinae (0.694–0.786) and Estrildinae (0.456–0.571), which had similar survival estimates across all members except one (*Ploceus luteolus* and *S. cucullata*, respectively). Mean survival varied significantly across all families (Figure 1, Table 3; ANOVA, $F_{8,25} = 2.9$, $p = 0.018$; Levene's test $F_{8,25} = 0.5$, $p = 0.83$) most likely because of the generally lower survival in the estrildine finches (Tukey,

Estrildinae vs Sylviiidae, mean difference = -0.3 , $p = 0.035$; all other tests between families $p > 0.05$). Substantially lower annual survival was also reported in the Passeridae, Emberizidae and Zosteropidae than for the other passerine families (with estimates lower than for Estrildinae); however, these were not formally tested because the study contained only one representative species for each family. Survival varied significantly between the four guilds represented in the study (ANOVA, $F_{3,36} = 3.9$, $p = 0.016$; Levene's test $F_{3,36} = 0.4$, $p = 0.74$) with lowest survival in the granivores and highest in the insectivores (Tukey, mean difference = -0.165 , $p = 0.012$). Standard errors of the parameter estimates were acceptable for most species (< 0.10), although the confidence intervals reflected the relatively low precision resulting from the generally small sample sizes (Lebreton et al. 1992), e.g. see *Melocichla mentalis* and *M. cinnamomeiventris*.

Lower parameter rates are often reported in the first year after catching than in subsequent years (Pradel et al. 1995, Sandercock 2006). However, in the eight species for which the TSM was applied here, parameter estimates of the two periods were not found to differ significantly (p_1 mean = 0.095, p_{2+} mean = 0.073) ($t_{14} = 0.6$, $p = 0.55$). Recapture rates were generally low across all 40 species (range 0.002–0.283; mean \pm SE = 0.102 ± 0.012) and did not differ significantly between families (ANOVA, $F_{16,24} = 0.4$, $p = 0.98$; Levene's test $F_{15,24} = 0.7$, $p = 0.8$). Return rates across all species varied between 0.064 (*S. cucullata*) and 0.563 (*S. brachyura*), and species with low return rates had low survival estimates (Pearson $r_{37} = 0.42$, $p < 0.01$).

Since a time-dependent survival component was not found to be the most appropriate in models for any species (even those identified as having a $\phi_t p_t$ starting model), it was not possible to test for the effects of any annual variation in climate (e.g. rainfall).

Comparisons with other Afrotropical studies

Estimates of adult survival in this study were similar to those obtained in other Afrotropical studies in Malawi (Peach et al. 2001) and Nigeria in 2004 (McGregor et al. 2007; Table 3) both when assessed collectively (ANOVA, Welch $F_{2,44.1} = 0.4$, $p = 0.70$; Levene's test, $F_{2,85} = 5.3$, $p = 0.007$) and when using only the five species common to all three studies (ANOVA, Welch $F_{2,6.6} = 0.01$, $p = 0.99$; Levene's test, $F_{2,12} = 4.2$, $p = 0.04$). The high standard errors in both the Malawi (0.115) and earlier Nigeria (0.129) data sets may have masked any true differences between estimates for the same species. Estimates of mean adult survival were found to be slightly higher in the current study than those of McGregor et al. (2007) (0.614 ± 0.023 vs 0.596 ± 0.048 , $N = 21$), but lower than those of Peach et al. (2001) (0.589 ± 0.056 vs 0.632 ± 0.115 , $N = 5$) when using species common to each study. However, neither of these differences was significant (matched pairs t : current vs Nigeria 2004 $t_{20} = 0.3$, $p = 0.75$; current vs Malawi $t_4 = -0.5$, $p = 0.67$). Across all passerine species assessed, mean adult survival estimates were similar between the current study and that in Malawi (0.649 ± 0.024 vs 0.638 ± 0.027 ; $t_{61} = -0.3$, $p = 0.75$; Levene's test, $F = 0.03$, $p = 0.85$) and 7% higher here than previous estimates for the study area (0.584 ± 0.045 ; $t_{52} = -1.4$, $p = 0.17$; Levene's test, $F = 2.9$,

Table 2: Model selection and estimates of apparent annual survival (ϕ), recapture probability (p), standard error (SE) and 95% confidence intervals for 40 bird species at Amurum Community Forest Reserve, Jos, Nigeria, in 2000–2008. Models are ranked according to quasi-Akaike information criterion (QAIC_c) and show the model set, departure from the best-supported model (Δ QAIC_c) and relative weight of support for the model (W_i). Catch identifies the interval for which the estimate is given (i.e. across all or for the second and subsequent (2+) intervals). Avg. = Weighted average estimate across all models with $W_i > 0.05$.

Species	Model	ΔQAIC_c	W_i	Survival			Recapture		
				Catch	$\phi \pm \text{SE}$	95% CI	Catch	$p \pm \text{SE}$	95% CI
Columbidae									
<i>T. abyssinicus</i>	$\phi_c p_c$	0	0.44	All	0.606 ± 0.078	$0.449\text{--}0.745$	All	0.105 ± 0.025	$0.065\text{--}0.165$
	$\phi_c p_{a2-c/c}$	0.91	0.28						
	$\phi_{a2-c/c} p_c$	1.76	0.18						
	$\phi_{a2-c/c} p_{a2-c/c}$	2.99	0.10						
				Avg.	0.547 ± 0.187	$0.216\text{--}0.841$	All	0.095 ± 0.035	$0.045\text{--}0.188$
Coliidae									
<i>C. striatus</i>	$\phi_c p_c$	0	0.49	All	0.619 ± 0.054	$0.509\text{--}0.718$	All	0.045 ± 0.007	$0.033\text{--}0.06$
	$\phi_c p_{a2-c/c}$	1.37	0.25						
	$\phi_{a2-c/c} p_c$	2.03	0.18						
	$\phi_{a2-c/c} p_{a2-c/c}$	3.37	0.09						
				Avg.	0.631 ± 0.259	$0.162\text{--}0.938$	All	0.041 ± 0.011	$0.025\text{--}0.069$
Lybiidae									
<i>P. chrysoconus</i>	$\phi_c p_c$	0	0.65	All	0.416 ± 0.05	$0.322\text{--}0.516$	All	0.096 ± 0.014	$0.072\text{--}0.127$
	$\phi_c p_{a2-c/c}$	1.23	0.35						
				Avg.	0.412 ± 0.051	$0.317\text{--}0.513$	Avg.	0.090 ± 0.019	$0.059\text{--}0.135$
<i>L. vieillotii</i>	$\phi_c p_c$	0	0.74	All	0.599 ± 0.094	$0.410\text{--}0.763$	All	0.182 ± 0.047	$0.106\text{--}0.294$
	$\phi_c p_{a2-c/c}$	2.14	0.26						
				Avg.	0.602 ± 0.096	$0.409\text{--}0.768$	Avg.	0.186 ± 0.056	$0.099\text{--}0.321$
Pycnonotidae									
<i>P. barbatus</i>	$\phi_c p_{a2-c/c}$	0	0.40	All	0.668 ± 0.052	$0.560\text{--}0.760$	1st	0.045 ± 0.012	$0.027\text{--}0.075$
							2nd	0.027 ± 0.005	$0.019\text{--}0.038$
	$\phi_c p_c$	0.46	0.32						
	$\phi_{a2-c/c} p_{a2-c/c}$	1.83	0.16						
				Avg.	0.614 ± 0.212	$0.215\text{--}0.902$	1st	0.039 ± 0.012	$0.021\text{--}0.072$
							2nd	0.029 ± 0.005	$0.020\text{--}0.041$
<i>C. flavicollis</i>	$\phi_c p_c$	0	0.51	All	0.844 ± 0.075	$0.639\text{--}0.943$	All	0.125 ± 0.033	$0.073\text{--}0.206$
	$\phi_{a2-c/c} p_c$	1.74	0.22						
	$\phi_c p_{a2-c/c}$	1.93	0.20						
	$\phi_{a2-c/c} p_{a2-c/c}$	3.88	0.07						
				Avg.	0.776 ± 0.199	$0.289\text{--}0.970$	Avg.	0.121 ± 0.043	$0.059\text{--}0.232$
Cisticolidae									
<i>C. brachyura</i>	$\phi_c p_c$	0	0.51	All	0.636 ± 0.055	$0.523\text{--}0.735$	All	0.098 ± 0.015	$0.072\text{--}0.132$
	$\phi_c p_{a2-c/c}$	1.71	0.22						
	$\phi_{a2-c/c} p_c$	1.93	0.19						
	$\phi_{a2-c/c} p_{a2-c/c}$	3.55	0.09						
				Avg.	0.603 ± 0.167	$0.280\text{--}0.856$	Avg.	0.104 ± 0.026	$0.063\text{--}0.166$
<i>C. guinea</i>	$\phi_c p_c$	0	0.60	All	0.510 ± 0.088	$0.343\text{--}0.674$	All	0.233 ± 0.053	$0.145\text{--}0.353$
	$\phi_c p_{a2-c/c}$	0.83	0.40						
				Avg.	0.498 ± 0.089	$0.331\text{--}0.665$	Avg.	0.209 ± 0.065	$0.109\text{--}0.364$
<i>C. aberrans</i>	$\phi_c p_{a2-c/c}$	0	0.60	All	0.650 ± 0.145	$0.348\text{--}0.866$	1st	0.141 ± 0.051	$0.068\text{--}0.273$
							2nd	0.055 ± 0.026	$0.021\text{--}0.133$
	$\phi_c p_c$	0.82	0.40						
				Avg.	0.611 ± 0.141	$0.330\text{--}0.834$	1st	0.121 ± 0.050	$0.051\text{--}0.258$
							2nd	0.068 ± 0.032	$0.027\text{--}0.163$
<i>C. cantans</i>	$\phi_c p_c$	0	0.71	All	0.806 ± 0.107	$0.520\text{--}0.941$	All	0.077 ± 0.023	$0.043\text{--}0.135$
	$\phi_c p_{a2-c/c}$	1.83	0.29						
				Avg.	0.800 ± 0.108	$0.515\text{--}0.938$	Avg.	0.071 ± 0.029	$0.031\text{--}0.152$
Sylviidae									
<i>M. mentalis</i>	$\phi_c p_c$		1	All	0.948 ± 0.130	$0.092\text{--}0.999$	All	0.082 ± 0.024	$0.046\text{--}0.142$
<i>E. pusilla</i>	$\phi_c p_{a2-c/c}$	0	0.63	All	0.586 ± 0.129	$0.332\text{--}0.801$	1st	0.033 ± 0.035	$0.004\text{--}0.228$
							2nd	0.161 ± 0.053	$0.082\text{--}0.292$
	$\phi_c p_c$	1.04	0.37						
				Avg.	0.612 ± 0.139	$0.335\text{--}0.832$	1st	0.065 ± 0.055	$0.012\text{--}0.289$
							2nd	0.145 ± 0.052	$0.070\text{--}0.278$

Table 2: (cont.)

Species	Model	ΔQAIC_c	W_i	Survival			Recapture		
				Catch	$\phi \pm \text{SE}$	95% CI	Catch	$p \pm \text{SE}$	95% CI
<i>S. brachyura</i>	$\phi_c p_{a2-cl/c}$	0	0.78	All	0.875 ± 0.119	0.452–0.984	1st	0.259 ± 0.085	0.127–0.455
	$\phi_c p_c$	2.58	0.22	2nd			2nd	0.080 ± 0.035	0.034–0.180
				Avg.	0.854 ± 0.121	0.467–0.975	1st	0.232 ± 0.093	0.098–0.456
							2nd	0.092 ± 0.043	0.036–0.216
Muscicapidae									
<i>C. niveicapilla</i>	$\phi_c p_c$	0	0.74	All	0.779 ± 0.064	0.631–0.880	All	0.080 ± 0.017	0.052–0.119
	$\phi_c p_{a2-cl/c}$	2.09	0.26						
				Avg.	0.780 ± 0.064	0.629–0.881	Avg.	0.080 ± 0.023	0.045–0.139
<i>M. cinnamomeiventris</i>	$\phi_c p_c$	0	0.56	All	0.657 ± 0.252	0.177–0.945	All	0.069 ± 0.054	0.014–0.279
	$\phi_c p_{a2-cl/c}$	2.13	0.19						
	$\phi_{a2-cl/c} p_c$	2.15	0.19						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	4.31	0.06						
				Avg.	0.597 ± 0.404	0.052–0.975	Avg.	0.077 ± 0.070	0.012–0.363
<i>C. familiaris</i>	$\phi_c p_c$	0	0.45	All	0.539 ± 0.064	0.414–0.659	All	0.144 ± 0.027	0.099–0.206
	$\phi_c p_{a2-cl/c}$	1.28	0.24						
	$\phi_{a2-cl/c} p_c$	1.77	0.19						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	2.69	0.12						
				Avg.	0.585 ± 0.177	0.252–0.855	Avg.	0.131 ± 0.035	0.077–0.215
Turdidae									
<i>T. pelios</i>	$\phi_c p_c$	0	0.52	All	0.799 ± 0.059	0.659–0.891	All	0.052 ± 0.009	0.037–0.073
	$\phi_c p_{a2-cl/c}$	1.77	0.21						
	$\phi_{a2-cl/c} p_c$	2.05	0.19						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	3.86	0.08						
				Avg.	0.793 ± 0.167	0.342–0.966	Avg.	0.050 ± 0.012	0.031–0.080
Platysteiridae									
<i>P. cyanea</i>	$\phi_c p_c$	0	0.54	All	0.700 ± 0.065	0.560–0.810	All	0.153 ± 0.030	0.103–0.221
	$\phi_c p_c$	0	0.54						
	$\phi_c p_{a2-cl/c}$	0.35	0.46						
				Avg.	0.709 ± 0.067	0.563–0.822	Avg.	0.183 ± 0.059	0.094–0.326
Zosteropidae									
<i>Z. senegalensis</i>	$\phi_c p_c$	0	0.56	All	0.527 ± 0.079	0.375–0.675	All	0.076 ± 0.018	0.047–0.119
	$\phi_c p_{a2-cl/c}$	0.45	0.44						
				Avg.	0.547 ± 0.088	0.376–0.707	Avg.	0.087 ± 0.028	0.046–0.159
Nectariniidae									
<i>C. verticalis</i>	$\phi_c p_{a2-cl/c}$	0	0.65	All	0.654 ± 0.059	0.530–0.760	1st	0.069 ± 0.034	0.025–0.174
	$\phi_c p_c$	1.28	0.35	2nd			2nd	0.160 ± 0.029	0.111–0.225
				Avg.	0.661 ± 0.060	0.534–0.768	1st	0.093 ± 0.045	0.034–0.228
							2nd	0.153 ± 0.029	0.104–0.219
							All	0.026 ± 0.006	0.017–0.039
<i>C. senegalensis</i>	$\phi_c p_c$	0	0.63	All	0.769 ± 0.068	0.611–0.876			
	$\phi_c p_{a2-cl/c}$	1.06	0.37						
	$\phi_c p_t$	10.55	<0.01						
				Avg.	0.779 ± 0.072	0.608–0.889	Avg.	0.031 ± 0.027	0.006–0.155
<i>C. venustus</i>	$\phi_c p_c$	0	0.69	All	0.534 ± 0.064	0.410–0.655	All	0.035 ± 0.007	0.023–0.052
	$\phi_c p_{a2-cl/c}$	1.65	0.31						
				Avg.	0.529 ± 0.065	0.402–0.653	Avg.	0.033 ± 0.009	0.020–0.055
Malaco-notidae									
<i>M. sulfureopectus</i>	$\phi_c p_c$	0	0.72	All	0.923 ± 0.087	0.523–0.992	All	0.112 ± 0.030	0.065–0.187
	$\phi_c p_{a2-cl/c}$	1.87	0.28						
				Avg.	0.917 ± 0.087	0.536–0.991	Avg.	0.104 ± 0.037	0.050–0.203
<i>T. senegalus</i>	$\phi_c p_c$	0	0.64	All	0.660 ± 0.097	0.455–0.819	All	0.093 ± 0.027	0.051–0.161
	$\phi_c p_{a2-cl/c}$	1.18	0.36						
				Avg.	0.674 ± 0.103	0.452–0.838	Avg.	0.107 ± 0.044	0.046–0.228
Emberizidae									
<i>E. tahapisi</i>	$\phi_c p_c$	0	0.35	All	0.491 ± 0.125	0.266–0.721	All	0.017 ± 0.006	0.008–0.035
	$\phi_{a2-cl/c} p_c$	0.65	0.25						
	$\phi_c p_{a2-cl/c}$	0.72	0.24						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	1.70	0.15						
				Avg.	0.522 ± 0.143	0.262–0.771	Avg.	0.021 ± 0.010	0.008–0.051

Table 2: (cont.)

Species	Model	ΔQAIC_c	W_i	Survival			Recapture		
				Catch	$\phi \pm \text{SE}$	95% CI	Catch	$p \pm \text{SE}$	95% CI
Passeridae									
<i>S. frontalis</i>	$\phi_c p_c$	0	0.60	All	0.592 ± 0.177	0.257–0.859	All	0.095 ± 0.035	0.045–0.189
	$\phi_c p_{a2-cl/c}$	0.85	0.40	Avg.	0.623 ± 0.200	0.240–0.900	Avg.	0.114 ± 0.054	0.043–0.270
Ploceinae									
<i>P. luteolus</i>	$\phi_c p_c$	0	0.53	All	0.487 ± 0.114	0.280–0.700	All	0.201 ± 0.061	0.107–0.345
	$\phi_{a2-cl/c} p_c$	1.75	0.22	Avg.	0.421 ± 0.200	0.127–0.784	Avg.	0.207 ± 0.075	0.096–0.391
	$\phi_c p_{a2-cl/c}$	2.17	0.18						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	3.97	0.07						
<i>P. cucullatus</i>	$\phi_c p_c$	0	0.51	All	0.694 ± 0.091	0.496–0.840	All	0.013 ± 0.004	0.008–0.022
	$\phi_{a2-cl/c} p_c$	1.75	0.21	Avg.	0.691 ± 0.092	0.489–0.839	Avg.	0.012 ± 0.005	0.006–0.250
	$\phi_c p_{a2-cl/c}$	1.87	0.20						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	3.61	0.16						
<i>P. nigricollis</i>	$\phi_c p_{a2-cl/c}$	0	0.66	All	0.786 ± 0.075	0.606–0.900	1st	0.129 ± 0.032	0.077–0.206
	$\phi_{a2-cl/c} p_{a2-cl/c}$	1.56	0.30	Avg.	0.784 ± 0.075	0.602–0.900	2nd	0.043 ± 0.011	0.026–0.071
	$\phi_c p_c$	6.87	0.02				1st	0.127 ± 0.034	0.074–0.209
	$\phi_{a2-cl/c} p_c$	7.59	0.01				2nd	0.044 ± 0.012	0.026–0.073
<i>P. vitellinus</i>	$\phi_c p_c$	0	0.44	All	0.726 ± 0.085	0.534–0.860	All	0.052 ± 0.010	0.036–0.074
	$\phi_{a2-cl/c} p_c$	1.11	0.25	Avg.	0.599 ± 0.240	0.174–0.914	Avg.	0.050 ± 0.013	0.030–0.084
	$\phi_c p_{a2-cl/c}$	1.56	0.20						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	2.89	0.10						
<i>E. hordeaceus</i>	$\phi_c p_{a2-cl/c}$	0	0.35	All	0.786 ± 0.084	0.581–0.907	1st	0.013 ± 0.008	0.004–0.046
	$\phi_c p_c$	0.38	0.29	Avg.	0.808 ± 0.087	0.585–0.926	2nd	0.013 ± 0.010	0.020–0.059
	$\phi_{a2-cl/c} p_{a2-cl/c}$	0.92	0.22				1st	0.020 ± 0.011	0.007–0.056
	$\phi_{a2-cl/c} p_c$	1.67	0.15				2nd	0.031 ± 0.009	0.017–0.056
<i>E. franciscanus</i>	$\phi_{a2-t/c} p_t$	0	0.86	2+	0.720 ± 0.034	0.649–0.782	Min.	0.002 ± 0.002	0.001–0.011
	$\phi_c p_t$	4.51	0.09	Avg.	0.646 ± 0.149	0.337–0.868	Max.	0.183 ± 0.028	0.135–0.244
	$\phi_{a2-cl/c} p_t$	5.64	0.05				Min.	0.002 ± 0.002	0.001–0.008
							Max.	0.187 ± 0.030	0.135–0.253
Estrildinae									
<i>E. caeruleus</i>	$\phi_{a2-cl/c} p_t$	0	0.56	2+	0.566 ± 0.040	0.486–0.643	Min	0.012 ± 0.013	0.001–0.094
	$\phi_c p_t$	0.45	0.44	Avg.	0.565 ± 0.040	0.485–0.643	Max	0.283 ± 0.083	0.151–0.468
<i>E. melpoda</i>	$\phi_c p_c$	0	0.5	All	0.571 ± 0.134	0.312–0.796	All	0.029 ± 0.011	0.014–0.060
	$\phi_{a2-cl/c} p_c$	1.60	0.22	Avg.	0.581 ± 0.143	0.305–0.814	Avg.	0.031 ± 0.013	0.013–0.070
	$\phi_c p_{a2-cl/c}$	1.84	0.20						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	3.56	0.08						
<i>U. bengalus</i>	$\phi_c p_{a2-cl/c}$	0	0.39	All	0.456 ± 0.040	0.379–0.535	1st	0.067 ± 0.012	0.047–0.093
	$\phi_c p_c$	0.33	0.33	Avg.	0.470 ± 0.149	0.216–0.741	2nd	0.048 ± 0.006	0.037–0.061
	$\phi_{a2-cl/c} p_{a2-cl/c}$	1.97	0.15				1st	0.060 ± 0.012	0.047–0.093
	$\phi_{a2-cl/c} p_c$	2.14	0.13				2nd	0.050 ± 0.007	0.038–0.066
<i>L. rufopicta</i>	$\phi_c p_c$	0	0.41	All	0.564 ± 0.087	0.392–0.722	All	0.164 ± 0.039	0.100–0.256
	$\phi_c p_{a2-cl/c}$	0.81	0.27	Avg.	0.580 ± 0.183	0.240–0.858	Avg.	0.168 ± 0.047	0.095–0.280
	$\phi_{a2-cl/c} p_c$	1.16	0.23						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	2.94	0.09						

Table 2: (cont.)

Species	Model	ΔQAIC_c	W_i	Survival			Recapture		
				Catch	$\phi \pm \text{SE}$	95% CI	Catch	$p \pm \text{SE}$	95% CI
<i>L.senegala</i>	$\phi_c p_c$	0	0.42	All	0.515 ± 0.056	0.407–0.622	All	0.047 ± 0.008	0.034–0.064
	$\phi_c p_{a2-cl/c}$	0.88	0.28						
	$\phi_{a2-cl/c} p_c$	1.44	0.20						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	2.60	0.11						
<i>L.sanguinodorsalis</i>				Avg.	0.525 ± 0.060	0.409–0.638	Avg.	0.051 ± 0.012	0.033–0.080
	$\phi_c p_t$	0	1	All	0.559 ± 0.039	0.482–0.632	Min.	0.011 ± 0.011	0.001–0.078
							Max.	0.270 ± 0.072	0.153–0.432
<i>L.rara</i>							All	0.249 ± 0.095	0.110–0.472
	$\phi_c p_c$	0	0.54	All	0.528 ± 0.146	0.263–0.779			
	$\phi_c p_{a2-cl/c}$	1.95	0.20						
	$\phi_{a2-cl/c} p_c$	2.12	0.19						
<i>S.cucullata</i>	$\phi_{a2-cl/c} p_{a2-cl/c}$	4.16	0.07						
				Avg.	0.570 ± 0.177	0.244–0.845	Avg.	0.270 ± 0.105	0.115–0.513
	$\phi_c p_c$	0	0.5	All	0.269 ± 0.065	0.162–0.413	All	0.022 ± 0.005	0.014–0.036
	$\phi_c p_{a2-cl/c}$	1.59	0.23						
	$\phi_{a2-cl/c} p_c$	2.00	0.18						
	$\phi_{a2-cl/c} p_{a2-cl/c}$	3.56	0.09						
				Avg.	0.280 ± 0.213	0.047–0.756	Avg.	0.021 ± 0.006	0.011–0.038

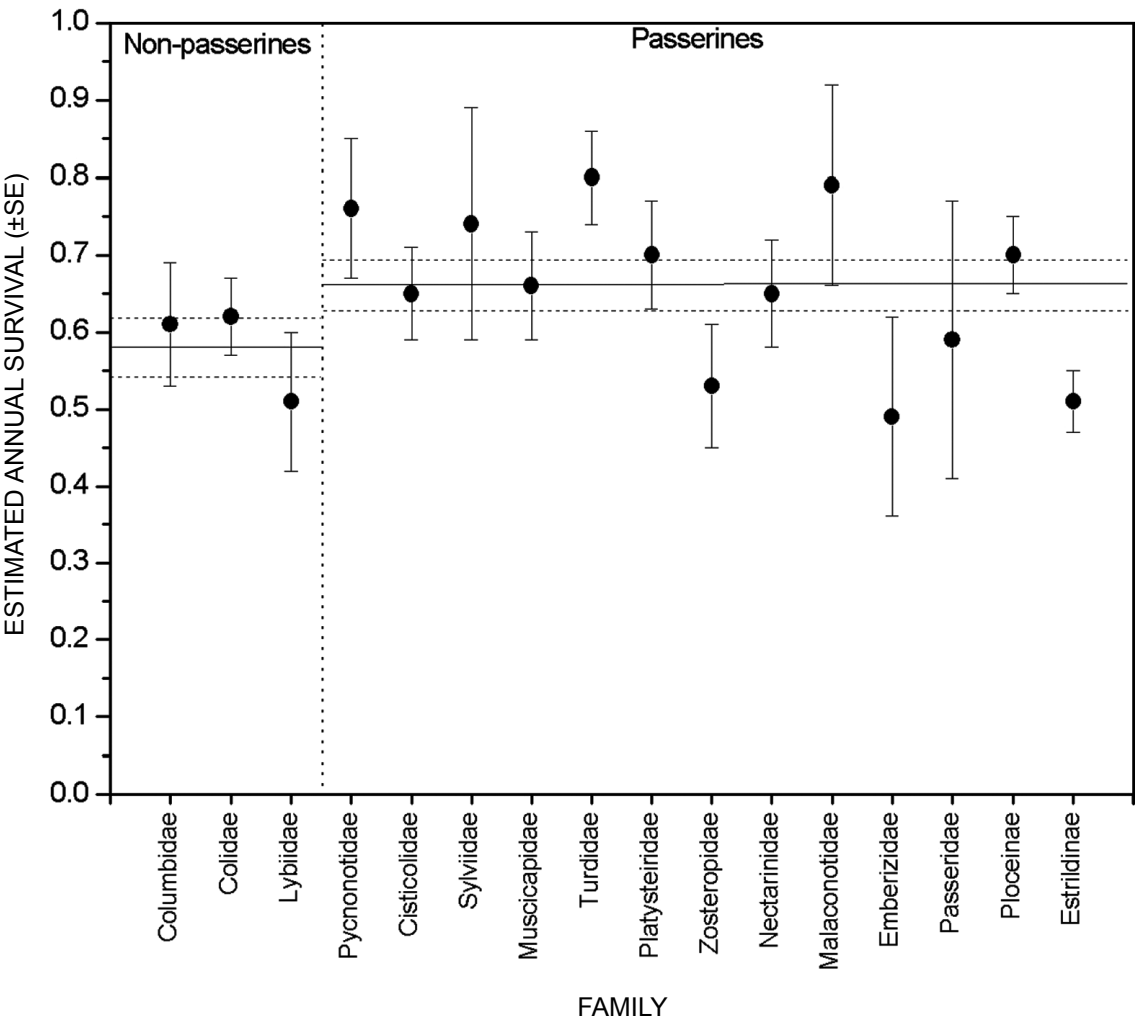


Figure 1: Mean estimated annual survival by family in West African savanna birds. Error bars denote the SE, horizontal solid and dashed lines represent the mean \pm SE across the non-passerine and passerine families

Table 3: Comparison of reported annual adult survival rates (\pm SE) of Afrotropical bird species between the current study (Nigeria 2008), previous work by McGregor et al. (2007) in the same study area in Nigeria between 2000 and 2004 (Nigeria 2004), and from Malawi in 1974–1989 (Peach et al. 2001)

Species	Nigeria 2008	Nigeria 2004	Malawi 1989	Mean
Columbidae				
<i>Turtur abyssinicus</i>	0.61 \pm 0.08	0.90 \pm 0.05	—	0.76 \pm 0.15
Coliidae				
<i>Colius striatus</i>	0.62 \pm 0.05	0.19 \pm 0.19	—	0.41 \pm 0.22
Lybiidae				
<i>Pogoniulus chrysoconus</i>	0.42 \pm 0.05	—	—	
<i>Lybius vieilloti</i>	0.60 \pm 0.09	0.90 \pm 0.08	—	0.75 \pm 0.15
Mean for family by study	0.51 \pm 0.09			
Overall mean for family				0.64 \pm 0.14
Non-passerine families overall mean (study)	0.58 \pm 0.04	0.66 \pm 0.24	—	
Non-passerine families overall mean				0.62 \pm 0.49
Pycnonotidae				
<i>Pycnonotus barbatus</i>	0.67 \pm 0.05	0.36 \pm 0.08	0.74 \pm 0.04	0.59 \pm 0.12
<i>Phyllastrephus terrestris</i>	—	—	0.74 \pm 0.05	
<i>Andropadus importunus</i>	—	—	0.68 \pm 0.03	
<i>Chlorocichla flavicollis</i>	0.84 \pm 0.08	0.45 \pm 0.26	—	
Mean for family by study	0.76 \pm 0.09	0.41 \pm 0.05	0.72 \pm 0.02	
Overall mean for family				0.61 \pm 0.07
Cisticolidae				
<i>Camaroptera brachyura</i>	0.64 \pm 0.06	0.46 \pm 0.11	0.74 \pm 0.06	0.61 \pm 0.08
<i>Prinia subflava</i>	—	—	0.60 \pm 0.08	
<i>Apalis flava</i>	—	—	0.68 \pm 0.07	
<i>Cisticola erythrops</i>	—	—	0.53 \pm 0.08	
<i>Cisticola guinea</i>	0.51 \pm 0.09	—	—	
<i>Cisticola cantans</i>	0.81 \pm 0.11	—	—	
<i>Cisticola aberrans</i>	0.65 \pm 0.15	—	—	
Mean for family by study	0.65 \pm 0.06		0.64 \pm 0.05	
Overall mean for family				0.62 \pm 0.04
Sylviidae				
<i>Acrocephalus baeticatus</i>	—	—	0.77 \pm 0.07	
<i>Acrocephalus gracilirostris</i>	—	—	0.56 \pm 0.09	
<i>Eremomela pusilla</i>	0.59 \pm 0.13	—	—	
<i>Sylvietta brachyura</i>	0.88 \pm 0.12	—	—	
<i>Sylvietta rufescens</i>	—	—	0.80 \pm 0.07	
Mean for family by study	0.74 \pm 0.15		0.71 \pm 0.08	
Overall mean for family				0.72 \pm 0.06
Muscicapidae				
<i>Cossypha niveicapilla</i>	0.78 \pm 0.06	—	—	
<i>Cossypha heuglini</i>	—	—	0.83 \pm 0.07	
<i>Cercomela familiaris</i>	0.54 \pm 0.06	—	—	
<i>Myrmecocichla cinnamomeiventris</i>	0.66 \pm 0.25	—	—	
Mean for family by study	0.66 \pm 0.07			
Overall mean for family				0.70 \pm 0.07
Turdidae				
<i>Turdus pelios</i>	0.80 \pm 0.06	—	—	0.80 \pm 0.06
Platysteiridae				
<i>Platysteira cyanea</i>	0.70 \pm 0.07	0.73 \pm 0.15	—	0.72 \pm 0.02
Zosteropidae				
<i>Zosterops senegalensis</i>	0.53 \pm 0.08	0.34 \pm 0.17	—	0.44 \pm 0.1
Nectariniidae				
<i>Hedydipna collaris</i>	—	—	0.76 \pm 0.08	
<i>Cyanomitra verticalis</i>	0.65 \pm 0.06	0.60 \pm 0.24	—	0.63 \pm 0.03
<i>Chalcomitra senegalensis</i>	0.77 \pm 0.07	0.39 \pm 0.19	0.90 \pm 0.08	0.69 \pm 0.15
<i>Cinnyris venustus</i>	0.53 \pm 0.06	0.96 \pm 0.03	0.55 \pm 0.08	0.68 \pm 0.14
<i>Cinnyris bifasciatus</i>	—	—	0.76 \pm 0.09	
<i>Cinnyris cupreus</i>	—	—	0.60 \pm 0.07	
Mean for family by study	0.65 \pm 0.07	0.65 \pm 0.17	0.71 \pm 0.06	
Overall mean for family				0.68 \pm 0.05

Table 3: (cont.)

Species	Nigeria 2008	Nigeria 2004	Malawi 1989	Mean
Malaeonotidae				
<i>Malaeonotus sulfureopectus</i>	0.92 ± 0.09	–	–	
<i>Tchagra senegalus</i>	0.66 ± 0.1	0.45 ± 0.24	–	0.56 ± 0.11
Mean for family by study	0.79 ± 0.13			
Overall mean for family				0.68 ± 0.14
Emberizidae				
<i>Emberiza tahapisi</i>	0.49 ± 0.13	–	–	0.49 ± 0.13
Passeridae				
<i>Sporopipes frontalis</i>	0.59 ± 0.18	0.42 ± 0.25	–	0.51 ± 0.09
Ploceinae				
<i>Ploceus xanthopterus</i>	–	–	0.70 ± 0.03	
<i>Ploceus luteolus</i>	0.49 ± 0.19	0.53 ± 0.5	–	0.51 ± 0.02
<i>Ploceus vitellinus</i>	0.73 ± 0.09	0.87 ± 0.09	–	0.80 ± 0.07
<i>Ploceus cucullatus</i>	0.69 ± 0.09	–	–	
<i>Ploceus nigricollis</i>	0.79 ± 0.08	0.48 ± 0.16	–	0.64 ± 0.16
<i>Euplectes hordaceus</i>	0.79 ± 0.08	–	–	
<i>Euplectes franciscanus</i>	0.72 ± 0.03	–	–	
<i>Euplectes orix</i>	–	–	0.72 ± 0.04	
<i>Euplectes capensis</i>	–	–	0.54 ± 0.09	
Mean for family by study	0.70 ± 0.05	0.63 ± 0.12	0.65 ± 0.06	
Overall mean for family				0.67 ± 0.04
Estrildinae				
<i>Pytilia melba</i>	–	–	0.52 ± 0.04	
<i>Estrilda caerulea</i>	0.57 ± 0.04	0.68 ± 0.13	–	0.63 ± 0.06
<i>Estrilda troglodytes</i>	0.57 ± 0.13	–	–	
<i>Estrilda astrild</i>	–	–	0.61 ± 0.05	
<i>Uraeginthus angolensis</i>	–	–	0.46 ± 0.09	
<i>Uraeginthus bengalus</i>	0.46 ± 0.04	0.53 ± 0.2	–	0.50 ± 0.04
<i>Lagonosticta rufopicta</i>	0.56 ± 0.09	0.75 ± 0.11	–	0.66 ± 0.1
<i>Lagonosticta senegala</i>	0.52 ± 0.06	0.89 ± 0.39	0.23 ± 0.1	0.55 ± 0.19
<i>Lagonosticta rhodopareia</i>	–	–	0.50 ± 0.06	
<i>Lagonosticta sanguinodorsalis</i>	0.56 ± 0.04	0.66 ± 0.18	–	0.61 ± 0.05
<i>Lagonosticta rara</i>	0.53 ± 0.15	–	–	
<i>Spermestes cucullata</i>	0.27 ± 0.07	–	–	
<i>Vidua chalybeata</i>	–	–	0.54 ± 0.12	
Mean for family by study	0.51 ± 0.04	0.70 ± 0.06	0.48 ± 0.05	
Overall mean for family				0.55 ± 0.03
Fringillidae				
<i>Serinus mozambicus</i>	–	–	0.65 ± 0.08	
<i>Serinus sulphuratus</i>	–	–	0.52 ± 0.07	
Mean for family by study			0.59 ± 0.06	
Overall mean for family				0.59 ± 0.06
Passerine families overall mean (study)	0.66 ± 0.03	0.52 ± 0.05	0.64 ± 0.03	
Passerine families overall mean				0.61 ± 0.02
Overall family mean (study)	0.63 ± 0.02	0.60 ± 0.05	0.64 ± 0.03	
Overall family mean				0.63 ± 0.02

$p = 0.10$). In all cases, apparent precision of estimates was greater in the current study.

Comparisons with Temperate studies

Published survival rates are similar for Palearctic and Nearctic species (range = 0.32–0.67 vs 0.29–0.76; mean ± SE = 0.515 ± 0.02 vs 0.540 ± 0.01) and no significant difference in mean annual estimates was detected between the two regions ($t_{77} = -1.2$, $P = 0.23$; Levene's test, $F = 0.3$, $P = 0.61$). Mean survival was significantly higher in Afrotropical species (0.64 ±

0.023, $n = 40$) than in those from the Holarctic (0.53 ± 0.01, $n = 79$); $t_{55.5} = -4.4$, $P < 0.001$; Levene's test, $F = 10.5$, $P = 0.002$).

Discussion

Average adult survival across our 40 Afrotropical species was similar to (or higher than) means derived in other multispecies Afrotropical studies (Peach et al. 2001, McGregor et al. 2007). Although the range of survival estimates in the current Nigeria data set was wide and

with quite a low minimum (0.27–0.95), the majority (23/40) of species assessed here had annual survival estimates >0.6 . Indeed, only five had estimates <0.5 and these were mostly for species (or families) found to have lower survival elsewhere (i.e. the Estrildine finches), were suspected of being very mobile (and therefore likely to exhibit higher levels of transience, e.g. *Spermestes cucullata*), or had small data sets (e.g. *Ploceus luteolus*).

Too few species were caught for us to make many generalisations about survival rates in tropical non-passerine landbirds. Of those caught in sufficient numbers to allow estimation of survival, all four species were frugivorous. Survival was fairly consistent at around 0.61 for three of the four species, but was markedly lower in *Pogoniulus chrysoconus*. This is most likely the result of the difference in size between the species involved (Sæther 1989, Ricklefs 2000), as *P. chrysoconus* has a mean mass (10.8 ± 0.04 , $N = 331$) less than 25% of that of the other species in the analysis.

Among the passerine species, apparent adult survival varied widely across all species and between species within families and the only apparent trend was based on size – smaller species generally having lower survival rates. The potential reasons behind this and the overall variability between species and among families are unclear but may relate to factors such as differential vulnerability to predation (van den Hout et al. 2008) or stresses arising from climate variability, variable levels of competition between certain species groups or guilds (e.g. among the nectarivores; Gill and Wolf 1979, Chaskda and Mwansat 2006), differential mortality of the sexes and sex-biases in mist-net captures (Oatley 1982, Dowsett 1985), or simply a result of estimates for certain species being derived using much smaller data sets. Estimates for certain species (and closely related species) were comparable with those achieved in other studies and this geographical replication suggests that these estimates are reasonably robust. On a broader scale, mean survival was reasonably stable and high (0.65–0.79) for all except three predominantly granivorous families (Estrildidae, Emberizidae and Passeridae) and the Zosteropidae (range 0.49–0.53).

In contrast to previous work (Brawn et al. 1995), we found significant differences in survival across families. Four of the passerine families assessed here had significantly lower survival estimates than others. Some of this may be attributed to lack of data (i.e. only one species assessed from each of Emberizidae, Passeridae and Zosteropidae). However, low survival in the remaining family (Estrildinae) has also been recorded from other Afrotropical studies (Morel 1966, Woodall 1975, Peach et al. 2001). A lack of site fidelity and a tendency to disperse away from the ringing site, as recorded in other members of the Estrildinae (Benson et al. 1971, Herremans et al. 1995), will often result in reduced recapture probability and consequently low survival estimates. A number of species were identified here that showed a seasonal variation in catches (see Table 1). Movements into and away from the study area may have resulted in reduced recapture probabilities and survival estimates. This scenario could be a factor behind the very low survival estimate for *Spermestes cucullata*, a species which, in our study area at least, formed mobile and ranging flocks. In general, however, variation in survival

estimates existed in both the resident and migratory species tested here. High survival estimates were identified here in other species shown to have high dispersal tendencies (e.g. members of the Ploceinae), which may suggest that our methodology was sound and that the estimates reflect a true family-specific variation in survival. Our results may also be indicative of the reduced severity of the seasonal variation in rainfall (i.e. a comparatively short dry season) in our study area and a less marked impact on survival on species here compared with other locations at this latitude.

In most instances closely related species will have similar ecological niches. It, therefore, follows that the family-specific effect on survival observed here may relate more to foraging guild than phylogeny, as found by Brawn et al. (1995). Across all species and guilds the lowest estimate of apparent annual survival in passerines was found in the granivores (0.27 in *S. cucullata*) and highest in an insectivorous species (0.92 in *Malaconotus sulfureopectus*). The significantly lower survival of estrildine species in this study mirrors the low survival in small, granivorous tropical passerines reported from a number of other studies. This has been linked to seasonality (Morel 1966, Yom-Tov et al. 1992, Peach et al. 2001) and the consequent variation in both food (Maclean 1971, Harrison et al. 1997) and water availability (Peach et al. 2001).

Invertebrates in tropical Africa remain sufficiently numerous throughout the year that insectivorous birds are rarely thought to suffer serious food shortages (Lack 1986, Chambers and Samways 1998). Species dependent upon insects or able to switch between foods should, therefore, rarely face increased mortality as a result of food limitation. In addition, several of the ploceids (e.g. *Euplectes franciscanus* and *E. hordeaceus*) show an increased tendency to undertake short-scale, local movements thereby overcoming the problems associated with temporal and spatial unpredictability in food and water availability. The potential causes for the markedly lower survival recorded here for *Ploceus luteolus* are uncertain because they have similarly varied diets, but may reflect more on the sample sizes and precision of the estimates than on species ecology. Both recent survival estimates for this species have had relatively high standard errors (0.194 here; 0.503 by McGregor et al. 2007). The recapture rate for this species (0.201), however, was greater than for many other members of this family, possibly suggesting that low survival may be a true ecological effect.

Methodological considerations and potential sources of bias

Attempts were made to overcome biases associated with species representation by including as many families as possible in the generation of survival estimates for this study. Given the nature of the capture method employed here, however, our study has focused mainly on those species foraging at lower levels and which are more frequently associated with open or scrub-dominated habitats.

We met the majority of the key assumptions relating to the independence of individuals and their detection and movements (Lebreton et al. 1992) required for generation of biologically meaningful estimates of annual survival. We found no evidence of trap-dependence or shyness (despite

a high proportion of the recaptures taking place during the 14-consecutive-day constant-effort periods) and evidence of transience in only three of the 40 species assessed. The lack of detailed information relating to the ageing and sexing of many West African bird species meant that we anticipated an effect of transience in our data set arising from errors in identification of the age of individuals. Inclusion of subadults within samples will often depress estimated survival rates (Pradel et al. 1997, Jullien and Clobert 2000, Parker et al. 2006) as a result of both direct (higher mortality in the first year of life; Ricklefs 2000) and indirect (age-specific variation in site-fidelity and natal dispersal) effects. Insufficient sample sizes may have reduced the power of tests for transience, however, because in Peach et al. (2001) transience was detected in species with relatively small sample sizes (i.e. *Cyanomitra verticalis*) and not in those with the largest samples. Despite being unable to find evidence of significant transience in the majority of species, and attempts to counter it in those we did using TSM models, it is still likely that these results underestimate true survival because we cannot distinguish death from dispersal.

This study ran for eight years, a significant duration given the long average lifespan reported for tropical birds (Jullien and Clobert 2000). This duration should have been sufficient to encompass annual fluctuations in environmental conditions (e.g. food availability, rainfall and fire) and give a representative picture of survival in these species. Although we noted an increase in fuel-wood collection throughout the duration of the study, the general habitat structure remained reasonably stable. Despite this, it is possible that habitat in the study area may have been modified in ways too subtle for us to detect but which nevertheless reduced suitability for certain species. Such an effect will have increased the likelihood of emigration of individuals from the site resulting in reduced recapture probability and, possibly, further underestimation of survival.

Comparisons of adult survival rates with other Afrotropical studies

Despite using some of the same species and working at the same study site, our estimates differed markedly from those generated by McGregor et al. (2007). This is almost certainly the result of an increase in sample sizes for each species (inclusion of data from four more years of catching) and the use of a differing modelling approach (retraps rather than resightings). Although other authors have suggested that survival studies incorporating resightings often result in the generation of higher estimates (Clobert and Lebreton 1991, Sandercock et al. 2000), previous assessments of this approach using our data (Stevens 2010) identified significant overparameterisation and difficulties in generation of reliable estimates. Estimates for certain species were considerably higher in the earlier Nigeria study, e.g. *Cinnyris venustus* (0.96 cf. 0.53). This species is especially apparent around the study site and its behaviour is such that resightings are more easily made than recaptures. Despite this, most estimates were higher in the current study. A number of other, smaller, negative biases in the mark–resighting approach not typical of mark–recapture methods may have influenced precision and resulted in lower estimates in the 2004 data set.

Loss or removal of colour-rings by birds, errors in resightings or duplication in application of colour-rings will all affect resighting rates and, ultimately, survival estimates. It appears, however, that the methodology adopted here and the resolution of reliability and precision issues may be the cause of our higher estimates compared with the resighting methodology used by McGregor et al. (2007). This may also explain the similarity in derived estimates between our study and the results of Peach et al. (2001) in Malawi, where resightings were not used. That our estimates are similar to those from Malawi is perhaps surprising given the difference in latitudes of the two sites (AFR: 09°52' N; Nchalo, Malawi: 16°16' S). Using the assumption that water and food availability are dependent on rainfall, one would expect mean survival to be higher for species at the wetter Nigerian site (annual rainfall 1 332 mm cf. 800–1 000 mm for Nchalo; data from Malawi Meteorological Services). There may be differences in food and water availability between the two sites, but any of a number of other factors (e.g. differing predation pressures or habitat quality) may serve to counteract this.

Comparison of tropical and temperate estimates

Our findings, of higher average survival rates of adult birds in tropical areas compared with temperate zones, suggest that the long-held view of latitudinal variation in life histories still holds weight. Distribution of survival rates tends to be equally variable across the studies used here. Although lower than those predicted from earlier studies (e.g. Snow 1962, Fogden 1972), rates were nevertheless significantly higher than for similar-sized temperate species. This higher likelihood of survival may provide a suitable mechanism to compensate for the generally smaller clutch sizes and reduced frequency of breeding attempts reported for tropical species (Moreau 1944, Jullien and Clobert 2000) that would help maintain stable populations. Unpublished data from this study identified higher juvenile survival among tropical species, which may further assist in compensating for the lower reproductive output of tropical adult pairs (Cody 1966, MacArthur 1972, Martin 1996).

Although our attempts to make comparisons of survival rates between ecozones are useful as initial assessments, they must, nevertheless, be treated with caution since we neither accounted for phylogenetic non-independence nor randomly selected species for inclusion. Despite this, our data have enabled the production of a useful 'general estimate' of survival across Afrotropical species and allowed for further examination of the potential differences in survival between Afrotropical and temperate species.

Survival estimates for several of the species included here have been produced previously in other areas of Africa. However, we consider these new estimates for 40 species to be valuable additions to the data set for Afrotropical species. In comparison with the Neotropics, there are still relatively few published survival estimates for Afrotropical species and we hope that this, and future work, will eventually result in sufficient estimates to enable a more complete examination of the tropical–temperate life history paradigm and permit further meaningful comparisons between Afrotropical/Palaearctic and Neotropical/Nearctic systems.

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Ethical note — Although the research work described here does not require any licences within Nigeria, all ringing was directly carried out and supervised by British Trust for Ornithology 'C' or 'A' permit ringing licence holders (or European equivalent) to the standards required for ringing in the UK. All ringing activities were also approved in advance by the APLORI Scientific Committee, which oversees research ethics at the site using the Association for the Study of Animal Behaviour ethical guidelines.

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