TITLE PAGE

Prediction of mean adult survival rates of southern African birds from demographic and ecological covariates

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Estimates of annual survival rates of birds are valuable in a wide range of studies of population ecology and conservation. These include modelling studies to assess the impacts of climatic change and anthropogenic mortality for many species for which no reliable direct estimates of survival are available. In this paper, we evaluate the performance of regression models in predicting adult survival rates of birds from values of demographic and ecological covariates that are available from textbooks and databases. We estimated adult survival for 67 species using dead recoveries of birds ringed in southern Africa and fitted regression models using five covariates: mean clutch size, mean body mass, mean age at first breeding, diet and migratoriness. Models including these explanatory variables performed well in predicting adult survival in this set of species, both when phylogenetic relatedness of the species was taken into account using phylogenetic generalised least squares (51% of variation in logit survival explained) and when it was not (48%). Two independent validation tests also indicated good predictive power, as indicated by high correlations of observed with expected values in a leave-one-out cross validation (LOOCV) test performed using data from the 67 species and when annual survival rates from independent mark–recapture studies of 38 southern African species were predicted from covariates and the regression using dead recoveries (LOOCV: 35% of variation in logit survival explained: mark-recapture estimates: 48%). Clutch size and body mass were the most influential covariates, both with and

without the inclusion of phylogenetic effects, and a regression model including only these two variables performed well in both of the validation tests (LOOCV: 39% of variation in logit survival explained: mark-recapture estimates: 48%). We conclude that our regression models, including the version with only clutch size and body mass, are likely to perform well in predicting adult survival rate for southern African species for which direct survival estimates are not available.

In this paper, we build and test regression models in which easily obtained biometric and biological variables were used to predict the mean annual adult survival of bird species. Estimates of annual survival rates of birds are valuable in studies of population ecology and conservation for several reasons. Comparisons among survival estimates specific to age classes and calendar years or other time periods can be used to assist in identifying the demographic mechanisms of population declines and increases (Green 2002). Even if there are insufficient data to permit survival estimation by time periods and pre-adult age classes, an estimate of the mean survival rate of adults is valuable for assessing the relative sensitivity of a species' population growth rate to changes in different demographic rates (Caswell 2001), and the capacity of a population to show density-dependent compensation for additional mortality from anthropogenic causes (Niel & Lebreton 2005, Dillingham & Fletcher 2008). A method to obtain the mean adult survival expected for a species might indicate that the rate measured directly during a period of unusual population decline is low by comparison. This might be useful in revealing the demographic mechanism underlying a decline of a species of conservation concern, though it would usually be preferable to do this by comparing survival and other demographic rates among areas or time periods with differing population trends (Green 2002).

An important new use of mean survival estimates is in dynamic models of the responses of species' distribution and abundance to climatic change. There is growing evidence that climatic change during the twentieth century has already changed the distribution (Parmesan 2006, Parmesan & Yohe 2003) and abundance (Gregory *et al*. 2009, Green *et al*. 2008) of species from a wide range of taxonomic groups (Hickling *et al*. 2006) and future projected climatic change is widely expected to have further substantial effects during the remainder of the present century (Huntley *et al*. 2008, Hill et al. 2002, Thuiller et al. 2006, Huntley et al. 2012). Most published projections of these impacts have used climatic envelope models of some form; such static models offer no insights into the rates at which, or even the extent to which, species may achieve potential changes in abundance and/or distribution. However, evidence indicates that, whilst at least some species are shifting their ranges and/or changing in abundance patterns in response to recent climatic changes, many are doing so at rates that lag behind the rate of climatic change (Devictor *et al.* 2008). Actual outcomes are affected both by the speed with which climate-induced changes in biotic factors directly affecting the species occur and by the interacting effects of the species' demographic characteristics and dispersal capacity. To improve upon climate envelope models, dynamic models of responses to climatic change are needed, incorporating estimates or assumptions about dispersal, demographic rates and the degree to which these are affected, directly or indirectly, by climatic changes (Huntley *et al.* 2010). Although some initial progress has been made in this direction (Anderson *et al.* 2009, Keith *et al.*

2008, Midgley *et al.* 2010, Midgley *et al.* 2006), a key limiting factor is the lack of data for most species on the demographic and dispersal attributes for which such mechanistic models typically require at least mean values (e.g. Collingham *et al.* 1996). Hence, to apply dynamic models of response to climatic change, methods are needed for estimating appropriate values of demographic parameters for a wide range of species.

Annual adult survival rate is amongst the most useful of these demographic parameters. Along with fecundity (number of independent young produced per adult per year) and pre-reproductive survival rate, it determines the potential maximum rate of population growth. A recent approach, based upon the theory of demographic invariants (Niel & Lebreton 2005), suggests that the potential maximum rate of population growth can be estimated reasonably accurately if just the mean annual adult survival rate under favourable conditions and the mean age at first reproduction are known, without information on other aspects of reproduction. Adult survival is also likely indirectly to influence patterns of juvenile dispersal in many actively-dispersing species in which occupation of a breeding territory by surviving adults excludes settlement by juveniles as they reach breeding age, especially in species that do not practice cooperative breeding. Survival rates of birds can be estimated from the ages at death of ringed birds reported by members of the public. Recaptures or re-sightings of live individually marked birds can also be used, although permanent emigration from the area under surveillance by the researchers may cause under-estimation of survival from such data. Inventory methods for survival estimation, which use the proportions of different age classes in counts of unmarked birds, can also be used (e.g. Green 2004). Extensive bodies of data from which annual adult survival rates can be estimated are available for few taxonomic groups, of which recoveries after death of ringed birds are the largest datasets in existence for the largest number of species. Although national datasets of this kind often include information on more than a million ringed individuals of all species, the proportion of these that are recovered dead is on average only a few percent, with highest proportions for large conspicuous species and those that are hunted, and lowest values for small, inconspicuous species and especially for migrants that spend a large part of the year in regions with low human population densities and/or where reporting of finds of ringed individuals is unlikely. Furthermore, the number of ringed individuals, and hence of recoveries, is higher for common species and often very low for rarer species including many of those that are of conservation concern. These latter species, however, are those for which we most urgently need the more reliable predictions of the potential impacts of climatic change that dynamic models should be able to provide.

The avifauna of southern Africa includes a high proportion of endemic species and other species of conservation concern, and is also relatively well studied. Hockey *et al.* (2005) provide comprehensive accounts of the biology of all species, including their diet, migratory behaviour and habitat preferences, as well as morphometric data. The Bird Ringing Scheme in South Africa (SAFRING: http://safring.adu.org.za/search_public.php?type=species) holds over 2.1 million ringing records, of which 1.4 million ringed since 1960 were eligible for the analyses reported below. Here we present an approach to estimating annual adult survival rate for land-bird species that is based upon modelling its relationship with a small number of biometric and biological characteristics that are readily obtainable from published sources. Mean annual adult survival was first estimated for all of those species with ten or more dead recoveries in the SAFRING database, filtered to remove estimates with low precision and the resulting values then used to develop predictive regression models in which biometric and biological variables were covariates of survival. The resulting models were evaluated both using leave-one-out cross validation and by applying them to predict annual adult survival rate for species for which we were able to locate independent published mark–recapture survival estimates. The results presented provide a widely applicable method for obtaining annual adult survival rate estimates for southern African species, especially rare and little-studied species. Our models may be of use in dynamic models of the impacts of climatic change upon such species and may also have wider applications in other studies of the demography of bird species.

METHODS

SAFRING ring recovery data

Records of individuals of all species ringed with metal rings labelled with a unique alphanumeric code, and recoveries of those birds found dead and subsequently reported, were obtained from the South African bird ringing scheme SAFRING (Animal Demography Unit, University of Cape Town, South Africa) in February 2011. We restricted our analysis to species that occur naturally as breeding birds in southern Africa and excluded results for those that occur only as non-breeders and breeding species introduced artificially to the region from elsewhere.

Our model of the mortality, ring recovery and ring reporting process was appropriate for dead recoveries only, so all other types of recovery, mainly recaptures and re-sightings of living birds, were excluded. Ringing years were taken to begin on 1 July and end on 30 June of the following year, so the last complete year of records in our dataset was July 2009 to June 2010. Birds ringed on or after 1 July 2009 and any recoveries from them were excluded from the analysis so as to ensure there was at least one year during which they could be recovered. All recoveries after June 2010 were excluded as this year was incomplete in our dataset. Data relating to rings issued before July 1960, or with five alphanumeric characters and a three-digit numeric prefix, were removed from the dataset, because the metal from which these rings were made may have been subject to ring wear or premature loss sufficient to affect the probability and timing of ring recovery (Piper 1995). The dataset was also screened to remove the small percentage of records where errors in data entry appear to have occurred, for example duplicated ring identities and non-matching species codes between recovery and ringing records with matching ring identities. Data for ringed or recovered birds were split according to whether the bird was ringed as an adult ($\geq$ 1yr old) or juvenile (fledged birds $<$ 1 year old). Data from birds ringed as nestlings were excluded. The number of years elapsed between recovery and ringing was calculated as the number of days between ringing and recovery divided by 365.25 and rounded down to the nearest integer.

Estimation of adult survival from dead recoveries

We used the statistical model of survival and recovery of Lebreton *et al.* (1995) which provides expressions for the probabilities of observing the recovery of a dead bird in each successive year after ringing, up to the end of the period over which recoveries are compiled. In addition, an expression is available for the combined probability that a ringed bird either survives the whole period from ringing to the end of the series, or dies during that period but is not recovered. The probabilities are expressed in terms of the parameters ϕ_J – the probability that a bird ringed as a juvenile survives beyond one year after ringing, ϕ_A – the probability that an adult bird survives for a year, λ_J – the probability that a bird that dies within a year of ringing as a juvenile is recovered, and λ_A – the probability that a bird that dies as an adult is recovered.

We did not attempt to fit models with calendar year-specific values for survival and recovery rates because of the large number of years in which birds were ringed and the lack of sufficient recoveries for most species to permit the fitting of models with large numbers of year-specific parameters. The log-likelihood of the observed recovery data, including birds ringed but not recovered, was calculated for a given set of values of the parameters λ_J, λ_A, ϕ_J and ϕ_A, but with logit parameter transformation to avoid out-of-range estimates (less than zero or greater than one). Those values of the transformed parameters that maximised the log-likelihood were obtained numerically by the Newton-Raphson method (Kalbfleisch 1979). We attempted to fit models for all species with at least ten dead recoveries of birds that died as adults (84 species). For many species, estimates of λ_J, and ϕ_J were imprecise because of relatively small numbers of birds ringed as young, low juvenile recovery rates, or both. We therefore concentrated on annual adult survival rate, ϕ_A, as the parameter of primary interest. Some of our estimates of ϕ_A also had low precision. Hence, we used only those estimates of ϕ_A with standard error of logit(ϕ_A) ≤ 0.4 (67 species) in our subsequent modelling.

Regression analysis of adult survival in relation to covariates

In order to explore the prediction of annual adult survival rate from biometric and biological properties of the species, we fitted regression models to our 67 estimates of adult survival. We used both ordinary least squares and PGLS phylogenetically-adjusted regression. PGLS accounts for the statistical non-independence, and consequent pseudo-replication, introduced into the analysis by the inclusion of related species with similar traits which might arise from descent from a common ancestor and is therefore preferred for unbiased assessment of the precision of regression parameter estimates. However, prediction of expected values for individual species from PGLS regression, whilst possible, is problematic because of the way that differences in traits among taxa are modelled. This difficulty arises most prominently for species outside the range of taxa included in our regression models. Prediction for such species is an important reason for our study and is also necessary for our validation tests, which are described later. For these reasons, we used both ordinary least squares and PGLS regression, but only used the ordinary least squares method for the validation tests.

Our covariates were mean body mass, mean clutch size, diet and migratoriness, with species-specific covariate values for the regression models obtained principally from Hockey *et al.* (2005), with additional input of expert advice where necessary. In addition, we obtained mean age at first breeding from a database maintained by BirdLife International (BirdLife International 2012, World Bird Database). We used the mean body mass, irrespective of sex, given by Hockey *et al.* (2005) where this was available, and otherwise the mean of the male and female means. Mean body mass, mean clutch size and mean age at first breeding were $\log_e$ transformed. The principal diet of full-grown birds was assigned to one of seven categories: Vertebrate carnivore; Vegetative herbivore; Omnivore; Nectarivore; Invertebrate carnivore; Granivore; or Frugivore. The migratoriness of species was categorised as: Resident; Mobile (combining the categories nomad, some local movement and altitudinal migrant of Hockey *et al.* (2005)); or intra-African migrant.

Ordinary least squares linear regression models were fitted with logit of adult survival as the dependent variable. Models that included all possible combinations of the main effects of the five covariates were fitted, together with the null model with no effects of covariates. This set comprised 32 models. We did not fit models with interaction terms because some of them would have required larger numbers of fitted parameters relative to the number of data points than is usually considered acceptable, and also to avoid data dredging because we did not have clear *a priori* justifications for biological mechanisms underlying any of the possible interactions (Burnham & Anderson 2002).

For each fitted regression model we calculated the Akaike Information Criterion, corrected for the effects of small sample size (AIC_C) (Burnham &

Anderson 2002). Weighted average regression coefficients for each variable were calculated across all of the models in the set, including the null model, using AICc model weights. These model-averaged coefficients were then used to calculate model-averaged expected values for logit adult survival for each species.

Regression analysis of adult survival in relation to covariates, adjusting for phylogeny

We repeated our analysis using an alternative method that adjusts for phylogenetic relationships among the species in our dataset. We obtained a bifurcating phylogeny for the 67 species using available literature (Figure S1, Supplementary Information). An unresolved polytomy was retained for three closely-related *Pycnonotus* spp. which could not be easily split. Branch lengths were unavailable so were initially set to equal length ($x = 1$) representing a "punctuated" or "speciational" model of evolution (Martins & Garland Jr 1991; Fisher, Blomberg & Owens 2002).

We fitted phylogenetic generalised least squares (PGLS) models to the data using the pgls function of the caper package in R (R Development Core Team 2011; Orme *et al.* 2012). Pagel's λ, a branch length transformation indicating the strength of the phylogenetic signal, (Pagel 1999) was optimised in each model by a maximum-likelihood method. All other branch length transformations (κ and δ) were set as constant in each model, at a level which assumed a Brownian motion model of evolution (equal to 1). We fitted separate models with all 32 of the combinations of covariates, as described above for the ordinary least squares analysis without phylogenetic adjustment, and then performed model averaging over this model set using AIC_c weights as described previously.

Validation test 1: Leave-one-out cross validation of the ordinary least squares regression models

We used a leave-one-out cross validation (LOOCV) procedure (Zuur *et al.* 2009) in which the set of 32 ordinary least squares regression models was fitted, omitting data for each of the 67 species in turn and using the resulting model-averaged regression coefficients to calculate an expected value for logit of adult survival of the omitted species. The Pearson correlation coefficient was then calculated between the directly estimated logit survival values and the LOOCV predicted values.

Validation test 2: Prediction of independent mark–recapture estimates of adult survival using covariates and model-averaged ordinary least squares regressions

We searched the literature for published estimates of annual adult survival rate made in southern Africa for species that breed there, according to Hockey *et al.* (2005), excluding non-native species. Only those published estimates that met the following criteria were included in our compilation: (1) the survival analysis accounted for incomplete detection of marked birds by an appropriate method for mark–recapture, mark–re-sighting or dead recovery data; (2) where data from both juvenile and adult birds were included in the analysis, the possible dependency of survival and recovery/recapture/re-sighting rates upon age was allowed for in the analyses; and (3) the data upon which the analyses were based were collected in Africa south of 15°S, but were not the same as or a subset of the dead recovery data used to make our survival estimates. Estimates that met these criteria were located for 38 species and were all based upon data obtained using mark–recapture methods. Two estimates available for *Acrocephalus baeticatus* were averaged. Nine of these estimates were for species for which we also had made estimates based upon dead recoveries, but the published estimates were based upon different data and thus could be considered independent of our estimates. These 38 estimates were of adult return rate rather than true survival, because some marked individuals might have permanently emigrated from the study area rather than died. This caveat applies less to estimates based upon dead recoveries, which are more likely to represent true survival rates, rather than return rates to study sites. Where the standard error of the untransformed survival rate SE_U was reported we took $(\text{logit}(\phi_A + SE_U) - \text{logit}(\phi_A - SE_U))/2$ as an approximation of the standard error of $\text{logit}(\phi_A)$.

Body mass, age at first breeding, clutch size, diet and mobility were determined for each of the 38 species as described above. The expected logit annual adult survival rate for each species was then calculated using its covariates and the regression models fitted to the dead recovery data for the 67 species. Pearson correlations between the published estimates and model predictions of logit survival rates were calculated.

RESULTS

Estimates of adult survival from dead recoveries

We made estimates of adult survival for the 84 species which met our criteria for inclusion in the analyses. Estimates for 67 of these species were sufficiently precise to be used in further regression analyses (Table 1). The adult survival estimates ranged from a maximum of 0·901 for Cape Gannet *Morus capensis* to a minimum of 0·240 for Cape Teal *Anas capensis*, with most values (48) falling between 0·5 and 0·8.

Ordinary least squares regression models of adult survival in relation to covariates

Thirty-two ordinary least squares regression models were fitted relating the logit of adult survival estimate for each of the 67 species to all possible combinations of the five covariates singly and in combination. The covariate values used for each species and the number of recoveries upon which the survival estimates were based are shown in Table S1 (Supplementary Information), whilst the performance of the top models is summarised in Table 2, with details of all models being given in Table S2 (Supplementary Information). Expected values obtained using model averaging across all models gave a Pearson correlation between observed and expected logit survival rates of 0·695 (Figure 1a). Model-averaged estimates of regression parameters and the relative importance of covariates are shown in Table 3.

Clutch size was the most important covariate, and had a strongly negative relationship with survival. Body mass was the next most important variable and had a positive relationship. The model with these two variables alone had the lowest AIC*c*, and the top five models with the lowest AIC*c* all included body mass and clutch size (Table 2). There was also a weak positive relationship of survival to age at first breeding and this variable was ranked third in terms of relative importance. Diet was the least important covariate, with a relative importance slightly less than half that of migratoriness.

Phylogenetic regression models of adult survival in relation to covariates

Thirty-two phylogenetic regression models were fitted relating the logit of adult survival estimate for each of the 67 species to all possible combinations of the five covariates singly and in combination. The performance of the top models is summarised in Table 2, with details of all models being given in

Table S3 (Supplementary Information). Expected values obtained using model averaging across all models gave a Pearson correlation between observed and expected logit survival rates of 0·712 (Figure 1b). Model-averaged estimates of regression parameters and the relative importance of covariates are shown in Table 4.

Clutch size was the most important covariate, and had a strongly negative relationship with survival. Body mass was the next most important variable and had a positive relationship. The model with these two variables alone had the lowest AIC*c*, and the top four models with the lowest AIC*c* all included body mass and clutch size (Table 2). There was a weak positive relationship of survival to age at first breeding and this variable was ranked third in terms of relative importance. Diet was nearly as important as age at first breeding with the relative importance of migratoriness being considerably lower.

Consistency of conclusions from ordinary least squares and phylogenetic regression models

Both ordinary least squares and phylogenetic regression methods identified clutch size, body mass and age at first breeding as the three most important covariates and agreed on their order. Model-averaged regression coefficients were also the same in sign and similar in magnitude for the two regression methods (compare Tables 3 and 4).

Ordinary least squares and phylogenetic regression disagreed on the relative importance of diet and migratoriness, though there was agreement that these were the two least important covariates. The model-averaged ordinary least squares regression model ranked the expected adult survival of the diet classes from lowest to highest in the following order: Granivore, Vegetative herbivore, Frugivore, Nectarivore, Invertebrate carnivore, Vertebrate carnivore, Omnivore. The ranking of these classes was the same for the phylogenetically adjusted PGLS model, except that the order of Vegetative herbivore and Frugivore was reversed. Hence, there was close agreement between the relationships of survival to diet estimated using the two regression methods (Spearman rank correlation coefficient, $r_S = 0.964$). However, the two regression methods did not agree on the pattern of modelled effects of migratoriness. The model-averaged ordinary least squares regression model ranked the expected adult survival of the migratoriness classes from lowest to highest in the following order: intra-African migrant, Resident, Mobile, whereas the phylogenetically adjusted PGLS model ranked them Resident, intra-African migrant, Mobile.

Mark–recapture estimates of survival from the literature

We identified eligible estimates of adult survival from the literature for 38 species of southern African birds (Table S4, Supplementary Information). Although we searched for estimates derived from dead recoveries and mark-recapture of live birds, all eligible estimates were from mark–recapture studies. They included estimates for nine species for which we also made estimates of adult survival from the analysis of dead recoveries (see Table 1 and Tables S1 & S4 (Supplementary Information)). There was a strong correlation ($r = 0.865$, one-tailed $P = 0.001$) between the independent literature-derived mark–recapture estimates of logit(ϕ_A) for the nine species and the estimates of logit(ϕ_A) that we derived from dead recoveries for the same species. The mark–recapture estimates were similar, on average, to the dead recovery estimates for the same species (means of logit(ϕ_A) back-transformed to ϕ_A: 0.710 for mark-recapture estimates and 0.697 for dead recovery estimates). There was no statistically significant difference between the two types of estimate (matched-pairs t test, $t_8 = 0.46$, two-tailed $P = 0.66$).

Validation test 1: Leave-one-out cross validation of the ordinary least squares regression models

The results of the LOOCV validation test are presented in Table 2, Figure 2 and in Tables S2 and S3 (Supplementary Information). The correlation between the observed logit(ϕ_A) values for a focal species and that expected from its covariates and model-averaged regression performed on all the other species was highly significant ($r = 0{\cdot}589$, one-tailed $P = < 0{\cdot}001$). Correlations between observed logit(ϕ_A) values and LOOCV expected values were statistically significant for 28 of the 31 models in the set, excluding the null model (Table S2, Supplementary Information).

Validation test 2: Prediction of independent mark–recapture estimates of adult survival using covariates and model-averaged ordinary least squares regressions

There was a strong correlation (*r* = 0.695, one-tailed *P* = 0.0006) between the independent literature-derived estimates of logit(ϕ_A) for 38 species from mark–recapture studies (see Table S4, Supplementary Information) and the expected values from the covariates for these species and the model-averaged regression fitted to the survival estimates from dead recoveries for 67 species (Figure 3). However, the mark–recapture estimates tended to be higher than the predictions based upon the models fitted to the dead recovery data by an average of 0.32 logit(ϕ_A) units. The means of logit(ϕ_A) back-transformed to ϕ_A were 0.690 for mark-recapture estimates and 0.617 for expected values for the same species from the regression. The mark–recapture estimate was higher than the expected value for 26 of the 38 species. The difference was highly significant (matched-pairs *t* test, $t_{37} = 3.78$, two-tailed *P* = 0.0005).

It can be argued that this validation test should exclude the nine species represented in both the SAFRING dead recovery data and the literature-derived mark–recapture estimates (see Table 1 for the identity of these species) because they are the same, even though the mark–recapture and dead recovery estimates for these species used different data. However, even when this exclusion was made, the correlation between observed values from the independent literature mark–recapture estimates for the remaining 29 species and the expected values from the model-averaged regression fitted to the survival estimates from dead recoveries remained highly significant (r = 0.663, one-tailed P = 0.0004).

Correlations between observed logit(ϕ_A) values from the literature and expected values from regression models derived from estimates from dead recoveries were statistically significant for 30 of the 31 models in the set, excluding the null model (Table S2, Supplementary Information).

Consistency of conclusions from the two independent validation tests of the ordinary least squares models

The pattern of variation in the degree of correlation between observed and expected values among regression models with different combinations of covariates was similar for the two validation tests. Table S2 (Supplementary Information) shows correlation coefficients between observed and expected logit(ϕ_A) values for 31 regression models for the two validation tests based upon LOOCV and upon the mark–recapture estimates from the literature, after excluding the null model. The correlation between these two sets of correlation coefficients for the two tests across the 31 models was high (r = 0.863, one-tailed P < 0.000001).

DISCUSSION

We obtained estimates of adult survival for 67 species of breeding birds of southern Africa from dead recoveries. For nine of these species, our estimates could be compared with previously published mark-recapture estimates of adult survival made in southern Africa for the same species. The two sets of estimates were similar to one another and highly correlated. We had expected that mark–recapture estimates would, if anything, be somewhat lower than those from dead recoveries because mark–recapture studies measure return rate rather than survival, and some adults may emigrate permanently from the study areas. However, this was not the case.

The main objective of this paper was to assess whether or not mean adult survival rates of bird species can be estimated reliably from values of demographic and ecological covariates that are available from accessible textbooks and databases. Our analyses of adult survival estimates for 67 species derived from dead recoveries of birds ringed in southern Africa indicate that regression models of survival with mean clutch size, mean body mass, mean age at first breeding, diet and migratoriness as predictor variables performed well in this regard, both when phylogenetic relatedness of the species was taken into account using PGLS and when it was not. Except for migratoriness, all covariates had relationships with survival that were similar for the two regression methods.

The two independent validation tests of our regression models are particularly informative in making an assessment of their usefulness. Good predictive power was indicated by high correlations of observed with expected values in a leave-one-out cross validation (LOOCV) test performed using data from the 67 species, and also for a validation test involving prediction from covariates and the regression using dead recoveries of annual survival rates from independent mark–recapture studies of 38 southern African species. Unexpectedly, despite their high correlation, the observed survival rates obtained from mark–recapture data were significantly higher than the expected values from the model based upon dead recoveries. We have no definitive explanation for this result. A previous comparison of mark-recapture and dead recovery estimates of adult survival for the same 19 species also indicated a tendency for the mark-recapture estimates to be higher (Saether 1989). The mark–recapture estimates for 27 of our 38 species came from a single study area in lowland Malawi (Peach *et al.* 2001), which is at a lower latitude (16°16'S), than the area of southern Africa where most of the birds contributing to the dead recovery analysis were ringed. It seemed possible that conditions at this site or in the region within which it was set may have been unusually favourable. However, the difference between mark-recapture estimates and expected values from the regression was similar for the results from Malawi and those from other parts of southern Africa, so this does not appear to be the correct explanation. Another possible explanation is that capture of birds for ringing in mark-recapture studies, which are usually done intensively at one or a few sites and sometimes for restricted periods of the year, such as the breeding season, selects individuals with higher than average survival prospects.

An assessment of the relative importance of the five covariates in our regression models, made using summed AIC_c weights, indicated that clutch size and body mass were the most influential covariates in the analyses, both with and without the inclusion of phylogenetic effects. Both regression methods identified the model with clutch size and body mass and no other covariates as that with the lowest AIC_c value. In addition, the model with just these two covariates ranked third in terms of the correlation between observed and expected values in the LOOCV validation test and second in the validation test using independent mark–recapture estimates of survival. In both of these tests the models with observed *vs.* expected correlation coefficients that ranked higher than that for the clutch size and body mass model did so only marginally.

The high importance of clutch size and body mass indicated by our analyses is convenient because these are the covariates that are most readily available for most species in most parts of the world from published sources and most likely to be reliable and robust against differences in interpretation. The information available on all of the other covariates is less reliable and more subject to variation due to differences in definitions than are clutch size and body mass. We note that mean age of first breeding is known from detailed field studies for relatively few species and many of the values for this covariate in the BirdLife database are extrapolated from those of related species. Our categorisations of diet and migratoriness were crude and different sources classify these variables in different ways. Given these shortcomings in the covariates age of first breeding, diet and migratoriness, we propose that adult survival could be estimated adequately just from clutch size and body mass using the ordinary least squares regression model $\mathrm{logit}(\phi_A) = 0.5419 + 0.1595 * \log_e(\text{body mass}) - 0.7246 * \log_e(\text{clutch size})$, where body mass is in grams. This is model m+c in the upper half of Table 2.

Clutch size, body mass and age at first breeding have been recognised for a long time as covarying with adult survival (Saether 1988; 1989) with the directions of the relationships found in previous studies being as found in our analysis. Such patterns may be the result of the evolution of optimal life histories in which a reduction in current fecundity is more likely to be compensated by increased reproductive success later in life if adult survival is high. Alternatively, survival may be reduced in species with large clutch size because of higher levels of competition for resources (Saether 1988).

There was substantial variation in observed survival rate that was not accounted for by our regression model, which suggests that inclusion of some variables that we overlooked or could not find data for might have improved model performance. We considered the possibility of including the likely degree to which species are killed deliberatley by humans as a covariate, though the absence of robust estimates of proportions of birds killed in the region precluded anything other than a simple expert-based measure. Based upon death rates from hunting and trapping of birds in Europe and North America, we intended to use expert opinion to assess whether more or less than 10% of all adult deaths of each southern African bird species were caused by deliberate killing as a crude measure of exposure to mortality due to these causes. However, advice from experts, especially Rob Little and Aldo Berruti (*in litt.*), was that the assessment would be difficult to make reliably, and also that few, if any, of the species included in our study would have more than 10% of adult deaths attributable to this cause. We therefore abandoned the idea of including this covariate. However, we note that one species with a low observed survival rate relative to the expected value from the ordinary least squares regression is the Red-billed Quelea *Quelea quelea*, a pest species subject to killing of large numbers of individuals to reduce crop damage. During parts of the period of our study, tens of millions of individuals of this species were killed per year using explosives and chemicals in South Africa (Garanito, Botha & van der Westhuizen 2000), so it is plausible that the proportion of adult deaths caused by deliberate killing might have exceeded 10% and that this contributed to the low observed survival rate. However, the size of the population and the proportion killed are unknown and the size of the cull has also varied over time, being lower in recent decades than in the 1990s, so no firm conclusion can be drawn about the impact of deliberate killing upon the long-term mean adult survival of this species.

Although our models performed well for southern African bird species, we do not propose that they should be used outside the region without further testing. Many previous studies have suggested that there is geographical variation in adult survival of birds, especially with regard to latitude. Species that breed in tropical and subtropical regions have been suggested to have higher survival rates than those breeding at higher latitudes (Cody 1971; MacArthur 1972; Ricklefs 1973; Murray 1985; Skutch 1985; Faaborg & Arendt 1995; Johnston *et al.* 1997; Francis *et al.* 1999; Jullien & Clobert 2000; Sandercock *et al.* 2000; de Swardt & Peach 2001; Ghalambor & Martin 2001; Peach *et al.* 2001). However, other authors have pointed out that this pattern does not always apply (Karr *et al.* 1990; McGregor *et al.* 2007). The differences in geographical patterns revealed by these studies suggest that it would be unwise to use a regression model relating survival to covariates fitted to data in one region to estimate survival from covariates in another region until the performance of such a model has been tested thoroughly. Ideally, a predictive regression model would be fitted using comparable survival estimates from as many regions as possible.

This study would not have been possible without the efforts of the large numbers of ringers who have contributed ringing records to SAFRING, and the many members of the public in southern Africa and elsewhere who have reported dead recoveries of ringed birds. Les Underhill and Michael Brooks at the Animal Demography Unit, University of Cape Town, are thanked for agreeing to our use of the data and for assisting in their provision, respectively. Andrew Bladon is thanked for helping to compile the phylogenetic tree. The advice of Rob Little and Aldo Berruti on the degree to which bird species are hunted in southern Africa is gratefully acknowledged. Stu Butchart of BirdLife International, Cambridge, kindly made available the BirdLife database from which covariate values were obtained for species where these were not available from Roberts Birds of Southern Africa. The research was supported by a research grant from the Leverhulme Trust (F/00 128/BI). RA was supported by the South African National Research Foundation.

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Supplementary Information

Figure S1. Phylogenetic tree of the 67 southern African bird species used in the comparative analysis. The phylogeny is based on Sibley and Ahlquist (1990), with additional information taken from Brown *et al.* (1982), Keith *et al.* (1992), Fry et al. (2004), del Hoyo *et al.* (1992-2009), Gonzalez *et al.* (2009), and Johnson & Sorenson (1999). We made the assumption that all branches in the phylogeny were of equal length.

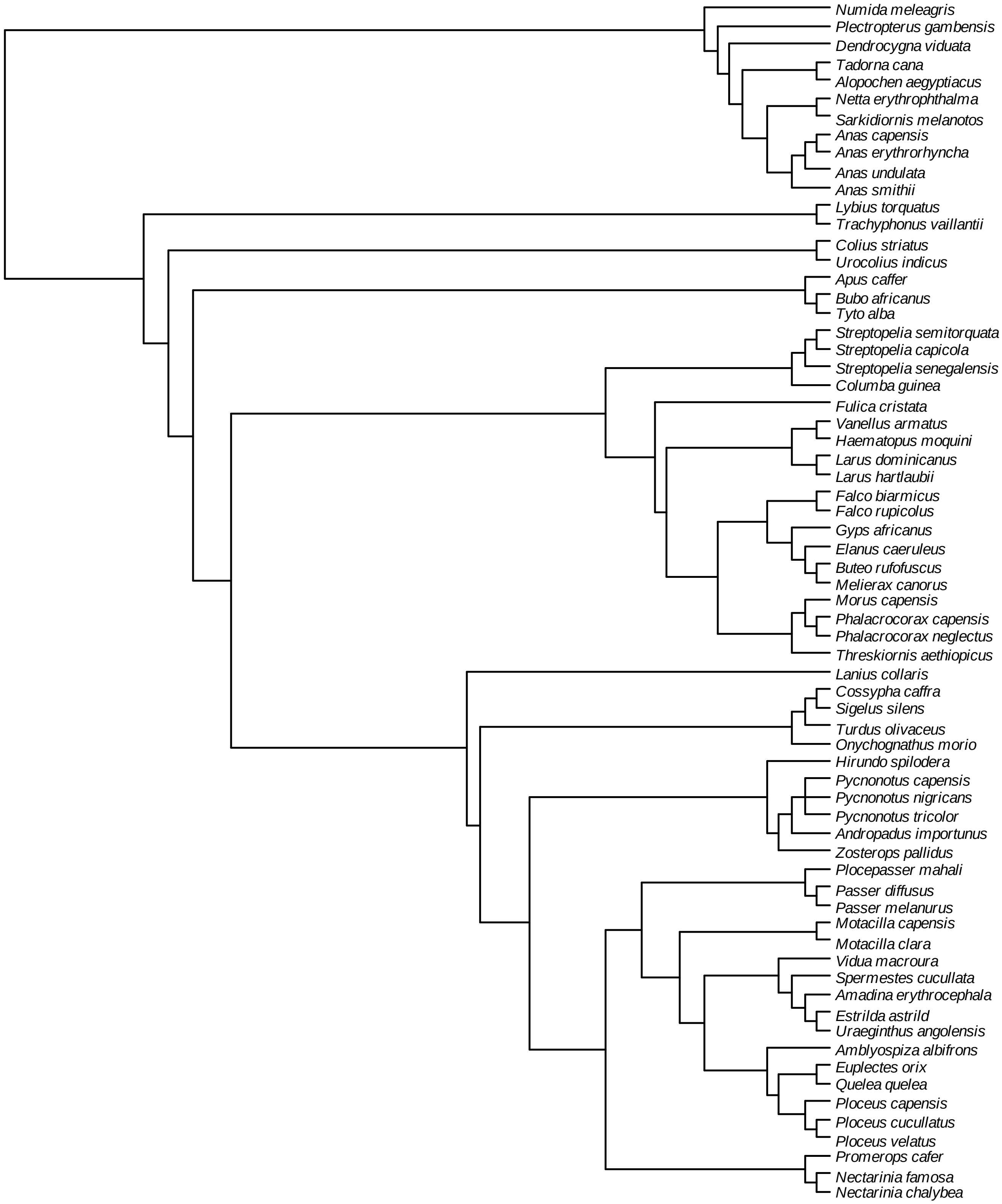

Table S1: Numbers of dead recoveries as adults (*n*) and covariate values for 67 species for which estimates of adult survival rate (ϕ_A) were made using dead recoveries from SAFRING

SAFRING No.	English name	Scientific name	*n*	m[a]	c[b]	fb[c]	d[d]	mv[e]	logit ϕ_A
44	Cape Gannet	*Morus capensis*	225	7.878534196	0	1.252763	1	2	2.210405
48	Cape Cormorant	*Phalacrocorax capensis*	47	7.106606138	0.85866162	0.952009	1	2	1.402561
49	Bank Cormorant	*Phalacrocorax neglectus*	19	7.575584652	0.70309751	0.916291	1	1	0.346259
81	African Sacred (Sacred) Ibis	*Threskiornis aethiopicus*	18	7.390181428	0.83290912	1.098612	5	2	0.948632
88	Spur-winged Goose	*Plectropterus gambensis*	42	8.407378325	2.37954613	1.098612	3	2	-0.15004
89	Egyptian Goose	*Alopochen aegyptiacus*	132	7.595889918	1.99061033	0.693147	2	2	0.236942
90	South African Shelduck	*Tadorna cana*	64	7.122866659	1.94591015	1.098612	3	2	0.902924
91	Comb Duck	*Sarkidiornis melanotos*	20	7.339537695	2.2512918	0.693147	3	3	0.511551
94	Cape Shoveler	*Anas smithii*	27	6.401917197	2.19722458	0.068993	3	3	0.659731
96	Yellow-billed Duck	*Anas undulata*	575	6.795705775	2.05412373	0.068993	3	2	0.410051
97	Red-billed Teal (Duck)	*Anas erythrorhyncha*	180	6.385194399	2.20827441	0.068993	3	2	0.371287
98	Cape Teal	*Anas capensis*	182	5.996452089	1.97408103	0.068993	3	2	-1.15224
100	White-faced (Whistling-) Duck	*Dendrocygna viduata*	26	6.549650742	2.35137526	0	2	2	-0.46627
102	Southern Pochard	*Netta erythrophthalma*	114	6.706862337	2.21920348	0	3	2	0.00932
107	African White-backed Vulture	*Gyps africanus*	21	8.61974978	0	1.791759	1	1	1.611792
114	Lanner Falcon	*Falco biarmicus*	13	6.380800273	1.25276297	0.693147	1	3	0.912395
123	Rock Kestrel	*Falco rupicolus*	18	5.375278408	1.20447268	0	1	2	1.167208
130	Black-shouldered (Winged) Kite	*Elanus caeruleus*	36	5.512420173	1.24990174	0.693147	1	2	0.477596
152	Jackal Buzzard	*Buteo [augur] rufofuscus*	62	7.060476366	0.68309684	1.098612	1	2	1.726
165	Southern Pale Chanting Goshawk	*Melierax canorus*	116	6.711740395	0.64185389	1.098612	1	2	1.899368
192	Helmeted Guineafowl	*Numida meleagris*	40	7.207859871	2.30258509	0.693147	3	1	-0.08922
212	Red-knobbed Coot	*Fulica cristata*	551	6.602587892	1.48160454	0	2	2	-0.33436
231	African Black Oystercatcher	*Haematopus moquini*	39	6.549650742	0.65232519	1.386294	5	2	1.42397
245	Blacksmith Lapwing	*Vanellus armatus*	13	5.093750201	1.25276297	0.650588	5	2	0.609427
287	Kelp Gull	*Larus dominicanus* (incl. *vetula)*	71	6.915227294	0.74193734	1.386294	3	2	1.849173
289	Hartlaub's Gull	*Larus hartlaubii*	34	5.631211782	0.58778666	1.098612	3	2	0.937726
311	Speckled (Rock) Pigeon	*Columba guinea*	34	5.840641657	0.69314718	0	6	1	0.56453
314	Red-eyed Dove	*Streptopelia semitorquata*	33	5.529429088	0.60431597	0	6	1	0.529258
316	Cape Turtle-dove	*Streptopelia capicola*	74	5.029784113	0.64185389	0	6	1	0.480221
317	Laughing Dove	*Streptopelia senegalensis*	446	4.620058798	0.67803354	0	6	1	0.073673
359	Barn Owl	*Tyto alba*	21	5.811140993	1.75785792	0	1	1	0.216279
368	Spotted Eagle-Owl	*Bubo africanus*	41	6.54534966	0.95551145	1.041454	1	1	-0.20625
383	White-rumped Swift	*Apus caffer*	13	3.18221184	0.66782937	1.386294	5	3	0.595735
390	Speckled Mousebird	*Colius striatus*	39	4.007333185	1.09861229	0.405465	7	2	0.160021
392	Red-faced Mousebird	*Urocolius indicus*	29	4.028916757	0.95551145	0	7	2	0.080684

Table S1 (continued)

SAFRING No.	English name	Scientific name	*n*	m[a]	c[b]	fb[c]	d[d]	mv[e]	logit ϕ_A
431	Black-collared Barbet	*Lybius torquatus*	26	3.988984047	1.19392247	0.405465	7	1	-0.19679
439	Crested Barbet	*Trachyphonus vaillantii*	31	4.298645026	1.25276297	0.405465	3	2	0.565785
504	South African Cliff-Swallow	*Hirundo spilodera*	230	3.025291076	0.87546874	0	5	3	-0.48119
543	Cape Bulbul	*Pycnonotus capensis*	46	3.653252276	1.00795792	0	7	1	0.525273
544	African Red-eyed Bulbul	*Pycnonotus nigricans*	49	3.42751469	0.95551145	0	7	2	0.516291
545	Dark-capped (Black-eyed) Bulbul	*Pycnonotus tricolor*	114	3.618993327	0.97455964	0	7	1	0.899565
551	Sombre Greenbul	*Andropadus importunus*	16	3.575150689	0.70309751	0	7	1	0.628812
553	Olive Thrush (pre-split)	*Turdus olivaceus*	141	4.192680463	1.06471074	0	3	2	0.615964
581	Cape Robin-Chat	*Cossypha caffra*	82	3.346389145	0.91629073	0	3	2	0.929333
665	Fiscal Flycatcher	*Sigelus silens*	19	3.265759411	1.02961942	0	5	1	0.537368
686	Cape Wagtail	*Motacilla capensis*	18	3.04927304	1.09861229	0	5	1	0.722421
688	Mountain (Long-tailed) Wagtail	*Motacilla clara*	15	2.975529566	0.83290912	0	5	1	1.11543
707	Common Fiscal	*Lanius collaris*	31	3.708682081	1.25276297	0.305382	3	1	0.472943
745	Red-winged Starling	*Onychognathus morio*	76	4.905274778	1.09861229	0.182322	3	1	0.868964
749	Cape Sugarbird	*Promerops cafer*	24	3.545297726	0.69314718	0.693147	4	2	0.518513
751	Malachite Sunbird	*Nectarinia [Cinnyris] famosa*	14	2.859339649	0.69314718	0	4	2	0.518941
760	Southern Double-collared Sunbird	*Nectarinia [Cinnyris] chalybea [chalybeus]*	26	2.079441542	0.78845736	0	4	1	0.781717
775	Cape White-eye (pre-split)	*Zosterops pallidus*	131	2.388762789	1.09861229	0	3	1	0.278017
780	White-browed Sparrow-weaver	*Plocepasser mahali*	19	3.850147602	0.69314718	0	6	1	0.224863
786	Cape Sparrow	*Passer melanurus*	215	3.384390263	1.28093385	0	6	2	0.316373
787	Greyheaded Sparrow (pre-split)	*Passer diffusus*	30	3.186352633	1.25276297	0	6	2	0.0136
797	Village (Spotted-backed) Weaver	*Ploceus cucullatus*	103	3.620332912	0.95551145	0.405465	3	2	0.687857
799	Cape Weaver	*Ploceus capensis*	125	3.815512105	0.95551145	0.405465	6	2	0.639454
803	Southern Masked-Weaver	*Ploceus velatus*	403	3.521938999	0.95551145	0.405465	6	2	0.522191
804	Thick-billed (Grosbeak) Weaver	*Amblyospiza albifrons*	20	3.827553849	1.13140211	0.405465	6	2	0.559384
805	Red-billed Quelea	*Quelea quelea*	302	2.952302716	1.02961942	0.405465	6	3	-1.09648
808	Southern Red (Red) Bishop	*Euplectes orix*	131	3.139832618	1.09861229	0.405465	6	2	0.37634
820	Red-headed Finch	*Amadina erythrocephala*	31	3.117949906	1.43508453	0	6	2	-0.32244
823	Bronze Mannikin	*Spermestes (Lonchura) cucullata*	48	2.282382386	1.5260563	0	6	1	-1.08755
839	Blue Waxbill	*Uraeginthus angolensis*	22	2.292534757	1.25276297	0	6	1	0.262456
843	Common Waxbill	*Estrilda astrild*	24	2.098017927	1.64865863	0	6	1	-0.37038
846	Pin-tailed Whydah	*Vidua macroura*	17	2.708050201	1.13140211	0	6	1	0.562972

[a] log$_e$ body mass (g); [b] log$_e$ clutch size; [c] log$_e$ age at first breeding (yr); [d] diet category (coded as follows: 1. vertebrate carnivore; 2. vegetative herbivore; 3. omnivore; 4. nectarivore; 5. invertebrate carnivore; 6. granivore; and 7. frugivore); [e] movement category ('migratoriness', coded as follows: 1. resident; 2. mobile (local or partial migrants and nomads); and 3. intra-African migrant).

Table S2. Performance of 32 regression models relating the logit of adult survival of 67 species of birds, estimated from dead recoveries, to all possible combinations of the following five covariates: m = $\log_e$(mean body mass); c = $\log_e$ (mean clutch size); fb = $\log_e$ (mean age at first breeding); d = diet category; mv = migratoriness category. Models are ranked in order of their Δ AICc values. The Pearson correlation coefficient *r* is shown between the logit of observed adult survival and the expected value from each model for the full data set (real data). Observed *vs*. expected Pearson correlation coefficients are also shown for two validation tests using independent data; one for observed values for the 67 species *vs*. leave-one-out-cross-validation (LOOCV) expected values, and another for logit (ϕ_A) values from mark–recapture estimates reported in the literature for 38 southern African species (Table S4) in relation to expected values for those species from their covariates and the model-averaged regression fitted to data for the 67 species. The statistical significance of the *r* values from the validation tests is shown as * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, all tests being one-tailed.

Model specification	Δ AIC$_c$	Real data *r*	LOOCV *r*	Literature test *r*
m+c	0.00	0.667	0.626***	0.695***
m+c+fb	1.04	0.675	0.622***	0.683***
m+c+mv	2.00	0.683	0.595***	0.663***
m+c+fb+mv	3.41	0.690	0.587***	0.653***
m+c+d	4.00	0.728	0.641***	0.724***
c+fb	5.11	0.633	0.589***	0.708***
m+c+d+mv	5.75	0.747	0.619***	0.706***
c+fb+mv	6.49	0.656	0.549***	0.605***
m+c+fb+d	6.69	0.729	0.629***	0.722***
c+fb+d	7.06	0.713	0.616***	0.699***
c+d	7.35	0.697	0.606***	0.679***
c+d+mv	7.62	0.725	0.589***	0.668***
c+fb+d+mv	8.41	0.735	0.592***	0.684***
m+c+fb+d+mv	8.75	0.748	0.604***	0.704***
c+mv	16.07	0.564	0.438***	0.531***
c	17.08	0.509	0.460***	0.624***
fb	18.46	0.493	0.441***	0.538***
fb+mv	19.70	0.529	0.424***	0.484**
m+fb	20.71	0.493	0.411***	0.540***
m+fb+mv	22.11	0.529	0.398***	0.501**
fb+d	23.15	0.591	0.460***	0.675***
fb+d+mv	23.44	0.632	0.470***	0.618***
m+fb+d	25.83	0.592	0.444***	0.680***
m+fb+d+mv	26.40	0.632	0.455***	0.620**
d+mv	27.65	0.576	0.410***	0.489**
m+d	27.90	0.549	0.408***	0.668***
d	28.09	0.520	0.385***	0.576***
m+d+mv	28.39	0.594	0.424***	0.516**
m	30.32	0.311	0.202	0.555***
m+mv	33.10	0.348	0.170	0.421**
null	34.94	0.000	0.000	0.000
mv	36.63	0.201	-0.041	-0.085
Model averaged	-	0.695	0.589***	0.695***

Table S3. Performance of 32 phylogenetic generalised least squares (PGLS) models relating the logit of adult survival of 67 species of birds, estimated from dead recoveries, to all possible combinations of five covariates. See Table S2 for variable codes. Models are ranked in order of their Δ AICc values. The Pearson correlation coefficient *r* is shown between the logit of observed adult survival and the expected value from each model for the full data set.

Model specification	Δ AIC_c	*r*
m+c	0	0.666
m+c+d	0.72	0.724
m+c+fb	0.85	0.674
m+c+mv	2.16	0.678
c+fb	2.56	0.627
m+c+fb+d	3.48	0.724
m+c+d+mv	3.50	0.739
m+c+fb+mv	3.58	0.684
c+d	3.84	0.692
c+fb+d	4.30	0.707
c+d+mv	5.54	0.717
c+fb+mv	6.23	0.651
c	6.24	0.509
m+c+fb+d+mv	6.47	0.739
c+fb+d+mv	6.84	0.726
c+mv	9.39	0.551
fb	9.46	0.493
m+fb	11.65	0.493
fb+mv	12.79	0.515
m+fb+mv	15.07	0.515
null	15.99	0.000
m	16.82	0.311
fb+d	17.71	0.554
d	19.39	0.448
mv	19.48	0.166
m+fb+d	20.36	0.552
m+mv	20.46	0.309
m+d	20.71	0.476
fb+d+mv	21.22	0.593
d+mv	22.49	0.519
m+fb+d+mv	24.09	0.593
m+d+mv	24.26	0.526
Model averaged	-	0.712

Table S4. Mark–recapture estimates of adult survival of southern African birds obtained from the literature and values of covariates used to estimate their survival using a regression model. Species marked with an asterisk also have independent estimates of survival derived from dead recoveries (see Table 1).

Species	ϕ_A	s.e. of logit ϕ_A	Mean body mass (g)	Mean clutch size	Mean age at first breeding (yr)	Diet	Migratoriness	Source
Anthropoides paradiseus	0.875	0.31	4870	1.87	4.5	Omnivore	Mobile	Altwegg & Anderson (2009)
*Larus dominicanus**	0.840	0.23	1008	2.1	4	Omnivore	Mobile	Altwegg *et al.* (2007)
Sterna balaenarum	0.870	0.45	51.8	1	3.2	Vertebrate carnivore	Intra-African migrant	Braby *et al.* (2011)
Falco peregrinus	0.852	0.24	628.8	3	2	Vertebrate carnivore	Mobile	Altwegg *et al.* (2014)
*Morus capensis**	0.886	0.18	2640	1	3.5	Vertebrate carnivore	Mobile	Altwegg *et al.* (2008)
Spheniscus demersus	0.731	0.06	3135	1.82	4	Vertebrate carnivore	Mobile	Crawford *et al.* (2011)
Hirundo smithii	0.635	0.40	13.4	2.9	1	Invertebrate carnivore	Mobile	Peach *et al.* (2001)
*Pycnonotus tricolor**	0.743	0.20	37.3	2.65	1	Omnivore	Resident	Peach *et al.* (2001)
Phyllastrephus terrestris	0.737	0.23	31.8	2.13	1	Invertebrate carnivore	Resident	Peach *et al.* (2001)
*Andropadus importunus**	0.681	0.15	35.7	2.02	1	Frugivore	Resident	Peach *et al.* (2001)
Sylvietta rufescens	0.795	0.45	11.6	1.8	1	Invertebrate carnivore	Resident	Peach *et al.* (2001)
Acrocephalus baeticatus	0.765 0.670	0.39 0.47	9.5	2.4	1	Invertebrate carnivore	Intra-African migrant	Peach *et al.* (2001) Jansen *et al.* (2014)
Acrocephalus gracilirostris	0.557	0.36	18.6	2.3	1	Invertebrate carnivore	Mobile	Peach *et al.* (2001)
Apalis flavida	0.680	0.33	8.2	2.9	1	Invertebrate carnivore	Resident	Peach *et al.* (2001)
Camaroptera brachyura	0.735	0.32	11.3	2.39	1	Invertebrate carnivore	Mobile	Peach *et al.* (2001)
Cisticola erythrops	0.529	0.32	14.9	2.7	1	Invertebrate carnivore	Resident	Peach *et al.* (2001)
Prinia subflava	0.598	0.34	9.0	3.1	0.915	Invertebrate carnivore	Resident	Peach *et al.* (2001)
*Motacilla clara**	0.688	0.07	19.6	2.3	1	Invertebrate carnivore	Resident	Piper (2002)
Cossypha heuglini	0.833	0.54	34.9	2	1	Invertebrate carnivore	Resident	Peach *et al.* (2001)
Promerops gurneyi	0.807	0.39	35.3	1.6	2	Nectarivore	Mobile	de Swardt & Peach (2001)
*Promerops cafer**	0.620	0.43	34.7	2	2	Nectarivore	Mobile	Altwegg & Underhill (2006)
Chalcomitra senegalensis	0.903	1.29	13.6	2	1	Nectarivore	Mobile	Peach *et al.* (2001)
Hedidypna collaris	0.757	0.42	7.6	2.2	1	Nectarivore	Resident	Peach *et al.* (2001)
Cinnyris bifasciatus	0.761	0.50	7.2	1.8	1	Nectarivore	Mobile	Peach *et al.* (2001)
Cinnyris cupreus	0.599	0.29	9.7	1.8	1	Nectarivore	Resident	Peach *et al.* (2001)
Cinnyris venustus	0.549	0.32	6.9	1.8	1	Nectarivore	Resident	Peach *et al.* (2001)
Philetairus socius	0.662	0.08	27.4	3.54	1	Granivore	Resident	Covas *et al.* (2004)
Ploceus xanthopterus	0.696	0.12	23.8	2.4	1.5	Omnivore	Resident	Peach *et al.* (2001)
*Euplectes orix**	0.715	0.22	23.1	3	1.5	Granivore	Mobile	Peach *et al.* (2001)
Euplectes capensis	0.540	0.36	34.0	2.9	1.5	Granivore	Resident	Peach *et al.* (2001)
Pytilia melba	0.519	0.16	11.9	3.3	1	Omnivore	Mobile	Peach *et al.* (2001)
Lagonosticta senegala	0.228	0.61	8.9	3.4	1	Granivore	Mobile	Peach *et al.* (2001)
Lagonosticta rhodopareia	0.499	0.23	9.3	3.9	1	Granivore	Mobile	Peach *et al.* (2001)
*Uraeginthus angolensis**	0.466	0.37	9.9	3.5	1	Granivore	Mobile	Peach *et al.* (2001)
*Estrilda astrild**	0.612	0.21	8.2	5.2	1	Granivore	Mobile	Peach *et al.* (2001)
Vidua chalybeata	0.542	0.49	13.2	3	1	Granivore	Mobile	Peach *et al.* (2001)
Crithagra mozambicus	0.648	0.37	13.3	3.2	1	Granivore	Mobile	Peach *et al.* (2001)
Crithagra sulphuratus	0.522	0.28	18.2	2.8	1	Granivore	Mobile	Peach *et al.* (2001)

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TABLES

Table 1. Estimates of the annual survival rate ϕ_A of adults of 67 southern African bird species, based upon dead recoveries reported to the SAFRING ringing scheme. Species marked with an asterisk also have independent estimates of survival derived from published mark–recapture studies (see Table S4 (Supplementary Information).

Scientific name	ϕ_A	s.e. of logit ϕ_A	Scientific name	ϕ_A	s.e. of logit ϕ_A
*Morus capensis**	0.901	0.13	*Urocolius indicus*	0.520	0.29
Phalacrocorax capensis	0.803	0.17	*Lybius torquatus*	0.451	0.34
Phalacrocorax neglectus	0.586	0.31	*Trachyphonus vaillantii*	0.638	0.28
Threskiornis aethiopicus	0.721	0.25	*Hirundo spilodera*	0.382	0.11
Plectropterus gambensis	0.463	0.23	*Pycnonotus capensis*	0.628	0.21
Alopochen aegyptiaca	0.559	0.12	*Pycnonotus nigricans*	0.626	0.22
Tadorna cana	0.712	0.15	*Pycnonotus tricolor**	0.711	0.14
Sarkidiornis melanotos	0.625	0.28	*Andropadus importunus**	0.652	0.38
Anas smithii	0.659	0.24	*Turdus olivaceus*	0.649	0.12
Anas undulata	0.601	0.05	*Cossypha caffra*	0.717	0.17
Anas erythrorhyncha	0.592	0.10	*Sigelus silens*	0.631	0.35
Anas capensis	0.240	0.15	*Motacilla capensis*	0.673	0.33
Dendrocygna viduata	0.386	0.34	*Motacilla clara**	0.753	0.36
Netta erythrophthalma	0.502	0.13	*Lanius collaris*	0.616	0.27
Gyps africanus	0.834	0.32	*Onychognathus morio*	0.705	0.17
Falco biarmicus	0.713	0.38	*Promerops cafer**	0.627	0.28
Falco rupicolus	0.763	0.33	*Nectarinia famosa*	0.627	0.37
Elanus caeruleus	0.617	0.23	*Cinnyris chalybeus*	0.686	0.28
Buteo rufofuscus	0.849	0.21	*Zosterops capensis*	0.569	0.13
Melierax canorus	0.870	0.17	*Plocepasser mahali*	0.556	0.37
Numida meleagris	0.478	0.23	*Passer melanurus*	0.578	0.10
Fulica cristata	0.417	0.07	*Passer diffusus*	0.503	0.28
Haematopus moquini	0.806	0.25	*Ploceus cucullatus*	0.665	0.14
Vanellus armatus	0.648	0.39	*Ploceus capensis*	0.655	0.13
*Larus dominicanus**	0.864	0.34	*Ploceus velatus*	0.628	0.07
Larus hartlaubii	0.719	0.28	*Amblyospiza albifrons*	0.636	0.34
Columba guinea	0.638	0.24	*Quelea quelea*	0.250	0.12
Streptopelia semitorquata	0.629	0.28	*Euplectes orix**	0.593	0.13
Streptopelia capicola	0.618	0.17	*Amadina erythrocephala*	0.420	0.32
Streptopelia senegalensis	0.518	0.07	*Spermestes cucullatus*	0.252	0.30
Tyto alba	0.554	0.36	*Uraeginthus angolensis**	0.565	0.35
Bubo africanus	0.449	0.25	*Estrilda astrild**	0.408	0.35
Apus caffer	0.645	0.38	*Vidua macroura*	0.637	0.34
Colius striatus	0.540	0.26			

Table 2. Performance of the best (lowest AIC_c) ten regression models relating the logit of adult survival of 67 species of birds, estimated from dead recoveries, to all possible combinations of the following five covariates: m = $\log_e$(mean body mass); c = $\log_e$ (mean clutch size); fb = $\log_e$ (mean age at first breeding); d = diet category; mv = migratoriness category. The upper part of the table shows results from ordinary least squares regression and the lower part those from PGLS regression, which allows for phylogenetic relationships. Models are ranked in order of their Δ AICc values. The Pearson correlation coefficient *r* is shown between the logit of observed adult survival and the expected value from each model for the full data set (real data). For the ordinary least squares regressions, observed *vs.* expected Pearson correlation coefficients are also shown for two validation tests using independent data; one for observed values for the 67 species *vs.* leave-one-out-cross-validation (LOOCV) expected values, and another for logit (ϕ_A) values from mark–recapture estimates reported in the literature for 38 southern African species (Table S4) in relation to expected values for those species from their covariates and the model-averaged regression fitted to data for the 67 species. The statistical significance of the *r* values from the validation tests is shown as * = *P* <0.05, ** = *P* <0.01, *** = *P* <0.001, all tests being one-tailed.

Model specification	Δ AIC_c	Real data *r*	LOOCV *r*	Literature test *r*
Ordinary least squares regression				
m+c	0.00	0.667	0.626***	0.695***
m+c+fb	1.04	0.675	0.622***	0.683***
m+c+mv	2.00	0.683	0.595***	0.663***
m+c+fb+mv	3.41	0.690	0.587***	0.653***
m+c+d	4.00	0.728	0.641***	0.724***
c+fb	5.11	0.633	0.589***	0.708***
m+c+d+mv	5.75	0.747	0.619***	0.706***
c+fb+mv	6.49	0.656	0.549***	0.605***
m+c+fb+d	6.69	0.729	0.629***	0.722***
c+fb+d	7.06	0.713	0.616***	0.699***
Model averaged	-	0.695	0.589***	0.695***
PGLS regression				
m+c	0	0.666	-	-
m+c+d	0.72	0.724	-	-
m+c+fb	0.85	0.674	-	-
m+c+mv	2.16	0.678	-	-
c+fb	2.56	0.627	-	-
m+c+fb+d	3.48	0.724	-	-
m+c+d+mv	3.50	0.739	-	-
m+c+fb+mv	3.58	0.684	-	-
c+d	3.84	0.692	-	-
c+fb+d	4.30	0.707	-	-
Model averaged	-	0.712	-	-

Table 3. Parameter estimates for the ordinary least squares regression of the logit of adult survival of 67 species of birds, estimated from dead recoveries, on covariates. Values were averaged over models with all possible combinations of covariates using AIC_c weights. Coefficients for diet and migratoriness represent estimated differences in the log-odds of survival between the category shown and the reference category (Vertebrate carnivore for diet and Resident for migratoriness). Also shown is the relative importance of each covariate, obtained by model averaging across models with all possible combinations of five covariates.

Parameter	Coefficient value	Lower C.L.	Upper C.L.	Relative importance
Intercept	0.626	0.101	1.151	-
log(mean body mass)	0.128	0.022	0.234	0.919
log(mean clutch size)	-0.692	-0.955	-0.429	1.000
log(mean age at first breeding)	0.089	-0.200	0.377	0.380
Diet	-	-	-	0.128
Vertebrate carnivore	0.000	-	-	-
Vegetative herbivore	-0.064	-0.313	0.186	-
Omnivore	0.004	-0.060	0.069	-
Nectarivore	-0.030	-0.189	0.129	-
Invertebrate carnivore	-0.016	-0.114	0.082	-
Granivore	-0.065	-0.301	0.172	-
Frugivore	-0.043	-0.217	0.132	-
Migratoriness	-	-	-	0.268
Resident	0.000	-	-	-
Mobile	0.049	-0.122	0.220	-
Intra-African migrant	-0.022	-0.182	0.138	-

Table 4. Parameter estimates for phylogenetic generalised least squares (PGLS) models of the logit of adult survival of 67 species of birds, estimated from dead recoveries, in relation to covariates. Values were averaged over models with all possible combinations of covariates using AIC_c weights. Conventions are as given in the legend for Table 3. Also shown is the relative importance of each covariate, obtained by model averaging across models with all possible combinations of five covariates.

Parameter	Coefficient value	95% confidence limits		Relative importance
		Lower	Upper	
Intercept	0.745	0.057	1.433	-
log(mean body mass)	0.098	0.014	0.182	0.814
log(mean clutch size)	-0.685	-0.955	-0.415	0.996
log(mean age at first breeding)	0.076	-0.088	0.240	0.381
Diet	-	-	-	0.362
Vertebrate carnivore	0.000	-	-	-
Vegetative herbivore	-0.122	-0.386	0.142	-
Omnivore	0.044	-0.122	0.210	-
Nectarivore	-0.058	-0.345	0.228	-
Invertebrate carnivore	-0.036	-0.229	0.157	-
Granivore	-0.160	-0.423	0.104	-
Frugivore	-0.151	-0.411	0.109	-
Migratoriness	-	-	-	0.218
Resident	0.000	-	-	-
Mobile	0.040	-0.041	0.121	-
intra-African migrant	0.018	-0.082	0.119	-

FIGURE LEGENDS

Figure 1. Observed values of the logit of adult survival of 67 species of birds, estimated from dead recoveries, in relation to the expected value obtained by averaging over regression models of survival in relation to covariates using AIC_c weights. Each point represents one species. The diagonal line shows the result expected if observed and expected values were equal. (a) Model-averaged expected results estimated from ordinary least squares regression, $r = 0.695$. (b) Model-averaged expected results estimated from phylogenetic generalised least squares (PGLS) models, $r = 0.712$.

Figure 2. Observed values of the logit of adult survival of 67 species of birds, estimated from dead recoveries, in relation to the expected value obtained by averaging over ordinary least squares regression models of survival fitted to all the data, except those for the species for which the expected value was being calculated, using AIC_c weights (leave-one-out-cross-validation, LOOCV). Each point represents one species. The diagonal line shows the result expected if observed and expected values were equal. $r = 0.589$.

Figure 3. Observed values of the logit of adult survival of 38 species of southern African birds, estimated from mark–recapture studies, in relation to the expected values obtained from covariates for these species and the model-averaged ordinary least squares regression model of survival fitted to estimates derived from dead recoveries for 67 species. Each point represents one species. Vertical lines show ±1 S.E.. The diagonal line shows the result expected if observed and expected values were equal. Filled circles show results for nine species with estimates available from both mark–recapture and dead recovery data. For all species, $r = 0.695$. After excluding the species with estimates from both types of data, $r = 0.663$.

Figure 1. Observed values of the logit of adult survival of 67 species of birds, estimated from dead recoveries, in relation to the expected value obtained by averaging over regression models of survival in relation to covariates using AIC$_c$ weights. Each point represents one species. The diagonal line shows the result expected if observed and expected values were equal. (a) Model-averaged expected results estimated from ordinary least squares regression, *r* = 0.695. (b) Model-averaged expected results estimated from phylogenetic generalised least squares (PGLS) models, *r* = 0.712.

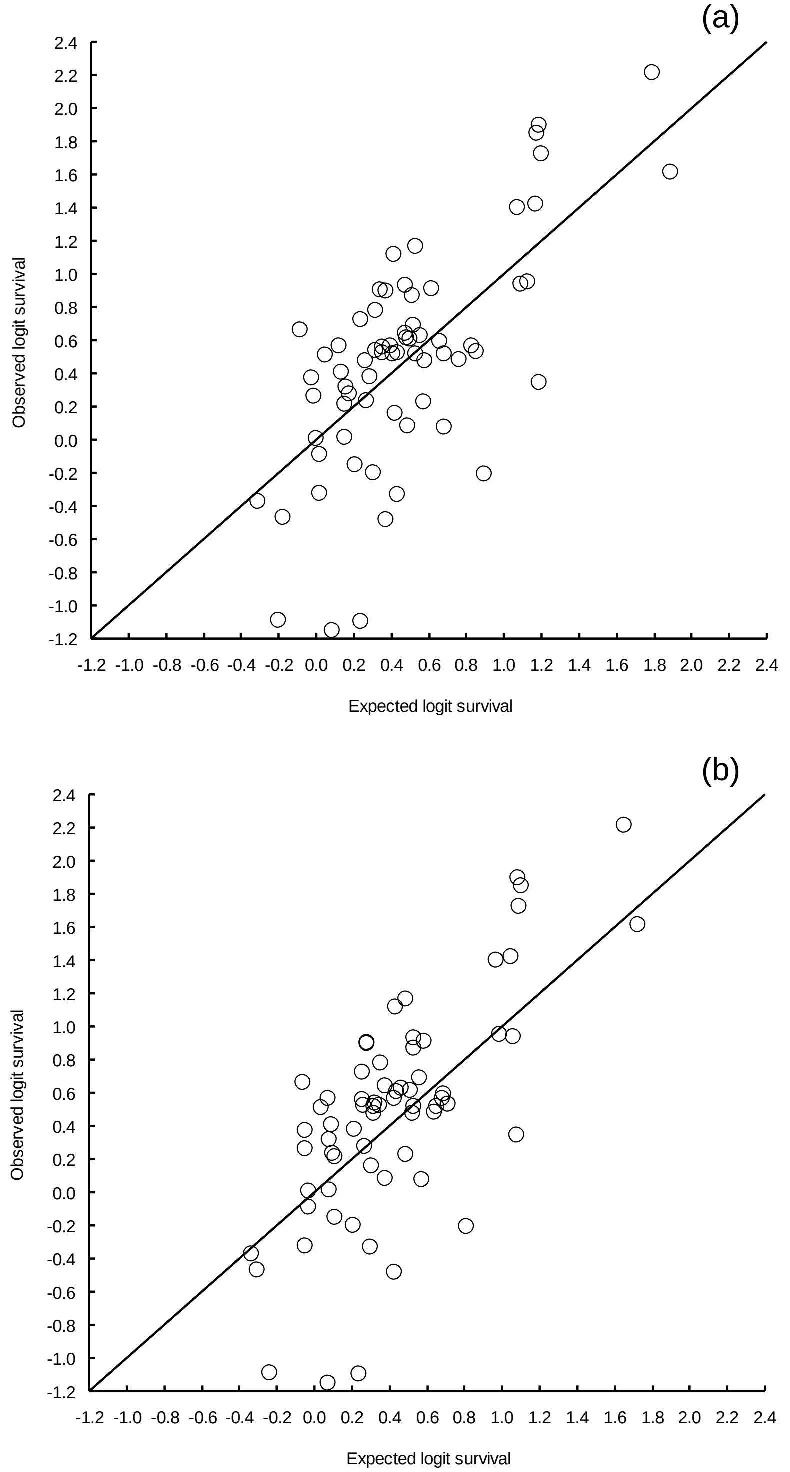

Figure 2. Observed values of the logit of adult survival of 67 species of birds, estimated from dead recoveries, in relation to the expected value obtained by averaging over ordinary least squares regression models of survival fitted to all the data, except those for the species for which the expected value was being calculated, using AIC$_c$ weights (leave-one-out-cross-validation, LOOCV). Each point represents one species. The diagonal line shows the result expected if observed and expected values were equal. $r = 0.589$.

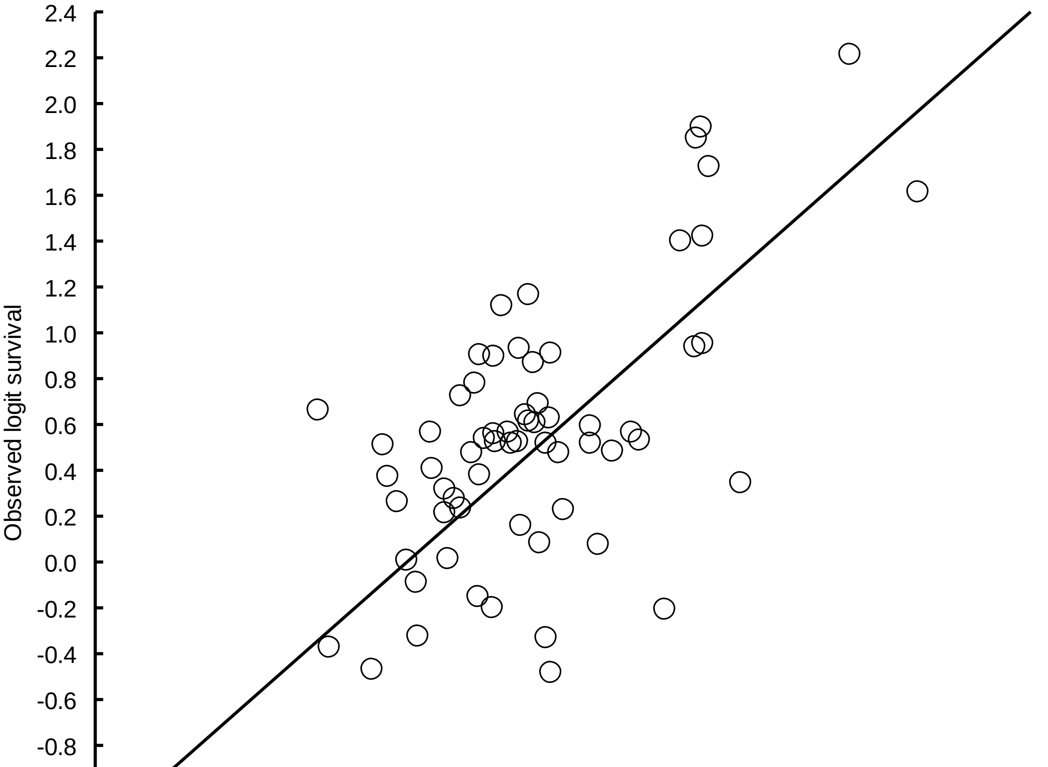

Figure 3. Observed values of the logit of adult survival of 38 species of southern African birds, estimated from mark–recapture studies, in relation to the expected values obtained from covariates for these species and the model-averaged ordinary least squares regression model of survival fitted to estimates derived from dead recoveries for 67 species. Each point represents one species. Vertical lines show ±1 S.E.. The diagonal line shows the result expected if observed and expected values were equal. Filled circles show results for nine species with estimates available from both mark–recapture and dead recovery data. For all species, $r = 0.695$. After excluding the species with estimates from both types of data, $r = 0.663$.