Mass gained during breeding positively correlates with adult survival because both reflect life history adaptation to seasonal food availability.

Daniel T. C. Cox\textsuperscript{1,2} and Will Cresswell\textsuperscript{1,2}

\textsuperscript{1}School of Biology, University of St Andrews, Bute Building, St Andrews, Fife, KY16 9TS, UK

\textsuperscript{2}A.P. Leventis Ornithological Research Institute, Jos, Nigeria

Email D.T.C.Cox\textregistered@exeter.ac.uk; wrle@st-andrews.ac.uk

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Both mass (as a measure of body reserves) during breeding, and adult survival should reflect variation in food availability. Those species that are adapted to less seasonally variable foraging niches and so where competition dominates during breeding, will tend to have a higher mass increase via an interrupted foraging response, because their foraging demands increase and so become more unpredictable. They will then produce few offspring per breeding attempt, but trade this off with higher adult survival. In contrast, those species that occupy a more seasonal niche will not gain mass because foraging remains predictable, as resources become superabundant during breeding. They can also produce more offspring per breeding attempt, but with a trade-off with reduced adult survival. We tested whether the then predicted positive correlation between levels of mass gained during seasonal breeding and adult survival was present across 40 species of tropical bird measured over a 10 year period in a West African savannah. We showed that species with a greater seasonal mass increase had higher adult survival, controlling for annual mass variation (i.e. annual variation in absolute food availability) and variation in the timing of peak mass (i.e. annual predictability of food availability), clutch size, body size, migratory status and phylogeny. Our results support the hypothesis that the degree of seasonal mass variation in birds is probably an indication of life-history adaptation: across tropical bird species it may therefore be possible to use mass gain during breeding as an index of adult survival.
Both mass (as a measure of body reserves, e.g. Rogers 1987; Gosler 1996) during breeding and adult survival should reflect variation in food availability. Many tropical bird species vary their mass across the year (e.g. 12.6% ± 1.0, Cox et al 2011), showing a seasonal mass change that is comparable with both northern (e.g. 7-12%, Haftorn 1989) and southern temperate species (8 – 14%, Rozman et al 2003). In tropical (and possibly southern hemisphere, Rozman et al. 2003) birds however, body reserves peak in the breeding season, before decreasing and being maintained at low levels during the non-breeding season. This is because foraging probably remains predictable due to constant day lengths and warm temperatures (Fogden 1972; Fogden and Fogden 1979; Cox et al. 2011). Thus birds are able to reduce mass-dependent energy use (Rogers and Heath-Coss 2003) and predation costs (Witter and Cuthill 1993) when not breeding.

When species subsequently commence breeding activities the energy requirements of chicks are timed to coincide with predictable seasonal increases in food availability (Perrins 1970; Martin 1987). The energetic expenditure for parents increases during the breeding season due to the energetic demands of chick rearing (e.g. Hambly et al. 2007), while at the same time, activities such as mate guarding, territoriality, nest building, incubation and parental care conflict with the time available for adults to maintain their own body condition (i.e. they interrupt their foraging). Such interruptions lead to mass gain generally in birds because they reduce the time or the space available in which to feed. Thus, effectively reducing the availability of food so that birds need to add fat reserves to insure against the increased unpredictability of foraging, termed an Interrupted Foraging response (Lima 1986; Houston et al. 1993). So despite an increase in food availability during the breeding season, foraging predictability may actually decrease, and so a bird may increase its reserves (and so mass) through an Interrupted Foraging response, independent of any mass increase from egg or gonad growth (Cox and Cresswell In submission).
The level of fat reserves gained, and so mass of an animal, during periods where the foraging intake rate might be unpredictable, such as during breeding, will depend on the absolute levels of food available, with higher levels of reserves being associated with poorer foraging environments (MacLeod et al. 2008; Cresswell et al. 2009). In animals that opportunistically exploit periods of food abundance during breeding, the decrease in the time available for foraging caused by breeding activities may be offset by the increase in food abundance, so there may be a reduced Interrupted Foraging response (Fig. 1). Thus, an increase in the seasonality of food availability leads to a more predictable energy budget during breeding. In contrast, animals that breed in more constant environments will have higher food requirements as they raise young without an increase in the absolute level of food resources (Ricklefs 1980; Martin 1987; McNamara et al. 2008), so there may be a greater Interrupted Foraging response (Fig. 1).

Adult survival, as a key life history trait, is also a consequence of availability of food, mediated through competition (Bennett and Owens 2002). If food availability remains reasonably constant for a species (at carrying capacity), there is always intense competition so reducing levels of parental investment available to any one offspring at any one time (Ghalambor and Martin 2001), and selection will favour those individuals that raise smaller broods (Roff 2002; McNamara et al. 2008). Selection will then act on those adults that prioritise their own long term survival so that there can be many breeding events to compensate (Bennett and Owens 2002). In contrast, in environments that vary in absolute levels of food abundance, such as strongly seasonal environments, food availability may temporarily far exceed carrying capacity so that parents can successfully raise larger broods. Selection can then favour a strategy of producing as many offspring as possible but with a trade-off with adult survival, probably through reduced
immunocompetence (Norris and Evans 2000) and increased susceptibility to fluctuations in environmental conditions (Bennett and Owens 2002).

Therefore, both life history and mass of a species should reflect the levels of food abundance in the environment, or whether a particular species is adapted to more seasonally fluctuating resources. Here we make the novel prediction that there will be a clear link between mass during breeding and life history. We propose that those species that are adapted to less seasonal foraging niches, with reduced seasonal peaks in food availability, will experience increased competition and subsequently have increased foraging unpredictability during breeding (Thiollay 1988) and so will show an increased interrupted foraging response (MacLeod et al. 2008) and have higher adult survival (Peach et al. 2001). Those species that occupy a more seasonal niche, where resources vary both within and across the years in response to fluctuations in environmental conditions, such as the annual seed crop which goes from almost negligible at the start of the rains to superabundant when the seeds ripen and fall (Crowley and Garnett 1999; Molokwu et al. 2008), will invest more in breeding when food availability increases and as a consequence are less likely to survive as adults (Ghalambor and Martin 2001; Peach et al. 2001; McNamara et al. 2008). Establishing a link between a key demographic life history parameter such as survival and strategic mass regulation has wide implications in ecology, because mass regulation is easy to measure, so providing researchers with a potential opportunity to efficiently establish life history strategies for species.

In this paper we test whether mass gain in tropical birds during breeding is greatest for those birds that have the highest survival, to test the hypothesis that variation in fat reserves is part of life history adaptation to variation in food availability. We tested whether there was a positive correlation between levels of mass gained during seasonal breeding and adult survival in 40
species of tropical bird collected over a 10 year period in a West African savannah, controlling for annual mass variation and variation in the timing of peak mass, along with potentially confounding variables of clutch size, body size, migratory status and phylogeny. We included annual mass variation to control for annual variation in absolute food availability: all species should show a reduced survival in years with reduced rainfall (Gibbs and Grant 1987). We included variation in the timing of peak mass to control for annual predictability of food availability: species that have greater variation in the annual timing of their mass peak will be breeding more opportunistically and are likely to have a lower survival (Tokolyi et al. 2012). We controlled for clutch size because, all other things being equal, a higher clutch size will indicate a species with higher absolute food availability, allowing a greater investment in each breeding attempt (e.g. Saether 1988; Peach et al. 2001). We controlled for migratory status because, all other things being equal, transient species might show lower mass because they buffer seasonal unpredictability in food supply through movement rather than body reserves as in sedentary species. We controlled for body mass because larger animals have different costs of acquiring and maintaining reserves (Witter and Cuthill 1993). Finally we controlled for phylogeny to account for possible non-independence of variables due to common evolutionary descent (Bennett and Owens 2002).

Methods

We tested the relationship between mass variation and adult survival at three temporal scales in 40 species of tropical savannah birds caught using understory mist nets in Guinea savannah woodland at Amurum Forest Reserve on the Jos Plateau (09°55’N, 08°53’E), and at Yankari Game Reserve (09°45’N, 10°30’E) in central Nigeria. These sites are situated in the middle of
the guinea savannah forest zone with very strong seasonality due to a single rainy season.

Amurum Forest Reserve consists of four main habitat types: degraded guinea savannah woodland, gallery forest, rocky outcrops (inselbergs) and farmland. Much of the land surrounding the reserve has been degraded by anthropogenic pressures. Yankari Game Reserve comprises more Sudan, rather than Guinea savannah, and therefore has some changes in floral composition. However, the overall degree of seasonality and climate was similar to Amurum Forest Reserve.

Details of survival estimation are given in Stevens et al. (2013), but in summary survival estimates of adults were calculated for 40 species (6939 individuals, 2099 recaptures) caught in Amurum over a nine-year period, between January 2000 and December 2008 (Table 1). 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). The data were analysed and parameter estimates developed, using the program MARK (White and Burnham 1999). When possible we used Cormack-Jolly-Seber time-dependent models (i.e. $\Phi t p t$, where $\Phi$ 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). Goodness of fit tests performed on the general starting models ($\Phi_t p_t$) for all species. The median c-hat technique within MARK was used to derive the variance inflation factor ($\hat{c}$) and assess the extent of lack of fit (i.e. over- or under-dispersion) of the model to the data. Model selection was performed using information theoretic methods.

Estimates of mass variation were given in Cox et al 2011; in summary 40 species (11,654 individuals) were caught in Guinea savannah in Amurum and Yankari, between November 2000 – March 2011 (Table 1). Note: Due to the survival and mass estimates used in the analysis
coming from papers published at different times, there is a small mismatch between dates. We built a general linear model for each species testing the effect of the parameters: season (S), year (Y) and the variation in the annual timing of mass change (SY, the interaction between season and year) on the mass of a bird while controlling for seasonal rainfall, age, wing length and sex where sexes were distinguishable. We calculated the degree of seasonal mass change for each species from the seasonal parameter estimates of mean mass across years (where SY was not significant) as the proportional difference in predicted mass between the lightest and heaviest seasons. Where SY was significant we calculated the seasonal mass change as above but for each year separately (where there was a sufficiently large sample size) before averaging the proportional difference across years. We calculated the degree of annual mass change as the proportional difference in mass change between the years in which the birds were lightest and heaviest. For species not covered in Cox et al. (2011) but for which we had survival estimates, we followed the same methods to calculate their mass change parameters. Time of day was not found to influence seasonal or annual parameter estimates, probably because data was most commonly collected between 07:00 09:00 h (see Cox et al. 2011 for a full description).

Statistical analysis

We ran a general linear mixed model testing for relationships between adult survival and all the predictor and potentially confounding variables. Mass variation within years (S) was the key predictor variable (covariate) that tested our hypothesis. We included mass variation across years (Y) as a covariate to control for annual variation in absolute food availability. We included variation in the timing of peak mass between years (SY) to control for annual predictability of food availability. Individual parameter estimates for the variation in the annual timing of mass
change had large confidence limits because of small sample sizes (resulting from the split
between each of four seasons over ten years) so we treated variable peak mass simply as a factor
(1 significant annual variation in seasonal mass peak; 0 not significant). We also controlled for
clutch size, migratory status and body size. Mean clutch size estimates were taken from the Birds
of Africa series Vol. 3-7 (Fry et al. 1992-2004). Where multiple estimates of clutch size were
given we used those that were geographically closest to our study area. Migratory status was
assigned to any species that had >50% reduction in capture rates between the end of the wet
season and the end of the dry season (see, Cox et al. 2011). Mean body mass data for a species
were used from this study (Table 1). To account for possible non-independence of variables
across species, we controlled for phylogenetic variation by including nesting of family within
order as random factors in the model. Finally to control for possible experimental noise due to
species with small sample size, we weighted the model by the number of individuals used to
calculate mass variation. We tested the statistical significance of our predictor and potentially
confounding variables on adult survival, by dropping each from the full model in turn, and
applying a likelihood ratio test (Table 2). Analysis was conducted using R.2.15.0 (R
Development Core Team 2011) and the nlme package (Pinheiro et al. 2011). The final model
structure was: survival ~ S + Y + SY + clutch size + body size + migratory status + (~1 | family
%in% order), weight = “n”.

**Results**

There was a significant positive correlation between adult survival and seasonal mass variation
across species controlling for the degree of annual mass variation, body size and phylogeny.
There was an increase in survival of 0.91 ± 0.29% for every 1% increase in seasonal mass
variation (Table 2, Fig. 2, and an increase of 0.78 ± 0.30% in the unweighted model). There was no correlation between adult survival and annual mass variation (Table 2). Species which showed significant variation in the timing of the seasonal mass peaks among years had significantly lower adult survival (SY; 0= 0.60, 1= 0.44 using parameter values from Table 2 and average values for each variable from each SY class from the study). However, this result was dependent on weighting the model by sample size (without weighting). We also reconfirmed the negative relationship between clutch size and adult survival (survival decreased by 7% for every 1 egg increase in clutch size, Table 2). Migratory status did not significantly affect adult survival.

Discussion

We show that across tropical bird species, in the same habitat, the degree of seasonal mass variation correlates positively with adult survival. Those species that showed an increased mass response during breeding also had higher adult survival (Fig. 2), while species that varied their mass at different times in different years may also have had lower adult survival. These results are consistent with life history theory, where increased seasonal variation in food availability drives both adaptive management of energy reserves and also adult survival.

A key assumption in our study is the seasonal pattern of food availability. Here we assume that if a species has a clear breeding season (and this is true for at least 55% of the species considered here, Cox et al. 2013) then this reflects an increase in food availability. This is a reasonable assumption as almost all birds breed when resources peak, but with a great deal of variation between species in the size of this peak, which is perhaps indicative of variable underlying levels of resource peaks (Perrins 1970). Previous research at the study site (e.g. Brandt 2007, Molokwu et al. 2008, Molokwu et al. 2010) does strongly suggest that patterns of food availability
probably follow those found in other tropical savannah regions (e.g. Dingle 1972; Poulin 1992),
with peaks associated with the onset or finish of the rainy season when most species breed (Gill
and Haggerty 2012). But a clear prediction from our study remains untested to prove that food
limitation drives the results of our study: species with greater mass increases during breeding
should show less annual fluctuation in food availability.

We predicted that mass during breeding should be highest for those species with the highest
survival because both are a consequence of density-dependent competition for food availability,
and our results were consistent with this. In a highly seasonal savannah environment, as in this
study, there is not a period of high density-dependent mortality that acts across all species, such
as winter in the northern hemisphere. This has allowed the evolution of a wide range of life
history strategies under the same environmental conditions (e.g. see the variation in survival
rates in Stevens et al. 2013). Those species that inhabit a less seasonal foraging niche will
experience increased density-dependent mortality in the breeding season and therefore
populations will be governed more by competition during breeding with fewer resources
available per individual (Ricklefs 1980; Martin 1987). Therefore parents will experience reduced
foraging predictability because of breeding activities and so could gain a selective advantage by
storing more reserves to insure against this increased starvation risk. Such environments also
favour those individuals that invest less in each breeding attempt (i.e. smaller broods) but over a
longer period (i.e. extended parental care) and over many years with a concomitant increase in
adult survival (Allcorn et al. 2012; Gill and Haggerty 2012). In contrast, those species that rely
on a more seasonal food source, such as specialized seed eating finches (Crowley and Garnett
1999; Brandt 2007), probably experience a period of reduced density-dependent mortality during
the breeding season when food availability may far exceed carrying capacity. This will then
affect life history through its effects on provisioning rates, nest predation and chick growth rates (Markman et al. 2002). As a consequence larger clutch sizes can evolve (e.g. Ricklefs 1980), which has negative implications for adult survival. Thus adaptation to seasonal food availability, mediated by density-dependent competition, drives both strategic mass regulation in birds while breeding and overall adult survival.

We expected that in years of higher food availability (i.e. because of variable rainfall which is characteristic across years in West African savannahs, Sylla et al. 2010) birds were likely to show a reduced level of mass increase because foraging will be generally less of a constraint during breeding (MacLeod et al. 2008). However, we did not find a relationship between adult survival and inter-annual mass variation. This is perhaps because any fluctuations in resource availability and so foraging predictability at this level are reflected in offspring fitness (Ghalambor and Martin 2001; Markman et al. 2002), or poorer adults showing reduced reproductive effort during that year (Grant et al. 2000; Renton and Salinas-Melgoza 2004) and not adult survival.

We expected species that had greater variation in the annual timing of their mass peak were likely to have a lower survival. We did find a suggestion that where peak mass occurred at different times in different years, mass variation was associated with lower adult survival (16% lower). Species where peak mass occurred at different times in different years were likely to be opportunistic breeders or those that rely on a food source which varies in predictability across the years (e.g. lavender waxbill *Estrilda coerulescens* and the bronze manikin *Lonchura cucullata*). Thus, species with more unpredictable peaks in food availability will be less likely to survive as adults and so need to produce more young when conditions allow, as predicted by life-history theory (Boyce 1984). Many finch species breed opportunistically (e.g. Grant et al. 2000; Cox et
al. *In submission*), maintaining an active or semi-active reproductive system in the non-breeding season despite fitness costs (Perfito et al. 2007) which further drives investment in an r-selected life history (Bennett and Owens 2002).

**General conclusions**

We provide evidence to support the generality of interrupted foraging hypothesis as a single explanation of how animals regulate their mass under variable environmental conditions, by showing how it links with life history. As population dynamics depend on individual survival, a bird’s mass provides a framework to predict the behaviour, fitness, population dynamics and community structure of birds (McNamara and Houston 1987). Several studies have investigated how fat regulation acts as an indication of survival and population change (MacLeod et al. 2007; MacLeod et al. 2008; Cresswell et al. 2009). However, these studies have focused on the relationship between mass variation and survival in the non-breeding season. These studies were conducted in the northern hemisphere where food is unlikely to be limiting for most species in the breeding season (e.g. Houston and McNamara 1993; Witter and Cuthill 1993) and more likely to be limited in the non-breeding season. In tropical environments the reverse may apply for many species that occupy a foraging niche with smaller seasonal peaks in food availability.

The positive relationship between adult survival and mass variation provides empirical evidence to support recent theoretical models which have concluded that food limitation, expressed as the seasonality of resources, as opposed to nest predation and/or the length of the breeding season is the driving evolutionary force behind life history evolution (McNamara et al. 2008; Griebeler et al. 2010). Here we show that in a tropical environment there is probably a direct relationship between food limitation in the breeding season and adult survival, which has wide implications
for life history strategy. This study does not prove that food limitation is driving the relationship, and this still needs to be done. However, if this is the case then the degree of mass gain during breeding provides both a potential index of life history adaptation (i.e. survival rates) across species, and a potential index of food availability within species – both of these variables being much harder to measure than mass gain.

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Table 1: Life history data of 40 species of West African savannah bird. Showing the total number of individuals of caught of each species (I), along with the number of individuals recaptured (R) to calculate species survival estimates*. The number of individuals used to calculate mass change parameters (n mass), and the percentage mass change between the season (S) and year (Y) of lowest and highest mean mass. Whether seasonal mass variation varied significantly with year was included as a factor (SY; 1 yes, 0 no). Transient status (T) was identified over resident status (R) by a >50% change in capture rate between dry and wet seasons.

<table>
<thead>
<tr>
<th>Species</th>
<th>n survival</th>
<th>% Survival (No. of individuals recaptured)</th>
<th>Survival estimate</th>
<th>Clutch</th>
<th>n mass</th>
<th>% Seasonal mass change</th>
<th>% Annual mass change</th>
<th>SY</th>
<th>Mean mass (g)</th>
<th>Migratory status</th>
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<td>60.8</td>
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<td>10</td>
<td>1</td>
<td>52.3</td>
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<td>7</td>
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<td>10.8</td>
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<td>Cisticolidae</td>
<td>Camaroptera brachyura</td>
<td>137 (53)</td>
<td>0.636</td>
<td>2.7</td>
<td>226</td>
<td>5</td>
<td>0</td>
<td>10.9 R</td>
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<tr>
<td></td>
<td>Cisticola aberrans</td>
<td>30 (16)</td>
<td>0.650</td>
<td>2.5</td>
<td>85</td>
<td>4</td>
<td>11</td>
<td>0  13.4 R</td>
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<tr>
<td></td>
<td>C. cantans*</td>
<td>57 (12)</td>
<td>0.806</td>
<td>2</td>
<td>60</td>
<td>8</td>
<td>4</td>
<td>4  11.5 T</td>
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<tr>
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<td>C. guinea*</td>
<td>39 (12)</td>
<td>0.510</td>
<td>3</td>
<td>39</td>
<td>15</td>
<td>26</td>
<td>0  9.0 R</td>
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<tr>
<td>Plastysteiridae</td>
<td>Platysteira cyanea</td>
<td>51 (24)</td>
<td>0.700</td>
<td>3</td>
<td>94</td>
<td>27</td>
<td>21</td>
<td>0  11.7 R</td>
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<tr>
<td>Zosteropidae</td>
<td>Zosterops senegalensis</td>
<td>152 (31)</td>
<td>0.527</td>
<td>2.5</td>
<td>241</td>
<td>2</td>
<td>7</td>
<td>0  9.5 R</td>
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<td>Nectarinidae</td>
<td>Cyanomitra verticalis</td>
<td>87 (34)</td>
<td>0.654</td>
<td>2</td>
<td>130</td>
<td>12</td>
<td>4</td>
<td>0  12.4 R</td>
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<tr>
<td></td>
<td>Chalcomitra senegalensis</td>
<td>202 (39)</td>
<td>0.769</td>
<td>2</td>
<td>476</td>
<td>4</td>
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<td>0  10.3 T</td>
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<td></td>
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<td></td>
<td>Cinyris venustus</td>
<td>206 (25)</td>
<td>0.534</td>
<td>2</td>
<td>354</td>
<td>5</td>
<td>9</td>
<td>0  6.3 R</td>
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<tr>
<td>Malacoontidae</td>
<td>Malacocontus sulfureopectus*</td>
<td>25 (12)</td>
<td>0.923</td>
<td>1.8</td>
<td>46</td>
<td>10</td>
<td>21</td>
<td>0  28.7 R</td>
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<tr>
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<td>Tchagra senegalus*</td>
<td>41 (15)</td>
<td>0.660</td>
<td>2</td>
<td>58</td>
<td>8</td>
<td>30</td>
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<td>Passeridae</td>
<td>Sporopipes frontalis</td>
<td>62 (19)</td>
<td>0.592</td>
<td>4</td>
<td>62</td>
<td>12</td>
<td>14</td>
<td>0  17.0 R</td>
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<td>Ploceus cucullatus</td>
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<td>2.3</td>
<td>738</td>
<td>11</td>
<td>9</td>
<td>1  36.6 R</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>P. luteolus</td>
<td>45 (17)</td>
<td>0.487</td>
<td>2.5</td>
<td>147</td>
<td>8</td>
<td>8</td>
<td>0  14.5 R</td>
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<tr>
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<td>P. nigricollis</td>
<td>116 (41)</td>
<td>0.786</td>
<td>2</td>
<td>209</td>
<td>6</td>
<td>9</td>
<td>0  26.5 T</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P. vitellinus</td>
<td>205 (45)</td>
<td>0.726</td>
<td>2.4</td>
<td>284</td>
<td>20</td>
<td>14</td>
<td>0  20.2 R</td>
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<tr>
<td></td>
<td>Euplectes franciscanus</td>
<td>1252 (200)</td>
<td>0.720</td>
<td>3</td>
<td>1762</td>
<td>5</td>
<td>8</td>
<td>1  15.2 T</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>E. hordeaceus</td>
<td>165 (27)</td>
<td>0.786</td>
<td>3</td>
<td>169</td>
<td>28</td>
<td>15</td>
<td>0  20.0 T</td>
<td></td>
<td></td>
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<tr>
<td>Estrildidae</td>
<td>Estrilda caerulescens</td>
<td>378 (144)</td>
<td>0.566</td>
<td>5</td>
<td>530</td>
<td>6</td>
<td>16</td>
<td>1  9.3 T</td>
<td></td>
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<tr>
<td></td>
<td>E. troglodytes</td>
<td>136 (14)</td>
<td>0.571</td>
<td>5</td>
<td>149</td>
<td>5</td>
<td>24</td>
<td>0  7.6 T</td>
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<tr>
<td></td>
<td>Uraeginthus bengalus</td>
<td>498 (104)</td>
<td>0.456</td>
<td>4.7</td>
<td>692</td>
<td>5</td>
<td>10</td>
<td>0  10.1 T</td>
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<tr>
<td></td>
<td>Lagonosticta rufopicta</td>
<td>62 (21)</td>
<td>0.564</td>
<td>4.5</td>
<td>113</td>
<td>9</td>
<td>10</td>
<td>0  9.3 R</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>L. rara</td>
<td>34 (14)</td>
<td>0.528</td>
<td>3.5</td>
<td>84</td>
<td>7</td>
<td>7</td>
<td>0  9.8 T</td>
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<tr>
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<td>L. sanguinodorsalis</td>
<td>305 (109)</td>
<td>0.559</td>
<td>4</td>
<td>480</td>
<td>11</td>
<td>8</td>
<td>1  10.5 R</td>
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<td></td>
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<tr>
<td></td>
<td>L. senegala</td>
<td>400 (88)</td>
<td>0.515</td>
<td>3.4</td>
<td>763</td>
<td>7</td>
<td>18</td>
<td>0  8.7 T</td>
<td></td>
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<tr>
<td></td>
<td>Lonchura cucullata</td>
<td>424 (27)</td>
<td>0.269</td>
<td>5</td>
<td>768</td>
<td>5</td>
<td>8</td>
<td>1  8.9 T</td>
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<td></td>
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<tr>
<td>Emberizidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Embergiza tahapisi</td>
<td>226 (16)</td>
<td>0.491</td>
<td>2.6</td>
<td>361</td>
<td>9</td>
<td>9</td>
<td>0</td>
<td>13.5</td>
<td>T</td>
<td></td>
</tr>
</tbody>
</table>

Note: * see Stevens et al (2013) Table 1 for details of starting models used to determine goodness of fit of model set in MARK and variance inflation factors used to adjust parameter estimates. Values come from data already published except for seven additional species (labelled with *) where we calculated new values of seasonal mass change, SY and mass.
Table 2: Summary statistics of the minimum adequate model testing for relationships with adult survival. Each variable was dropped from the model in turn, before applying a likelihood ratio test.

<table>
<thead>
<tr>
<th>Variable</th>
<th>estimate</th>
<th>error</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.75</td>
<td>0.11</td>
<td>6.9</td>
<td>&lt;0.0001</td>
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<tr>
<td>Seasonal mass</td>
<td>0.91</td>
<td>0.29</td>
<td>3.1</td>
<td>0.005</td>
</tr>
<tr>
<td>Annual mass</td>
<td>0.17</td>
<td>0.25</td>
<td>0.7</td>
<td>0.52</td>
</tr>
<tr>
<td>Variable peak mass</td>
<td>-0.14</td>
<td>0.05</td>
<td>-3.0</td>
<td>0.007</td>
</tr>
<tr>
<td>Clutch size</td>
<td>-0.07</td>
<td>0.03</td>
<td>-2.7</td>
<td>0.01</td>
</tr>
<tr>
<td>Mean mass</td>
<td>-0.0007</td>
<td>0.001</td>
<td>-0.6</td>
<td>0.54</td>
</tr>
</tbody>
</table>

Note: The model includes order/family as a random factor, to control for any variation due to phylogeny and the model was weighted by sample size (df = 20). Migratory status was removed from the model during model simplification.
**Figure 1:** The theoretical relationship across species between seasonal variation in food availability and adult survival in small tropical birds.

**Figure 2:** Relationship between adult survival and seasonal mass variation by feeding guild in 40 species of small tropical savannah bird: filled square = Frugivore; filled circle = Insectivore; blank triangle = Nectivore; blank diamond = Granivore. Parameter estimate = 0.91 ± 0.29, $t = 0.31$, $P = 0.005$. Fitted line is the predicted line from the model in Table 2, with values of seasonal mass variation with year set to zero and a clutch size of 3.
Fig. 1
Adult survival vs. % annual mass variation.

Fig. 2