

1 **Running heading:** Mass variation and life history

2 **Mass gained during breeding positively correlates**
3 **with adult survival because both reflect life**
4 **history adaptation to seasonal food availability**

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14 **Key words** Fat · Interrupted foraging · Life history · Seasonality · Tropical birds

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15 Both mass (as a measure of body reserves) during breeding, and adult survival should reflect
16 variation in food availability. Those species that are adapted to less seasonally variable foraging
17 niches and so where competition dominates during breeding, will tend to have a higher mass
18 increase via an interrupted foraging response, because their foraging demands increase and so
19 become more unpredictable. They will then produce few offspring per breeding attempt, but
20 trade this off with higher adult survival. In contrast, those species that occupy a more seasonal
21 niche will not gain mass because foraging remains predictable, as resources become
22 superabundant during breeding. They can also produce more offspring per breeding attempt, but
23 with a trade-off with reduced adult survival. We tested whether the then predicted positive
24 correlation between levels of mass gained during seasonal breeding and adult survival was
25 present across 40 species of tropical bird measured over a 10 year period in a West African
26 savannah. We showed that species with a greater seasonal mass increase had higher adult
27 survival, controlling for annual mass variation (i.e. annual variation in absolute food availability)
28 and variation in the timing of peak mass (i.e. annual predictability of food availability), clutch
29 size, body size, migratory status and phylogeny. Our results support the hypothesis that the
30 degree of seasonal mass variation in birds is probably an indication of life-history adaptation:
31 across tropical bird species it may therefore be possible to use mass gain during breeding as an
32 index of adult survival.

33 Both mass (as a measure of body reserves, e.g. Rogers 1987; Gosler 1996) during breeding and
34 adult survival should reflect variation in food availability. Many tropical bird species vary their
35 mass across the year (e.g. $12.6\% \pm 1.0$, Cox et al 2011), showing a seasonal mass change that is
36 comparable with both northern (e.g. 7-12%, Haftorn 1989) and southern temperate species (8 –
37 14%, Rozman et al 2003). In tropical (and possibly southern hemisphere, Rozman et al. 2003)
38 birds however, body reserves peak in the breeding season, before decreasing and being
39 maintained at low levels during the non-breeding season. This is because foraging probably
40 remains predictable due to constant day lengths and warm temperatures (Fogden 1972; Fogden
41 and Fogden 1979; Cox et al. 2011). Thus birds are able to reduce mass-dependent energy use
42 (Rogers and Heath-Coss 2003) and predation costs (Witter and Cuthill 1993) when not breeding.

43 When species subsequently commence breeding activities the energy requirements of chicks are
44 timed to coincide with predictable seasonal increases in food availability (Perrins 1970; Martin
45 1987). The energetic expenditure for parents increases during the breeding season due to the
46 energetic demands of chick rearing (e.g. Hambly et al. 2007), while at the same time, activities
47 such as mate guarding, territoriality, nest building, incubation and parental care conflict with the
48 time available for adults to maintain their own body condition (i.e. they interrupt their foraging).
49 Such interruptions lead to mass gain generally in birds because they reduce the time or the space
50 available in which to feed. Thus, effectively reducing the availability of food so that birds need
51 to add fat reserves to insure against the increased unpredictability of foraging, termed an
52 Interrupted Foraging response (Lima 1986; Houston et al. 1993). So despite an increase in food
53 availability during the breeding season, foraging predictability may actually decrease, and so a
54 bird may increase its reserves (and so mass) through an Interrupted Foraging response,
55 independent of any mass increase from egg or gonad growth (Cox and Cresswell *In submission*).

56 The level of fat reserves gained, and so mass of an animal, during periods where the foraging
57 intake rate might be unpredictable, such as during breeding, will depend on the absolute levels of
58 food available, with higher levels of reserves being associated with poorer foraging
59 environments (MacLeod et al. 2008; Cresswell et al. 2009). In animals that opportunistically
60 exploit periods of food abundance during breeding, the decrease in the time available for
61 foraging caused by breeding activities may be offset by the increase in food abundance, so there
62 may be a reduced Interrupted Foraging response (Fig. 1). Thus, an increase in the seasonality of
63 food availability leads to a more predictable energy budget during breeding. In contrast, animals
64 that breed in more constant environments will have higher food requirements as they raise young
65 without an increase in the absolute level of food resources (Ricklefs 1980; Martin 1987;
66 McNamara et al. 2008), so there may be a greater Interrupted Foraging response (Fig. 1).

67 Adult survival, as a key life history trait, is also a consequence of availability of food, mediated
68 through competition (Bennett and Owens 2002). If food availability remains reasonably constant
69 for a species (at carrying capacity), there is always intense competition so reducing levels of
70 parental investment available to any one offspring at any one time (Ghalambor and Martin
71 2001), and selection will favour those individuals that raise smaller broods (Roff 2002;
72 McNamara et al. 2008). Selection will then act on those adults that prioritise their own long term
73 survival so that there can be many breeding events to compensate (Bennett and Owens 2002). In
74 contrast, in environments that vary in absolute levels of food abundance, such as strongly
75 seasonal environments, food availability may temporarily far exceed carrying capacity so that
76 parents can successfully raise larger broods. Selection can then favour a strategy of producing as
77 many offspring as possible but with a trade-off with adult survival, probably through reduced

78 immunocompetence (Norris and Evans 2000) and increased susceptibility to fluctuations in
79 environmental conditions (Bennett and Owens 2002).

80 Therefore, both life history and mass of a species should reflect the levels of food abundance in
81 the environment, or whether a particular species is adapted to more seasonally fluctuating
82 resources. Here we make the novel prediction that there will be a clear link between mass during
83 breeding and life history. We propose that those species that are adapted to less seasonal foraging
84 niches, with reduced seasonal peaks in food availability, will experience increased competition
85 and subsequently have increased foraging unpredictability during breeding (Thiollay 1988) and
86 so will show an increased interrupted foraging response (MacLeod et al. 2008) and have higher
87 adult survival (Peach et al. 2001). Those species that occupy a more seasonal niche, where
88 resources vary both within and across the years in response to fluctuations in environmental
89 conditions, such as the annual seed crop which goes from almost negligible at the start of the
90 rains to superabundant when the seeds ripen and fall (Crowley and Garnett 1999; Molokwu et al.
91 2008), will invest more in breeding when food availability increases and as a consequence are
92 less likely to survive as adults (Ghalambor and Martin 2001; Peach et al. 2001; McNamara et al.
93 2008). Establishing a link between a key demographic life history parameter such as survival and
94 strategic mass regulation has wide implications in ecology, because mass regulation is easy to
95 measure, so providing researchers with a potential opportunity to efficiently establish life history
96 strategies for species.

97 In this paper we test whether mass gain in tropical birds during breeding is greatest for those
98 birds that have the highest survival, to test the hypothesis that variation in fat reserves is part of
99 life history adaptation to variation in food availability. We tested whether there was a positive
100 correlation between levels of mass gained during seasonal breeding and adult survival in 40

101 species of tropical bird collected over a 10 year period in a West African savannah, controlling
102 for annual mass variation and variation in the timing of peak mass, along with potentially
103 confounding variables of clutch size, body size, migratory status and phylogeny. We included
104 annual mass variation to control for annual variation in absolute food availability: all species
105 should show a reduced survival in years with reduced rainfall (Gibbs and Grant 1987). We
106 included variation in the timing of peak mass to control for annual predictability of food
107 availability: species that have greater variation in the annual timing of their mass peak will be
108 breeding more opportunistically and are likely to have a lower survival (Tokolyi et al. 2012). We
109 controlled for clutch size because, all other things being equal, a higher clutch size will indicate a
110 species with higher absolute food availability, allowing a greater investment in each breeding
111 attempt (e.g. Saether 1988; Peach et al. 2001) . We controlled for migratory status because, all
112 other things being equal, transient species might show lower mass because they buffer seasonal
113 unpredictability in food supply through movement rather than body reserves as in sedentary
114 species. We controlled for body mass because larger animals have different costs of acquiring
115 and maintaining reserves (Witter and Cuthill 1993). Finally we controlled for phylogeny to
116 account for possible non-independence of variables due to common evolutionary descent
117 (Bennett and Owens 2002).

118 **Methods**

119 We tested the relationship between mass variation and adult survival at three temporal scales in
120 40 species of tropical savannah birds caught using understory mist nets in Guinea savannah
121 woodland at Amurum Forest Reserve on the Jos Plateau (09°55'N, 08°53'E), and at Yankari
122 Game Reserve (09°45'N, 10°30'E) in central Nigeria. These sites are situated in the middle of

123 the guinea savannah forest zone with very strong seasonality due to a single rainy season.
124 Amurum Forest Reserve consists of four main habitat types: degraded guinea savannah
125 woodland, gallery forest, rocky outcrops (inselbergs) and farmland. Much of the land
126 surrounding the reserve has been degraded by anthropogenic pressures. Yankari Game Reserve
127 comprises more Sudan, rather than Guinea savannah, and therefore has some changes in floral
128 composition. However, the overall degree of seasonality and climate was similar to Amurum
129 Forest Reserve.

130 Details of survival estimation are given in Stevens et al. (2013), but in summary survival estimates of
131 adults were calculated for 40 species (6939 individuals, 2099 recaptures) caught in Amurum over a
132 nine-year period, between January 2000 and December 2008 (Table 1). Analysis of survival was
133 performed using the general methods of capture-mark-recapture modelling outlined by Lebreton et
134 al. (1992) and Burnham and Anderson (2002) . The data were analysed and parameter estimates
135 developed, using the program MARK (White and Burnham 1999). When possible we used
136 Cormack-Jolly-Seber time-dependent models (i.e. $\Phi_t p_t$, where Φ is the probability that an animal
137 alive at time i is alive at time $i + 1$, and p is the probability that an animal at risk of capture at
138 time i is captured at $i + 1$, t indicates time-dependence). Goodness of fit tests performed on the
139 general starting models ($\Phi_t p_t$) for all species. The median c-hat technique within MARK was
140 used to derive the variance inflation factor (\hat{c}) and assess the extent of lack of fit (i.e. over- or
141 under-dispersion) of the model to the data. Model selection was performed using information
142 theoretic methods.

143 Estimates of mass variation were given in Cox et al 2011; in summary 40 species (11,654
144 individuals) were caught in Guinea savannah in Amurum and Yankari, between November 2000
145 – March 2011 (Table 1). Note: Due to the survival and mass estimates used in the analysis

146 coming from papers published at different times, there is a small mismatch between dates. We
147 built a general linear model for each species testing the effect of the parameters: season (S), year
148 (Y) and the variation in the annual timing of mass change (SY, the interaction between season
149 and year) on the mass of a bird while controlling for seasonal rainfall, age, wing length and sex
150 where sexes were distinguishable. We calculated the degree of seasonal mass change for each
151 species from the seasonal parameter estimates of mean mass across years (where SY was not
152 significant) as the proportional difference in predicted mass between the lightest and heaviest
153 seasons. Where SY was significant we calculated the seasonal mass change as above but for each
154 year separately (where there was a sufficiently large sample size) before averaging the
155 proportional difference across years. We calculated the degree of annual mass change as the
156 proportional difference in mass change between the years in which the birds were lightest and
157 heaviest. For species not covered in Cox et al. (2011) but for which we had survival estimates,
158 we followed the same methods to calculate their mass change parameters. Time of day was not
159 found to influence seasonal or annual parameter estimates, probably because data was most
160 commonly collected between 07:00 09:00 h (see Cox et al. 2011 for a full description).

161 *Statistical analysis*

162 We ran a general linear mixed model testing for relationships between adult survival and all the
163 predictor and potentially confounding variables. Mass variation within years (S) was the key
164 predictor variable (covariate) that tested our hypothesis. We included mass variation across years
165 (Y) as a covariate to control for annual variation in absolute food availability. We included
166 variation in the timing of peak mass between years (SY) to control for annual predictability of
167 food availability. Individual parameter estimates for the variation in the annual timing of mass

168 change had large confidence limits because of small sample sizes (resulting from the split
169 between each of four seasons over ten years) so we treated variable peak mass simply as a factor
170 (1 significant annual variation in seasonal mass peak; 0 not significant). We also controlled for
171 clutch size, migratory status and body size. Mean clutch size estimates were taken from the Birds
172 of Africa series Vol. 3-7 (Fry et al. 1992-2004). Where multiple estimates of clutch size were
173 given we used those that were geographically closest to our study area. Migratory status was
174 assigned to any species that had >50% reduction in capture rates between the end of the wet
175 season and the end of the dry season (see, Cox et al. 2011). Mean body mass data for a species
176 were used from this study (Table 1). To account for possible non-independence of variables
177 across species, we controlled for phylogenetic variation by including nesting of family within
178 order as random factors in the model. Finally to control for possible experimental noise due to
179 species with small sample size, we weighted the model by the number of individuals used to
180 calculate mass variation. We tested the statistical significance of our predictor and potentially
181 confounding variables on adult survival, by dropping each from the full model in turn, and
182 applying a likelihood ratio test (Table 2). Analysis was conducted using R.2.15.0 (R
183 Development Core Team 2011) and the nlme package (Pinheiro et al. 2011). The final model
184 structure was: survival ~ S + Y + SY + clutch size + body size + migratory status + (~1 | family
185 %in% order), weight = “n”.

186 **Results**

187 There was a significant positive correlation between adult survival and seasonal mass variation
188 across species controlling for the degree of annual mass variation, body size and phylogeny.
189 There was an increase in survival of $0.91 \pm 0.29\%$ for every 1% increase in seasonal mass

190 variation (Table 2, Fig. 2, and an increase of $0.78 \pm 0.30\%$ in the unweighted model). There was
191 no correlation between adult survival and annual mass variation (Table 2). Species which
192 showed significant variation in the timing of the seasonal mass peaks among years had
193 significantly lower adult survival (SY; $0 = 0.60$, $1 = 0.44$ using parameter values from Table 2 and
194 average values for each variable from each SY class from the study). However, this result was
195 dependent on weighting the model by sample size (without weighting). We also reconfirmed the
196 negative relationship between clutch size and adult survival (survival decreased by 7% for every
197 1 egg increase in clutch size, Table 2). Migratory status did not significantly affect adult survival.

198 **Discussion**

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

205 A key assumption in our study is the seasonal pattern of food availability. Here we assume that if
206 a species has a clear breeding season (and this is true for at least 55% of the species considered
207 here, Cox et al. 2013) then this reflects an increase in food availability. This is a reasonable
208 assumption as almost all birds breed when resources peak, but with a great deal of variation
209 between species in the size of this peak, which is perhaps indicative of variable underlying levels
210 of resource peaks (Perrins 1970). Previous research at the study site (e.g. Brandt 2007, Molokwu
211 et al. 2008, Molokwu et al. 2010) does strongly suggest that patterns of food availability

212 probably follow those found in other tropical savannah regions (e.g. Dingle 1972; Poulin 1992),
213 with peaks associated with the onset or finish of the rainy season when most species breed (Gill
214 and Haggerty 2012). But a clear prediction from our study remains untested to prove that food
215 limitation drives the results of our study: species with greater mass increases during breeding
216 should show less annual fluctuation in food availability.

217 We predicted that mass during breeding should be highest for those species with the highest
218 survival because both are a consequence of density-dependent competition for food availability,
219 and our results were consistent with this. In a highly seasonal savannah environment, as in this
220 study, there is not a period of high density-dependent mortality that acts across all species, such
221 as winter in the northern hemisphere. This has allowed the evolution of a wide range of life
222 history strategies under the same environmental conditions (e.g. see the variation in survival
223 rates in Stevens et al. 2013). Those species that inhabit a less seasonal foraging niche will
224 experience increased density-dependent mortality in the breeding season and therefore
225 populations will be governed more by competition during breeding with fewer resources
226 available per individual (Ricklefs 1980; Martin 1987). Therefore parents will experience reduced
227 foraging predictability because of breeding activities and so could gain a selective advantage by
228 storing more reserves to insure against this increased starvation risk. Such environments also
229 favour those individuals that invest less in each breeding attempt (i.e. smaller broods) but over a
230 longer period (i.e. extended parental care) and over many years with a concomitant increase in
231 adult survival (Allcorn et al. 2012; Gill and Haggerty 2012). In contrast, those species that rely
232 on a more seasonal food source, such as specialized seed eating finches (Crowley and Garnett
233 1999; Brandt 2007), probably experience a period of reduced density-dependent mortality during
234 the breeding season when food availability may far exceed carrying capacity. This will then

235 affect life history through its effects on provisioning rates, nest predation and chick growth rates
236 (Markman et al. 2002). As a consequence larger clutch sizes can evolve (e.g. Ricklefs 1980),
237 which has negative implications for adult survival. Thus adaptation to seasonal food availability,
238 mediated by density-dependent competition, drives both strategic mass regulation in birds while
239 breeding and overall adult survival.

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

249 We expected species that had greater variation in the annual timing of their mass peak were
250 likely to have a lower survival. We did find a suggestion that where peak mass occurred at
251 different times in different years, mass variation was associated with lower adult survival (16%
252 lower). Species where peak mass occurred at different times in different years were likely to be
253 opportunistic breeders or those that rely on a food source which varies in predictability across the
254 years (e.g. lavender waxbill *Estrilda coerulescens* and the bronze manikin *Lonchura cucullata*).
255 Thus, species with more unpredictable peaks in food availability will be less likely to survive as
256 adults and so need to produce more young when conditions allow, as predicted by life-history
257 theory (Boyce 1984). Many finch species breed opportunistically (e.g. Grant et al. 2000; Cox et

258 al. *In submission*) , maintaining an active or semi-active reproductive system in the non-
259 breeding season despite fitness costs (Perfito et al. 2007) which further drives investment in an r
260 selected life history (Bennett and Owens 2002).

261 *General conclusions*

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

274 The positive relationship between adult survival and mass variation provides empirical evidence
275 to support recent theoretical models which have concluded that food limitation, expressed as the
276 seasonality of resources, as opposed to nest predation and/or the length of the breeding season is
277 the driving evolutionary force behind life history evolution (McNamara et al. 2008; Griebeler et
278 al. 2010). Here we show that in a tropical environment there is probably a direct relationship
279 between food limitation in the breeding season and adult survival, which has wide implications

280 for life history strategy. This study does not prove that food limitation is driving the relationship,
281 and this still needs to be done. However, if this is the case then the degree of mass gain during
282 breeding provides both a potential index of life history adaptation (i.e. survival rates) across
283 species, and a potential index of food availability within species – both of these variables being
284 much harder to measure than mass gain.

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

Species	<i>n</i> survival (No. of individuals recaptured)	Survival estimate	Clutch	<i>n</i> mass	% Seasonal mass change	% Annual mass change	SY	Mean mass (g)	Migratory status
COLUMBIFORMES Columbidae									
<i>Turtur abyssinicus</i>	68 (20)	0.606	2	230	9	34	0	60.8	R
COLIIFORMES Coliidae									
<i>Colius striatus</i>	223 (51)	0.619	1.9	298	12	10	1	52.3	R
PICIFORMES Capitonidae									
<i>Pogoniulus chrysoconus</i>	186 (45)	0.416	2.5	239	3	7	0	10.8	T
<i>Lybius vieilloti</i>	36 (16)	0.599	2.5	65	17	9	0	36.7	R
PASSERIFORMES Pycnonotidae									
<i>Pycnonotus barbatus</i>	311 (68)	0.668	2	614	12	30	1	37.6	R
<i>Chlorocichla flavicollis*</i>	34 (14)	0.844	2	49	14	23	0	50.7	T
Turdidae									
<i>Turdus pelios</i>	190 (55)	0.799	2.4	516	8	7	0	65.2	T
Muscicapidae									
<i>Cossypha niveicapilla</i>	80 (27)	0.779	2.5	176	1	12	0	36.6	R
<i>Cercomela familiaris</i>	45 (15)	0.539	3	117	11	13	0	17.2	T
<i>Myrmecocichla cinnamomeiventris</i>	41 (7)	0.657	2	63	17	16	0	39.5	R
Sylviidae									
<i>Melocichla mentalis*</i>	24 (11)	0.948	2	37	11	12	0	33.2	R
<i>Eremomela pusilla</i>	33 (13)	0.586	2	70	7	23	1	8.6	T
<i>Sylvietta brachyuran*</i>	32 (18)	0.875	2	60	2	6	0	13.8	R

Cisticolidae									
<i>Camaroptera brachyura</i>	137 (53)	0.636	2.7	226	8	5	0	10.9	R
<i>Cisticola aberrans</i>	30 (16)	0.650	2.5	85	4	11	0	13.4	R
<i>C. cantans</i> *	57 (12)	0.806	2	60	8	4	0	11.5	T
<i>C. guinea</i> *	39 (12)	0.510	3	39	15	26	0	9.0	R
Plastysteiridae									
<i>Platysteira cyanea</i>	51 (24)	0.700	3	94	27	21	0	11.7	R
Zosteropidae									
<i>Zosterops senegalensis</i>	152 (31)	0.527	2.5	241	2	7	0	9.5	R
Nectarinidae									
<i>Cyanomitra verticalis</i>	87 (34)	0.654	2	130	12	4	0	12.4	R
<i>Chalcomitra senegalensis</i>	202 (39)	0.769	2	476	4	7	0	10.3	T
<i>Cinnyris venustus</i>	206 (25)	0.534	2	354	5	9	0	6.3	R
Malaconotidae									
<i>Malaconotus sulfureopectus</i> *	25 (12)	0.923	1.8	46	10	21	0	28.7	R
<i>Tchagra senegalus</i> *	41 (15)	0.660	2	58	8	30	1	51.1	T
Passeridae									
<i>Sporopipes frontalis</i>	62 (19)	0.592	4	62	12	14	0	17.0	R
Ploceidae									
<i>Ploceus cucullatus</i>	301 (27)	0.694	2.3	738	11	9	1	36.6	R
<i>P. luteolus</i>	45 (17)	0.487	2.5	147	8	8	0	14.5	R
<i>P. nigricollis</i>	116 (41)	0.786	2	209	6	9	0	26.5	T
<i>P. vitellinus</i>	205 (45)	0.726	2.4	284	20	14	0	20.2	R
<i>Euplectes franciscanus</i>	1252 (200)	0.720	3	1762	5	8	1	15.2	T
<i>E. hordeaceus</i>	165 (27)	0.786	3	169	28	15	0	20.0	T
Estrildidae									
<i>Estrilda caerulescens</i>	378 (144)	0.566	5	530	6	16	1	9.3	T
<i>E. troglodytes</i>	136 (14)	0.571	5	149	5	24	0	7.6	T
<i>Uraeginthus bengalus</i>	498 (104)	0.456	4.7	692	5	10	0	10.1	T
<i>Lagonosticta rufopicta</i>	62 (21)	0.564	4.5	113	9	10	0	9.3	R
<i>L. rara</i>	34 (14)	0.528	3.5	84	7	7	0	9.8	T
<i>L. sanguinodorsalis</i>	305 (109)	0.559	4	480	11	8	1	10.5	R
<i>L. senegala</i>	400 (88)	0.515	3.4	763	7	18	0	8.7	T
<i>Lonchura cucullata</i>	424 (27)	0.269	5	768	5	8	1	8.9	T
Emberizidae									

<i>Emberiza tahapisi</i>	226 (16)	0.491	2.6	361	9	9	0	13.5	T
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418 *Note:* ⁺ see Stevens et al (2013) Table 1 for details of starting models used to determine
419 goodness of fit of model set in MARK and variance inflation factors used to adjust parameter
420 estimates. Values come from data already published except for seven additional species
421 (labelled with *) where we calculated new values of seasonal mass change, SY and mass.

422 **Table 2:** Summary statistics of the minimum adequate model testing for relationships with
423 adult survival. Each variable was dropped from the model in turn, before applying a
424 likelihood ratio test.

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

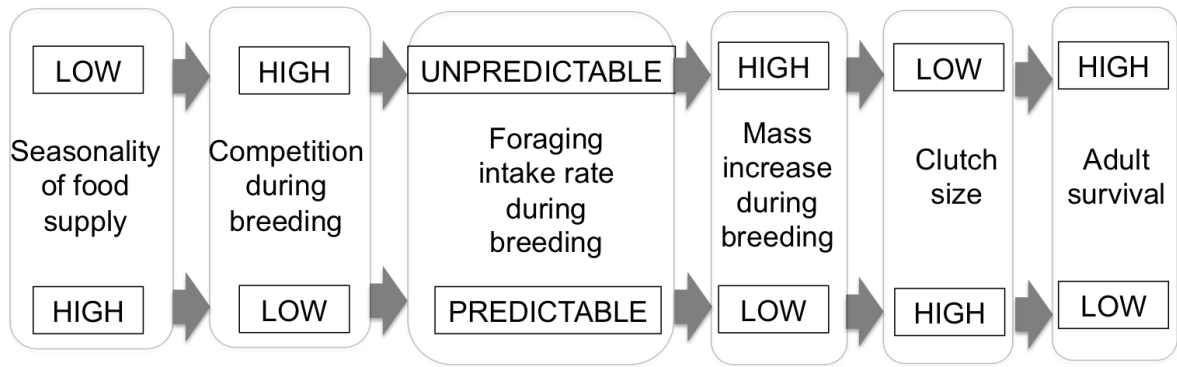
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426 *Note:* The model includes order/family as a random factor, to control for any variation due to
427 phylogeny and the model was weighted by sample size ($df = 20$). Migratory status was
428 removed from the model during model simplification.

429 **Figure 1:** The theoretical relationship across species between seasonal variation in food
430 availability and adult survival in small tropical birds.

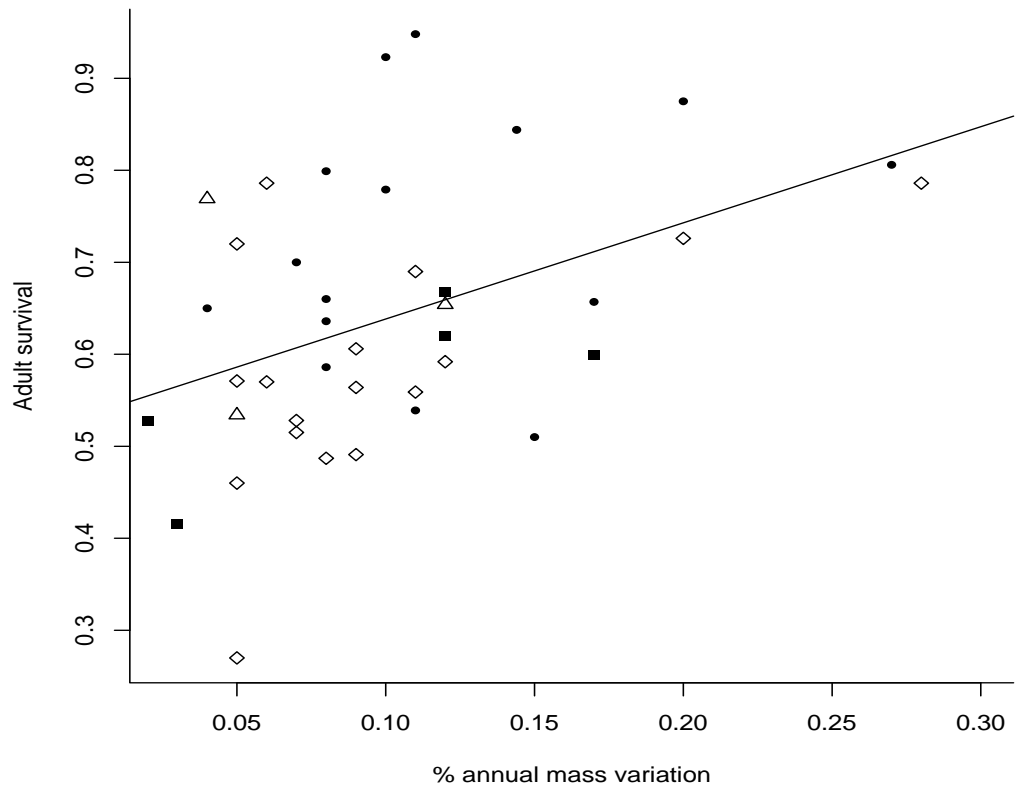
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432 **Figure 2:** Relationship between adult survival and seasonal mass variation by feeding guild
433 in 40 species of small tropical savannah bird: filled square = Frugivore; filled circle =
434 Insectivore; blank triangle = Nectivore; blank diamond = Granivore. Parameter estimate =
435 0.91 ± 0.29 , $t = 0.31$, $P = \mathbf{0.005}$. Fitted line is the predicted line from the model in Table 2,
436 with values of seasonal mass variation with year set to zero and a clutch size of 3.



437

438 Fig. 1



440

441 Fig. 2