

# **Seasonal mass variation as a life history trait in West African savannah birds**

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to the University of St Andrews

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# Publications

This document is a declaration of the roles of different authors in the production of peer-review published and submitted chapters, which were submitted by Daniel Cox for a degree of doctor of philosophy.

**Thesis title:** Seasonal mass variation as a life history trait in West African Savannah birds

This thesis used field data collected over a 10 year period between 2001 and 2011 at the A. P. Leventis Research Institute on the Jos Plateau in Nigeria.

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Daniel Cox, collected the field data from between 2009 and 2011 and was responsible for designing the methodology from inception, carrying out the statistical analysis and producing the first and successive paper drafts.

Miriam Brandt, Ross McGregor, Ulf Ottosson and Matthew Stevens collected field data between 2001 and 2009. Will Cresswell supervised the project and commented on successive drafts of the paper before submission.

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Miriam Brandt, Ross McGregor, Ulf Ottosson and Matthew Stevens collected field data between 2001 and 2009. Will Cresswell supervised the project and commented on successive drafts of the paper before submission.

A handwritten signature in black ink, reading "Daniel Cox". The signature is written in a cursive style with a horizontal line underneath it.

Daniel Cox

8<sup>th</sup> January 2013

# Abstract

Seasonality influences life history through its effect on the availability of essential resources, with birds timing breeding to occur during peak food availability. Due to density-dependence, investment in breeding is determined largely by the seasonality of food availability, with an increased investment being traded-off against adult survival. A bird's mass acts as an index of a species' foraging environment, because a bird bases its foraging decisions on a trade-off between the risk of predation and the risk of starvation. Under constant predation risk a bird increases its mass as insurance against increased foraging unpredictability. In tropical savannahs day length and temperature remains relatively constant, and there is not a season of increased density-dependent mortality which acts across all species. Thus species have evolved a broad range of life history traits under the same environmental conditions, although how a species experiences seasonality depends largely on its foraging niche. This thesis shows that most savannah species varied their mass across the year, having a reduced mass in the non-breeding season which suggests that foraging remained predictable. Independent of gonad or egg growth they then increased their mass as they started to breed, with the timing of breeding coinciding with peak food availability. Across species in the *same* foraging niche mass acts as an index of breeding investment, with females increasing their mass more than males. While across species in *different* foraging niches an increased mass response was associated with higher adult survival, probably because breeding strategy and subsequently adult survival are governed by food limitation. This thesis shows that birds adaptively manage their mass during breeding and that mass is not a result of energetic stress, thus under constant predation risk a bird's mass is a result of foraging predictability as a function of competition for available food and investment in breeding.

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# Chapter 1: General Introduction

Seasonality influences life history through its effect on the availability of essential resources (Ashmole 1963, Ricklefs 1980, Martin 1987). Birds reduce the costs of breeding by timing the provisioning of chicks to coincide with peak food availability (e.g., Perrins 1970). Due to density-dependence, investment in breeding is determined largely by the seasonality of food availability, with an increased investment being traded-off against adult survival (McNamara et al. 2008, Griebeler et al. 2010). Mass acts as an index of a species foraging environment because a bird bases its foraging decisions on a trade-off between the risk of predation and the risk of starvation (Lima 1986, Houston and McNamara 1993, Witter and Cuthill 1993). Under constant predation risk a bird will increase its mass in response to a decrease in foraging predictability, so as to reduce the risk of starvation (Rogers 1987, Houston and McNamara 1993, MacLeod et al. 2008). In tropical savannahs day length and temperature remain relatively constant, and there is not a season of increased density-dependent mortality which acts across all species such as winter in the Northern hemisphere. Therefore how a species experiences seasonality will depend on seasonal variation in its essential resources, and so how a bird manages its mass across the year may provide insights into life history evolution. This thesis investigates how birds in the highly seasonal but predictable environments of a West African savannah, manage their mass within the starvation vs predation framework across seasonally changing resource availability and in response to life history events.

## Seasonality and life history evolution

All animals live in a seasonally changing environment where there is spatial and temporal variation in the availability of essential resources. Within an animal's genetic and phenological constraints this variation is thought to be the driving force in the evolution of different life history traits (Boyce 1979, Roff 1992, Stearns 1992). Life history theory tries to explain how an animal maximises the number of surviving young when resources are limited by the environment (Lack 1968), and is based on the model that growth is costly and reduces the amount of resources that can be used in reproduction, and similarly, that reproduction is costly and reduces subsequent survival (Williams 1966, Stearns 1976, Ricklefs 1977, Calow 1979). Thus the beneficial evolution of one trait is a trade-off against a detrimental change in

another trait, where environmental constraints often determine the relative importance of each trait for survival. For example, reproductive rate is determined by clutch size, nesting success, season length, and nest cycle length, each of which represents the outcome of many different interactions of an individual's life history with its environment (Ricklefs 2000).

Evolutionarily, birds have adjusted the seasonal regulation of life history stages to the seasonality of the environments in which they live. Most birds live in an environment with predictable seasonal changes in conditions within and between years, with species evolving a suite of life history traits that maximise overall fitness (Roff 1992, Stearns 1992). The characteristics of the traits depend on the predictability and seasonality of the environment, with general life history patterns being expressed as r or K selection (MacArthur and Wilson 1967, Pianka 1970, Saether et al. 2002). Species which evolve under r selection inhabit an environment where resources are superabundant for a predictable but short period, followed by a less favourable period, for example a period of extreme temperatures and minimal food availability, e.g. in the arctic. So selection acts on populations during the non-breeding season when competition for remaining resources intensifies and populations experience a period of increased density-dependent mortality. There are then more resources per individual when conditions improve, and so species maximise fitness by producing large numbers of young when conditions allow. An increased investment in breeding has both immediate and longer term consequences for survival which results in higher adult mortality. Conversely, species which evolve under K selection inhabit environments which do not experience such climatic seasonal extremes, and as a result populations remain at, or close to, their carrying capacity throughout the year. As such, populations are more limited by density-dependent factors such as competition during breeding and so species invest fewer resources into reproduction and more into self-maintenance and as a consequence are more likely to survive as adults. This results in species which breed more slowly and parents which dedicate a longer period to parental care in order to maximise the fitness of their offspring in a highly competitive environment (Horn and Rubenstein 1984, Richard et al. 2002). No species undergoes either complete r or K selection but evolves through a combination of both, the degree of each determined by the environment (Pianka 1970).

Seasonality becomes less acute with decreasing latitude, and as such species adopt a more K selected life history (MacArthur and Wilson 1967), with life history traits in birds close to the equator differing from Northern temperate species in many ways, such as: higher survival

rates (Yom-Tov 1994, Johnston et al. 1997, Geffen and Yom-Tov 2000, Peach et al. 2001), lower clutch sizes (Lack 1947, Cody 1966, Ricklefs 1980, Skutch 1985, for review see Martin 1996, Cardillo 2002, Schaefer et al. 2004), lower annual fecundity (Schaefer et al. 2004), longer post fledging care (Geffen and Yom-Tov 2000, Russell 2000, Russell et al. 2004, Schaefer et al. 2004), slower growth rates (Ricklefs 1976, Martin et al. 2011) and increased immunity (Martin et al. 2008). Bird species in the Southern hemisphere show traits more consistent with tropical bird species than Northern hemisphere bird species (Yom-Tov 1987, Rowley and Russell 1991, Russell et al. 2004). This may be due to reduced seasonality in the availability of food in the Southern hemisphere, together with high ambient temperatures, lack of severe winters, and the high proportion of predators in these regions (Ashmole 1963, Skutch 1985, Rowley and Russell 1991, Martin et al. 2000b, Martin et al. 2006).

### **Seasonality and life history traits**

The host of different trade-offs which influence each life history trait mean that it has been difficult to determine the driving force behind life history evolution. More recent analytical models have concluded that because of density-dependence it is the degree of seasonality of resources which is the primary driver of life history evolution, with factors such as levels of nest predation and the length of the breeding season refining a species' optimal strategy within its environment (McNamara et al. 2008, Griebeler et al. 2010). The seasonality of food availability can influence a range of life history traits such as laying date (Perrins 1970), offspring growth rate (Blancher and Robertson 1987), interval between breeding attempts (Arcese and Smith 1988), predation rate (Arcese and Smith 1988), nest attentiveness during incubation (Chalfoun and Martin 2007) and parental care tactics (Markman et al. 2002). Specifically I will discuss how seasonal variation in resource availability influences the following core life history traits:

#### *The timing of breeding*

The costs of reproduction are widely assumed to be fundamentally important to the evolution of life-history strategies, because breeding is the largest single cost that a bird will experience in a year (Roff 1992, Stearns 1992). In order to maximise off-spring survival and minimise the cost of breeding to adults, provisioning for chicks should coincide with the period of

highest food availability because an increase in food delivery per chick increases growth rate, condition and immunological resistance (e.g., Perrins 1970, Gustafsson et al. 1994).

Therefore the predictability and scale of the seasonal food peaks is vital for determining how a bird maximises its fitness by producing the greatest number of surviving young. In a predictable but highly seasonal environment where there is a single short breeding season where food may not be limiting (reviewed in Martin 1987), there may only be a narrow window of opportunity for breeding with those individuals which breed earlier in the season being able to increase the number of surviving young (Perrins 1970, Martin 1987). In the tropics where seasonality is reduced, breeding seasons are longer and there is a less defined peak in food availability. So birds are not as constrained as to when they can breed, and there may be sufficient time to attempt multiple broods should previous nests fail (Stutchbury and Morton 2001, Stutchbury and Morton 2008). As day length remains relatively constant, species probably rely less on increases in photoperiod to initiate breeding and more on environmental cues such as food availability (e.g., Wikelski, Hau & Wingfield 2000; Hau, Perfito & Moore 2008). As such, the timing of breeding tends to be population specific, depending on the local climatic conditions that drive seasonal peaks in food availability (Wingfield 1980, Moore et al. 2005), and there is increased variation in the timing of breeding across species in the same habitat, because seasonality depends more on a species' particular foraging niche.

Species living in an unpredictable environment have to trade off maintaining physiological preparedness (which can be costly) with being unprepared (which decreases the chances of successful reproduction; Tokolyi *et al.* 2012). Consequently selection favours those individuals that can maximise reproductive success through rapid breeding attempts when conditions allow, even at a cost to their own survival (Grant et al. 2000, Hau et al. 2004). The Zebra Finch *Taeniopygia guttata* is a classic example of an opportunistic breeder because it is capable of breeding throughout the year in the arid interior of Central Australia (Zann et al. 1995, Perfito et al. 2007), where rainfall is unpredictable. In the non-breeding season many individuals in the population maintained increased physiological readiness for breeding, even at a cost to body condition compared to zebra finches inhabiting a more predictable seasonal habitat (Perfito et al. 2007).

### *Clutch size*

One of the best known latitudinal gradients in life history is the increase in avian clutch size with increasing latitude (Moreau 1944, Lack 1947, Ricklefs 1980, Martin 1996, Cardillo 2002). The clutch size of a species should correspond to the number of young that parents can nourish adequately so as to maximise their individual fitness (Lack 1947, 1948). Thus the reproductive rate should depend on the seasonality of resources and population density during the breeding season (Ashmole 1963). Therefore clutch sizes increase with increasing seasonality because there are more resources available per individual during breeding (McNamara et al. 2008), with clutch sizes tending to be larger in years or habitats with greater food availability (Reviewed in Martin 1987). An increase in clutch size and therefore reproductive effort is then traded off against adult survival (Saether 1988, Martin 1995, Ghalambor and Martin 2001), and so the seasonality of an individual's foraging niche directly shapes life history evolution.

### *Nest predation*

Seasonal variation in essential resources causes movements of predators on many scales (e.g., Thiollay & Clobert; Sperry et al. 2008), and subsequently there is thought to be high variability between species, seasons and years in the levels of nest predation experienced (Robinson et al. 2000). Nest predation is the primary cause of reproductive failure in most birds, thus acts as a strong selective force on parental care tactics, which directly influence life history through their effect on nestling success and therefore fitness (Slagsvold 1982, Martin et al. 2000a, Martin et al. 2000b). An increase in the risk of a nest being predated is associated with a reduced total feeding rate and per-nestling feeding rate, because more frequent nest visits by parents increase the probability of a nest being detected by predators (Martin et al. 2000a, Martin et al. 2000b, Eggers et al. 2005, Fontaine and Martin 2006, Massaro et al. 2008, Martin et al. 2011). Birds are thought to be able to assess nest predation risk and adjust egg size, clutch size and the rate they feed the nestlings accordingly, with parents investing more in the young when there is reduced predation risk. Thus perceived predation risks yield significant fitness consequences for the young (Fontaine and Martin 2006, Martin 2011). Although food limitation is probably the dominant force behind variation in clutch size, high levels of nest predation may reduce both the number of eggs laid

(McNamara et al. 2008, Griebeler et al. 2010) and chick growth strategies (Martin et al. 2011) below the limits set by food availability.

### *Post-fledging care*

The seasonality of a bird's foraging environment has a strong influence on parental care tactics, which determine life history through their effects on juvenile survival and therefore fitness. Those species that inhabit a less seasonal environment experience reduced density-dependent mortality during the non-breeding season, resulting in an increase in competition for food during the breeding period. Consequently density-dependent factors will be increasingly important in determining population dynamics; as such an individual's ability to compete in a highly competitive environment is a strong selective force on its fitness (Ashmole 1963). In such an environment, species that provide extended parental care may allow juveniles to survive until they become sufficiently competitive. High adult survival and low territory turnover also favour longer parental care and delayed dispersal, and have been related to increased survival of the young (Willis 1967, Fogden 1972, Willis 1972, Skutch 1976), partly through increased immunocompetence of the chicks (Ricklefs 1992). In accordance with this idea, birds inhabiting tropical and/or Southern hemisphere habitats tend to have longer post-fledgling parental care and delayed dispersal, relative to Northern hemisphere species (Martin 1996, Ghalambor and Martin 2000, Russell 2000, Russell et al. 2004).

### *Survival*

Survival depends on the seasonality of resources and its effects on breeding, because breeding is costly and an increased investment in each breeding attempt and/or numerous breeding attempts carries physiological and behavioural costs which reduce the chances of immediate and longer term survival (Bryant 1988, Dufty Jr 1989, Cressler et al. 2010). An increase in seasonality and thus an increase in the food available to an individual during breeding, allows individuals to invest more in each breeding attempt. An increase in reproductive effort has immediate physiological costs such as a reduction in immunity to disease (Sheldon and Verhulst 1996, Norris and Evans 2000) as well as possible longer term consequences (Gustafsson et al. 1994, Daan et al. 1996). Breeding also leads to behavioural changes, which can reduce survival (reviewed by Lima 2009), such as increased aggression

(Dufty Jr 1989) or nest defence (Caro 2005), and therefore risk of injury. An increase in reproductive effort also means that birds need to spend more time foraging to feed chicks and so spend a greater proportion of their time exposed to predators, and as such are less likely to survive to the next breeding season (reviewed in Stephens *et al.* 2007).

### *Mass variation*

A bird's mass acts as a bridge between the seasonality of its foraging environment and life history because how a bird adaptively manages its mass is a reflection of environmental conditions (Pravosudov & Grubb 1997). Seasonal mass variation can therefore be considered a life history trait because it is a function of seasonal variation in resource availability. A bird regulates its mass as a trade-off between the risk of starvation and the risk of predation, in a way consistent with maximising overall survival (Lima 1986, Lemon 1991, Houston *et al.* 1993, Rogers and Smith 1993, Gentle and Gosler 2001, Olsson *et al.* 2002). In order to avoid the risk of starvation a bird is as heavy as possible because greater fat reserves allow birds to survive longer periods of unpredictable foraging (Rogers 1987). However, in order to reduce the risk of predation a bird needs to be as lean as possible because increased mass reduces acceleration when escaping predators (Lima 1986, McNamara and Houston 1990, Houston and McNamara 1993, Witter and Cuthill 1993, Gosler *et al.* 1995). Being fat also carries costs in terms of increased metabolic expenditure and extended exposure to predators while foraging to maintain the mass (Witter and Cuthill 1993). Therefore fat reserves are not maintained when foraging is more predictable and starvation risk is reduced.

Interruptions to a bird's foraging, such as from an increase in predation risk, severe weather events or conflict with time spent engaged in breeding activities causes a bird to increase its reserves against the increased risk of starvation, i.e. an interrupted foraging response (Houston and McNamara 1993, Pravosudov and Grubb 1997, Lilliendahl 1998, Gentle and Gosler 2001, McNamara *et al.* 2005, MacLeod and Gosler 2006). This adaptive increase in body mass can increase the chances of survival through the availability of stored energy reserves as insurance against starving due to unpredictable foraging conditions (Houston and McNamara 1993, Bednekoff and Houston 1994, Gosler 1996). Macleod *et al.* (2008) found that in European starlings *Sturnus vulgaris* subjected to constant predation risk, the scale of a bird's mass response gave an index to the quality of the foraging environment. They



concluded that a larger mass increase was indicative of a poorer foraging environment and thus an indication of population decline.

Mass can act as an index of life history strategy because a bird's foraging decisions have direct influence on its immediate and future survival (Lima 1998a, Caro 2005). Birds show many behavioural and physiological changes to reduce mortality from predation and these are likely to have negative effects on other aspects such as fitness and population dynamics, as well as affecting the ecology of their own prey and predators (Cresswell 2008). If a bird is not starving, how it manages its mass as a consequence of interruptions to its foraging is dependent on the quality of the foraging environment and provides a framework to predict life history, behaviour, fitness, population dynamics and community structures (Abrams 1984, McNamara and Houston 1987, Bolker et al. 2003, Cresswell 2008).

### **Seasonal mass variation: tropical savannahs as model systems**

High levels of species diversity combined with the lack of the driving evolutionary force of winter means that tropical environments offer a powerful tool for disentangling mass variation in response to life history events. The absence of seasonally short day lengths and in most environments, low temperatures, may mean that foraging remains predictable throughout the year. Or at the least a possible 'lean' season may be reduced (Ward 1969, Fogden 1972). The non-lethal effects (or perception) of predation may also remain relatively constant across the year because communities are driven more by density-dependent than independent forces, so there are higher numbers of competitors and con-specifics to spread the risk of being depredated (Brandt 2007, Cresswell 2008). If foraging remains predictable and perception of predation does not vary significantly across the seasons, then in the non-breeding season birds may not need to store excess fat as in the Northern hemisphere and so any seasonal variation in mass may be due to other factors such as from interruptions to foraging (Rogers and Smith 1993) or birds compensating for seasonal water constraints with increased metabolic water (Macmillen 1990).

In particular, the savannahs of West Africa may be ideal for understanding the effects of seasonality of a bird's foraging environment on mass variation and subsequently life history. This is because they lack a period of high density-dependent mortality which acts across all species, and day length and temperatures remain relatively constant across the year, as does the timing, intensity and duration of the rains (Bourlière and Hadley 1970), which are driven

by the annual movement of the Inter-Tropical Convergence Zone (Bourlière and Hadley 1970, Perry and Walker 1977, Tyson 1986, Osborne 2000). The seasonal availability of water, which goes from almost negligible at the end of the dry season to superabundant at the end of the wet season, has a considerable influence on leaf production, and the flowering and fruiting of savannah trees (de Bie et al. 1998). Young leaves are eaten by numerous adult insects and/or their larval stages, and so the abundance of such insects is related to the seasonality of leaf production (Poulin et al. 1992). Ground-dwelling arthropods are present in low numbers throughout the dry season, but the arrival of the rains then causes an explosion in the density and diversity of arthropod populations (Dingle and Khamala 1972, Poulin et al. 1992). Those species that rely directly on water for survival may experience increased seasonality, incurring greater costs when water is limiting such as from increased travel (Brandt and Cresswell 2008). Many insectivorous, nectivorous and frugivorous species live relatively independent of standing water (Fisher et al. 1972, Fogden and Fogden 1979, Gill 2007), so are affected by rainfall through its effect on primary productivity. However, food and water are often strongly complimentary in granivorous birds (Kotler et al. 1998); with many species relying on drinking water to facilitate the digestion of seeds during the dry season, particularly during high midday temperatures (Immelmann and Immelmann 1967, Skaed 1975, Ward 1978, MacMillen and Baudinette 1993, MacMillen and Hinds 1998). Therefore how species or populations experience seasonality is likely to be determined by their foraging niche, because different food types will vary in the timing and scale of their peak abundance (Poulin et al. 1992, Peach et al. 2001).

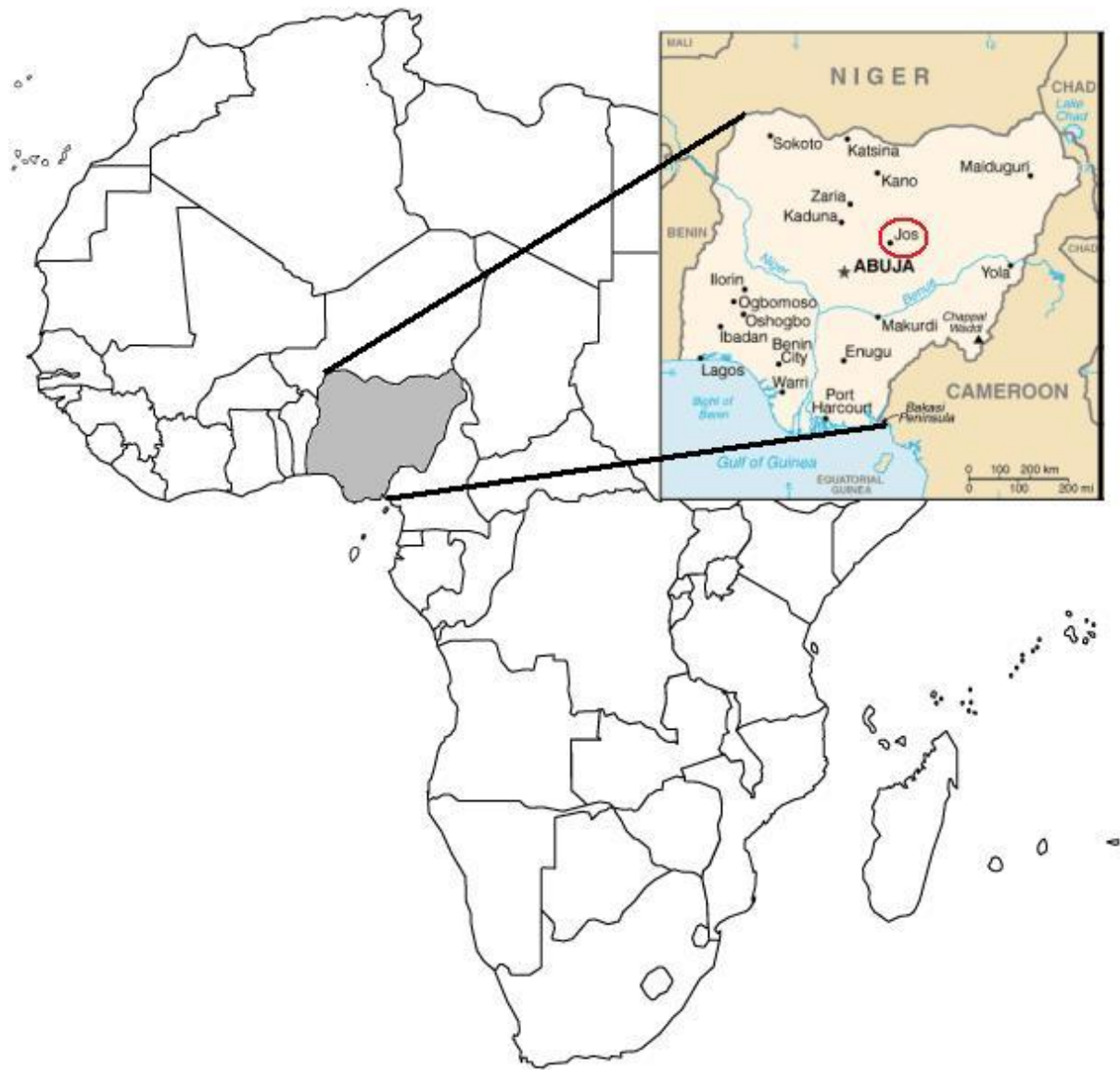
#### *Dispersal reduces the seasonality of competition*

In tropical savannahs seasonal variation in food availability causes the movement of populations on many scales, with avifaunal communities consisting of both transient and sedentary populations of many species (Fry et al. 1992-2004, McGregor 2005). Therefore, although food availability increases during breeding, an increase in energetic expenditure coupled with an increase in the number of competitors and con-specifics for available food sources may mean that foraging predictability actually decreases. Therefore some populations will be increasingly constrained by density-dependent factors during breeding, so selection acts on those individuals who invest in smaller clutch sizes and longer parental care. These species may be more similar in their life history strategy to lowland tropical forest species having smaller clutch sizes and higher rates of adult survival (McGregor et al. 2007a). If

populations do remain close to their carrying capacity then it may be less costly, e.g. through reduced competition for resources, for some individuals to either breed out of the main breeding season or to have extended breeding seasons.

### **The study site**

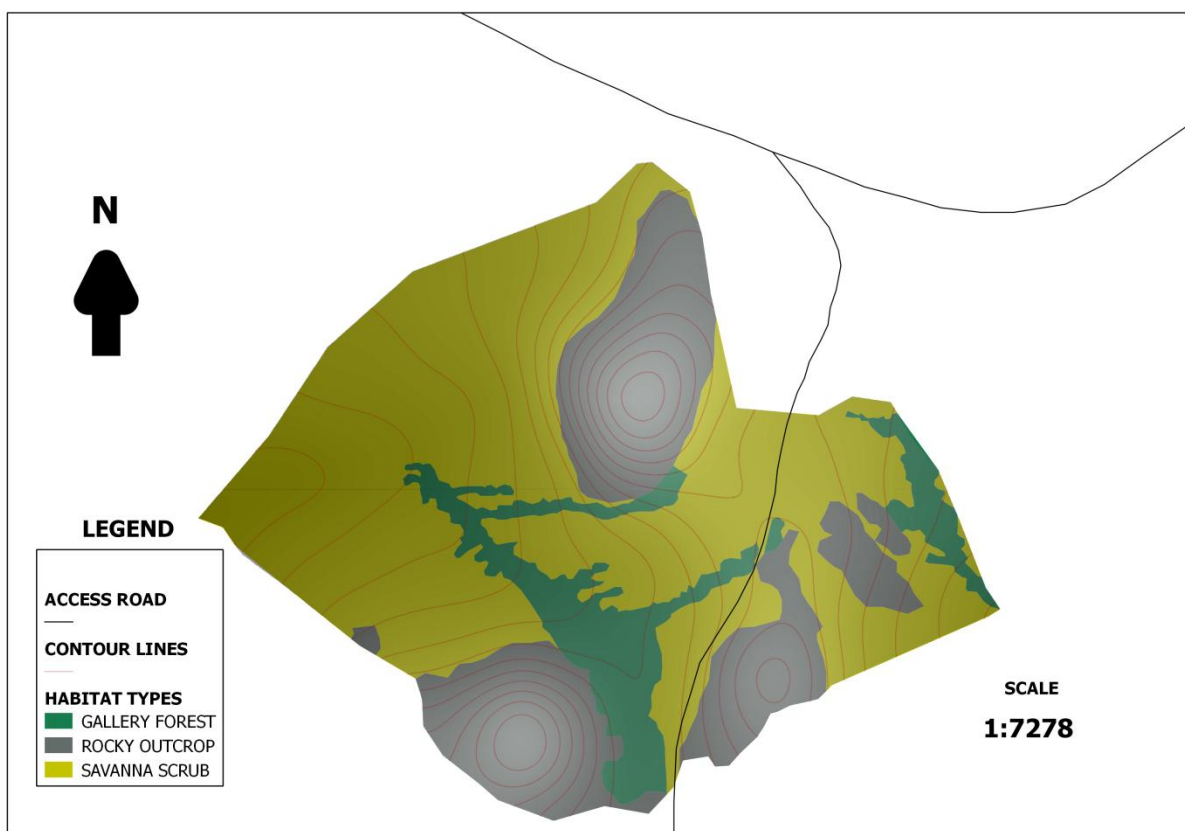
This study was conducted on the Jos Plateau in Nigeria, which lies midway along a rainfall gradient from rainforest in the south to dry Sahel and deserts in the north (Figure 1). The plateau is situated on the interface between humid (annual rainfall  $> 1500\text{mm}$ ) and semi-humid habitats ( $< 1500\text{ mm}$ ) where seasonality may be more pronounced (Omorie and Akenova 1999), at least in West Africa, because there is a single intense wet season (Dowsett-Lemaire 1997), which retains a relatively high year to year stability compared to two wet season regimes (Herrmann and Mohr 2011). Combined with cooler temperatures due to the altitude of the site (1300 m asl), this may mitigate some of the factors causing the decline in arthropod abundance (Poulin et al. 1992), thus allowing for slightly increased diversity in life history strategies compared to more arid habitats. The Jos plateau therefore combines components of both more arid and more humid environments.



**Figure 1:** Location of the study site in Nigeria, West Africa.

Amurum Community Forest Reserve (Amurum; N 09° 52'; E 08° 58') is located in the centre of the Guinea savannah zone in Nigeria and consists of 120 hectares of four main habitat types; gallery forests, rocky outcrops 'inselbergs', degraded guinea savannah and mixed farmland (Figure 2). The site contains areas of vegetation typical of the Guinea savannah zone with small patches of 13m-17m high broadleaved woodlands and gallery forests (*Brachystegia eurycoma*, *Parkia bigobosa*, *Vitellaria paradoxa*, *Terminalia*, spp.). Most of the site is dominated by low growing scrub of *Combretum* spp., occasional *Acacia* spp., and large areas of grassland dominated by species such as *Andropogon* spp., and *Hyparrhenia* spp. (Figure 3, Elgood et al. 1994). Due to its close proximity to Jos (12km to the West) much of the habitat surrounding the reserve has been severely degraded by anthropogenic

pressures. Relatively Amurum is a high quality heterogenic habitat, and as such probably acts as a source habitat to the surrounding area. Across the plateau, forest and savannah patches are linked by a network of gallery/riverine forest which may act as corridors for the dispersal of both forest and savannah species (Omotoriogun et al. 2011). In Amurum Forest Reserve the rainy season lasts for approximately six months, from the 10th of April  $\pm$  9 days until the 13th of October  $\pm$  11 days, there was an annual rainfall of  $1337 \pm 159$  mm (2001-2011), with the heaviest rainfall occurring in August ( $290 \text{ mm} \pm 28 \text{ mm}$ ). Maximum temperatures range from between 20 and 25 °C during the coldest months, rising to 30 to 35 °C at the end of the dry season. Day length varies annually by 68 minutes.



**Figure 2:** Amurum Community Forest Reserve. The reserve is surrounded by land that is farmed by subsistence farmers.

Data were also used from birds caught in Yankari Game Reserve, Bauchi State (N09° 20'; E10° 30'). The habitat comprised more Sudan, rather than Guinea, savannah and therefore had some differences in floral composition. However, overall the degree of seasonality and climate was similar to Amurum.



**Figure 3:** Typical habitat within Amurum Community Forest Reserve, showing degraded guinea savannah, galley forest and inselberg habitats.

#### *Methodological details*

This thesis uses data collected from birds caught using four-panelled mist nets in Amurum. On capture the bird was first aged and sexed, before the maximum wing chord was measured using a stopped wing rule (Svensson 1992). The mass was recorded using electronic scales to the nearest 0.1g. The bird was assessed for body and wing moult (Redfern and Clark 2001) and whether or not there was a brood patch present (Redfern and Clark 2001). Each bird was then fitted with an individually numbered ring so that it could be identified if recaptured, before being released unharmed. The ringing program at the A. P. Leventis Research Institute (APLORI) commenced in November 2001 and has been run continuously by PhD students at the University of St Andrews. Ringing is conducted throughout the year, and until 2010 it was concentrated over two 14 day Constant Effort Sites (CES), utilising 272m of mist net. The CES was carried out at the end of the end of the dry season in March-April and again at



the end of the wet season in September-October. In order to increase the numbers of species and individuals caught, as well as to have systematic ringing during the most biologically interesting period during the wet season (June), since 2010 the CES program changed to being conducted at two sites alternately over six days, five times a year. The CES has then been conducted at the end of the dry season (March), start of the wet season (April), middle of the wet season (June), end of the wet season (October) and start of the dry season (November). Nets were reduced to 153m at the original site, and 171m of new net were set at a site surrounding APLORI, totalling 324m.

Ringing activities also provided an opportunity to instruct West African APLORI MSc students in this field technique, several competent ringers have now been produced who are currently expanding APLORI's ringing activities through different research projects within Nigeria. During this thesis I concentrated on expanding APLORI's current ringing activities, along with updating the database to Access 2007 and managing the writing of the Ringing Guide to the Birds of West Africa which is available on APLORI's website <http://www.aplori.org>. In total there have now been 25,000 individuals caught of 366 species, along with 7,300 recaptures.

### **Aims of the study and hypotheses to be tested**

In the following five chapters of this thesis: 1) Firstly, I established patterns of seasonal and annual mass variation across 47 species of small savannah birds; 2) I then explored the use of two breeding indicators to ascertain to what degree there was seasonality of breeding in 25 species of savannah bird and how timing of peak breeding was related to feeding guild; 3) This allowed me to expand on the previous two chapters to investigate how birds increased their mass during breeding through an interrupted foraging response, and how the scale of any mass gain was related to sex and species-specific investment in breeding activities; 4) The next chapter established mass variation as a life history trait by exploring the relationship between seasonal mass variation and variation in the timing of peak mass across the years with adult survival; 5) Finally, I summarise the subjects researched in this thesis and how these relate to one another to establish mass variation as a bridge between foraging theory and life history in tropical birds.

## **Chapter 2:** Patterns of seasonal and annual mass variation in West African Tropical Savannah birds

A bird regulates its mass as a trade-off between the risk of predation and the risk of starvation (Brodin 2001). Birds in the Northern hemisphere increase mass reserves in response to seasonally low temperatures and shorter day lengths that increase foraging unpredictability and so starvation risk (Houston and McNamara 1993, Cresswell 1998, Brodin 2007). However, in many tropical environments day length and temperatures remain relatively constant across the year and so bird species may not need to increase their reserves in the non-breeding season because foraging remains predictable (e.g., Ward 1969, Fogden 1972, Rozman, Runciman & Zann 2003). If food availability remains high then any seasonal variation in reserves may provide insights into individual investment in life history events. Mass variation in the savannah species of this study is probably representative of mass variation in tropical environments which don't experience seasonally cold temperatures (see also Ward 1969, Fogden 1972, Crowe et al. 1981, Wikelski et al. 2000, Rozman, Runciman & Zann 2003).

This chapter tested two hypotheses:

- I. That tropical bird species vary their mass seasonally,
- II. Species that vary their mass do so in response to seasonally variable foraging opportunities characterized by a dry and wet season, moderated by their foraging guild and migratory status.

## **Chapter 3:** The seasonality of breeding in savannah birds of West Africa assessed from brood patch and juvenile occurrence

Breeding is a costly life-history activity which conflicts with adult survival (Saether 1988, Bennett and Owens 2002). Animals reduce the costs of reproduction by timing their breeding around periods of increased resource availability, avoiding periods of resource constraint (Lack 1968). In the tropics the rains drive distinct seasonal peaks in resource availability and many species time their breeding around these peaks (Poulin et al. 1992), despite the fact that foraging probably remains predictable for much of the year. So how a species experiences seasonality will determine the timing and length of its breeding season. This chapter assessed the suitability of two potential breeding indicators, proportion of brood patches in adult birds and the ratio of juveniles to adults, to test two hypotheses:



- I. That species will show a distinct seasonal peak in breeding activity even though individuals of most species can potentially nest throughout the year,
- II. That seasonal peaks are coincident with peak food availability so that timing of breeding will depend on the feeding guild.

***Chapter 4:*** Breeding as interrupted foraging – seasonal mass gain in tropical savannah birds

Birds put on mass reserves in response to interruptions to their foraging which may arise from a number of sources such as predators, disturbances, long winter nights or extreme weather events (Lima 1986). Theoretically, breeding should also represent a similar interruption in foraging because adult birds have to divert time away from their own foraging to incubate eggs, feed chicks and to guard mates, nests and territories. So within the same foraging environment the scale of any mass response will reflect foraging predictability as determined by an individual's level of investment in breeding. This chapter tested two specific hypotheses:

- I. That mass gain occurs during the breeding season for both incubating and non-incubating birds (i.e. mass increases during the breeding season and is not solely due to gonad or egg development),
- II. That the scale of mass gain due to breeding of males and females differs due to sex specific costs associated with different breeding stages.

***Chapter 5:*** Mass variation during breeding as an indication of food limitation and its consequences for adult survival

If foraging is predictable in the non-breeding season a bird will reduce its mass to avoid mass-dependent costs. Within such a foraging environment the scale of any subsequent mass increase during breeding is an index of breeding investment, with higher levels of reserves also being associated with poorer quality environments (MacLeod et al. 2008). However, in tropical savannahs where day length and temperatures remain relatively constant, how a population experiences seasonality will depend on its foraging niche. If predation risk remains relatively constant across the year then the level of body reserves should reflect life history events, as a consequence of adaptation to the quality of the foraging environment. Animals that are r selected exploit super abundances of often unpredictable food availability, so during breeding they are not constrained by absolute levels of resources or competition and so might show a reduced mass response. In contrast animals that are K selected exploit

lower levels of predictable food availability and are constrained during breeding by the absolute level of food resources and competition for them and so may show an increased mass response. This chapter tested two specific hypotheses:

- I. That savannah species which show a larger interrupted foraging response will have higher apparent survival
- II. That species which show peaks in mass at different times in different years will have reduced apparent adult survival.

## **Chapter 2: Patterns of seasonal and yearly mass variation in West African tropical savannah birds**

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### **Summary**

Birds in the Northern hemisphere usually increase mass reserves in response to seasonal low temperatures and shorter day length that increase foraging unpredictability and so starvation risk. In the lowland tropics relatively low temperatures and short day lengths are absent and so the risk of starvation may be reduced, leading to much smaller seasonal effects on mass. Nevertheless, other factors such as high temperatures and water and food availability may vary greatly between tropical wet and dry seasons leading to variable starvation risk and seasonal mass effects. Using data collected from 47 species of birds caught over a 10-year period in a tropical savannah region in West Africa we tested for seasonal variation in mass in response to a predictable, strongly seasonal tropical climate. Many species (91%) showed seasonal variation in mass, and this was often in a clear annual pattern that was constant across the years. Many species (89%) varied their mass in response to seasonally predictable rainfall. Annual variation in mass was also important (45% of species). Relatively few species (13%) had a seasonal pattern of mass variation that varied between years. Feeding guild or migratory status was not found to affect seasonal or annual mass variation. Seasonal mass change was on average 8.1% across the 21 species with very large sample size and was comparable to both northern and southern temperate species. Our study showed that biologically significant consistent seasonal mass variation is common in tropical savannah bird species, and this is most likely in response to changing resource availability brought about by seasonal rainfall and the interrupted foraging response due to the constraints of breeding.

### **Introduction**

Birds regulate their mass as part of the trade-off between the risk of starvation and the risk of predation (Brodin 2001). For example, birds lay down fat deposits to insure against unpredictable foraging opportunities in winter, when day length and temperature are reduced (Cresswell 1998, Brodin 2007). Carrying fat, however, bears a cost in terms of increased

mass-dependent predation risk, due to reduced acceleration during escape flights of fatter birds (Lima 1986, McNamara and Houston 1990, Houston and McNamara 1993, Witter and Cuthill 1993), and higher metabolic costs and extended exposure to predation while foraging (Lima 1987). Therefore fat reserves are not maintained when starvation risk is reduced, such as during the summer in northern temperate regions when temperatures are higher and foraging is more predictable. A bird's mass is therefore a reflection of environmental conditions (Pravosudov and Grubb 1997).

Regular cold temperatures and short day length occurring in the winter of temperate and boreal regions are the main reason for seasonal weight variation in birds occurring in northern latitudes (Rogers and Heath-Coss 2003). In the tropics, however, temperature and day length remain relatively constant throughout the year, and so there is no season when birds have a particularly high risk of starvation due to longer and colder nights (Brodin 2007). Warmer, shorter nights, followed by predictable foraging conditions suggest that tropical birds can afford to avoid the cost of carrying elevated fat reserves throughout the year. Furthermore, the cost of increased fat reserves may be higher in the tropics. Perceived or actual risk of predation may be different in the tropics compared to northern temperate regions (Brandt and Cresswell 2009), because survival rates appear to be higher (Jullien and Clobert 2000, Peach et al. 2001, McGregor et al. 2007a) and there is an increase in the density and diversity of predators (Thiollay 1991, 1999). Nevertheless significant adaptive mass variation has been recorded in tropical birds (McNeil 1971, Fogden and Fogden 1979, Brandt and Cresswell 2009), although there are surprisingly few studies that have measured this in non-migrating birds. For example, across its geographical range, 59 different populations of a common African species (Common Bulbul *Pycnonotus barbatus*) have been shown to display a degree of plasticity in their weight variation in response to varied environmental conditions: individual birds tended to be heavier at sites with lower temperatures and populations responded to increased seasonality by increasing their body mass in colder months (Crowe et al. 1981).

Although the risk of starvation caused by seasonal low temperatures may be less important in determining seasonal mass change in tropical birds, other factors may still cause mass reserves to vary seasonally. In particular, tropical environments are characterised by rainfall seasonality, with the monsoon rains driving predictable peaks in the abundance of food sources and the availability of standing water (Osborne 2000). Seasonal availability of water

(Macmillen 1990) and its interaction with high diurnal temperatures (Goulart and Rodrigues 2007) have both been shown to affect mass reserves in birds. Consequently many tropical species schedule costly activities, such as breeding, moult and migration seasonally (Fogden 1972, Elgood et al. 1973, Sinclair 1978, Dittami and Gwinner 1985, Cruz and Andrews 1989, Abrams 1991, Poulin et al. 1992). Any effects of seasonal variation in starvation risk because of variable rainfall may however be dependent on feeding guild. Granivores may have a peak of food availability after the rains as grasses set seed (Crowley and Garnett 1999, Brandt and Cresswell 2009), whereas insectivores may have a peak of food availability during the rains as invertebrate numbers peak (Dingle and Khamala 1972).

Temporally variable resources may also result in seasonal movements on many scales (Elgood et al. 1973, Karr 1976, Newton 2008). Seasonal mass change could be expected to occur in intra-African migrants as they increase their fuel reserves in preparation for migration (Fry 1967, Jones and Ward 1977, Ward and Jones 1977) due to the high energy demands of migration (King and Farner 1965, Ramenofsky 1989). Starvation risk, and therefore mass reserves in the tropics might also be caused by density-dependent processes associated with a higher population density of con-specifics and competitors (Rohde 1992, Gaston 2000). For example, spatial redistribution of birds due to migration may change local competition levels and so seasonal foraging uncertainty for both migrants and residents that the migrants join or leave, again leading to seasonal mass variation (Rogers 1987).

In this paper we use data collected over a ten year period in a tropical west African savannah to test two hypotheses: 1) that tropical bird species vary their mass seasonally and 2) species that vary their mass do so in response to seasonally variable foraging opportunities characterised by a dry and wet season, moderated by their foraging guild and migratory status.

## **Methods**

### **Study site**

We estimated the seasonal weight variation of small tropical birds in Guinea savannah woodland at the AP Leventis Ornithological Research Institute (APLORI) Amurum Forest Reserve on the Jos Plateau (09°52'N, 08°58'E) and at Yankari Game Reserve (09°45'N, 10°30'E) in Nigeria: we caught 13,353 individuals of 47 species (Table 1). All retraps of

birds were excluded from the analysis to avoid pseudoreplication or over parameterisation of the model. We included all species where more than 60 individuals were caught: species with smaller sample sizes did not have a sufficient spread of captures across seasons and years to allow meaningful analysis.

Birds were trapped using understory mist nets between November 2001 and March 2011. Trapping occurred year round but was concentrated at a Constant Effort Site (CES) conducted biannually in Amurum for a 14 day period, at the end of the dry season (March-April) and the end of the wet season (September-October). During the CES, 272 meters of 4 shelf net was used between 06:00 to 10:30 h WAT (although with few captures after 09:30 h). Trapped birds were aged and sexed where possible. Maximum wing-chord was measured using a stopped wing rule to 1mm (Svensson 1992). Mass was measured to 0.1g using digital scales (Ohaus Scout). For each species the time of year was classified into four seasons estimated from the approximate start and finish of the rains: end of dry season (February-April), start of wet season (May-July), end of wet season (August-October), start of dry season (November-January). Seasonal rainfall at the site was estimated from monthly rainfall summaries from Jos Airport (09°52'N, 08°53'E), which is located in the centre of Jos Plateau and 26km from Amurum Forest Reserve. Each species was assigned a residency status on the basis of seasonal variation in capture rates. Migratory status was assigned to any species that had > 50% reduction in capture rate between the end of the wet season and the end of the dry season CES (Table 1). A species was considered sedentary if there was a less than 50% variation in catching totals between CESs. Species were assigned to feeding guilds according to diet (Elgood *et al.* 1994, Urban *et al.* 1997 and Fry *et al.* 2004).

### *Variables and statistical analysis*

We adopted the Information Theoretic statistical approach to test for the relative importance of six parameters on mass variation in each species (AICc, Burnham & Anderson 2002). Parameters included in the model were season (S), year (Y), variation in the annual timing of mass variation (S\*Y), age, seasonal rainfall (mm), sex (where sexes could be reliably distinguished in the hand), and wing length (as an index of overall size, mm). We included the interaction (S\*Y) to test if seasonal patterns were consistent between years. If S\*Y was not significant ( $n = 40$  species), we reran the model excluding this interaction. If S\*Y was

significant ( $n = 7$  species) we ran separate models for every year and averaged effect size across years.

The mass of a species for a particular season was calculated from the parameter estimates (for example,  $\text{mass} = \text{Intercept} + (\text{mean wing} * \text{wing estimate}) + \text{year estimate} + (\text{total rain} * \text{rain estimate}) + \text{age estimate for adults} + \text{sex estimate (if included)} + \text{season estimate}$ ). The predicted mass of a species in the lightest and heaviest season within a year was calculated by using the season with the lowest and highest parameter estimate respectively. The proportional difference in predicted mass between the lightest and heaviest season was then calculated  $((\text{mass in the heaviest season} - \text{the mass in the lightest season}) / \text{mass in the lightest season})$ . To standardise effects across species the estimate for year was either arbitrarily set for 2006 (the year of largest sample size and mid-point of the study) for species with models that did not show a significant interaction of season with year ( $S*Y$ ). For species where this interaction was significant, we simply averaged effect sizes across the different years' models.

The best models were then evaluated using AICc to calculate the Akaike weight ( $W_1$ ) of the top model.  $W_1$  converts the deviance of all possible models to a scale of zero to one. Each weight then represents the likelihood that that model is the best model. We also calculated the number of models which showed equal support for the top model ( $\Delta < 2$  (Burnham & Anderson 2002, Richards 2005)). We recorded which variables were represented in models where  $\Delta < 2$  (Table 1, Fig. 1) before model averaging all possible models to obtain relative variable weights. There was a positive relationship between sample size and the weight of the top model and a negative relationship between sample size and the number of models where  $\Delta < 2$ . Analysis was conducted using the MuMIn and lme4 packages in R 2.13.0 (R Development Core Team 2011).

We examined to what extent the range of species in our sample was phylogenetically representative of West African savannah birds. Although we sampled reasonably randomly with respect to species that might show seasonal mass variation (any species caught in sufficient numbers by mist-netting was included here), any overall estimate of the proportion of species showing seasonal mass gain may be confounded if some genera (or families, or orders) were sampled more frequently with respect to proportion of species than others, and some taxa are more likely to show seasonal mass change than others. We adjusted for any such effects of uneven sampling across species by multiplying the total number of species

within genera (or within families, or within order) available at the study site by the proportion of species sampled within that genus (or family, or order) that showed seasonal mass change. We then averaged this true estimate of the number of species within genera across all genera present at the study sites (or species within families across all families present at the study sites, or species within order across all orders present at the study sites) showing seasonal mass change.

Time of day was not included in analysis because these data were missing in many cases so greatly reducing our sample sizes. Inclusion of time of day to the nearest hour in the best model for each species did not significantly affect seasonal and annual parameter estimates except as might be expected by a reduction in sample size ( $n = 9\,010$ , species = 38). The lack of effect of time of day on seasonal results was expected because data were almost always collected between 06:30 and 10:30 h (and most commonly between 07:00 - 09:00 h), and any effects acted in an unbiased way across seasons.

## Results

There was strong evidence for consistent seasonal mass variation linked to rainfall variation in most species. Season was included as a parameter in at least one of the top models for 43 species (91%, Table 1, Fig. 1). All four species that did not include season in their top models had significantly different seasonal catching totals and small sample sizes (Table 1), suggesting that seasonal mass variation may have been detected in these species with a larger or more seasonally uniform dataset. The timing of the seasonal mass change varied across years for six species (13%, Table 1). Year was included as a parameter in at least one of the top models for 21 species (45%, Table 1). Rainfall was included as a parameter in at least one of the top models for 42 species (89%, Table 1). An example of a species showing predictable seasonal variation in mass (African Thrush *Turdus pelios*) and a species showing variation in the seasonal pattern of mass change dependent on year (Northern Red Bishop *Euplectus franciscanus*) are illustrated in Figure 2.

Seasonal mass change was on average 12.6% ( $\pm 1.6$ ) across the 47 species. Most species had their highest mean mass at the end of the wet season and start of the dry season, but there was no clear season in which most species were lightest (Table 1, Fig. 3). There was no significant difference in the frequency of the season with the lowest mass ( $\chi^2_3 = 0.3$ ,  $P = 0.96$ )



or highest mass ( $\chi^2_3 = 0.5$ ,  $P = 0.93$ ) according to resident or transient status (Table 1). The effects of the predictor variables were fairly consistent regardless of feeding guild, and there was no significant difference in the frequency of the season of lowest mass ( $\chi^2_9 = 9.8$ ,  $P = 0.37$ ) or highest mass ( $\chi^2_9 = 15.8$ ,  $P = 0.07$ ) according to guild (Table 2). There was no significant variation in percentage mass change by either residency status ( $F_{1,41} = 0.03$ ,  $P = 0.86$ ) or guild ( $F_{3,41} = 0.3$ ,  $P = 0.80$ ) controlling for overall mass ( $F_{1,41} = 0.4$ ,  $P = 0.53$ ).

There were 194 possible species caught during mist-netting at Amurum and Yankari, 47 (24.2%) provided mass data sufficient for meaningful analysis and 43 showed seasonal mass variation in their top models. Unbiased estimates of occurrence of seasonal mass change were high at all taxonomic levels. Seasonal mass change was estimated to occur in 91.9% ( $\pm 4.4$ ) of species within genera averaged across all genera present at the sites ( $n = 79$  possible species in the 32 genera caught), 90.8% ( $\pm 5.5$ ) of species within family averaged across all families present at the sites ( $n = 118$  possible species in the 20 families caught) and 97.9% ( $\pm 2.0$ ) of species within order averaged across all orders present at the sites ( $n = 163$  possible species in the five orders caught).

## Discussion

Our study showed that the mass of about 91% of tropical savannah species was affected by season grouped into wet and dry periods. Rainfall was in the top models for 89% of these species and in all top models for species where the seasonal timing of mass varied significantly between years, suggesting that annual variation in the arrival of the rains is important as well as its variability. There were no clear differences in seasonal mass patterns with migratory status or foraging guild again suggesting a reasonable consistency of selection for mass regulation in response to rainfall across species.

The magnitude of seasonal mass gain was of the order of 12.6%. Six species showed relatively high variation in seasonal mass ( $> 25\%$ ), but their analyses were probably less reliable because of small sample sizes ( $n < 200$ ). After controlling for sample size (by including only species where  $n > 200$ ) the maximum average degree of seasonal mass change in tropical species ( $8.1\% \pm 4.1$ , species = 21) was comparable to both northern temperate (maximum of 12%, Baldwin & Kendeigh 1938, 2-8%, Sep–Dec only, Haftorn 1989) and southern temperate species (8-14%, Rozman *et al.* 2003). Even the four species (9%) which

did not have season in their top models showed a comparable variation range in mass gain (9%).

That variation in the timing and amount of rainfall results in consistent mass variation across many bird species is perhaps not surprising. There is strong seasonality in the tropics brought about by the arrival of the rains, which causes a profound increase in primary productivity and the availability of standing water (Dingle and Khamala 1972, Wolda 1978, Poulin et al. 1992). Species were generally heaviest during the late wet season which probably coincided with high invertebrate population densities (Dingle and Khamala 1972), or at the start of the dry season when seed availability is most abundant (Crowley and Garnett 1999, Brandt and Cresswell 2009). This also coincided with the peak of breeding for many species (unpubl. data from the occurrence of brood patches during the CES). We conclude that although there is no “winter” period with a particularly high starvation risk, the arrival of the rains and the subsequent increase in resources changes the predictability of the foraging environment for many species, causing variation in fat reserves.

That mass reserves *peak* with favourable foraging conditions in tropical savannah birds presents an apparent conflict when considering the northern hemisphere paradigm of *low* fat reserves being associated with favourable foraging conditions. However, under increasingly favourable foraging conditions and constraints to foraging time such as high predation risk, an increase in resource availability may result in a shift from a mass-dependent predation risk response (where birds lose mass) to an interrupted foraging response (where birds increase in mass, Lima 1986, Houston & McNamara 1993, Houston *et al.* 1993). This is because overall mass levels are affected by foraging unpredictability as a direct consequence of environmental factors (such as temperature) but also foraging unpredictability caused by conflicts with foraging such as avoiding predators. For example, when prey avoid predators, both in time and space, the prey’s foraging options are reduced and this may then lead to mass increases as insurance against the increased unpredictability in foraging (Lilliendahl 1998, Gentle and Gosler 2001, Rands and Cuthill 2001). Interrupted foraging occurs, however, only if foraging conditions are sufficiently good to allow long term energy budgets to be met in the remaining time and space available after birds have avoided predators (Brodin 2007). Although it is well established that reduction in foraging predictability directly from the environment leads to high total body mass (e.g., Rogers 1987, Bednekoff *et al.* 1994, Gosler *et al.* 1995, Cresswell 1998), these studies are all associated with northern

temperate winters when environmental effects on foraging predictability are likely to be very severe. In tropical areas, however, the effects of behaviours that conflict with foraging may be relatively more important because baseline foraging certainty is always relatively high and so mass response by birds may be largely concerned with interrupted foraging responses. Such situations are possible, even in northern temperate species as demonstrated by a range of species (MacLeod *et al.* 2007) and particularly by Great Tits *Parus major* (Cresswell *et al.* 2009b).

Overall, our results of lowest mass, on average, in the non-breeding season suggest that foraging predictability in the tropics (and possibly in the Southern hemisphere, Rozman *et al.* 2003) remains high, probably because of relatively high temperatures and relatively little shortening of day length. Consequently birds can minimise mass to avoid mass-dependent costs. In contrast, in the northern temperate non-breeding season, much greater unpredictable foraging associated with very long nights followed by freezing days, when foraging is impossible, causes birds to increase fat reserves. Temperate species therefore accept a higher maintenance cost and a higher predation risk in the non-breeding season, which may account for some of the lower survival rates reported on average for temperate versus tropical species (McGregor *et al.* 2007a). Furthermore, we suggest that a seasonal breeding period in both temperate and tropical areas is associated with increased mass because the constraints of breeding reduce foraging predictability in terms of self-maintenance for an adult bird. In other words, breeding season priorities such as feeding chicks, singing, territory maintenance, mate guarding and nest building conflict with foraging, but increased mass reserves allow self-maintenance to be scheduled between these activities, rather than always taking priority. Consequently we see an interrupted foraging response associated with the breeding season because many breeding activities conflict with foraging for self-maintenance. However, in temperate areas this mass increase is not apparent because it is always measured relative to the greater mass increase in the non-breeding season preceding it. It is interesting to note, that in temperate species where annual mass variation has been analysed in detail that minimum annual mass occurs immediately after breeding, before moult (e.g., Macleod *et al.* 2005). This relatively brief period of long day length and favourable temperatures where only self-maintenance is required, is perhaps then equivalent to the non-breeding season in tropical areas.

We could find little evidence for the effects of seasonal mass gain associated with migrants. We suggest that many transient species only travel relatively short distances within Africa, and do not need to barrier cross, so they may be able to forage each day while they migrate in short daily legs (Elgood et al. 1973, Payne 1980). We also found little evidence for any effects of potential changes in density associated with some species migrating, despite major changes in abundance of many species across seasons. For example, resident populations of species, such as the Northern Red Bishop show increased population density during the rains as transient populations converge at breeding locations (Craig 1980). Our study was not designed specifically to test these hypotheses however and it seems likely that true migratory fattening occurs in long distance intra-African migrants, and as a result of competition. Further research is needed at sites which have greater variation in both these variables than we could measure.

Overall our results show that approximately nine out of ten tropical savannah species from West Africa vary their mass seasonally and we provide evidence that this is most likely in response to rainfall seasonality. We suggest that these birds vary their mass in response to a variation in resource availability and foraging constraint as in temperate birds, but with the season with the maximum mass being that with the highest resource availability as a consequence of the interrupted foraging response, and relatively high foraging predictability during the rest of the year.

**Table 1:** Seasonal mass variation in 47 species of West African savannah birds captured by mist-netting over a 10 year period in central Nigeria. Results of models to test whether there was seasonal (S), annual (Y) or variation across the years in season (S\*Y) of variation in mass controlling for rainfall, age, sex and wing length. We used AICc to calculate the Akaike weight ( $W_1$ ) of the top model and the number of models which show equal support to the top model ( $\Delta$ ,  $\Delta < 2$ ). We present which variables were present (■) or absent ( ) in the top models (- denotes that the variable was not analyzed in the model), and the relative importance ( $\Sigma$ ) of a predictor as the sum of the  $W_1$  of the models in which the predictor was present. Minimum and maximum mass and the proportional maximum mass change between seasons are given along with the season of the minimum and maximum mass. We identified species guilds from diet in Elgood *et al.* (1994), Urban *et al.* (1997) and Fry *et al.* (2004): **I** Insectivore, **F** frugivore, **N** nectivore, **G** granivore. Transient status was identified over resident status by a > 50% change in capture rate between dry and wet season CES.

Species	<i>n</i>		<i>W</i> <sub>1</sub>								$\Sigma$ S	$\Sigma$ Y	$\Sigma$ S*Y	Min. mass (g)	Max. mass (g)	% difference	Mean mass (g)	Season min. mass	Season max. mass		No. of dry season CES captures	No. of wet season CES captures	Migratory
		Guild		$\Delta$	season	year	season*year	rain	age	sex	wing												
COLUMBIFORMES																							
Columbidae																							
<i>Streptopelia hypopyrrha</i>	159	F	0.44	3		-				-		0.45	0		32.14	37.71	17	36.58	3	4	26	15	R
<i>Stigmatopelia senegalensis</i>	85	G	0.5	2		-						0.6	0		40.69	48.45	19	45.72	3	1	38	26	R
<i>Turtur nigrcollis</i>	230	G	0.41	2		-				-		>0.99	>0.99	>0.99	35.45	39.71	12	37.41	4	2	199	108	R
COLIIFORMES																							
Coliidae																							
<i>Colius striatus</i>	298	F	0.18	6						-		0.48	>0.99	0.42	51.01	57.09	12	52.27	4	3	98	64	R

CORACIIFORMES

Meropidae

<i>Merops bulocki</i>	205	I	0.26	4		-		-		0.15	0.03		22.77	24.45	7	23.91	3	1	73	16	T
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PICIFORMES

Capitonidae

<i>Pogoniulus chrysoconus</i>	239	F	0.23	6				-		0.81	0.37		10.50	10.84	3	10.86	1	4	106	23	T
<i>Lybius vieilloti</i>	62	F	0.21	5			-			0.45	0		32.14	37.71	17	36.58	3	4	26	15	R

Indicatoridae

<i>Indicator indicator</i>	111	I	0.22	4			-			0.6	0		40.69	48.45	19	45.72	3	1	38	26	R
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PASSERIFORMES

Pycnonotidae

<i>Pycnonotus barbatus</i>	614	F	0.65	2				-		>0.99	>0.99	>0.99	35.45	39.71	12	37.41	4	2	199	108	R
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Turdidae

<i>Turdus pelios</i>	516	I	0.38	3			-			>0.99	0.09		64.51	69.68	8	65.28	1	3	251	42	T
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Muscicapidae

<i>Cossypha niveicapilla</i>	176	I	0.36	3			-			0.99	0	0	34.00	37.23	10	36.28	2	1	60	23	T
<i>Ceromela familiaris</i>	117	I	0.43	1			-			0.69	0		15.59	17.37	11	16.88	4	2	43	10	T
<i>Myrmecocichla cinnamomeiventris</i>	63	I	0.28	3			-			0.59	0		39.03	45.59	17	39.35	1	2	18	9	R

Sylviidae

<i>Eremomela pusilla</i>	70	I	0.34	2		-		-		0.11	0.29		6.88	7.43	8	7.03	1	2	17	8	T
<b>Cisticolidae</b>																					
<i>Camaroptera brachyura</i>	226	I	0.66	1		-		-		0.66	>0.99		10.76	11.64	8	10.87	1	3	47	32	R
<i>Prinia subflava</i>	64	I	0.38	3		-		-		0.64	0		6.45	9.33	45	8.40	2	4	16	10	R
<i>Cisticola aberrans</i>	85	I	0.3	4		-		-		0.17	0.04		13.20	13.68	4	13.26	1	3	24	12	R
<b>Monarchidae</b>																					
<i>Terpsiphone viridis</i>	84	I	0.59	2		-		-		0.96	0.01		13.81	14.68	6	14.21	1	4	35	5	T
<b>Platysteiridae</b>																					
<i>Batis senegalensis</i>	68	I	0.38	3		-				0.29	0		7.92	10.82	37	9.88	2	4	23	10	T
<i>Platysteria cyanea</i>	94	I	0.38	2		-				0.1	0.98		13.94	14.86	7	13.79	1	1	23	26	R
<b>Zosteropidae</b>																					
<i>Zosterops senegalensis</i>	241	F	0.4	2		-		-		0.55	0.02		9.42	9.66	2	9.42	2	3	72	39	R
<b>Nectarinidae</b>																					
<i>Cyanomitra verticalis</i>	130	N	0.78	1		-				0.91	0.02		11.52	12.87	12	12.15	2	4	40	38	R
<i>Chlcomitra senegalensis</i>	476	N	0.39	3		-				0.97	>0.99		10.69	11.13	4	10.23	4	3	205	72	T
<i>Cinnyris venustus</i>	354	N	0.14	8		-				0.87	0.64		6.15	6.43	5	6.26	3	1	152	67	T
<i>Cinnyris pulchellus</i>	201	N	0.58	2		-				0.05	0.03		7.11	8.05	13	6.98	4	3	16	1	T
<b>Malaconotidae</b>																					

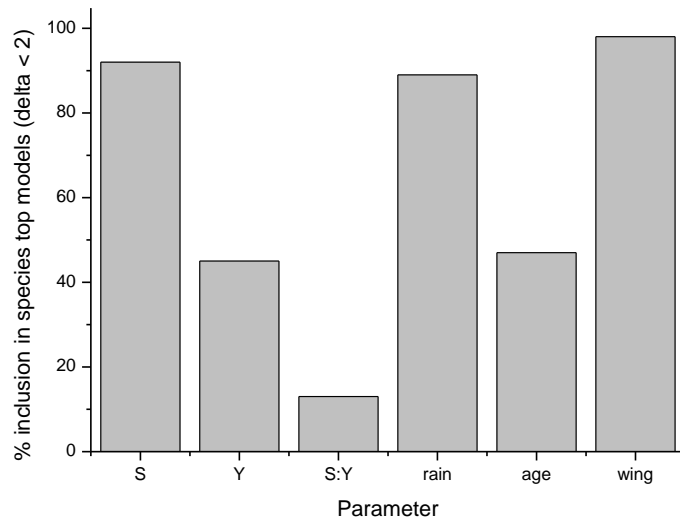
<i>Laniarius barbarus</i>	82	I	0.34	4		-		-		0.46	0.53		46.78	51.84	11	48.89	1	4	24	10	T
<b>Passeridae</b>																					
<i>Petronia dentata</i>	64	G	0.46	2		-		-		0.89	0		15.61	23.84	53	18.00	1	3	16	2	T
<b>Ploceidae</b>																					
<i>Sporopipes frontalis</i>	62	G	0.15	7		-		-		0.25	0.09		17.06	19.10	12	17.02	1	3	21	19	R
<i>Ploceus luteolus</i>	147	G	0.42	1		-		-		0.7	>0.99		13.67	14.79	8	14.44	2	3	28	24	R
<i>Ploceus vitellinus</i>	284	G	0.33	3		-		-		0.63	0.35		17.94	21.61	20	20.18	2	4	58	26	R
<i>Ploceus heuglini</i>	81	G	0.35	3		-		-		0.48	0.02		20.95	27.91	33	23.61	3	4	55	9	T
<i>Ploceus cucullatus</i>	738	G	0.61	2		-		-		0.99	>0.99	0.99	36.45	40.25	11	36.38	2	3	210	90	T
<i>Ploceus nigrcollis</i>	209	G	0.43	2		-		-		>0.99	0.31		25.01	26.63	6	26.40	1	4	59	50	R
<i>Euplectes hordeaceus</i>	169	G	0.86	1		-				>0.99	0.01		17.15	21.95	28	19.99	2	4	98	18	T
<i>Euplectes franciscanus</i>	1762	G	0.38	2				-		>0.99	>0.99	>0.99	14.67	15.46	5	15.22	1	3	222	1084	T
<b>Estrildidae</b>																					
<i>Estrilda melpoda</i>	88	G	0.27	3		-		-		0.34	0.14		7.06	7.93	12	7.21	4	3	23	7	T
<i>Estilda caeruleascens</i>	530	G	0.27	4				-		0.49	>0.99	0.05	8.92	9.46	6	9.22	4	3	158	73	T
<i>Estrilda troglodytes</i>	149	G	0.23	3		-		-		0.48	0.92		7.79	8.17	5	7.62	1	4	56	15	T
<i>Urarganthus bengalus</i>	692	G	0.46	3		-				0.78	>0.99		9.72	10.22	5	10.08	4	3	83	193	T
<i>Ortygospiza atricollis</i>	139	G	0.22	6		-				0.98	0		10.31	11.11	8	10.58	1	3	77	39	R



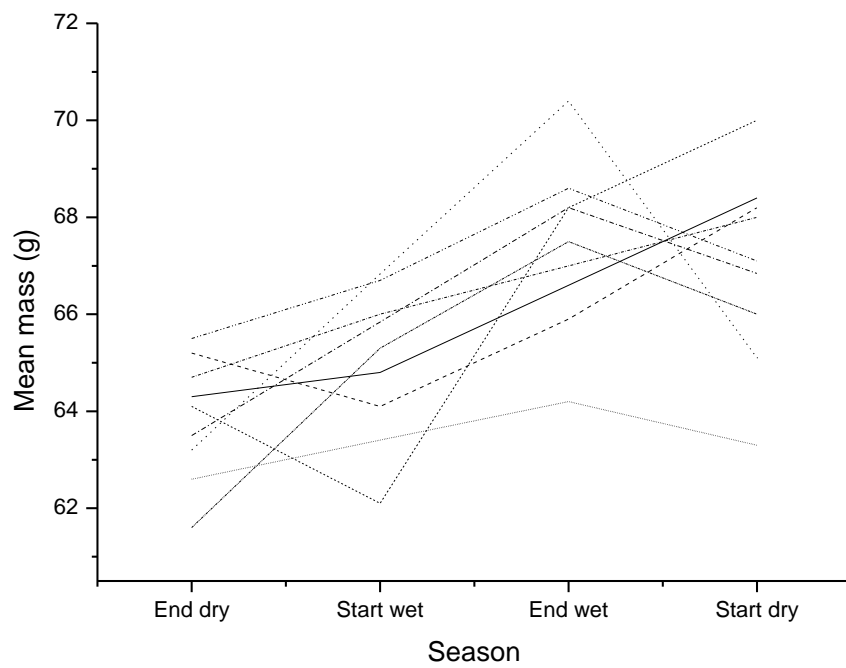
<i>Lagonosticta rufopicta</i>	113	G	0.24	3		-		-		0.6	0.13		9.43	10.23	9	9.27	4	3	14	28	R
<i>Lagonosticta senegala</i>	763	G	0.46	2			-			>0.99	0.93		8.06	8.60	7	8.69	2	4	120	185	T
<i>Lagonosticta sanguinodorsalis</i>	480	G	0.54	1						>0.99	>0.99	0.97	9.98	11.05	11	10.45	1	3	59	64	R
<i>Lagonosticta rara</i>	84	G	0.18	5			-			0.17	0.44		9.73	10.37	7	9.82	1	3	35	8	T
<i>Spermestes cucullatus</i>	768	G	0.5	2					-	>0.99	>0.99	>0.99	8.75	9.22	5	8.94	2	3	329	94	T
<b>Viduidae</b>																					
<i>Vidua chalybeata</i>	71	G	0.31	3			-			0.51	0		11.55	12.48	8	12.24	2	4	10	16	R
<b>Emberizidae</b>																					
<i>Emberiza tahapisi</i>	361	G	0.2	6			-			0.62	0.18		13.36	14.50	9	13.50	3	4	147	35	T

**Table 2:** Important parameters affecting mass in 47 species of West African tropical bird, summarized across four feeding guilds (mean values and percentage inclusions were calculated from Table 1, see also Table 1 for variable explanations).

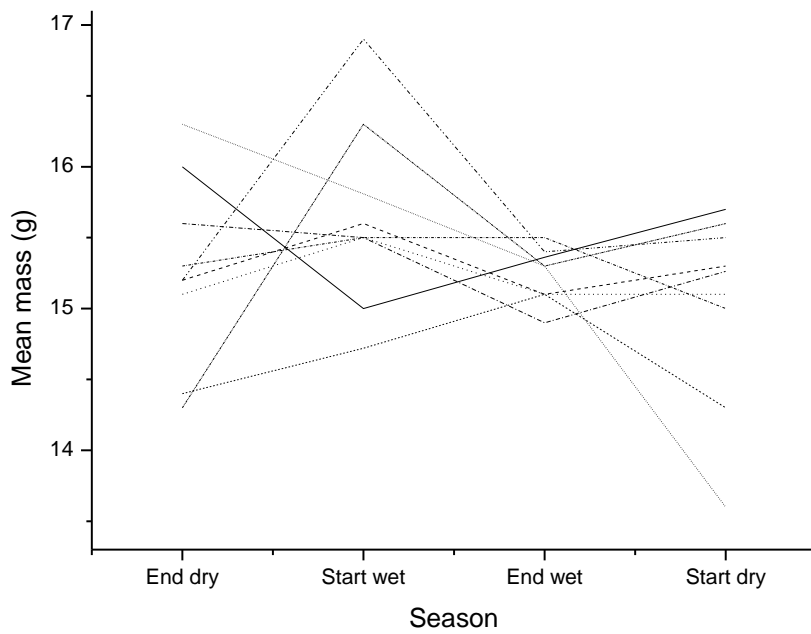
		Frugivores	Insectivores	Nectivores	Granivores	All species
<b>Migratory status</b>	<b>No. species</b>	6	14	4	23	47
	<b>Transient</b>	2	8	3	14	27
	<b>Resident</b>	4	6	1	9	20
	<b>Mean <math>W_1</math></b>	0.35	0.35	0.47	0.47	0.38
<b>% inclusion of each variable in the top models (<math>\Delta &lt; 2</math>)</b>	<b>Mean <math>\Delta</math></b>	4	3.5	3	3	3.4
	<b>S</b>	100	86	75	96	92
	<b>Y</b>	50	29	50	52	47
	<b>S*Y</b>	33	0	0	17	13
	<b>Rain</b>	100	86	100	87	89
	<b>Age</b>	66	57	100	35	47
	<b>Wing</b>	100	100	100	96	98
<b>Mean <math>\Sigma</math> of predictor variables</b>	<b>S</b>	0.6	0.53	0.7	0.68	0.63
	<b>Y</b>	0.4	0.21	0.42	0.43	0.37
<b>Season of min. mass</b>	<b>1</b>	1	8	0	9	18
	<b>2</b>	1	3	1	7	12
	<b>3</b>	1	2	1	3	7
	<b>4</b>	3	1	2	4	10
	<b>1</b>	0	4	1	0	5
<b>Season of max. mass</b>	<b>2</b>	2	3	0	1	6
	<b>3</b>	2	3	2	13	20
	<b>4</b>	2	4	1	9	16



**Figure 1:** Proportional representation in species' top models ( $\Delta < 2$ ) of the effect on a bird's mass of the parameters: season (S), year (Y), variation in seasonal mass change pattern (S\*Y), rain, age and wing (sex not shown because it was not tested for every species).

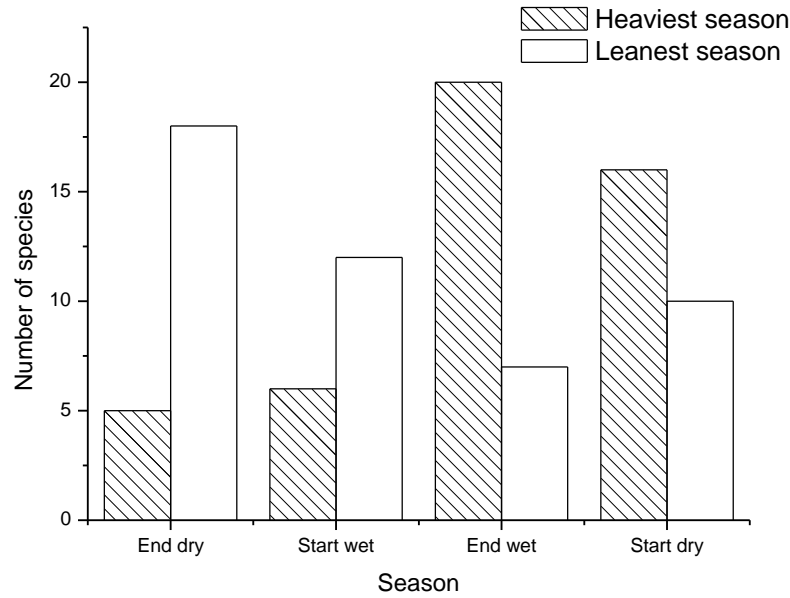


**Fig. 2a**



**Fig. 2b**

**Figure 2:** Species which displayed mass variation were found to either: A) vary their mass in a clear annual pattern that was consistent across the years ( $n = 37$ ), or B) vary their mass differently in different seasons across years ( $n = 6$ ). We present the mean mass of two case study species by season and year: individual lines represent different years. A) African Thrush ( $n = 516$ ), being heaviest at the end of the wet season (69.7g,  $n = 89$ ) and lightest at the end of the dry season (64g.5,  $n = 324$ ), resulting in an 8% annual change in mean mass. B) Northern Red Bishop ( $n = 1762$ ), being on average heaviest at the end of the wet season (15.2g,  $n = 511$ ) and lightest at the end of the dry season (14.7,  $n = 391$ ), resulting in a 5% annual change in mean mass.



**Figure 3:** Season of the highest and lowest mass for 47 species of tropical savannah bird, from data pooled across years. Most species were heaviest at the end of the wet season or start of the dry season ( $\chi^2_3 = 14.0$ ,  $P = 0.003$ ), while there was no season in which most species were lightest ( $\chi^2_3 = 5.5$ ,  $P = 0.14$ ).

# **Chapter 3: The seasonality of breeding in savannah birds of West Africa assessed from brood patch and juvenile occurrence**

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## **Summary**

In order to maximise breeding success in a seasonally fluctuating environment animals breed during periods of increased resource abundance, and avoid times of resource constraint. In tropical savannahs variation in resources in time and space is dependent on the amplitude of the rains and their predictability. We quantified the degree to which tropical savannah birds have breeding concentrated around predicted periods of increased food availability coincident with rainfall. We used the proportion of adults caught with brood patches and/or juvenile to adult ratio in birds caught over a ten year period in 25 species of small West African savannah bird to assess the degree to which there were clear seasonal peaks in breeding activity. We found two thirds of species bred in all seasons (68%), but that most species showed distinct seasonal peaks (96%) in the timing of their breeding. Over half of species (60%) varied the timing of their breeding across the years. Granivorous species bred later than insectivorous and frugivorous species, which probably indicates synchronisation with their respective food types' peak abundance. Overall we show distinct seasonal peaks in breeding effort (i.e. breeding seasons) and this is most likely in response to changing resource availability brought about by seasonal rainfall. We also demonstrated the potential utility of using brood patches to test for patterns in breeding in multi species long term datasets.

Breeding is the most costly life history activity, with energetic expenditure peaking while parents are rearing nestlings (e.g. Bryant 1988; Nilsson and Råberg 2001). Animals reduce the costs of reproduction by timing their breeding around periods of increased resource availability (Martin 1987, Bennett and Owens 2002). This then ensures maximum reproductive output for each breeding attempt by synchronising the production of young with seasonal peaks of resource abundance to enable rapid growth and to increase juvenile survival (e.g. Perrins 1970). Adult survival during breeding is also maximised because breeding is only initiated when there is anticipated to be sufficient food available for females during egg formation (e.g. Nager et al. 1997), without there being a significant risk of starvation to the female (Perrins 1970, Martin 1987).

In many tropical environments, variation in the timing of breeding in time and space is dependent on both the amplitude of the rains and their regularity (Wingfield et al. 1992, Komdeur 1996, Moore et al. 2005). In those environments where the dry period is less pronounced, clear breeding seasons may be absent (Voous 1950), and there is greater diversity across species in the timing of peak breeding (e.g. Thomson 1950; Brown and Britton 1980). A study conducted in Limonochocha National Biological Nature Reserve in equatorial Ecuador, for example, where rainfall and temperature remain relatively constant, found that 26 species of antbirds (Formicariidae) displayed almost no breeding seasonality (Tallman and Tallman 1997). However, most tropical environments are distinctly seasonal in their rainfall and correspondingly the timing and length of the breeding season may be both species and population specific (Komdeur 1996, Hau et al. 2000, Wikelski et al. 2003, Moore et al. 2005).

Seasonal rainfall drives fluctuations in food availability, which is a key factor for many species in determining annual fecundity, number of broods and the time taken between renesting attempts (Martin 1987, König and Gwinner 1995, Martin 1995, Komdeur 1996). In



almost all tropical habitats food availability across the breeding season fluctuates in relation to rainfall (e.g. Janzen 1973; Wolda 1978; Poulin et al. 1992 Mulwa et al. 2012), so with seasonally predictable rainfall patterns we expect to see predictable periods of increased food availability. Therefore although there is an extended season when birds can possibly breed (and many tropical species may be capable of breeding for much of the year; e.g. Franklin et al. 1999), a predictable period of increased food availability and subsequently higher juvenile survival means that there will be a strong selective pressure to breed during these periods. How a bird experiences seasonality will depend on the response of its foraging niche to variation in rainfall. The high degree of niche specialisation in the tropics thus leads to a diverse variety of breeding strategies, with the timing and predictability of seasonal fluctuations in food availability appearing to be the driving force determining the timing of breeding in most species (Poulin et al. 1992, Poulin et al. 1993, Komdeur 1996, Moore et al. 2005, Hau et al. 2008). However, other factors such as nest predation (e.g. Morton 1971), climate (e.g. Tye 1991) or juvenile survival during post-natal dispersion (Young 1994) might also be important in determining when to be species and population specific and dependent on environmental conditions at the site (Moore et al. 2005). Where there is not a season of particularly high starvation risk, individual pairs may initiate breeding outside of the main breeding season, thus giving a false impression of year round reproduction at the species level (Miller 1965, Wingfield et al. 1997), even though most individuals of the species may breed during a defined season. This season may vary however with different feeding guilds such as insectivores timing their breeding to coincide with the insect peak of the early rains and granivores with the seed peak at the end of the rains (Poulin et al. 1992).

There has been a lot of interest in the breeding seasons of species in humid tropical forests (e.g. Fogden 1972; Wikelski et al. 2000), in East Africa. However there have been no quantitative, across species studies in West African where the presence of a single,

predictable wet season may mean that birds are more constrained in when they can breed. Ideally, a study would follow a species at an individual level, tracking a large number of colour ringed individuals and recording breeding success, number of broods, time taken between nesting attempts and survival of fledged juveniles (e.g. Grzybowski et al. 2005; Nesbitt Styrsky and Brawn 2011). Unfortunately this is not practical in a multi species study in most tropical environments, where population densities are often low, nests hard to find and individuals difficult to track. We therefore used temporal changes in two breeding indicators, the proportion of adults with brood patches, or changes in juvenile to adult ratios within a population to quantify the degree to which there are specific periods of increased breeding costs which occur during egg laying, incubation and chick provisioning. This may provide insights into how seasonality affects the timing and length of the breeding seasons in a strongly seasonal savannah environment in West Africa. We used such indices to test two specific hypotheses: 1) that species will show a distinct seasonal peak in breeding activity even though individuals of most species can potentially nest throughout the year; and 2) that seasonal peaks are coincident with predicted peaks in food availability so that timing of breeding will depend on the feeding guild.

## **Methods**

We estimated the seasonality of breeding in small tropical birds in Amurum Community Forest Reserve, at the A.P. Leventis Ornithological Research Institute (APLORI), on the Jos Plateau (09°55'N, 08°53'E) in Nigeria. The site is located in the centre of the Guinea savannah forest zone with very strong seasonality due to a single rainy season. It consists of 120 hectares 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. In West African savannahs the seasons are divided into

a distinct wet and dry season. Daily rainfall summaries between January 2002 and November 2011 was obtained from Jos Airport (09°52'N, 08°53'E), located in the centre of Jos Plateau and 26 km from Amurum Forest Reserve. In Amurum where the rainy season lasts for approximately six months, from the 10th of April  $\pm$  9 days until the 13th of October  $\pm$  11 days, there was an annual rainfall of  $1337 \pm 159$  mm (2001-2011), 97.4 % of which fell within the wet season with the heaviest rainfall occurring in August ( $290 \text{ mm} \pm 28 \text{ mm}$ ). Maximum temperatures range from between 20 to 25 °C (<10 °C in extreme cases) during the coldest months, rising to 30 – 35 °C at the end of the dry season. Amurum is located 1270m asl, with day length varying annually by 68 minutes.

We caught 9,228 individuals of 25 species (Table 1). To avoid under representation of adult birds breeding over several years we retained individuals retrapped in different years in the analysis: 2280 records of 25 species. Birds were trapped using mist nets between January 2002 and November 2011. Trapping occurred year round but was concentrated at a Constant Effort Site (CES) conducted biannually in Amurum for a 14-day period at the end of the dry season (March–April) and at the end of the wet season (September–October). During the CES, 272 m of four shelf nets was used between 06:00 and 10:30 h WAT (although there were few captures after 09:30 h). Where possible birds were aged and sexed. Species were assigned to feeding guilds (Fry et al. 1992-2004). This methodology was repeated outside of the CES, with the exception that netting occurred opportunistically throughout the year, and there was variation in the number of net metres used. However, overall annual netting effort was approximately the same as a single CES.

#### *Determination of variables*

The presence of brood patches and of juveniles was used to identify timing of breeding periods. Assessment of brood patches was made using a six-stage scoring system: 0 (no

brood patch); 1 (patch forming; defeathering process has begun); 2 (breast and belly fully defeathered, some wrinkling of skin evident and signs of oedema); 3 (skin of belly opaque and engorged, broad swollen wrinkles); 4 (skin shows thin wrinkles, no longer engorged); 5 (reifeathering; Redfern 2008). It was assumed that tropical species show a similar progression of brood patch development to temperate species. Stages 2-4 generally occur during the period of incubation and brooding (Bailey 1952, Hinde 1962, Jones 1971), however a bird is also breeding at stages 1 and 5 (Redfern 2010). We therefore included all stages as an indication of breeding. To standardise across species where sexes could and could not be distinguished in the hand, all birds with brood patches were included in analyses irrespective of sex since males of a number of species included here were also known to incubate (e.g. Fry 2004). We only included species where there were > 10 adults with brood patches.

Trapped birds were aged as juvenile if they had a complete juvenile plumage containing no adult feathers; immature, if they had a mixture of juvenile and adult feathers, or had moulted into their sub-adult plumage (e.g. the African thrush *Turdus pelios*); adult, if birds no longer retained any juvenile feathers and as such were considered to be capable of breeding. Juvenile feathers were identified by feather shape and structure, as feathers tend to be weaker and looser than following generations of feathers (Svensson 1992). Ringing has been conducted in the reserve since 2001 and species can usually be reliably aged from plumage characteristics: birds of uncertain ages were excluded from the analysis. After fledging, birds only maintain their juvenile plumage for an approximate short period before they undergo post-juvenile moult. Therefore if a bird is caught with juvenile plumage it is possible to *estimate* the number of days since fledging and subsequently when it hatched. Most species of northern temperate passerines undergo post-juvenile moult between three and eight weeks after leaving the nest (e.g. Jenni and Winkler 1994), and tropical passerines may follow a similar timeframe (Franklin et al. 1999, Jones et al. 2002). If the mean fledging period for

tropical passerine species is approximately 16.8 days ( $se \pm 0.37$ ,  $n = 204$ , derived from data in Byers 1995; Feare et al. 1998; Cheke et al. 2001), then we can estimate when the chick hatched. Large confidence limits linked to the uncertainty of our estimate of individual variation in the timing of post juvenile moult, should be considered against the low temporal resolution of the study (i.e. three month seasons, see below). Across the 15 species, for where there was sufficient data, the period between peak juvenile abundance and the peak presence of brood patches correlated with the estimate of the number of days between presence of juveniles and hatching dates (see below). Therefore we assumed that the presence of juveniles estimated the timing of breeding in adult birds. Immature birds were assumed not be to actively breeding and so were excluded from the analysis. Only species where there were records for  $> 10$  juveniles were included.

### *Statistical analysis*

In total we identified 1594 individuals with brood patches and 999 juveniles. We assumed that the peak timing of breeding for the adults coincided with peak brood patch abundance and used brood patch data within the same species to then determine how peak juvenile abundance related to the timing of peak breeding. For each of the 15 species we modelled how the response variable varied across 26 two week periods, commencing from 1<sup>st</sup> January, included as a factor. The response variable was the relative proportion of birds with brood patches, or juveniles, to the total number of adult birds caught. This was included in the model as the real relative frequency of adult birds with brood patches, or juveniles, to the number of adult birds without brood patches, or adults. We used the `cbind` command in the R (version 2.14.0) statistical environment (R Development Core Team 2011) to do this and the `lme4` package (Bates and Maechler 2010).

The two weeks of peak breeding was then calculated from the parameter estimates. For each species we estimated the number of days between peak presence of brood patches and peak juvenile abundance, before averaging across species to estimate a lag of 35 days  $\pm$  17 days. The presence of juveniles in catches was therefore considered a suitable method of identifying breeding periods. We subsequently used this estimate to calculate peak breeding for the three species where there was insufficient brood patch data (Table 1). However, where both measures were available, the presence of brood patches was considered to be a more precise measure of breeding and was used over the presence of juveniles.

We categorised the year into four seasons of distinctly different resource availability correlated to the approximate start and finish of the rains: end of dry season (10<sup>th</sup> January – 09<sup>th</sup> April); start of wet season (10<sup>th</sup> April – 09<sup>th</sup> July); end of wet season (10<sup>th</sup> July – 09<sup>th</sup> October); start of dry season (10<sup>th</sup> October – 09<sup>th</sup> January). We estimated variation in seasonal rainfall as a covariate by dividing the actual rainfall (mm) for a season within year by the average rainfall (mm) for that season across years: thus a value above 1 indicated a season in which rainfall was above the seasonal average.

We tested for variation in seasonal breeding across species by building a generalized linear mixed model (GLMM) with a binomial error structure and with species as a random factor. We modelled how the response variable (proportion of adults with brood patches (across 22 species) or proportion of juveniles to adults (across 18 species); constructed with the cbind command in R) varied seasonally, annually or was affected by variation in rainfall. We justify the validity of fixed effects models across species because the variance absorbed by the random effect was relatively small (Table 2), allowing us to rerun each model as a GLM (i.e. without the random effect). We compensated for over dispersion in the GLM by fitting an empirical scale parameter. However, this suggested the GLMM may also be over dispersed, which was compensated for by including a random effect for each species/season

combination. This allowed for an additional variance component within species at the level of the linear predictor. The GLM and GLMM provided consistent estimates for the effects of each predictor variable, so here we present the results of the GLMM (Table 2).

For each species we modelled the occurrence of seasonal breeding by building a GLM with a pseudo-binomial error structure, logit link function and empirical scale parameter. We tested the statistical significance of season, year and variation in seasonal rainfall on our response variables, by dropping each from the full model, and applying a likelihood ratio test (Table 1). We corrected for multiple tests using sequential Bonferroni correction (Rice 1989). For each species and season we calculated the proportion of adults with brood patches or juveniles to adults predicted by the model by back-transforming the parameter estimates. Above we used a stepwise model opposed to an Akaike Information Criteria (AIC) approach to specifically test for the effect of predictor and confounding variables on the response variable. We provided further support for our model by excluding the predictor variable season, and rerunning the model, before comparing AIC values. Across all species we found that the model was significantly improved by including season.

For each species we calculated the two week period of peak breeding (as above), either from the two weeks with the highest proportion of brood patches or the two weeks with the highest proportion of juveniles minus the mean lag period between peak juveniles and peak brood patches (37 days). We built a linear model to test whether the two weeks of peak breeding (included as a continuous variable) varied by feeding guild across species.

## **Results**

There was strong evidence for the seasonality of breeding *across* savannah species. Mixed effect models testing for the effect of season, while controlling for the possible confounding effects of year and variation in rainfall on the proportion of brood patches (across 22 species)

or juveniles (across 18 species), showed that across species there was a seasonal effect (Table 2). Most species showed reduced breeding towards the end of the dry season, before increasing breeding after the onset of the rains (Fig. 1).

There was strong evidence for the seasonality of breeding *within* most savannah species. Of the 22 species where there were sufficient numbers of adults with brood patches caught, we found seasonal variation in 21 (95%) species (Tables 1 and 3). Only the Common bulbul *Pycnonotus barbatus* showed no significant evidence of seasonal breeding (Fig. 2a). All three species which lacked sufficient brood patch data showed significant seasonal variation in the proportion of juveniles (Table 1). Twelve (80%) of the 15 species for which there were sufficient data showed seasonal variation in both juveniles and brood patches (Table 1).

Overall (through the presence of brood patches or where there was insufficient data, juveniles) 24 species (96%) varied their timing of peak breeding within a year (20 species (80%) significantly after sequential Bonferroni correction and four marginally significant species (16%); Table 1). Fifteen species (60%) also varied their timing of peak breeding across years (12 species (48%) significantly after sequential Bonferroni correction and three marginally significant species (12%); Table 1). Seasonal variation in rainfall only affected breeding in seven species (28%; one species (4%) significantly after sequential Bonferroni correction and six species (24%) marginal; Table 1). We found evidence of breeding in all seasons in 20 species (80%; Table 1 and 3).

The timing of peak breeding across species was variable, with there being a strong interaction between season and species in the 21 species which showed seasonal variation in the proportion of brood patches (season \* species added to model in Table 2,  $df = 69$ , deviance = 1026,  $P < 0.0001$ ) and the 15 species which showed seasonal variation in the proportion of juveniles (season \* species added to model in Table 2,  $df = 51$ , deviance = 1049,  $P < 0.0001$ ).



At least one species showed a peak of breeding in each season (Table 3, e.g. compare *Tchagra senegalus* Fig. 2b with *Lonchura cucullatus* Fig. 2c and Fig. 2d that shows intra-annual variation in rainfall). Annual variation in seasonal rainfall was not found to influence breeding across species in the proportion of birds with brood patches ( $df = 1$ , deviance = 999,  $P = 0.1$ ), but did influence the proportion of juveniles to adults ( $df = 1$ , deviance = 678,  $P = 0.006$ ). This suggests that in a tropical environment such as our study site where rainfall is predictable across years, most species may time their breeding independent of annual environmental variation, but that seasonal rainfall may influence productivity and juvenile survival. At an increased temporal resolution the 14 day period of peak breeding varied by feeding guild ( $F_{3,22} = 8.5$ ,  $P < 0.001$ ), with granivores breeding later in the year than insectivorous and frugivorous species (Table 4, Fig. 3).

## Discussion

Our study tested for seasonality in breeding in a large dataset and showed that although two thirds of species (68%) in the savannah environment of West Africa were capable of breeding in all four seasons, most species (96%) showed distinct seasonal peaks in breeding activity which was coincident with predictable seasonal rainfall and was dependent on feeding guild.

### *Methodological considerations*

Modelling seasonal breeding at a population level through the use of a breeding indicator, such as the presence of brood patches or juveniles, appears to provide a robust method of using existing ringing datasets to investigate patterns of breeding across species. Identification of either a brood patch or a juvenile in the hand is a straight forward field technique for estimating the most costly stage of breeding for parent birds (Walsberg and King 1978, Redfern 2010). Although the presence of a brood patch may not be a reliable

indicator of breeding in some bird guilds (Tranquilla et al. 2003), in small passerine birds the different stages of brood patch development has been closely linked to breeding stages (Redfern 2008, 2010). For example; nest building (brood patch score 1), egg production and incubation (brood patch score 3) or parental care (brood patch score 4 and 5; Hinde 1962; Jones 1971). However, there are limitations to the resolution in breeding activities which can be inferred from using brood patches as a breeding indicator, as there may be variation in the stage of brood patch development, relative to actual egg production (Hinde 1962, Zann and Rossetto 1991), and as well as variation as to the extent of brood patch formation in males (Zann and Rossetto 1991). Further work is needed to determine how much individual variation there is within and across species and guilds in the development of brood patches in relation to stages of breeding.

We found that three species (*Cinnyris venustus*, *Lagonosticta sanguinodorsalis*, *Emberiza tahapisi*) showed seasonal variation in the proportion of brood patches but not the proportions of juveniles (Table 1). This suggests that the proportion of juveniles as a breeding indicator maybe confounded by seasonal variation both within and across species, by factors such as: the number of days before commencing post-juvenile moult (Ginn and Melville 1983) and variation in clutch size (Ludvig et al. 1995). Therefore, where possible, the proportion of adults with brood patches was used over the proportional presence of juveniles. However, despite these potentially confounding factors we found a strong correlation between our breeding indicators. There was a reasonably consistent lag (37 days  $\pm$  17 days) between the peak abundance of adults with brood patches and the peak presence of juveniles, and so the presence of juveniles was likely to be a reliable indicator of peak breeding activities for the three species (*Cloius striatus*, *Merops bulocki*, *Ploceus nigricollus*) where there was insufficient brood patch data. Clearly it is better to use brood patch data whenever possible

but on average juvenile ratio data is also likely to indicate seasonality of breeding at a population level at a seasonal temporal scale.

#### *Average seasonality of breeding*

Almost three quarters of species (16 out of the 22 species for where there was sufficient brood patch data) showed evidence of incubating eggs in all four seasons, while seven of these species (out of the 10 for which there was data) also managed to successfully fledge chicks in all seasons, indicating that breeding is possible outwith the main breeding season. Aside from possible density-dependent advantages of breeding out of season such as reduced competition, selection should favour breeding during peak food availability. Therefore we suggest that individuals which breed out of season may be doing so opportunistically, capitalising on localised increases in food availability. The common occurrence of a few individuals breeding out of the main season mean that studies with small sample sizes, or accounts of a few nests found in any one time of year, should be treated with caution when drawing conclusions about general seasonality (or aseasonality) of breeding in the tropics.

Although most species showed a peak in breeding during the late wet and/or early dry season, it is important to point out that this only indicates what is happening *on average*. Although most species time their peak breeding to occur at the end of the rains some species will specialise as dry season breeders: the lack of a season where resources are constrained, such as winter in the Northern hemisphere, has allowed species to evolve to occupy a wide variety of niches. For example, the familiar chat *Cercomela familiaris* forages on ground dwelling invertebrates, which may not vary across the seasons (Poulin et al. 1992), and thus foraging may become more predictable at the end of the dry season due to a reduction in grass cover. At the higher temporal resolution of two-week periods, the timing of peak breeding was dependent on feeding guild, with species probably synchronising their peak breeding season

with their particular feeding niche. Insectivorous and frugivorous species showed peak breeding during the wet season probably coinciding with the explosion in invertebrate numbers and peak fruit abundance, respectively (Poulin et al. 1992). In contrast granivorous birds bred later with respect to rainfall probably concentrating their breeding at the start of the dry season when the grain crop is at its peak (Fig. 3; Crowley and Garnett 1999). Specialised seed eating finches may breed later than other guilds because they experience greater increased seasonality in their food availability, with seeds going from negligible at the start of the rains to superabundant when seeds ripen and fall (Crowley and Garnett 1999, Brandt 2007). Carry over effects from the wet season probably mean that foraging for invertebrates to feed chicks remains reasonably predictable into the dry season, while seed availability becomes superabundant allowing parents to efficiently forage for themselves while providing for chicks. We also suggest that breeding maybe favourable during this period for some species due to increased nest survival resulting from changes in grass cover (e.g. Hovick et al. 2012). Some species, such as the cinnamon-breasted rock bunting *Emberiza tahapisi*, which breeds largely in the dry season, may then trade-off these benefits with declining invertebrate availability.

#### *Seasonal breeding in West Africa savannahs*

The savannahs of West Africa act as a model system for understanding how the seasonality of resources affects synchrony in breeding across species, because, although day length and temperature remain relative constant across the year, the rains drive a single wet and dry season of distinctly different resource availability. Where rainfall is less constrained such as in humid tropical forests or in East Africa, where there are two wet seasons, the seasonality of food availability is likely to be reduced because organisms experience a longer period where water is abundant which tends to result in species which reproduce more slowly and as a consequence live longer . However, increased seasonality leads to a period of increased

density-dependent mortality, therefore there is more food available when species start to breed, which leads to larger clutch sizes and subsequently reduced survival (McNamara et al. 2008). We might therefore predict an increase in breeding synchrony (and clutch size) within and across species relative to regions where rainfall is less constrained, because species respond to large peaks in food availability (Griebeler et al. 2010). However, although some species displayed distinct breeding seasons, three quarters of species from all four feeding guilds initiated breeding in all four seasons which suggests that despite relatively high seasonality, food availability for many species may not be constrained in any particular season.

The savannah communities of West Africa are dynamic with species movements on many scales as populations follow seasonal variation in food availability (e.g. Elgood et al. 1973; McGregor 2005; Cresswell et al. 2009). Thus an increase in the numbers of competitors and conspecifics at source habitats could result in the food available per individual not increasing significantly. Therefore the timing of breeding is likely to be more species, population and breeding pair specific with individuals capitalising on local increases in food availability. Consequently birds are unable to support the larger clutch sizes which we see in seasonal environments and instead clutch sizes in many species are more comparable to humid forest species (Fry et al. 1992-2004).

### *General conclusions*

Overall, most species of West African savannah bird bred seasonally, with distinct peaks in breeding occurring within a main breeding season, the timing of which was dependent on feeding guild and so that is probably related to peak food availability. However, small numbers of individuals of two-thirds of species were also able to incubate and successfully fledge young outside of the main breeding season. The ability to breed throughout the year

suggests that there is not a high risk of starvation in the non-breeding season. Nevertheless the existence of a seasonal peak in food abundance will select for an apparent breeding season as individuals are selected to breed at the optimum time. Other constraints on timing of breeding may of course also select for a fixed breeding season such as moult or migration. In addition, the correlation in peak timing between our breeding indicators provides support for the reliability of using brood patches to access the stages of breeding in small savannah birds.

**Table 1:** The seasonality of breeding in 25 species of savannah bird caught between 2002 and 2011 in West Africa. General linear models for each species tested the effect of season, year and variation in rainfall on two response variables; the proportion of adults caught with brood patches, and/or the proportion of juveniles to adults. Pooling data across years for each species, we show the season with the lowest proportion of adults with brood patches, and the approximate start (S.) or end (E.) of the month which best fits the two week period of the highest breeding activity (also numbered 1-26). From the literature we identified a species' feeding guild: F, frugivorous; G, granivorous; I, insectivorous; N, nectivorous.

Species	<i>n</i> adult	<i>n</i> adult with BP	<i>n</i> juv.	BP Season <sup>1</sup>	BP Year <sup>1</sup>	BP Rain <sup>1</sup>	Juv Season <sup>1</sup>	Juv Year <sup>1</sup>	Juv Rain <sup>1</sup>	Season min.	Month max. Breed <sup>2</sup>	Br. all seasons	Guild
COLIIFORMES													
<b>Coliidae</b>													
Speckled mousebird <i>Colius striatus</i>	385	-	16	-	-	-	<0.0001	0.03	0.01	-	E. Jun.	No	F
CORACIIFORMES													
<b>Meropidae</b>													
Red-throated bee-eater <i>Merops bullocki</i>	130	-	18	-	-	-	0.009	0.0009	0.02	-	S. Mar.	No	I
PICIFORMES													
<b>Capitonidae</b>													
Yellow-fronted tinkerbird <i>Pogoniulus chrysoconus</i>	342	109	-	0.002	0.0004	0.05	-	-	-	1	S. Aug.	Yes	I
PASSERIFORMES													
<b>Pycnonotidae</b>													
Common bulbul <i>Pycnonotus barbatus</i>	573	45	-				-	-	-	4	E. May.	Yes	I/F
<b>Turdidae</b>													
African thrush <i>Turdus pelios</i>	508	18	22	0.03			<0.0001	<0.0001		1	S. Aug.	Yes	I
<b>Muscicapidae</b>													
Familiar chat <i>Ceromela familiaris</i>	107	14	18	<0.0001	<0.0001		<0.0001	<0.0001		3	S. May.	Yes	I
<b>Cisticolidae</b>													
Grey-backed camaroptera <i>Camaropectera brachyura</i>	293	35	14	0.0003			0.002			1	S. Sep.	Yes	I
<b>Zosteropidae</b>													
Yellow white-eye <i>Zosterops senegalensis</i>	271	64	-	0.01			-	-	-	1	E. Sep.	Yes	F

<b>Nectariniidae</b>													
Red-chested sunbird <i>Chlcomitra senegalensis</i>	379	21	41	<b>0.002</b>			<b>&lt;0.0001</b>		0.04	1	S. Sep.	Yes	N
Variable sunbird <i>Cinnyris venustus</i>	314	16	35	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0005</b>				2	S. Sep.	Yes	N
Green-headed sunbird <i>Cyanomitra verticalis</i>	178	14		<b>0.003</b>	<b>0.0001</b>	<b>0.0003</b>	-	-	-	2	S. Sep.	Yes	N
<b>Malaconotidae</b>													
Black-crowned tchagra <i>Tchagra senegalus</i>	82	18	-	<b>0.0001</b>	<b>&lt;0.0001</b>		-	-	-	1	S. Sep.	Yes	
<b>Ploceidae</b>													
Village weaver <i>Ploceus cucullatus</i>	601	66	73	<b>&lt;0.0001</b>			<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.004</b>	1	E. Oct.	Yes	G
Little weaver <i>Ploceus luteolus</i>	120	11	13	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>		<b>0.002</b>	<b>&lt;0.0001</b>		1	S. Nov.	Yes	G
Black-necked weaver <i>Ploceus nigricollis</i>	222	-	16	-	-	-	<b>0.001</b>			-	<i>E. Oct.</i>	Yes	G
Vitelline masked weaver <i>Ploceus vitellinus</i>	242	42	47	<b>&lt;0.0001</b>	<b>0.0002</b>		<b>0.0006</b>	0.03	0.03	1	E. Oct.	Yes	G
Northern red bishop <i>Euplectes franciscanus</i>	204	515	369	<b>0.0002</b>			<b>&lt;0.0001</b>	<b>&lt;0.0001</b>		1	S. Dec.	No	G
<b>Estrildidae</b>													
Lavender waxbill <i>Estrilda caerulescens</i>	668	61	23	<b>&lt;0.0001</b>	<b>0.0004</b>	0.05	<b>&lt;0.0001</b>			2	E. Sep.	Yes	G
Red-cheeked cordon-bleu <i>Uraeginthus bengalus</i>	739	168	32	<b>&lt;0.0001</b>	<b>0.003</b>		<b>&lt;0.0001</b>	<b>0.002</b>		2	E. Nov.	Yes	G
Black-bellied firefinch <i>Lagonosticta rara</i>	92	21	-	<b>&lt;0.0001</b>	<b>0.003</b>	0.05	-	-	-	2	S. Dec.	Yes	G
Bar-breasted firefinch <i>L. rufopicta</i>	98	25	-	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>		-	-	-	2	S. Dec.	No	G
Rock firefinch <i>L. sanguinodorsalis</i>	541	71	49	<b>&lt;0.0001</b>			<b>&lt;0.0001</b>	<b>&lt;0.0001</b>		1	E. Dec.	Yes	G
Red-billed firefinch <i>L. senegala</i>	655	150	50	<b>0.0002</b>	<b>&lt;0.0001</b>					2	S. Dec.	Yes	G
Bronze mannikin <i>Lonchura cucullatus</i>	609	49	145	<b>&lt;0.0006</b>			<b>&lt;0.0001</b>			1	S. Oct.	Yes	G
<b>Emberizidae</b>													
Cinnamon breasted rock-bunting <i>Emberiza tahapisi</i>	315	31	18	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>					2	E. Nov.	Yes	G

<sup>1</sup>If the predictor variable was significant after sequential Bonferroni correction (Rice 1989) in bold.

<sup>2</sup>The start or end of the month which showed the highest annual breeding activity. Where possible this was calculated from the proportional brood patch data. Where BP data was insufficient we subtracted one month from peak juvenile abundance (*italics*).



**Table 2:** Estimates from mixed effects models testing seasonal variation in the occurrence of brood patches across 22 species (brood patch; no brood patch) and juveniles across 19 species (juveniles; adults), both as a proxy for breeding, while controlling for possible year effects and inter-annual variation in rainfall (included in the models below but parameter estimates not shown). We included species as a random effect, while compensating for possible over dispersion in the model by fitting an observational level random effect (random).

	Estimate	SE	Z value	<i>p</i>
<i>Brood patch</i>				
Intercept	-3.30	0.28	-11.6	<0.0001
Start wet	0.13	0.16	0.8	0.4
End wet	1.67	0.18	9.0	<0.0001
Start dry	1.65	0.14	12.0	<0.0001
Species	Variance 0.45 SE 0.67			
Random	Variance 0.55 SE 0.74			
<i>Juveniles</i>				
Intercept	-3.29	0.36	-9.1	<0.0001
Start wet	0.15	0.28	0.5	0.6
End wet	1.23	0.28	4.4	<0.0001
Start dry	2.19	0.22	9.7	<0.0001
Species	Variance 0.25 SE 0.50			
Random	Variance 1.65 SE 1.29			

**Table 3:** The proportion of adults with brood patches and/or the proportion of juveniles to adults caught per season in 25 species of West African savannah bird. The data were pooled by season between 2002 and 2011.

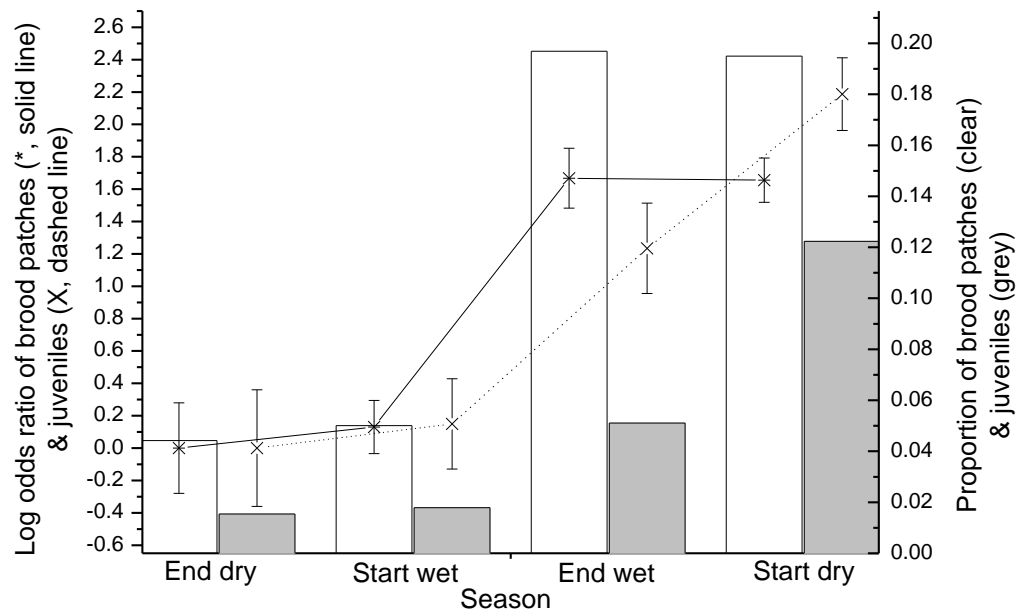
Species	% of adults with brood patches				% juveniles			
	End	Start	End	Start	End	Start	End	Start
<i>Colius striatus</i>	-	-	-	-	0.0	7.0	6.7	2.8
<i>Merops bulocki</i>	-	-	-	-	23.8	19.8	0.0	0.0
<i>Pogoniulus chrysoconus</i>	25.1	22.9	46.6	42.9	-	-	-	-
<i>Pycnonotus barbatus</i> *	7.3	12.4	9.5	5.1	-	-	-	-
<i>Turdus pelios</i>	1.4	4.8	12.1	4.9	0.0	2.3	22.6	8.8
<i>Cercomela familiaris</i>	12.3	16.4	0.0	0.0	1.8	22.6	22.5	23.2
<i>Camaroptera brachyuran</i> <sup>+</sup>	3.4	8.8	3.3	21.8	0.7	0.3	10.0	21.8
<i>Zosterops senegalensis</i>	12.2	30.3	58.2	25.7	-	-	-	-
<i>Chalcomitra senegalensis</i> <sup>+</sup>	2.2	5.7	22	3.0	4.2	4.5	19.1	27.2
<i>Cinnyris venustus</i>	8.3	0.0	2.3	10.7	13.7	6.5	12.7	9.0
<i>Cyanomitra verticalis</i>	2.0	3.9	9.9	7.5	-	-	-	-
<i>Tchagra senegalus</i>	6.0	24.9	46.4	19.9	-	-	-	-
<i>Ploceus cucullatus</i> <sup>+</sup>	0.8	7.9	17.7	20.5	0.9	5.0	11.4	20.9
<i>Ploceus luteolus</i>	0.0	0.0	13.5	18.5	2.4	5.3	5.2	13.1
<i>Ploceus nigricollis</i>	-	-	-	-	3.2	6.3	25.6	37
<i>Ploceus vitellinus</i> <sup>+</sup>	15.4	6.0	5.7	18.1	4.7	2.0	14	22.5
<i>Euplectes franciscanus</i>	0.0	1.3	49.0	33.0	0.0	0.0	1.2	18.9
<i>Estrilda caerulescens</i> <sup>+</sup>	6.1	2.6	25.4	27.4	2.6	0.5	6.1	12.6
<i>Uraeginthus bengalus</i>	2.1	7.3	19.5	39.1	1.8	0.0	0.0	9.6
<i>Lagonosticta rara</i>	6.2	11.6	75.0	47.5	-	-	-	-
<i>Lagonosticta rufopicta</i>	20.8	0.0	29.7	33.8	-	-	-	-
<i>Lagonosticta sanguinodorsalis</i>	11.2	9.0	25.4	36.4	3.6	0.0	1.0	15.9
<i>Lagonosticta senegala</i> <sup>+</sup>	22.4	9.1	26.7	32.6	9.9	10.8	2.7	5.9
<i>Lonchura cucullatus</i> <sup>+</sup>	3.5	10.1	19.6	23.9	0.9	0.6	16.1	53.7
<i>Emberiza tahapisi</i>	9.7	0.0	0.0	20.9	7.0	2.1	0.0	4.7

\*The only non-seasonal breeder

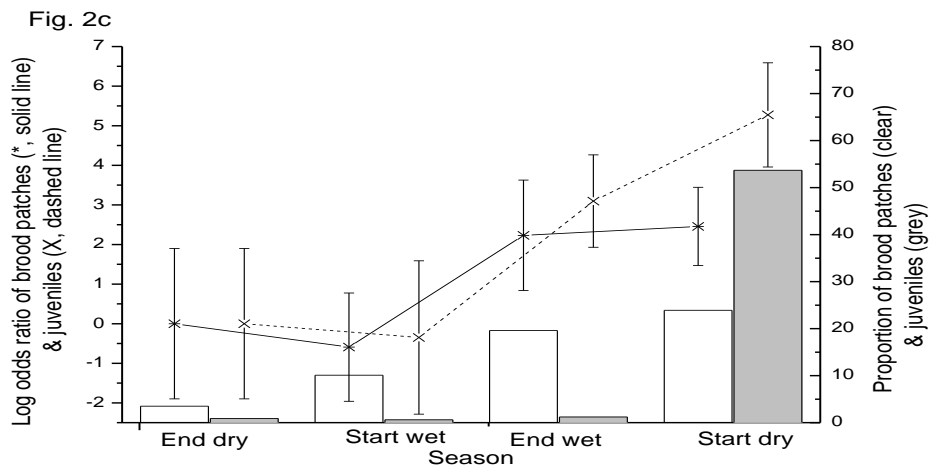
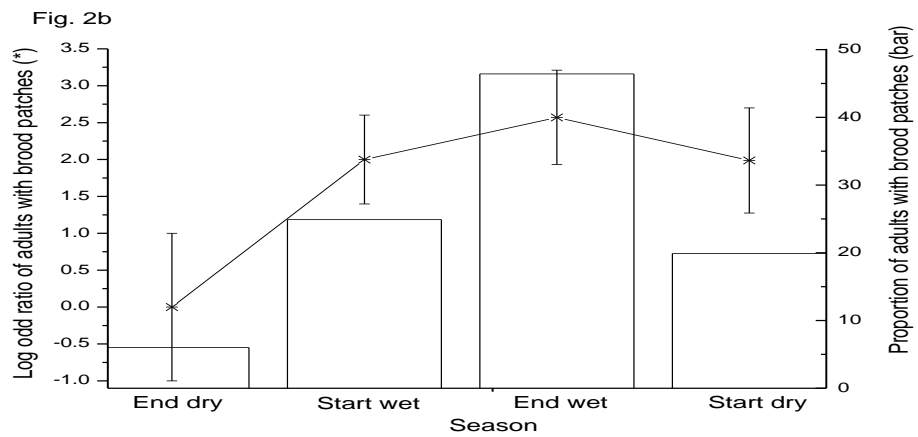
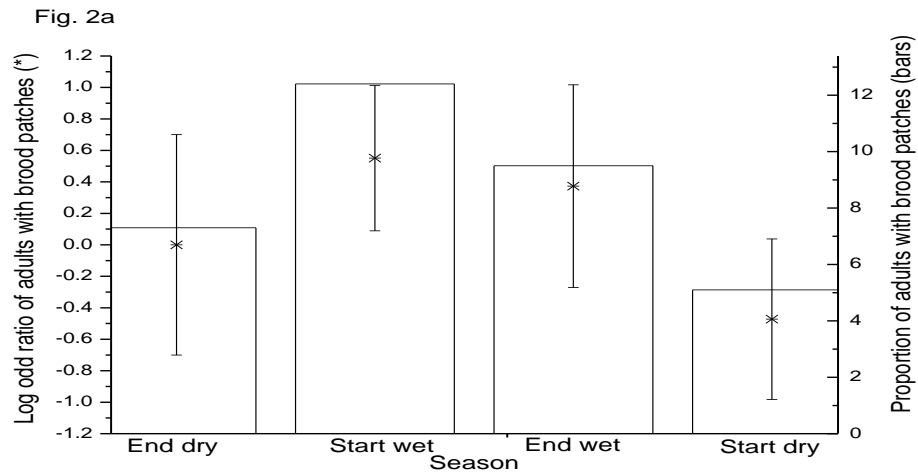
<sup>+</sup>Species which both incubated eggs and successfully fledged chicks in all four seasons

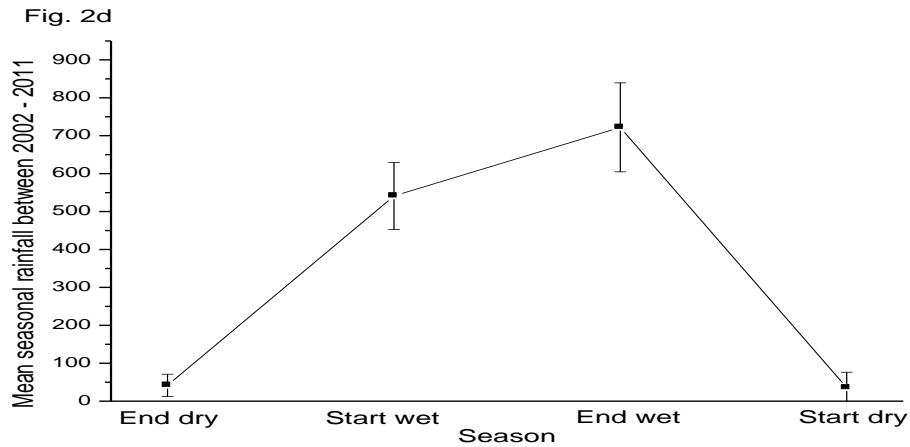
**Table 4:** A general linear model of how the two week period of peak breeding activity varied by feeding guild across 25 species of West African Savannah species.

<b>Guild</b>	<b>Estimate</b>	<b>Error</b>	<b><i>t</i></b>	<b><i>p</i></b>
Intercept (Frugivore)	15.7	2.2	7.2	<b>&lt;0.0001</b>
Granivore	7.0	2.4	2.9	<b>0.009</b>
Insectivore	-1.5	2.6	-0.6	0.6
Nectivore	2.0	3.1	0.6	0.5
Adjusted R <sup>2</sup>	0.49			

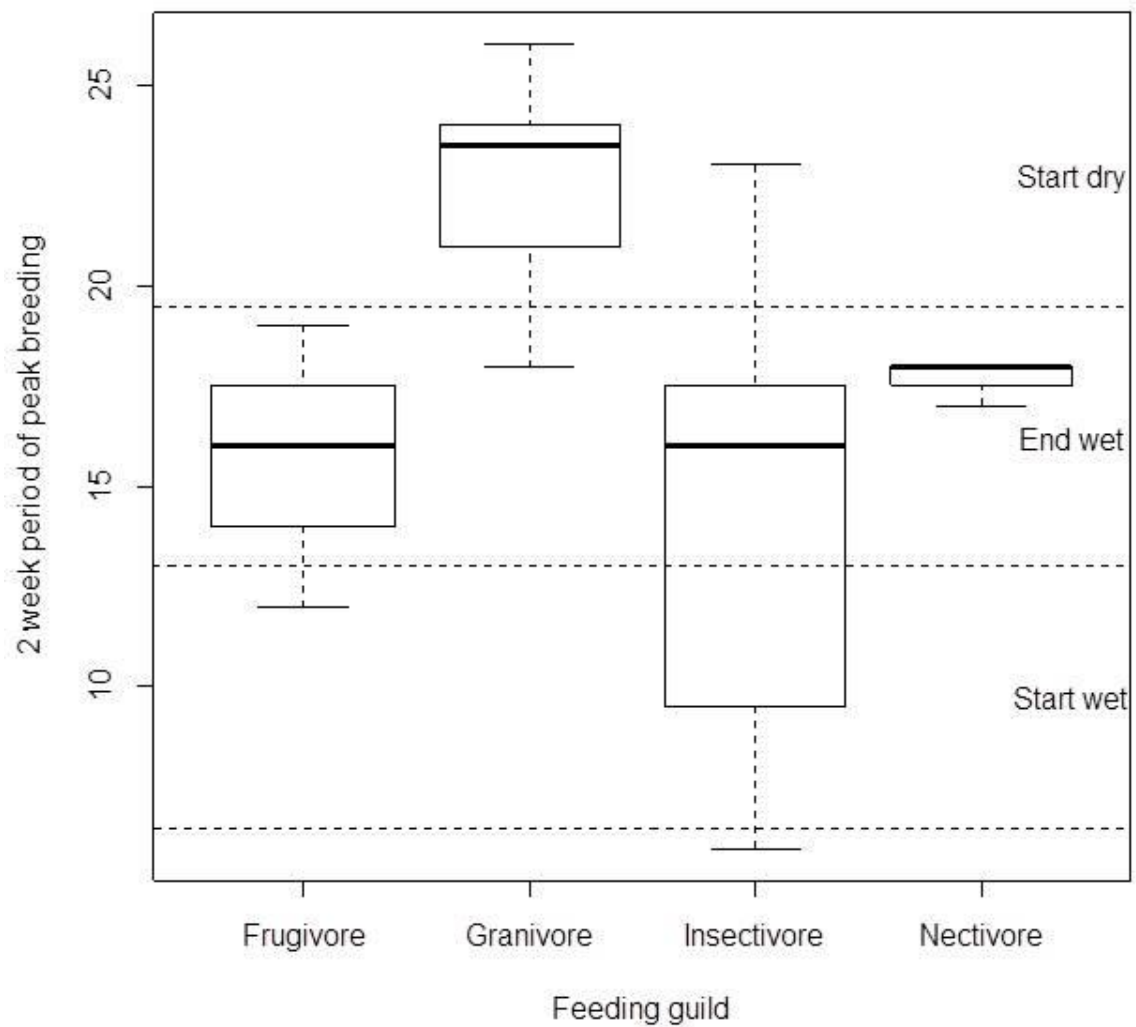


**Fig. 1** Average seasonal timing of breeding. Log odds ratios (as a measure of the effect size and non-independence of the two binary response variables) and proportions of adult birds caught with brood patches (across 22 species), and juveniles to adults (across 18 species)





**Fig. 2 a-d** Examples of individual species' seasonal timing of breeding. Log odds ratios (as a measure of the effect size and non-independence of the two binary response variables) and proportions of adult birds caught with brood patches, and/or juveniles to adults in three case study species: a species showing no significant seasonal peak in brood patch abundance (*Pycnonotus barbatus*; Fig. 2a); a species which showed a peak in brood patch abundance at the end of the wet season (*Tchagra senegalus*; Fig. 2b) and a species which showed a peak in brood patch abundance at the start of the dry season (*Lonchura cucullatus*; Fig. 2c). Mean seasonal rainfall (2002 – 2011; Fig. 2d) is also shown to demonstrate the general driver of these patterns.



**Fig. 3** Variation in the two weeks of peak breeding by feeding guild in 25 species of small West African savannah bird. Week 1 commences on January 1<sup>st</sup> and runs across the year.

# **Chapter 4: Breeding as interrupted foraging - seasonal mass gain in tropical savannah birds**

## **Summary**

1. Theoretically any interruption to foraging caused by, for example, predators, disturbance or environmental conditions should cause an increase in mass in birds as they compensate for the consequent increased risk of starvation. Breeding could also be considered an interruption in foraging because birds become constrained in the time and location of their foraging.
2. Therefore we predict that breeding birds should also show an interrupted foraging mass increase, independent of any increases due to gonad or egg development. We would also predict that the sex that invests more time and energy in reproduction should show a higher mass increase due to interrupted foraging.
3. We tested these predictions using data from ten species of three feeding guilds collected over a ten year period in a West African savannah.
4. We show that independent of egg production and probably gonad growth; 1) birds increased their mass during breeding and we provide evidence that this is due to an interrupted foraging response, and 2) females showed higher mass gain than males which probably represents an increased investment in breeding. We also show that females but not males, increased their mass during brood patch development, probably as a fixed cost due to increased fat reserves associated with egg formation.
5. We conclude that mass gain before breeding and mass loss during breeding is the result of adaptive management reflecting the level of investment in young, independent of sex or incubation stage and is not a consequence of energetic stress. As such the scale of any mass gain has important implications for food limitation theory and life history, as it reflects a trade-off between foraging predictability and breeding strategy.

## **Introduction**

Birds put on mass reserves in response to interruptions in their foraging, which reduces the predictability of foraging and so increases the risk of starvation (Rogers 1987, Houston and



McNamara 1993, Lilliendahl 1998). Interruptions to foraging may arise from a number of sources such as predators, disturbances, long winter nights or extreme weather events (Lima 1986). Theoretically, breeding should also represent a similar interruption to foraging because adult birds have to divert time away from their own foraging to incubate eggs, feed chicks and to guard mates, nests and territories. Therefore we should expect mass increases in birds during breeding (independent of any increases because of development of reproductive organs (Murton and Westwood 1977, Wikelski et al. 2000) or eggs (Lack 1968) and we should expect that if individuals, sexes or species invest more in their breeding attempts, that this should be reflected in greater increases in mass reserves during breeding.

Under constant predation risk, interrupted foraging theory is widely recognised to be the mechanism behind variation in mass during the non-breeding season in the northern hemisphere (e.g. Houston and McNamara 1993, Lilliendahl 1998, Pravosudov and Grubb 1997, McNamara et al. 2005). However, mass variation during the breeding season has not been investigated from an interrupted foraging theory perspective, because studies have focused on mass loss which occurs during the short, intense breeding season (e.g. Freed 1981, Nur 1984, Nagy et al. 2007). In tropical birds however, little or no mass may be gained during the non-breeding season because foraging remains predictable due to constant day lengths and warm temperatures (Fogden 1972, Fogden and Fogden 1979, Rozman et al. 2003, Cox et al. 2011). Mass, however, does peak in the breeding season (e.g., Fogden 1972; Fogden & Fogden 1979; Rozman *et al.* 2003; Cox *et al.* 2011) suggesting that an interrupted foraging mass gain could be occurring. Here we investigate the degree to which the mass increase in tropical savannah birds during the breeding season is due to an interrupted foraging response, rather than simply as a consequence of factors such as, egg production or gonad development.

The timing of mass gain or loss relative to food and breeding peaks, and any differences between the sexes related to differential investment are crucial in disentangling whether mass gain due to interrupted foraging during breeding occurs. Consider a hypothetical savannah bird species breeding in a strongly seasonal tropical environment. During the non-breeding dry season when foraging probably remains predictable (Cox et al. 2011), mass (as a proxy for body reserves) is maintained at low levels to reduce mass-dependent energy (Rogers and Heath-Coss 2003) and predation costs (Witter and Cuthill 1993). Food availability then increases with the arrival of the rains and birds will time the energy requirements of the chicks to coincide with a predictable seasonal food peak (Martin 1987). Although an increase

in food availability should result in a decrease in mass in adults, foraging predictability may actually *decrease*, because breeding activities conflict with the time available for foraging for self and the associated increased energetic expenditure result in a birds reserves being depleted more rapidly. Therefore we would predict an increase in mass during the breeding season, independent of any mass increases due to gonad and egg development (Figure 1). We would also expect more mass to be gained by the sex that invests most heavily in reproduction, and differences in the timing of mass gain to reflect sex-dependent differences in investment (e.g. males engaging in pre-breeding territoriality and mate guarding, and females investing more heavily in incubation and feeding young).

Any mass gain during the breeding period in birds is of course confounded by mass increases due to gonad and egg development (e.g., Lack 1968). Such mass increases occur during egg production and incubation (Martin 1987), the timing of which can be identified by the presence of a brood patch (Hinde 1962, Jones 1971, Redfern 2008). Therefore if females put on mass due to interrupted foraging, rather than simply because of gonad and egg production, we would expect birds without brood patches also to show increased mass during the breeding season. This is because during the breeding season most individuals in a population are likely to be engaged in breeding activities which interrupt their foraging, not only those which have a brood patch which designates a specific period during the breeding process. In addition, if the mass increase is due solely to gonad growth we would expect non-incubating males and females to show similar patterns of mass regulation

Females vary their mass during brood patch development (Redfern 2010). We predict that peak mass will occur during laying as a consequence of the mass of the egg which when fully formed can weigh ~10% of the females mass (Lack 1968, Payne 1977), because of an increase in fat reserves because the egg costs 40% of the basal metabolic rate to produce (Fogden and Fogden 1979, Rahn et al. 1985) and also to compensate for missed foraging opportunities. Females engaged in parental care will then maintain increased reserves due to the time and energy constraints of feeding the chicks, with the size of the mass increase reflecting the level of parental investment. Any mass increase in males with brood patches is expected to be less than females and will reflect their level of investment during incubation.

We use data collected over a 10 year period in a West African savannah region to test two general predictions that arise if birds show mass gain during breeding because of interrupted foraging:

- 1) That mass gain occurs during the breeding season for both incubating and non-incubating birds (i.e. mass increases during the breeding season and is not solely due to gonad or egg development)
- 2) That the scale of mass gain due to breeding of males and females differs due to sex specific costs associated with different breeding stages (accounting for any differences due to egg development).

## Methods

We estimated temporal variation in mass in relation to breeding in small tropical birds caught in Guinea savannah woodland at the A.P. Leventis Ornithological Research Institutes (APLORI), Amurum Forest Reserve on the Jos Plateau (09°52'N, 08°58'E) in Nigeria: we caught 3386 individuals of 10 species. To avoid under representation of adult birds breeding over several years we retained individuals retrapped in different years in the analysis: 1031 records of 10 species (Table 1).

Birds were trapped using mist nets between January 2002 and December 2011. Trapping occurred year round but was concentrated at a Constant Effort Site (CES) conducted biannually in Amurum for a 14-day period at the end of the dry season (March–April) and at the end of the wet season (September–October). During the CES, 272 m of four shelf nets were used between 06:00 and 10:30 h WAT (although there were few captures after 09:30 h). Species were assigned to feeding guilds (Fry et al. 1993, 2000, 2004). In West Africa the seasons are divided into a distinct wet and dry season. There was an annual rainfall of  $1337 \pm 159$  mm (2001–2011), with 97.4% of rain falling in the wet season from the 10th of April  $\pm 9$  days until the 13th of October  $\pm 11$  days. See Cox et al. *In submission* for a climatic description of the study site.

### *Determination of variables*

Where possible trapped birds were aged and sexed, only birds in full adult plumage were included in the analysis. Maximum wing-chord was measured using a stopped wing rule to 1 mm (Svensson 1992). Mass was measured to 0.1 g using digital scales (Ohaus Scout). Assessment of brood patches were made using a six-stage scoring system: 0 (no brood patch); 1 (brood patch forming; defeathering process has begun); 2 (breast and belly fully de-

feathered, some wrinkling of skin evident and signs of oedema); 3 (skin of belly opaque and engorged, broad swollen wrinkles); 4 (skin shows thin wrinkles, no longer engorged); 5 (refeathering; Redfern 2008). In European resident and migrant passerine species the different stages of brood patch development has been closely linked to breeding stages (Redfern 2008, 2010), and it was assumed that small savannah species show a similar progression of brood patch development to temperate species. Only species for which there were  $\geq 10$  females with brood patches were included in analyses.

All ten species showed evidence of breeding throughout the year, either through the presence of brood patches or juveniles, however at a population level, species showed distinct breeding seasons (Cox et al. *In submission*). During the main breeding season most individuals will be engaged in breeding activities, such as mate guarding, territoriality or parental care, even if they are not actively incubating (indicated by the presence of a brood patch). At the study site the period which the greatest proportion of a population had brood patches coincided with the period when food was likely to be most available : Granivore  $24.2 \pm 1.2$  (November; Crowley & Garnett 1999; Poulin, Lefebvre & McNeil 1992); Nectivore  $17.7 \pm 0.0$  (August; Poulin 1992); Frugivore  $17.5 \pm 2.1$  (August; Poulin 1992 ); variation in peak breeding activity across 26 two-week periods, numbered 1-26 where 1 is the first two weeks in the calendar year, taken from Cox et al. *In submission*). To increase sample size in statistical models when exploring whether mass gain is determined by sex-dependent breeding investment we pooled species by feeding guild.

In our models we controlled for the important potential effects of confounding variables on mass. We controlled for active wing moult because a bird may either increase mass to allow more choice in time and space as to when it can forage or decrease mass to compensate for reduced take-off ability (Swaddle and Witter 1997). We controlled for inter-annual fluctuations in environmental conditions by including year in the model, and body size because larger animals have different costs of acquiring and maintaining fat reserves (Witter and Cuthill 1993). We calculated variation in seasonal rainfall as a covariate by dividing the actual rainfall (mm) for a season within year by the average rainfall (mm) for that season across years: thus a value above one indicated a season in which rainfall was above the seasonal average. All analysis was conducted in the R (version 2.15) statistical environment (R Development Core Team 2011), and we used the nlme package (Pinheiro et al. 2011).

## *Statistical analysis*

Hypothesis 1: Mass gain occurs for both incubating and non-incubating breeding birds

For each species we built a General Linear Model to test whether birds with and without brood patches varied their mass across the months. We controlled for possible year effects, whether the bird was in active wing moult or not, rainfall and body size. Where sexes were distinguishable in the hand we controlled for sex, but did not test for its possible interactions with other variables because of large confidence intervals due to small sample sizes in some species and months. The mean mass and the predicted mass increase in birds with or without brood patches was calculated from the parameter estimates, we used the months where the mean mass was lightest and heaviest within a year, using the month with the lowest and highest parameter estimate, respectively (Table 1).

We used the parameter estimates to test three specific predictions:

- 1) Independent of incubation (i.e. birds without brood patches) birds increase their mass during the breeding season. We calculated the percentage difference in mass between the month of maximum and minimum mass, before running a match paired t-test of the maximum mass gain across species relative to no mass change (i.e. 0).
- 2) Across months, birds with brood patches are heavier than those without. We ran a matched pairs t-test of the mass change in birds with brood patches relative to those without. To increase sample size within months, we also pooled species by feeding guild and built Generalized Linear Mixed Models (GLMM) to test for the effects of the predictor and potentially confounding variables on the percentage difference in mass to the mean species mass (MASS DIFFERENCE). Species was included as a random factor. We used the parameter estimates to calculate the percentage change in mass for each feeding guild in birds with or without brood patches (Fig. 2a-c).
- 3) Birds without brood patches show a greater increase in mass during the breeding season, compared to mass gain which occurs because of brood patch development. We ran a matched paired t-test of percentage change in mass between the month of maximum and minimum mass, compared to the average mass gain across the months in birds with brood patches.

Hypothesis 2: mass gain is determined by sex-dependent breeding investment

We tested for sex-dependent differences in *monthly* mass gain across non-incubating males and females of two feeding guilds; across two sunbird (scarlet-chested sunbird *Chalcomita senegalensis*; variable sunbird *Cinnyris venustus*), and across three finch (red-cheeked cordon-bleu *Uraeginthus bengalus*; red-billed firefinch *Lagonosticta senegala*; rock firefinch *L. sanguinodorsalis*) species. We controlled for the confounding effects on mass of egg production by excluding birds with brood patches from the model. We built a GLMM for each feeding guild to test for the effect on mass difference of the interaction sex\*month. We controlled for possible year effects, whether the bird was in active wing moult or not, rainfall and body size. Species was included as a random factor.

We caught sufficient males with brood patches to test for sex-dependent differences in mass gain, dependent on the presence of a brood patch across three species of granivorous finch; red-cheeked cordon-bleu, red-billed firefinch and the rock firefinch, but only on a *seasonal* basis. We categorised the year into four seasons of distinctly different resource availability correlated with the approximate start and finish of the rains: end of dry season (10<sup>th</sup> January – 09<sup>th</sup> April); start of wet season (10<sup>th</sup> April – 09<sup>th</sup> July); end of wet season (10<sup>th</sup> July – 09<sup>th</sup> October); start of dry season (10<sup>th</sup> October – 09<sup>th</sup> January). We then built a GLMM (with species as a random factor) to determine the effect on mass difference of the interactions between sex\*season and sex\*brood patch; we controlled for possible year effects, whether the bird was in active wing moult or not, rainfall and body size.

We tested for sex-dependent variation in mass during brood patch development by pooling the individuals from the three species of granivorous finch (red-cheeked cordon-bleu; red-billed firefinch; rock firefinch) where we had caught sufficient males with brood patches (Table 2). We built a GLMM with species as a random factor to test for the effect on mass difference of the interaction sex\*brood patch score, while controlling for possible seasonal and year effects, whether the bird was in active wing moult or not, rainfall and body size. The mean mass and the predicted mass increase at each stage of brood patch development were calculated from the parameter estimates. We also caught sufficient numbers of birds with brood patches to test for variation in MASS DIFFERENCE dependent on brood patch score in two species of frugivorous birds (yellow-fronted tinkerbird *Pogoniulus chrysoconus*; yellow white-eye *Zosterops senegalensis*;) where sexes were indistinguishable in the hand (Table 1). We controlled for season, year, whether the bird was in active wing moult or not, rainfall and body size. Species was included as a random factor.

## Results

### *Mass gain occurs for both incubating and non-incubating breeding birds*

There was strong evidence that independent of the presence of a brood patch, birds varied their mass across the year in all ten species ( $8.9\% \pm 1.5\%$ ;  $t(9) = 18.8$ ,  $P < 0.0001$ ; Table 1), probably because even though birds did not display a brood patch they were engaged in activities which interrupted foraging during the breeding season. Birds with brood patches then showed a further mass increase relative to those without ( $5.0\% \pm 1.8\%$ ;  $t(9) = 8.9$ ,  $P < 0.0001$ ; Table 1). The average monthly mass gain in birds with brood patches relative to those without did not vary by feeding guild; granivores ( $4.2\% \pm 2.2\%$ ); nectivores ( $5.5\% \pm 1.2\%$ ); frugivores ( $3.5\% \pm 2.7\%$ ;  $F^2_7 = 2.6$ ,  $P = 0.1$ ; Fig. 2a-c). Across species, mass gained across the year in birds without brood patches, was larger than the additional mass increase in birds with brood patches ( $t(17.4) = 5.3$ ,  $P = < 0.0001$ ): i.e. mass is gained during the breeding season regardless of whether a brood patch is present, and this mass gain is larger than any mass gain associated with a brood patch.

### *Mass gain is determined by sex-dependent breeding investment*

We investigated *monthly* mass variation in, males and females without brood patches, i.e. independent of egg production, across two sunbird (scarlet-chested sunbird; variable sunbird) and across three finch species (red-cheeked cordon-bleu; red-billed firefinch; rock firefinch; Table 2).

Male and female sunbirds followed similar overall mass gain strategies, with both sexes increasing their mass during the breeding season, but with a significantly different seasonal pattern (the interaction month\*sex in Table 3a, Fig. 3a). Females showed a greater variation in mass across the year, with peak mass coinciding with peak breeding in the late wet season and minimum mass in the middle of the dry season (females 12.2%; males 5.5%; Fig. 3a).

Male and female granivores had quite different overall mass gain strategies (the interaction month\*sex in Table 3b, Fig. 3b). Initially, both sexes had reduced mass in the non-breeding season, they then increased their mass at the start of the wet season which coincided with a possible 'lean' season as remaining seeds started to germinate with the arrival of the rains (% difference between March and May in males  $3.7 \pm 2.5$ , and females  $3.7 \pm 1.9$ ; Fig. 3b). Males

then decreased their mass before maintaining a constant mass throughout the breeding and non-breeding seasons (Fig. 3b). In contrast, after the 'lean' period female granivores first decreased their mass as did males, before increasing their mass ( $6.2\% \pm 2.2\%$ ) to peak just after the start of the main breeding season. They then lost mass through the breeding season despite an increase in breeding effort (Fig. 3b). The largest drop in mass occurred during the month of peak breeding ( $4.9\% \pm 1.6\%$ ) which coincided with the ripening of the seed crop (Fig. 3b; Crowley 1999 ).

We further tested the hypothesis that mass gain occurs for both incubating and non-incubating males and females across three granivore species (red-cheeked cordon-bleu; red-billed firefinch; rock firefinch). Species were pooled by *season*, so that we had sufficient power to examine any sex-dependent differences on mass gain dependent on the presence of a brood patch (Table 4; Fig. 4). Females with brood patches were heavier in all seasons than those without ( $2.6\% \pm 0.2\%$ ), while the presence of a brood patch in males had no effect on mass ( $0.6\% \pm 0.2\%$ ; the interaction sex\*brood patch; Table 4; Fig. 4).

We tested for sex-dependent variation in mass during brood patch development across three finch species (red-cheeked cordon-bleu; red-billed firefinch; rock firefinch; Table 2; Fig. 5a). Males and females followed different overall mass gain strategies (the interaction sex\*brood patch score; Table 5a). Females showed no mass change while the brood patch was defeathering (brood patch score 1; Fig. 5a). They then gained mass, with peak mass occurring while they were laying and/or incubating eggs ( $9.9\% \pm 0.8\%$ ; brood patch score 3; Fig. 5a). After fledging, the parents reduced mass, but still showed a  $5.4\% \pm 0.8\%$  increase relative to birds without brood patches (Fig. 5a). Males showed no mass change during brood patch development relative to males without brood patches (Fig. 5a).

Across frugivore species (yellow-fronted tinkerbird; yellow white-eye) birds increased their mass during brood patch development (Table 5b), with peak mass also occurring during laying and incubation ( $5.9\% \pm 1.5\%$ ; brood patch score 3; Fig. 5b). They then reduced their mass directly after fledging but still retained a mass gain of  $3.4\% \pm 1.2\%$  relative to birds without brood patches (brood patch score 4). By the time that the brood patch had started to refeather they had regained their pre-incubation mass (brood patch score 5; Fig. 5b). We acknowledge that this result is likely confounded because females will show an increased mass gain during egg development bringing up the average, while males may not vary their mass (see also Redfern 2010), bringing down the average, nevertheless the pattern is



consistent with the results above from other species which are not confounded by egg development.

## **Discussion**

We show that tropical savannah birds increase their mass during breeding and we provide evidence that this is due to an interrupted foraging response and not simply due to a mass increase from egg or gonad growth. Independent of egg and gonad growth females showed a larger mass increase than males, which probably reflects their increased investment in breeding. Females but not males showed a further mass increase during brood patch development which was probably a fixed cost due to increased fat reserves associated with egg formation.

### *Evidence that the mass gain during breeding is due to an interrupted foraging response*

Research suggests that species may increase their mass during breeding in one or more of three ways; either due to egg production, gonad growth or through an interrupted foraging response. We found that in all three feeding guilds across the year mass variation occurred in birds with and without brood patches, and that birds with brood patches were consistently heavier than those without (Table 1; Fig. 2a-c). In passerine birds brood patch development closely follows the stages of breeding, with the defeathering process beginning well before birds lay down the extra fat associated with egg production (Hinde 1962, Jones 1971). Including the presence of a brood patch in the model controlled for any mass increase due to egg production. Although incubation and provisioning of young is the most costly period for parent birds (Bryant 1988, Nilsson and Råberg 2001), we found that the mass gain in birds without brood patches was greater than any subsequent mass increase which occurred during brood patch development (Table 1; Fig. 2a-c). This probably reflects the high physiological and energetic costs of breeding relative to non-breeding activities.

Similar to temperate species, many tropical species seasonally regress their reproductive organs, which might be an adaptation for minimising energy expenditure during the non-breeding season (e.g., King 1973; Dawson *et al.* 2001). In the northern hemisphere gonad mass can increase several hundred fold (Dawson *et al.* 2001), commencing 1-2 months before the onset of the breeding season (Wikelski *et al.* 2000), and tropical species may show a similar progression (Dittami 1987, Rödl *et al.* 2004). So if the mass increase which occurs in

birds without brood patches is due to gonad growth we would expect any mass response to take place a month before the breeding season and to follow the proportion of individuals breeding (i.e., Fig. 1).

Key to disentangling whether the mass increase during breeding is due to an interrupted foraging response and not due to gonad growth is through the differences in food types which adults feed themselves and their chicks. Invertebrates are a good source of nutrients for young (Ward 1969, Berthold 1976) and sunbirds and finches both feed their chicks on invertebrates while adults forage for nectar (Markman et al. 1999, Fry et al. 2000) and seeds, respectively (Dyer et al. 1982, Fry et al. 2004). Specialized seed eating finches inhabit a seasonal foraging environment with seed availability varying from almost negligible at the start of the wet season to super-abundant at the start of the dry season when seeds ripen and fall (Crowley and Garnett 1999). Despite seed availability remaining low during the second half of the wet season many individuals respond to peak invertebrate abundances (Poulin et al. 1992) by commencing breeding activities. This is because, in a seasonal environment, earlier clutches are often larger and more successful and so birds lay as early as they can find sufficient food (Perrins 1970). Seed availability, however, for the adults has not yet peaked and so females show an increased mass response because of this increased starvation risk. Food availability and thus foraging predictability for adults then peaks with the ripening of the seed crop in November, and there is a *decrease* in mass despite an *increase* in breeding effort (Fig. 3b). Thus we see a lag between the month of peak mass and peak breeding and so the mass gain at the start of breeding season must be due to an interrupted foraging response and not gonad growth because the gonads will still be fully grown during peak breeding (see theoretical model Fig. 6). Thus any mass increase due to gonad growth may be relatively small. We did not detect this lag in sunbird species probably because peak food availability for adults coincides with peak invertebrate abundance, at least at the temporal scale of this study (Poulin et al. 1992) and so foraging predictability approximately coincides with breeding effort (Fig. 3a).

Mass loss during breeding has been observed in many species in the northern hemisphere (e.g., Hillstrom 1995; Cavitt & Thompson 1997), particularly in females and was initially assumed to occur due to the energetic stress hypothesis (e.g., Ricklefs 1974). From an interrupted foraging perspective any mass loss which occurs during provisioning for young is perhaps a measure of the scale of the interrupted foraging response which occurred during laying and the early stages of chick provisioning, with individuals with larger broods storing

more mass (shown by greater mass loss). For example; female black-throated blue warblers (*Setophaga caerulescens*) in New Hampshire given supplementary food showed a smaller mass decrease while provisioning for chicks than did control females, which the authors attributed to the energetic stress hypothesis (Nagy et al. 2007). However, interrupted foraging theory predicts that those birds in a more predictable foraging environment (i.e. provided with supplementary food) would show a reduced interrupted foraging response (shown by a smaller mass loss during provisioning) which is what occurred.

*The scale of the interrupted foraging response is an index of sex-specific breeding investment*

Our results are consistent with mass change during the breeding season reflecting reproductive investment, mediated by the interrupted foraging response. Females and males are likely to occupy the same foraging niche in most species and so any change of mass may well reflect differing foraging predictability, which can be attributed to sex-specific roles during breeding. For example, male and female sunbirds both increased their mass during the breeding season, before decreasing their mass at the start of the dry season. Females lost twice as much mass as males, which may represent their increased investment in provisioning for chicks (Markman et al. 1995). Similarly, male and female finches showed distinctly different patterns of mass regulation across the year. After an interrupted foraging response associated with a possible 'lean' season, both sexes then decreased mass before females increased their mass during breeding (discussed above). However, males showed no subsequent change in mass, which suggests that they invest relatively little in chick production, or their investment is maintained at a constant low level throughout the year (for example, through territory maintenance, mate guarding, chick feeding, vigilance, and extended post-fledging care). Consequently males are likely to be prioritising their foraging over off spring survival.

Numerous other studies have shown that males invest less in chick care than females do and also that males have higher survival, so supporting our observations (Markman et al. 1995, McCleery et al. 1996, Verhulst 1998, Siefferman and Hill 2008). Increased mass loss in females relative to males has previously been recorded in birds in the northern hemisphere (e.g., Freed 1981, Gosler 1991), and was associated with larger broods and subsequently lower survival in females, while male mass or survival was not affected by brood size (Nur 1984). For example, females may incur a greater energetic expenditure which can be

attributed in part to an increased rate of provisioning young (Williams and Nagy 1985, Verhulst and Tinbergen 1997, Burness et al. 2001) and increased immune response (Pap et al. 2010) compared to males. If females invest more time and energy in their off spring they then have less time available to forage for themselves and expend reserves more rapidly, and so they may store more fat to allow them increased flexibility in time and space for foraging (Rogers 1987, Houston et al. 1997).

#### *Sex specific mass variation in relation to brood patch development*

We tested for sex-dependent *seasonal* mass variation in relation to brood patches across three finch species. Males did not vary their mass during incubation in any season, so they probably do not increase their overall investment during breeding (Fig. 4; see also Redfern 2010, Neto and Gosler 2010). We did not find a seasonal effect on the mass gain in females with brood patches, irrespective of the changing environmental conditions across the seasons, peak mass gain in females occurred during laying and incubation regardless of season. Therefore mass gain in females during incubation is probably a fixed cost resulting from the combination of increased fat reserves in the days immediately before laying (Fogden and Fogden 1979), the oedema of brood patch formation and the mass of the partly formed egg. After fledging, females maintained increased reserves ( $5.2\% \pm 0.2\%$ ; brood patch score 4 and 5), despite the ability of small passerines to lose up to 9% of their mass daily (e.g., Cresswell 1998). Thus females must retained fat reserves independent of egg production costs, most likely due to an interrupted foraging response in order to compensate for the demands of feeding chicks and of post fledgling care.

The yellow-fronted tinkerbird and yellow white-eye also varied their mass during brood patch development, with peak mass also occurring during laying and incubation (Fig. 5b). Birds maintained an increased mass while provisioning chicks, but had regained normal breeding mass by the time the brood patch was refeathering (brood patch score 5). Variation across species in the scale of the interrupted foraging response in females post fledging, probably represents a trade-off between the number of off spring, parental investment and foraging efficiency (see also Redfern 2010).

## *General conclusions*

In conclusion, we show that in ten West African savannah species, independent of egg and probably gonad growth birds increased their reserves during breeding through an interrupted foraging response. We conclude that within the starvation-predation framework the scale of any mass gain during breeding is likely to be a trade-off between foraging efficiency and the level of investment in breeding.

The presence of an interrupted foraging response during breeding has probably not previously been detected because most empirical studies have been conducted in Northern temperate regions where any mass increase is swamped by the greater mass loss which occurs as conditions improve in spring (Rogers 1987, Houston and McNamara 1993). Resident species show decreased mass directly after the breeding season when foraging remains predictable, because birds do not need to carry insurance against longer colder nights of winter or interruptions to foraging from life history activities (Cresswell 1998), i.e. mimicking conditions in the non-breeding season in tropical savannahs. The loss of mass post breeding in temperate birds should therefore reflect any interrupted foraging response which occurred during the breeding season.

Weight loss in females during breeding in the northern hemisphere has been well documented and has previously been explained as due to energetic deficiency (the energetic stress hypothesis; Ricklefs 1974, Johnson et al. 1990, Martins and Wright 1993, Woodburn and Perrins 1997, Nagy et al. 2007) or to an adaptive reduction in wing-loading to save energy during flight (the wing-loading hypothesis; Freed 1981, Norberg 1981, Moreno 1989, Jones 1994, Curlee and Beissinger 1995, Merkle and Barclay 1996, Gebhardt-Henrich et al. 1998), or through a combination of both (Neto and Gosler 2010). Interrupted foraging theory provides a more likely, universal explanation for mass regulation during breeding, where birds adaptively manage their mass in response to varying foraging predictability as in most other situations in birds (Rogers 1987, Houston and McNamara 1993, Rogers and Heath-Coss 2003, MacLeod et al. 2007, MacLeod et al. 2008), rather than energetic expenditure as, outwith situations of imminent starvation. Previous studies have investigated mass loss between incubation and provisioning of chicks which is only part of the breeding mass response. We show the greater mass change relative to predictable foraging in the non-breeding season, which allowed us to tease apart any mass response from egg production or

gonad growth and the mass change due to an interrupted foraging response at specific stages in the breeding cycle.

The scale of the mass gain during the breeding season varies between species within the same habitat (Cox et al. 2011), and we predict this will relate to the seasonality of a species' foraging niche. Those species which inhabit a foraging niche with smaller seasonal peaks in food availability will put on more mass gain against increased foraging unpredictability, related to breeding activities. As such they will allocate fewer resources to breeding aspects such as immunocompetence and so will live longer as adults (Norris and Evans 2000), but at a cost to investment in their own off spring (Lemon 1993). So during breeding, populations will be restricted more by density-dependent factors such as food limitation and competition, and as a consequence will be more K selected, trading-off a lower investment in each breeding attempt (i.e. smaller clutch sizes) but for longer (i.e. longer parental care).

Across populations of a species in different habitats, those birds which inhabit better quality foraging environments will be better able to meet their foraging needs and so will show a smaller mass response. This allows them to prioritize breeding activities around foraging without incurring fitness costs, so that they will produce better quality off spring and live longer as adults (MacLeod et al. 2007). Therefore across populations in different habitats the scale of the mass gain may give us an index of the demographics of bird populations in different habitats or of life history strategy as a consequence of food limitation across species in the same habitat.

**Table 1:** Mass variation in breeding birds in ten species of West African savannah bird, caught over a ten year period in Nigeria. For each species we tested for the effect the presence of a brood patch and month on mass (*P* values given), while controlling for the possible confounding effects of year, rainfall, body size, whether the bird was in active wing moult or not and in species where sexes were distinguishable in the hand, sex.

Species	<i>n</i> no brood patch	<i>n</i> brood patch	Mass* (g)	% mass increase in birds with brood patches*	% difference between months of max. & min. mass*	Brood patch ( <i>P</i> -value)	Month ( <i>P</i> -value)	Sex ( <i>P</i> -value)	Guild
Yellow-fronted tinkerbird	233	109	10.9 ± 0.7	2.7 ± 2.9	8.0	0.0008	0.002	-	Frugivore
Yellow white-eye	207	64	9.5 ± 0.7	3.2 ± 2.0	7.3	0.009	0.7	-	Frugivore
Variable sunbird	298	14	6.1 ± 0.5	8.2 ± 2.1	11.7	0.006	0.001	<0.0001	Nectivore
Scarlet-chested sunbird	354	20	10.6 ± 1.0	4.4 ± 1.5	7.9	0.008	<0.0001	<0.0001	Nectivore
Red-cheeked cordon-bleu	572	196	9.7 ± 0.8	3.6 ± 0.7	9.4	<0.0001	<0.0001	<0.0001	Granivore
Lavender waxbill	607	61	9.2 ± 1.2	5.0 ± 2.2	7.0	<0.0001	0.0001	-	Granivore
Red-billed firefinch	502	182	8.7 ± 0.7	4.2 ± 0.8	9.0	<0.0001	<0.0001	0.05	Granivore
Rock firefinch	438	117	10.3 ± 0.9	5.3 ± 1.0	10.6	<0.0001	<0.0001	0.4	Granivore
Black-faced quailfinch	120	10	10.8 ± 0.7	6.4 ± 2.5	8.3	0.01	0.003	0.06	Granivore
Cinnamon-breasted rock bunting	282	32	14.0 ± 1.1	7.2 ± 1.4	9.8	0.0001	0.001	0.8	Granivore

\* Values calculated from the parameter estimates.

**Table 2:** Mass variation in birds with brood patches in males and females of five species of West African savannah bird. For each species and sex we calculated the expected mean mass change in birds with brood patches and the maximum difference in mass between seasons in a year from the parameter estimates of the model  $\text{mass} \sim \text{brood patch} * \text{sex} + \text{sex} * \text{season} + \text{wing} + \text{rainfall} + \text{moult}$ .

Species	Sex	<i>n</i> no brood patch	<i>n</i> brood patch	Mass* (g)	% mass change in birds with brood patches*	% difference between seasons of max. & min. mass*
Scarlet-chested sunbird	Female	181	15	9.7 ± 0.7	6.1 ± 0.5	3.5
( <i>Chalcomitra senegalensis</i> )	Male	173	5	11.1 ± 0.7	4.0 ± 2.0	5.0
Variable sunbird	Female	144	12	6.0 ± 0.5	6.0 ± 1.5	4.5
( <i>Cinnyris venustus</i> )	Male	154	2	6.5 ± 0.5	0.2 ± 3.0	2.3
Red-cheeked cordon-bleu	Female	236	176	10.2 ± 0.9	4.7 ± 0.7	10.4
( <i>Uraeginthus bengalus</i> )	Male	336	20	9.9 ± 0.6	-4.2 ± 2.0	8.0
Red-billed firefinch	Female	202	151	8.7 ± 0.8	6.8 ± 0.9	6.7
( <i>Lagonosticta senegala</i> )	Male	300	31	8.8 ± 0.6	-2.2 ± 1.7	7.0
Rock firefinch	Female	172	90	10.4 ± 0.9	7.8 ± 1.0	5.1
( <i>L. sanguinodorsalis</i> )	Male	266	27	10.4 ± 0.7	2.4 ± 1.9	4.8

\* Values calculated from the parameter estimates.

Sample sizes of birds with brood patches were too small in sunbird species for robust analysis but the parameter estimates are included for comparison (*italics*)



**Table 3:** An ANOVA of the mixed effects models testing for mass variation across *months* in males and females a) across two species of sunbird (scarlet-chested sunbird; variable sunbird) b) across three species of finch (red-cheeked cordon-bleu; red-billed fire-finch; rock firefinch). We controlled for the possible confounding effects of egg production by excluding birds with brood patches from the analysis. We also controlled for possible year effects, rainfall, body size and whether a bird was in active wing moult or not. Species was included as a random factor.

Parameter	d.f.	F-value	P-value
a)			
Intercept ( <i>den df</i> 615)	1	31.3	<.0001
Sex	1	1.7	0.2
Month	11	2.9	0.0009
Year	9	2.7	0.004
Wing	1	69.0	<.0001
Wing moult	1	0.4	0.5
Rainfall	1	0.3	0.6
Month*sex	11	1.9	<b>0.04</b>
Species (Random)*	Intercept	10.8	Residual
b)			
Intercept ( <i>den df</i> 1474)	1	48.8	<.0001
Sex	1	5.8	0.0
Month	11	10.6	<.0001
Year	9	3.4	0.0
Wing	1	46.4	<.0001
Wing moult	1	0.8	0.4
Rainfall	1	0.1	0.8
Month*sex	11	9.3	<b>&lt;.0001</b>
Species (Random)*	Intercept	1.4	Residual

\* Where the intercept is the standard deviation of the variation across species and the residual is the standard deviation of the variation within species.

**Table 4:** An ANOVA of the mixed effects model testing for mass variation across the *seasons* in males and females across three species of finch (red-cheeked cordon-bleu; red-billed fire-finch; rock firefinch) in relation to the presence of a brood patch. We controlled for the possible confounding effects of year, rainfall, body size and whether a bird was in active wing moult or not. Species was included as a random factor. We model simplified by removing any non-significant interactions.

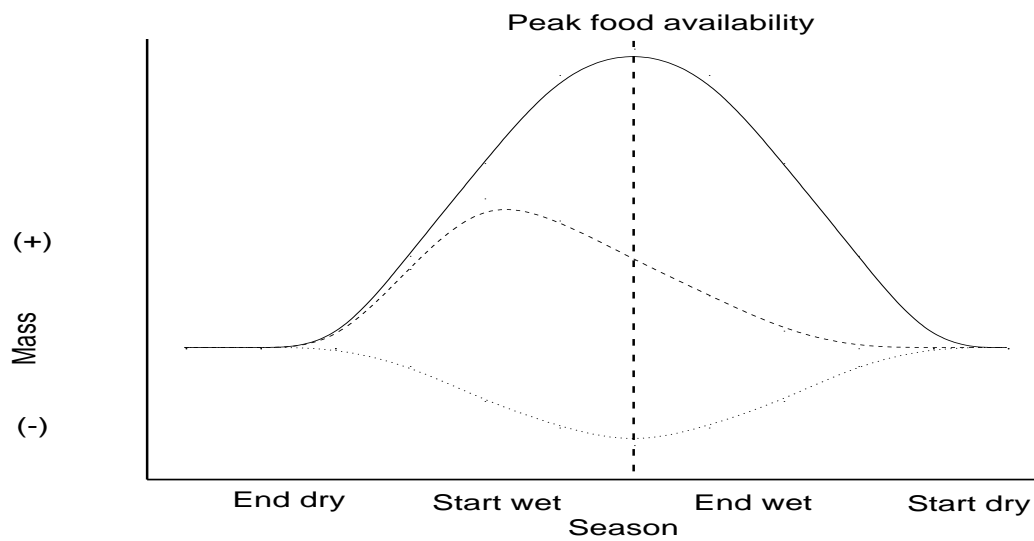
Parameter	d.f.	F-value	P-value
(Intercept <i>den df</i> 1983)	1	58.2	<.0001
Brood patch	1	51.9	<.0001
Sex	1	38.7	<.0001
Season	3	28.8	<.0001
Year	9	4.6	<.0001
Wing	1	52.9	<.0001
Wing moult	1	0.7	0.4
Rainfall	1	0.4	0.5
Sex*Brood patch	1	12.5	<b>0.0004</b>
Sex*Season	3	24.7	<.0001
Species (random)*	Intercept 1.7		Residual

\* Where the intercept is the standard deviation of the variation across species and the residual is the standard deviation of the variation within species.

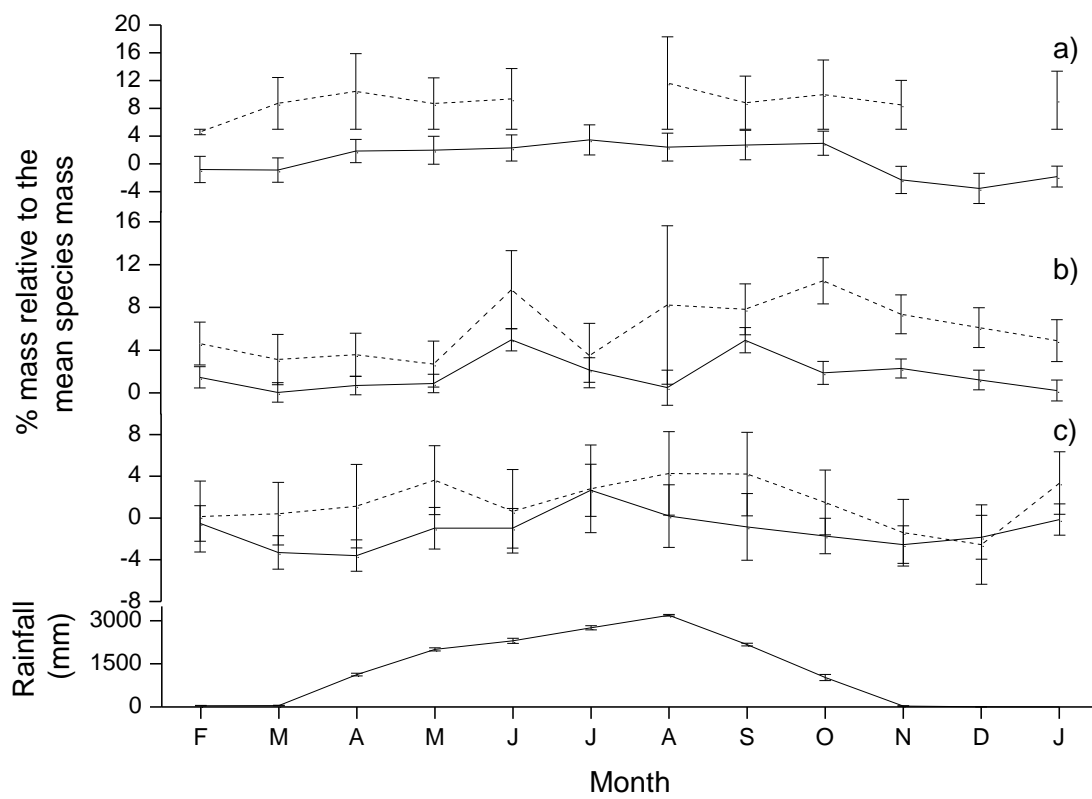
**Table 5:** ANOVA's of mixed effect models testing for variation in mass during brood patch development, of males and females; a) across three species of finch (red-cheeked cordon-bleu; red-billed fire-finch; rock firefinch), and b) across two frugivore species where sexes were indistinguishable in the hand (yellow-fronted tinkerbird; yellow white-eye). We controlled for the possible confounding effects of season, year, rainfall, body size and whether a bird was in active wing moult or not. Species was included as a random factor.

Parameter	d.f.	F-value	P-value
a)			
Intercept ( <i>den df</i> 1847)	1	50.1	<.0001
Brood patch score	5	29.0	<.0001
Sex	1	8.2	0.004
Season	3	9.7	<.0001
Year	9	5.5	<.0001
Wing	1	48.0	<.0001
Wing moult	1	0.5	0.5
Rainfall	1	0.03	0.9
Brood patch score*Sex	5	5.2	<b>0.0001</b>
Species (random)*	Intercept 1.7		Residual
b)			
Intercept ( <i>den df</i> 550)	1	39.1	<.0001
Brood patch score	1	5.2	<b>0.0001</b>
Month	11	2.1	0.1
Year	9	1.8	0.07
Wing	1	39.5	<.0001
Wing moult	1	0.1	0.8
Rainfall	1	0.5	0.5
Species (random)*	Intercept 1.4		Residual

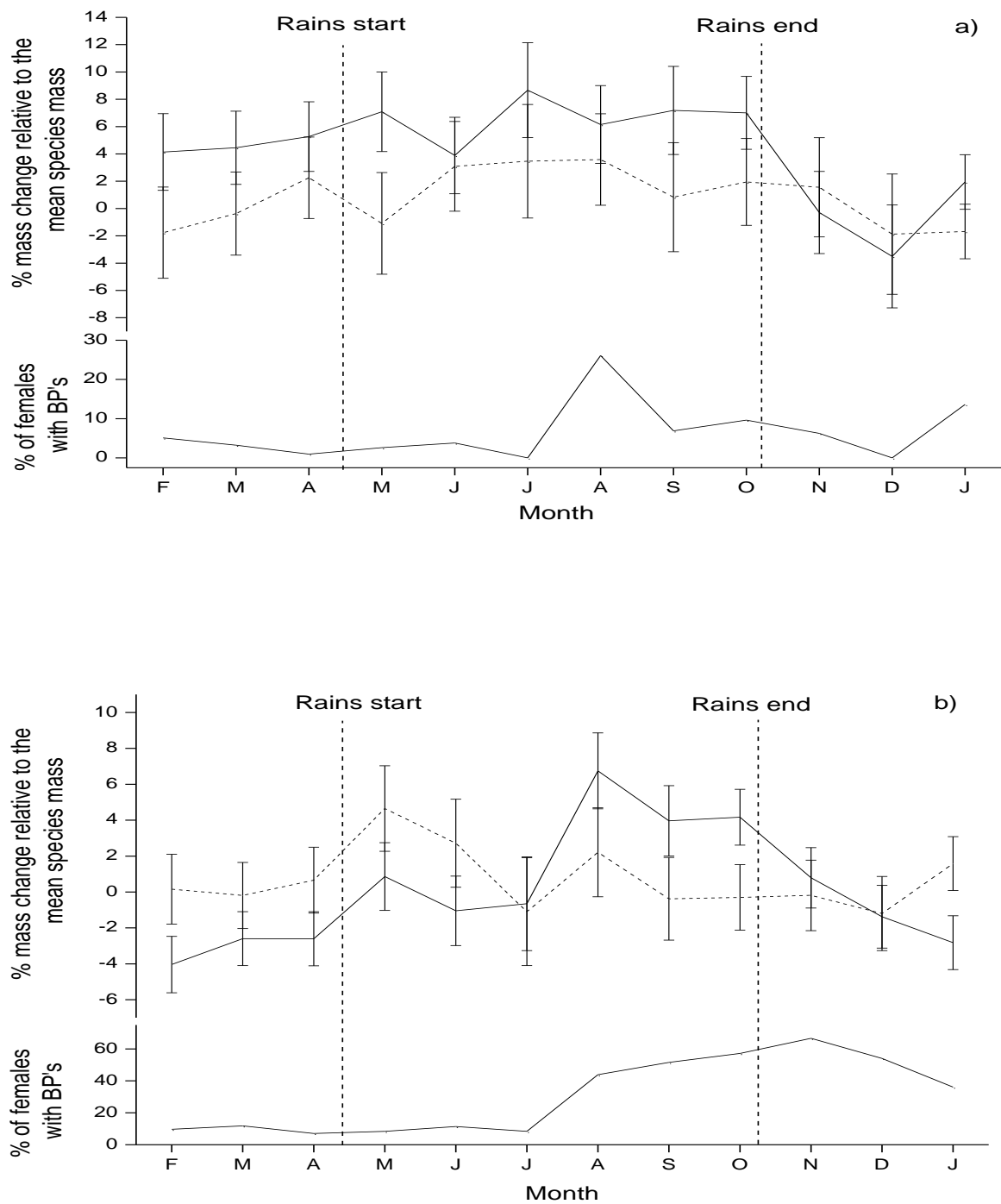
\* Where the intercept is the standard deviation of the variation across species and the residual is the standard deviation of the variation within species.



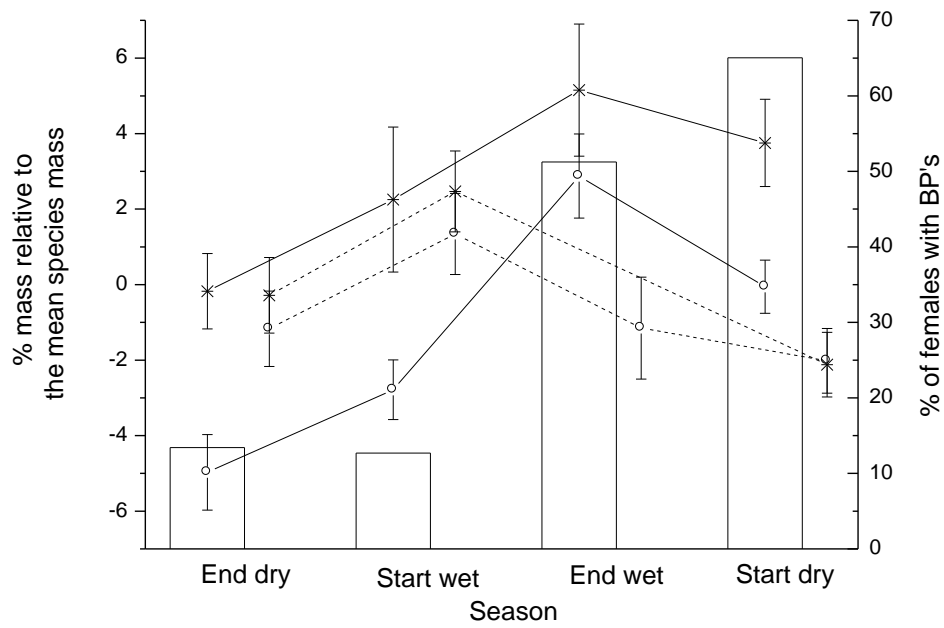
**Figure 1:** Theoretical model of how in the absence of any breeding effort the mass of either sex would decrease in response to increased food availability (dotted). If we consider breeding effort male (dashed) and female (solid) savannah birds will increase their mass in relation to sex specific investment. Therefore the actual mass in breeding birds will be a sum of the mass loss through increased food availability and the increase in mass due to an interrupted foraging response.



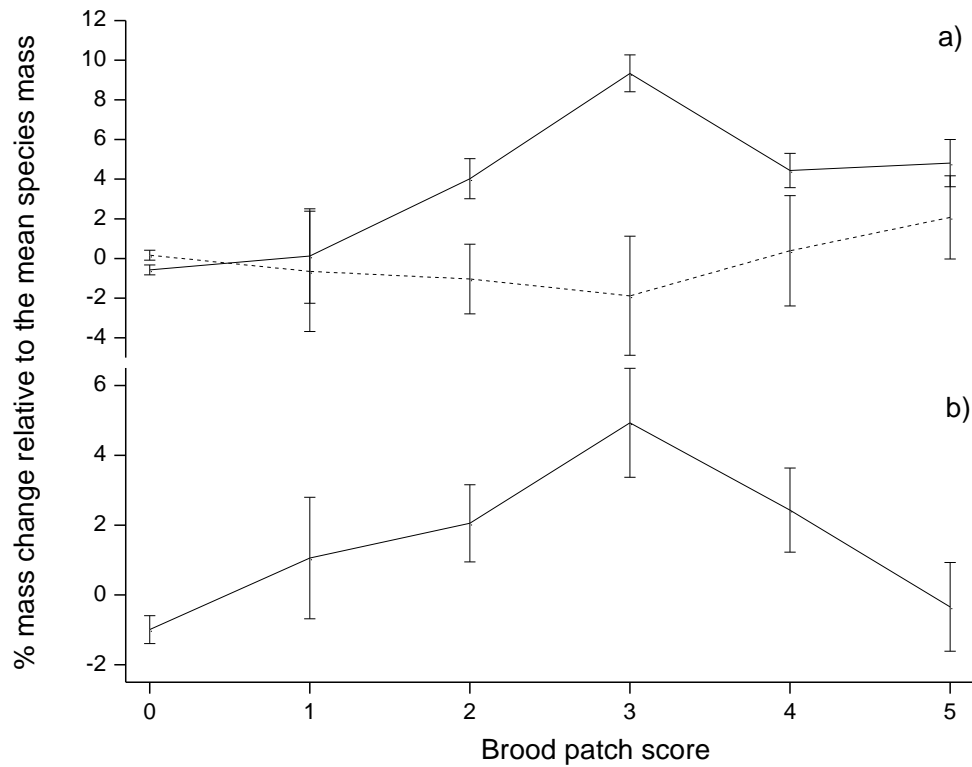
**Figure 2:** Monthly mass change in birds with (dashed) and without (solid) brood patches; a) across two sunbird species, b) across six species of finch, and c) across two frugivore species. Mean monthly rainfall (2002 – 2011) is also shown to demonstrate the general driver of these patterns.



**Figure 3:** *Monthly mass change in males (dashed) and females (solid) males without brood patches, a) across two species of sunbird and b) across three species of finch. The bottom graph shows the percentage of females caught with brood patches, as an indicator of the proportion of the population engaged in breeding activities.*

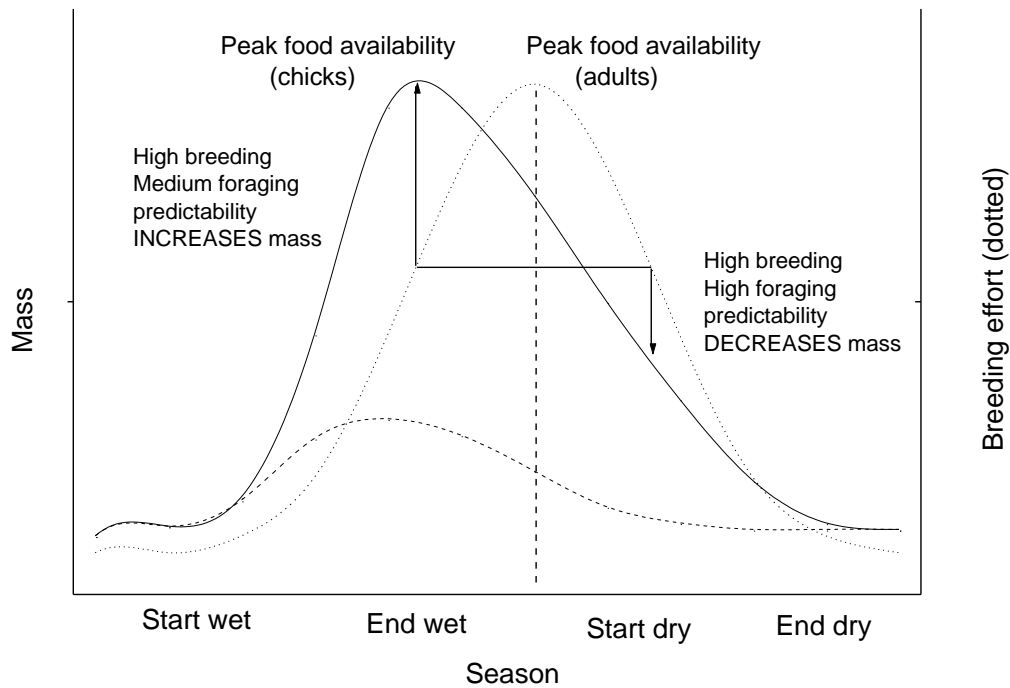


**Figure 4:** *Seasonal* mass change in incubating (solid, \*) and non-incubating (solid, o) females and incubating (dashed, \*) and non-incubating (dashed, o) males across three species of finch (red-cheeked cordon-bleu; red-billed fire-finch; rock firefinch), relative to the percentage of females caught with brood patches.



**Figure 5:** Mass variation during brood patch development across a) males (dashed) and females (solid) across three species of finch (red-cheeked cordon-bleu; red-billed fire-finch; rock firefinch), and b) two species of frugivore where sexes were indistinguishable in the hand (yellow-fronted tinkerbird; yellow white-eye).





**Figure 6:** Theoretical model of mass variation in females (solid) and males (dashed) across the year in relation to breeding effort (dotted). Food availability for chicks peaks at the end of the wet season, with the scale of the interrupted foraging response dependent on sex-specific investment. Then mass *decreases* despite an *increase* in breeding effort as food availability peaks for adults because foraging predictability increases. The lag between peak mass and peak breeding provides evidence that mass gain is also due to a bird regulating its mass through an interrupted foraging response and not solely due to gonad growth.

# **Chapter 5: Mass variation during breeding as an indication of food limitation and its consequences for adult survival**

## **Summary**

Levels of body reserves have been used as a proxy for survival in many studies because they reflect environmental variation and the degree to which an organism can buffer the consequent unpredictability of foraging. A universal source of increased foraging unpredictability is breeding, because animals become constrained in time and space (interrupted foraging), and have increased energy requirements. Animals consequently increase body reserves during breeding but this is dependent on the quality of the foraging environment, with higher levels of reserves being associated with poorer quality environments. This means that levels of body reserves should reflect life history which is a consequence of adaptation to the quality of the foraging environment. Species that are K selected exploit lower levels of predictable food availability and so are constrained during breeding by the absolute level of food resources and competition for them, whereas r selected species exploit super abundances of often unpredictable food availability and so are not so constrained. Therefore we would predict that, across species, there should be a positive relationship between survival and the level of mass reserves during breeding because this reflects life history adaptation to absolute food availability. We tested the direction of the relationship between levels of mass reserves gained during seasonal breeding and adult survival in 40 species of tropical bird collected over 10 years in a West African savannah, controlling for annual mass variation and variation in the timing of peak mass, clutch size, body size, guild, migratory status and phylogeny. We showed that species that had a greater seasonal mass increase had higher adult survival, supporting the hypothesis that life history determines the relative degree of the interrupted foraging response and so the relative level of body reserves during breeding. There was some evidence that those species which showed peaks in mass at different times in different years (i.e. breeding in response to unpredictable food availability) were less likely to survive as adults, further supporting the hypothesis. The

study shows that across tropical bird species the degree of seasonal mass variation is an indication of life-history adaptation and therefore survival.

## Introduction

Levels of body reserves have been used as a proxy for survival because they reflect environmental variation and the degree to which an organism can buffer the consequent unpredictability of foraging (e.g., Houston and McNamara 1993, Rogers and Smith 1993, Caro 2005, MacLeod et al. 2007). A universal source of increased foraging unpredictability is breeding, because animals become constrained in time and space (interrupted foraging), and have increased energy requirements. Many tropical (and possibly Southern hemisphere, (Rozman et al. 2003) bird species vary their mass across the year, decreasing their mass in the non-breeding season (e.g., Ward 1969, Fogden 1972, Fogden and Fogden 1979, Cox et al. 2011), because foraging may remain predictable (Sinclair 1978, Cox et al. 2011), and thus reducing mass-dependent energy requirements (Rogers and Heath-Coss 2003) and predation costs (Witter and Cuthill 1993). Species then commence breeding activities in anticipation of increased food availability, and birds will time the energy requirements of chicks to coincide with predictable seasonal food peaks (Martin 1987). Energetic expenditure increases during the breeding season (e.g., Anava et al. 2002, Hambly et al. 2007), at the same time activities such as mate guarding, territoriality, nest building, incubation and parental care conflict with the time available for foraging for self (i.e. interrupt foraging; Cox and Cresswell *in submission*). So despite an increase in food availability, foraging predictability may actually decrease during the breeding season, and so a bird increases its reserves through an interrupted foraging response, independent of any mass increase from egg or gonad growth (Cox and Cresswell *In submission*). Animals may increase body reserves during breeding but this is dependent on the quality of the foraging environment, with higher levels of reserves being associated with poorer quality environments (MacLeod et al. 2008).

If levels of body reserves reflect environmental quality then they should also reflect life history because this is also a consequence of adaptation to the quality of the foraging environment. Species that are K selected exploit lower levels of predictable food availability and so are constrained during breeding by the absolute level of food resources and competition for them (Ashmole 1963, MacArthur and Wilson 1967, Martin 1986, Martin 1987, McNamara et al. 2008). In tropical and southern hemisphere environments, if a bird is

unable to meet its foraging requirements it will prioritise its own future survival over that of its off-spring, with a loss in off spring fitness (Ghalambor and Martin 2001, Tieleman et al. 2008) and selection will favour those individuals that raise smaller broods (Ricklefs 1977, Roff 2002, McNamara et al. 2008). An increased investment in its own condition means that a bird has more flexibility in time and space as to when it can forage, and so can buffer fluctuations in environmental conditions and interruptions to its foraging (reviewed in Roff 2002), along with reducing physiological breeding trade-offs (Dufty Jr 1989, Hau et al. 2010), and so individuals are more likely to survival as adults, i.e. are more K selected. Therefore selection acts on individuals who prioritise their own foraging needs over breeding costs; trading off the reduced investment in each breeding attempt with longer parental care and thus increased survivorship of juveniles. In contrast, r selected species exploit super abundances of often unpredictable food availability and so are not so constrained during breeding by availability of food. Larger seasonal peaks in food availability mean that parents can meet their own foraging needs and successfully raise larger broods when conditions allow, and so selection favours more young but at a cost to adult survival, probably through reduced immunocompetence (Sinervo and Svensson 1998, Wingfield et al. 2001) and increased susceptibility to fluctuations in environmental conditions (Bennett and Owens 2002).

Therefore we would predict that, across species, there should be a positive relationship between survival and level of mass reserves during breeding because this reflects life history adaptation to absolute food availability. Those species that inhabit a less seasonal foraging environment with reduced seasonal peaks in food availability will have reduced foraging success during breeding (Thiollay 1988) and so species will show an increased interrupted foraging response (MacLeod et al. 2008). 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), will adopt a more r selected life history (Ghalambor and Martin 2001, Peach et al. 2001, McNamara et al. 2008).

We tested whether there was a positive correlation between levels of mass reserves gained during seasonal breeding and adult survival in 40 species of tropical bird collected over 10 years in a West African savannah, controlling for annual mass variation and variation in the timing of peak mass, clutch size, body size, guild, migratory status and phylogeny.

## 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. Details of survival estimation are given in Stevens et al. (in press), but in summary survival estimates were calculated for 40 species (6939 individuals, 2099 recaptures) caught in Amurum between January 2000 – December 2008 (Table 1). Analysis of survival was performed using the general methods of capture-mark-recapture modelling outlined by Lebreton et al. (1992). The data were analysed with the program MARK (White and Burnham 1999); using standard time-dependent, time-since-marking models (TSM) and Cormack-Jolly-Seber (CJS) models. Goodness of fit tests were 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 47 species (13,353 individuals) were caught in Guinea savannah in Amurum and Yankari, between November 2000 – March 2011 (Table 1). 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; time of day was not found to be an important predictor because almost all data were collected early in the morning. 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, using the annual parameter estimates of mean mass across years from models for each species without the SY interaction (2001 and 2011 were excluded because yearly data

were incomplete). 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.

In this analysis we also control for the potential confounding effects of other life history trade-offs (see Bennett and Owens 2002) by including clutch size because this has been shown to correlate with survival, so that species with larger clutch sizes tend to be more r selected (e.g., Saether 1988, Peach et al. 2001). 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 having the largest sample sizes that were geographically closest to our study area. Species were assigned to feeding guilds according to diet (Fry et al. 1992-2004). We also control for any confounding effects of guild and migratory status because these will change the degree of environmental certainty for different species under the same set of environmental conditions. Granivores for example, may experience higher levels of seasonal unpredictability in food supply than insectivores and so may compensate for decreased predictability by increasing fecundity at a cost to adult survival (Lloyd 1999). Similarly transient species might buffer variation through movement to track resources rather than body reserves as in sedentary species, so that transient species may favour K selection, being limited more by density-dependent factors (Boyce 1984). 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). We also control for body mass, which correlates positively with survival in birds (Saether 1989, Jeschke and Kokko 2009), and because larger animals have different costs of acquiring and maintaining reserves (Witter and Cuthill 1993).

### *Statistical analysis*

We ran a general linear mixed model testing for relationships between survival and all the predictor and potentially confounding variables. Mass variation within (S), and across (Y) years were included as covariates. Individual parameter estimates for the variation in the annual timing of mass change (the interaction between seasonal mass gain pattern and year, variable peak mass, SY) 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, feeding guild (g), migratory status (m) and body size (b).

Closely related species may share characteristics through common descent and are therefore not statistically independent (Harvey and Pagel 1991). To account for possible non-independence of variables across species, and for an increased level of variance in the model (Jeschke and Kokko 2009) 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 survival, by dropping each from the full model, 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:  $\text{survival} \sim S + Y + SY + \text{clutch size} + b + m + g + (\sim 1 | \text{family \%in\% order}), \text{weight} = "n"$ .

## Results

There was a positive correlation between survival and seasonal mass variation across species controlling for the degree of environmental predictability, body size and phylogeny (an increase in survival of 0.91% for every 1% increase in seasonal mass variation, Table 2, Fig. 1). There was no correlation between survival and annual mass variation (Table 2). Species which showed significant variation in the timing of the seasonal mass peaks between years had significantly lower 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; Fig. 2). However, this result was dependent on weighting the model by sample size (without weighting,  $F = 0.2$ ,  $P = 0.7$ ). We also reconfirmed the negative relationship between clutch size and survival (survival decreased by 6% for every 1% increase in clutch, Table 2). Neither, migratory status nor feeding guild, significantly affected survival and were subsequently removed from the minimal adequate model.

## Conclusion

We show that across tropical bird species, in the same habitat, the degree of seasonal mass variation acts as an indication of adult survival and therefore life-history adaptation. Those species which showed an increased mass response during breeding were more likely to survive as adults (Fig. 1), while species which varied their mass at different times in different

years had lower adult survival (Fig. 2). These results are consistent with the hypothesis that increased foraging unpredictability leads to increased mass as a result of the adaptive management of energy reserves.

In a highly seasonal savannah environment, as in this study, there is not a period of high density-dependent mortality which 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 McGregor et al. 2007; Stevens et al. 2012). 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 (Ashmole 1963, Martin 1986, Martin 1987). Therefore birds will experience reduced foraging predictability around breeding activities and so will store more reserves against this increased starvation risk. Selection may then favour those individuals that invest less in each breeding attempt (i.e. smaller broods) but over a longer period (i.e. extended parental care). This affects survival because an increased investment in self maintenance decreases the physiological (Dufty Jr 1989, Richner et al. 1995, Hau 2007) and energetic (McNamara and Houston 2008) costs and gives increased insurance against fluctuations in the foraging environment (Rogers 1987). Consequently birds are more likely to survive as adults. Therefore species which showed an increased interrupted foraging response in this study tended to be more K selected (Fig. 1).

In contrast, those species that rely on a more seasonal food source, such as specialized seed eating finches, probably experience a period of increased density-dependent mortality during the non-breeding season (Peach et al. 2001, Cox and Cresswell *In submission*). During the breeding season however, food availability may far exceed carrying capacity, which will affect life history through its effects on provisioning rates, nest predation and chick growth rates (Tveraa et al. 1998, Markman et al. 2002). Consequently larger clutch sizes can evolve (e.g., Ricklefs 1980), which has negative implications for adult survival. Increased food availability both leads to a decreased mass response as a bird can meet its foraging needs and also its higher breeding costs, although some of these will be offset by lower adult survival.

We found evidence that where peak mass occurred at different times in different years, mass variation was associated with lower adult survival (16% lower, see Fig. 2). This suggests that these species rely on a food source which varies in predictability across the years. Species



with a greater unpredictability of foraging will be less likely to survive as adults and so need to produce more young when conditions allow, as predicted by life-history theory (MacArthur and Wilson 1967, Pianka 1970). Many finch species breed opportunistically (e.g., Zann et al. 1995, 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 *r* selection.

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 off-spring fitness and not adult survival (Ghalambor and Martin 2001, Markman et al. 2002, Tieleman et al. 2008). We predict that those years which have increased food availability are likely to show a reduced level of mass increase (MacLeod et al. 2008) and probably increased juvenile survival (Markman et al. 2002), because foraging will be more predictable. Therefore the scale of the interrupted foraging response either within a population across the years or across populations, may act as an index of the quality of the foraging environment and so population productivity for that year (MacLeod et al. 2008).

### *General conclusions*

We provide evidence to support the generality of interrupted foraging theory as a single explanation of how animals regulate their mass under changing 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 (Abrams 1984, McNamara and Houston 1987, Bolker et al. 2003, Cresswell 2008, MacLeod et al. 2008). 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. 2009b). 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 in the breeding season (e.g., Houston and McNamara 1993, Witter and Cuthill 1993, Gosler et al. 1995) and more likely to be limited in the non-breeding season. In tropical environments the reverse may apply for many *K* selected species. 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. If food is a limiting factor through low availability and increased competition, then selection will favour smaller clutch sizes and consequent increased investment in promoting juvenile survival through extended parental care, as well as longer life spans for adults.

The positive relationship between adult survival and mass variation provides empirical evidence to support recent theoretical models which 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). Variance within this relationship may be due to varying levels of species specific nest predation or varying length of breeding seasons within the same habitat, for example: increased levels of nest predation or the fear of nest predation may cause smaller broods (Martin 1996, Martin 2011) and may vary considerably between years and species (Robinson et al. 2000). Our results support the hypothesis that within the starvation-predation framework, how a bird regulates its mass is a trade-off between foraging predictability and conflict with life history activities (Cox and Cresswell *In submission*). Determining how an individual balances its foraging needs (i.e. mass regulation) while maximising its fitness in a changing environment can act as an index of both life history strategies and the seasonality of a species' foraging niche. Although this study supports previous work in the northern hemisphere in that across species within the same habitat mass can act as a reliable indicator of environmental quality and population dynamics (Lima 1986, MacLeod et al. 2007), further work is needed to gather empirical data on the seasonality of food availability for a range of species. For example: how at an individual level does this relate to the scale of the interrupted foraging response and trade-offs between life history traits, such as adult and juvenile survival, nest predation, fecundity, brood sizes, and the length of the breeding season.

**Table 1:** Life history data of 40 species of West African savannah bird.

Species	<i>n</i> survival (recaptures)	Survival	Clutch	<i>n</i> mass	% Seasonal mass change	% Annual mass change	S Y	Mean mass (g)	Migratory status	Guild
<b>COLUMBIFORMES Columbidae</b>										
<i>Turtur abyssinicus</i>	68 (44)	0.606	2	230	9	34	0	60.8	R	G
<b>COLIIFORMES Coliidae</b>										
<i>Colius striatus</i>	223 (95)	0.619	1.9	298	12	10	1	52.3	R	F
<b>PICIFORMES Capitonidae</b>										
<i>Pogoniulus chrysoconus</i>	186 (134)	0.416	2.5	239	3	7	0	10.8	T	F
<i>Lybius vieilloti</i>	36 (33)	0.599	2.5	65	17	9	0	36.7	R	F
<b>PASSERIFORMES Pycnonotidae</b>										
<i>Pycnonotus barbatus</i>	311 (111)	0.668	2	614	12	30	1	37.6	R	F
<i>Chlorocichla flavicollis</i> *	34 (24)	0.844	2	49	14	23	0	50.7	T	I
<b>Turdidae</b>										
<i>Turdus pelios</i>	190 (87)	0.799	2.4	516	8	7	0	65.2	T	I
<b>Muscicapidae</b>										
<i>Cossypha niveicapilla</i>	80 (75)	0.779	2.5	176	1	12	0	36.6	R	I
<i>Cercomela familiaris</i>	45 (37)	0.539	3	117	11	13	0	17.2	T	I
<i>Myrmecocichla cinnamomeiventris</i>	41 (11)	0.657	2	63	17	16	0	39.5	R	I
<b>Sylviidae</b>										
<i>Melocichla mentalis</i> *	24 (17)	0.948	2	37	11	12	0	33.2	R	I
<i>Eremomela pusilla</i>	33 (21)	0.586	2	70	7	23	1	8.6	T	I
<i>Sylvietta brachyuran</i> *	32 (31)	0.875	2	60	2	6	0	13.8	R	I
<b>Cisticolidae</b>										
<i>Camaroptera brachyura</i>	137 (168)	0.636	2.7	226	8	5	0	10.9	R	I
<i>Cisticola aberrans</i>	30 (29)	0.650	2.5	85	4	11	0	13.4	R	I
<i>Cisticola cantans</i> *	57 (28)	0.806	2	60	8	4	0	11.5	T	I
<i>Cisticola guinea</i> *	39 (26)	0.510	3	39	15	26	0	9.0	R	I
<b>Platysteiridae</b>										
<i>Platysteira cyanea</i>	51 (53)	0.700	3	94	27	21	0	11.7	R	I
<b>Zosteropidae</b>										
<i>Zosterops senegalensis</i>	152 (55)	0.527	2.5	241	2	7	0	9.5	R	F
<b>Nectarinidae</b>										

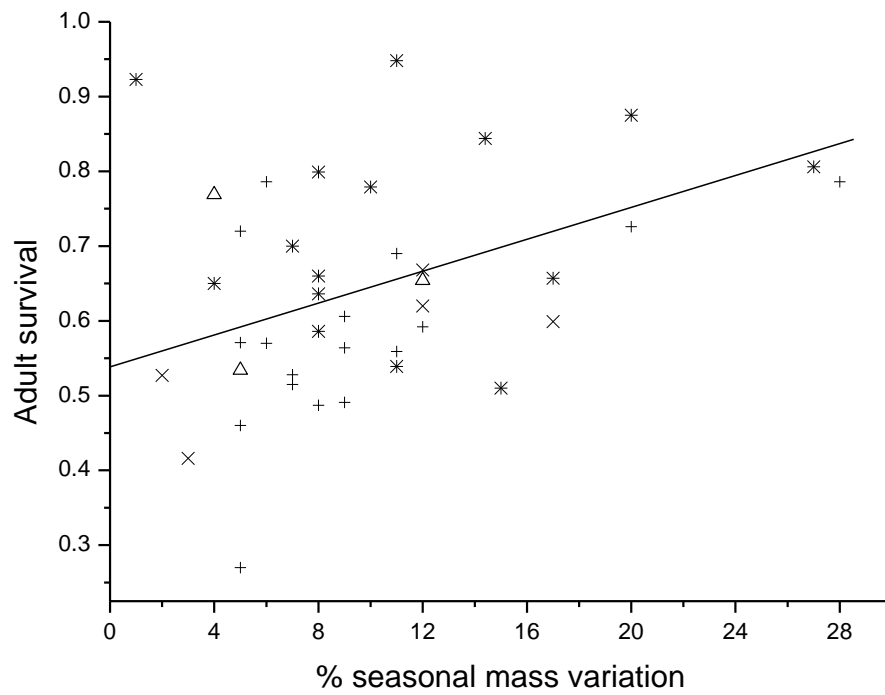
<i>Cyanomitra verticalis</i>	87 (80)	0.654	2	130	12	4	0	12.4	R	N
<i>Chalcomitra senegalensis</i>	202 (62)	0.769	2	476	4	7	0	10.3	T	N
<i>Cinnyris venustus</i>	206 (42)	0.534	2	354	5	9	0	6.3	R	N
<b>Malaconotidae</b>										
<i>Malaconotus sulfureopectus</i> *	25 (14)	0.923	1.8	46	10	21	0	28.7	R	I
<i>Tchagra senegalus</i> *	41 (24)	0.660	2	58	8	30	1	51.1	T	I
<b>Passeridae</b>										
<i>Sporopipes frontalis</i>	62 (41)	0.592	4	62	12	14	0	17.0	R	G
<b>Ploceidae</b>										
<i>Ploceus cucullatus</i>	301 (34)	0.694	2.3	738	11	9	1	36.6	R	G
<i>Ploceus luteolus</i>	45 (26)	0.487	2.5	147	8	8	0	14.5	R	G
<i>Ploceus nigricollis</i>	116 (63)	0.786	2	209	6	9	0	26.5	T	G
<i>Ploceus vitellinus</i>	205 (76)	0.726	2.4	284	20	14	0	20.2	R	G
<i>Euplectes franciscanus</i>	1252 (360)	0.720	3	1762	5	8	1	15.2	T	G
<i>Euplectes hordeaceus</i>	165 (47)	0.786	3	169	28	15	0	20.0	T	G
<b>Estrildidae</b>										
<i>Estrilda caerulea</i>	378 (326)	0.566	5	530	6	16	1	9.3	T	G
<i>Estrilda troglodytes</i>	136 (24)	0.571	5	149	5	24	0	7.6	T	G
<i>Uraeginthus bengalus</i>	498 (226)	0.456	4.7	692	5	10	0	10.1	T	G
<i>Lagonosticta rufopicta</i>	62 (38)	0.564	4.5	113	9	10	0	9.3	R	G
<i>Lagonosticta rara</i>	34 (26)	0.528	3.5	84	7	7	0	9.8	T	G
<i>Lagonosticta sanguinodorsalis</i>	305 (300)	0.559	4	480	11	8	1	10.5	R	G
<i>Lagonosticta senegala</i>	400 (137)	0.515	3.4	763	7	18	0	8.7	T	G
<i>Spermestes cucullatus</i>	424 (43)	0.269	5	768	5	8	1	8.9	T	G
<b>Emberizidae</b>										
<i>Emberiza tahapisi</i>	226 (31)	0.491	2.6	361	9	9	0	13.5	T	G

*Note:* Seasonal mass variation varied significantly with year (SY; 1 yes, 0 no). 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. We identified species guilds from the literature: I insectivore, F frugivore, N nectivore, G granivore. Transient status (T) was identified over resident status (R) by a >50% change in capture rate between dry and wet seasons.

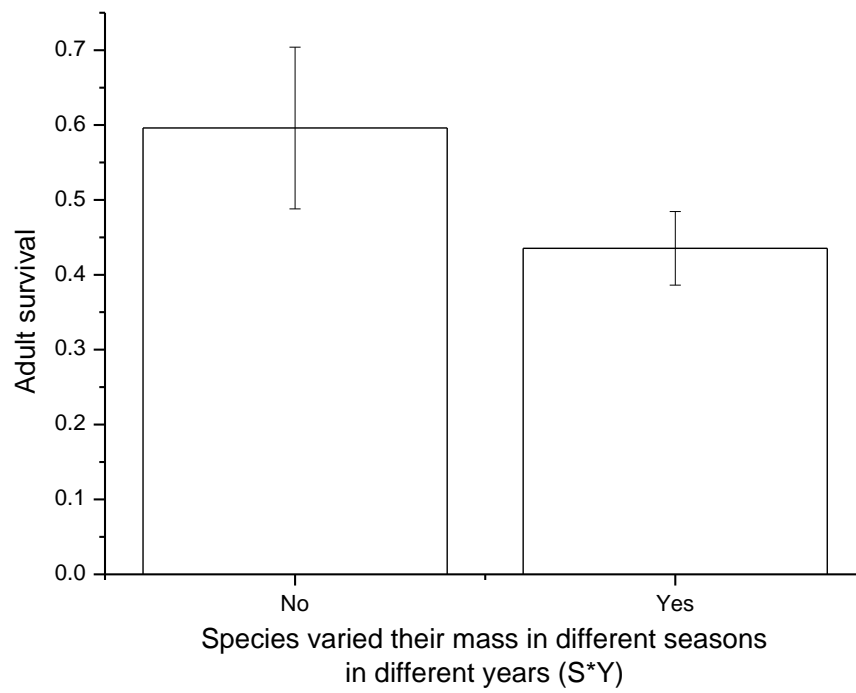
**Table 2:** ANOVA of the minimum adequate model testing for relationships with adult survival. Each variable was dropped from the model in turn, before applying a likelihood ratio test.

<b>Variable</b>		<b>estimate</b>	<b>error</b>	<b><i>t</i></b>	<b><i>P</i></b>
Intercept	( <i>df</i> 20)	0.75	0.11	6.9	<b>&lt;0.0001</b>
Seasonal mass		0.91	0.29	3.1	<b>0.005</b>
Annual mass		0.17	0.25	0.7	0.52
Variable peak mass		-0.14	0.05	-3.0	<b>0.007</b>
Clutch size		-0.07	0.03	-2.7	<b>0.01</b>
Mean mass		-0.0007	0.001	-0.6	0.54

*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. Migratory status and feeding guild were both removed from the model through model simplification.



**Figure 1:** Relationship between adult survival and seasonal mass variation by feeding guild in 40 species of small tropical savannah bird: X Frugivore; \* Insectivore; Δ Nectivore; + Granivore. Parameter estimate =  $0.91 \pm 0.29$ ,  $t = 0.31$ ,  $p = \mathbf{0.005}$ .



**Figure 2:** Relationship between species which varied their peak mass at different times in different years (included in the model as a two level factor) and adult survival. The model was weighted by sample size.

## Chapter 6: Concluding discussion

### Seasonal mass variation as a consequence of food limitation during breeding

Under constant predation risk a bird's mass acts as an index of the foraging environment, because a decrease in foraging predictability will cause a bird to increase its reserves against the increased risk of starvation. Breeding activities increase energetic expenditure and interrupt the time available for foraging for self and so foraging becomes less predictable. How a bird manages its mass during breeding can either be an index of investment in breeding in individuals in the *same* foraging habitat, or it can give an indication of breeding strategy and life history in populations across *different* foraging habitats. This thesis provides clear evidence that birds adaptively manage their mass during breeding and that mass change is not a response to the physiological stress of provisioning for chicks. Furthermore, this thesis provides support for food limitation being the main driving force behind patterns of life history variation, with variance around the predicted upper limits set by food limitation probably being set by other factors such as levels of nest predation and length of the breeding season which were not explored here. This thesis shows that how an individual manages its mass acts as a bridge between population dynamics, foraging theory and life history, and that the mass of a bird can be seen to provide an index of how a bird maximises its fitness in a changing environment.

### Tropical savannahs as model systems

The tropical savannahs of West Africa act as model systems for studying the effects of seasonality on life history, because they are highly seasonal environments where day length and temperature remain relatively constant, and so how a bird experiences seasonality will depend largely on its particular foraging niche (Peach et al. 2001). A broad range of K to r selected species within the same environment provides an increased understanding of the selective pressures of food limitation on the evolution of life history traits.

Close to the equator the absence of the universal driving evolutionary force of winter means that seasonality is driven primarily by the predictable annual movement of the rains, which cause increases in primary productivity and consequently invertebrate populations (Bourlière and Hadley 1970, de Bie et al. 1998). As day length and temperatures remain relatively



constant how a species experiences seasonality will largely be determined by variation in its essential resources such as food and water availability for itself and its off-spring (Ahumada 2001, Peach et al. 2001). The savannahs of West Africa are an ideal system for studying the effects of seasonality on life history, because there is only one wet season annually, the timing of which remains relatively predictable across the years (Bourlière and Hadley 1970). The single dry and the wet season each consist of distinctly different resource availability and species will have evolved to maximise their fitness across this changing environment. Specifically, Amurum Forest Reserve consists of a mosaic of four main habitat types (inselberg, gallery forest, degraded Guinea savannah, farmland) within a relatively small area (~4 hectares), thus providing a heterogenic landscape capable of supporting diverse communities of species.

An increase in species diversity means that many species have evolved to specialise in specific foraging niches, because where there is high competition for resources it is beneficial to outcompete competitors for a specific food type (Martin 1986). Therefore density-dependence results in seasonality not only being determined by the total food available but also by seasonal variation in competition for it. Savannah communities are dynamic with many species consisting of both transient and sedentary populations, therefore some populations may experience reduced seasonality because although the rains drive a significant increase in primary productivity, competition may increase proportionately and will likely influence life history through variation in foraging predictability. While species which inhabit a more seasonal environment may not be constrained in the same way as food becomes super-abundant. This makes tropical savannahs ideal systems for disentangling how life history traits evolved in response to seasonality.

### **Seasonality is dependent on a species' foraging niche**

Within a tropical savannah, if how a species experiences seasonality is largely to do with its foraging niche then we can expect a wide range of r to K selected species, which is what we find (Peach et al. 2001, McGregor 2005, Stevens 2010). At one end of the continuum there are specialized seed eating finches which are characterised by having large clutch sizes and low rates of adult survival. These are comparable with species in the Northern hemisphere (i.e. r selected). These species rely on the seasonal grain crop and the availability of free standing water to aid digestion of seeds, both of which go from negligible to superabundant

across the seasons (Peach et al. 2001, Brandt 2007). Therefore food availability and subsequently the breeding season will be limited to more rapid breeding attempts in response to predictable and unpredictable peaks in food availability (Zann et al. 1995, Grant et al. 2000). A period when resources are constrained means that there are more resources available per individual when food availability increases, allowing parents to support larger broods, which consequently has negative implications for adult survival. However, within these r selected species, the predictability of foraging for self-maintenance during breeding becomes predictable as the seed crop ripens and falls (food does not have to be caught and is abundant) despite an increase in energy expenditure and the demand for food associated with larger broods, so that these species can reduce their mass during breeding.

Conversely, specialised insectivorous species such as the sulphur breasted bush-shrike *Malaconotus sulfureopectus*, have high survival and small clutch sizes (i.e. K selected; Stevens 2010). These species forage on small and medium sized insects in the canopy and so individuals are likely to face quite different levels of foraging predictability which will be defined not only by the abundance of food and competition for it, but also by the time required to find, capture and process their prey (Martin 1986, Ahumada 2001). During the non-breeding season birds reduce their energy expenditure and there is sufficient food available to forage opportunistically. Because of density-dependence a reduction in the seasonality of food availability means that mortality will be reduced during the non-breeding season and so populations may stay closer to their carrying capacity. Therefore during breeding there will be fewer resources available per individual. Consequently the increased demand for food due to an increase in energy expenditure associated with breeding, and an increase in population size as young birds fledge, may mean that density-dependent mortality acts more strongly during the breeding season and so parents provide longer parental care in order to increase the competitive ability of fledged young. The unpredictability of foraging during breeding probably remains high throughout so resulting in increased mass reserves.

### **Seasonal mass variation in savannah birds**

Within the starvation vs. predation trade-off framework a birds' mass is the result of foraging predictability, where foraging predictability is a function of food availability, risk of predation while obtaining food, competition for food (density-dependence), and interruptions to the time available for foraging from say a predator, severe weather event or breeding

activities. If predation risk remains relatively constant across the year, and if a bird is not starving then a bird's mass will be a trade-off between food availability and interruptions to the bird's foraging which may occur due to life history events such as breeding or in preparation for migration. There was evidence that for most species foraging remained predictable throughout the year, because most species maintained a low mass and so avoided mass dependent costs and this may be a common strategy generally in the tropics (Ward 1969, McNeil 1971, Fogden 1972, Crowe et al. 1981, Crick and Fry 1986, Brown and Bhagabati 1998, Wikelski et al. 2000, Cox et al. 2011) and in the Southern hemisphere (Box et al. 2002, Rozman et al. 2003). There was also evidence that some individuals of two thirds of the species studied (68%) were capable of breeding in all four seasons, despite most individuals breeding during a specific period of increased food availability. This suggests there must be sufficient food available to instigate breeding activities without a risk of starvation to the female (Perrins 1970, Martin 1987). If a bird's mass is a function solely of food availability then we might have predicted that a bird would further decrease its mass with an increase in food availability. However, independent of egg production or gonad growth this thesis shows that birds actually increase their mass, which provided an opportunity to investigate mass variation in response to trade-offs during breeding. Only finch species were found to gain mass as a possible response to unpredictable food availability at the start of the rains which provided evidence of the increased seasonality experienced by this feeding guild. However, some individuals were still capable of successfully fledging young at this time despite an increased mass associated with reduced food availability, thus highlighting the opportunistic nature of this solely tropical family (Grant et al. 2000, Hau et al. 2004, Perfito et al. 2007).

### **Birds adaptively manage their mass during breeding**

Adaptive management of mass by birds in the non-breeding season is now well established (Rogers 1987, Houston and McNamara 1993, Rogers and Heath-Coss 2003, MacLeod et al. 2007, MacLeod et al. 2008), but there is still debate over whether a bird adaptively manages its mass during breeding (Norberg 1981, Croll et al. 1991, Merkle and Barclay 1996, Wojczulanis-Jakubas et al. 2012), or whether a bird's mass is a response to food limitation and physiological stress, known as the Energetic Stress Hypothesis (Ricklefs 1974, Johnson et al. 1990, Martins and Wright 1993, Merila and Wiggins 1997, Woodburn and Perrins 1997, Nagy et al. 2007), or possibly a combination of both (Neto and Gosler 2010). This

thesis provides clear support for the growing body of evidence which shows that birds adaptively manage their mass during breeding.

During the breeding season in the Northern hemisphere, many birds, particularly females, are heaviest during incubation before losing mass whilst they are feeding chicks (Ricklefs 1974, Hillstrom 1995, Merkle and Barclay 1996, Cavitt and Thompson 1997, Woodburn and Perrins 1997). However, this has previously been viewed from the perspective of a mass decrease relative to the much larger mass gain caused by poor foraging conditions in winter. Instead, if mass variation during breeding is viewed from the perspective of a mass increase relative to predictable foraging in the non-breeding season as is the case in many tropical and Southern hemisphere species (e.g., Fogden 1972; Rozman *et al.* 2003), then interrupted foraging provides a universal explanation for seasonal mass change. For example, breeding birds which were given more supplementary food lost less mass than control birds (i.e., smaller interrupted foraging response) because foraging was more predictable and therefore birds did not need to store increased reserves, although previously this was attributed to the energetic stress hypothesis (Garcia *et al.* 1993, Nagy *et al.* 2007). Interestingly, the presence of supplemented food during breeding does not always result in a reduction in mass. Instead the availability of an predictable food source means that a bird needs to spend less time searching for food, thus allowing it to dedicate more time to other breeding activities such as surveillance and mate guarding, and so birds actually increase their mass to compensate for the allocation of resources to other activities (Arcese 1989). Therefore predictions of mass consequences are problematic because foraging predictability directly affects how an individual-apportions its available resources to different activities.

Neto and Gosler (2010) examined variation in four indices of body condition; pectoral muscle, fat score, weight and lean weight in a breeding population of Savi's warbler *locustella luscinioides*, in Portugal. They argue that variation in mass was adaptive if they involved changes in fat that can be rapidly metabolised, whereas physiological stress should influence muscle score to a greater extent because muscle is a less efficient store of energy. They found that both males and females recovered fat reserves after each breeding attempt and thus showed evidence of adaptive management. They also observed a reduction in pectoral muscle mass across the breeding season that corresponded to increasing numbers of breeding attempts, and suggest that this was evidence of physiological stress. However, measures of fat scores have often been confounded in tropical species, because there is frequently little or no visible surface fat (Ward 1969, Fogden 1972, McGregor 2005), and this

was also found to be the case in this study. However, dissection of individuals has shown that males and females do vary their fat and protein reserves during breeding (McNeil 1971, Jones and Ward 1976, Fogden and Fogden 1979), and this also appears to also be the case in Zebra finches in the Southern hemisphere (Rozman et al. 2003). Individuals increased pectoral muscle with the onset of breeding, before then decreasing muscle mass through the breeding season (Ward 1969, Fogden 1972), while fat reserves increased directly before egg laying (Jones and Ward 1976, Fogden and Fogden 1979). This suggests that the larger increase in mass with the onset of the breeding season observed in this study maybe due to increases in pectoral muscle. While the further smaller mass increase associated with incubation in females is probably due to increases in fat related to stages of egg production.

The mass increase observed during the breeding relative to the non-breeding season, suggests that birds are able to adaptively manage both their longer term (protein) and more immediate (fat) energy reserves during breeding, and interrupted foraging theory currently provides the most universal explanation for this. If savannah birds experienced protein loss due to physiological stress we would expect to see individuals regain mass after breeding, instead of further decreasing their mass as they enter the non-breeding season. It may be that increased brood sizes and longer day lengths, and thus increased workloads, intensifies the stress of breeding in the Northern hemisphere. Thus birds may experience higher levels of physiological stress, which is why breeding birds lost protein mass during the breeding season. It would be interesting to investigate changes in internal protein and fat levels across a range of savannah species with different life history strategies, i.e. between specialised insectivorous species which have larger seasonal mass change but smaller clutch sizes, compared to the more r-selected finch species.

Interrupted foraging is the most current theory which is able to explain how birds manage their mass in response to stress both in the breeding and non-breeding season. It should be noted however that although this theory has proven to be robust across different systems, it is not yet conclusive and there may be other explanations for how birds vary their mass. This thesis provides further support for interrupted foraging theory.

### **Mass variation within species as an index of breeding investment**

Under constant predation risk interrupted foraging theory states that a bird's mass is a response to foraging predictability (Houston and McNamara 1993, MacLeod et al. 2008). If

foraging becomes less predictable a bird will increase its mass to reduce the risk of starvation, with foraging predictability being a consequence of food availability and life history demands. Therefore, within the same foraging niche, where food availability is constant across individuals, the mass of a bird during breeding acts as an index of investment in breeding. Numerous studies have found that in many species females show the greater mass increase and greater energetic expenditure compared to males, which is related to their increased investment in breeding (Williams and Nagy 1985, Verhulst and Tinbergen 1997, Burness et al. 2001). Therefore, should males and females show the same level of breeding investment and energetic expenditure, then we would expect that both parents would follow similar mass gain strategies, which is what is found in Little Auk (*Allie allie*; Wojczulanis-Jakubas *et al.* 2012). As such the scale of any mass change which occurs during breeding relative to predictable foraging in the non-breeding season can give us an index of how breeding affects foraging predictability, and consequently influences life history through food limitation theory (Martin 1987). Future studies should investigate how birds manage their mass under different breeding systems, for example as a measure of the investment of helpers relative to parents in cooperatively breeding species (Crick and Fry 1986), or parents feeding a larger brood-parasite chick rather than several of their own?

Birds act as a model system for studying mass variation as an index of breeding investment because they are relatively easy to catch and weigh and are capable of relatively large within day mass variation (e.g., Rogers & Smith 1993; Cresswell 1998). Adaptive management of mass is probably a universal strategy in bird species across both the breeding and non-breeding season; therefore it is highly likely that the mass of other animal groups during breeding were also a result of adaptive management. Body mass loss during breeding has also been observed to occur in females of other flying vertebrates, e.g. bats (Burnett & Kutz 1982) and non-flying vertebrates, including Adelie penguins (*Pygoscelis adeliae*; Johnson & West 1973), red deer (*Cervus elaphus*; Albon, Mitchell & Staines 1983), northern elephant seals (*Mirounga angustirostris*; Costa, Le Boeuf & Huntley 1986; Deutsch, Haley & Le Boeuf 1990) and brushtail possums (*Trichosurus vulpecula*; Isaac 2005), which has previously been interpreted as a result of reproductive stress. Researchers should therefore be cautious when assuming that mass loss is an indication of stress or cost of reproduction, because an animal's mass during breeding is probably also a trade-off between foraging predictability (as a function of competition and food availability) and investment in breeding, and it is possible to explain the above studies from this perspective.

## **Mass variation across species as an index of life history strategy**

This study provides empirical support for recent theoretical models which show that the seasonality of food limitation through density-dependence is the defining evolutionary force behind life history evolution (McNamara et al. 2008, Griebeler et al. 2010). Food availability during breeding limits the number of off spring produced or negatively influences the quality or condition of the off spring or parents, such that future survival or breeding success is reduced (reviewed in Martin 1986). Decreased food availability (either from abundance or competition), increases search time which decreases feeding rate with birds needing to spend more time foraging to store reserves against this increased foraging unpredictability (i.e. large mass response), and so less time is available for other activities (reviewed in Martin 1986). As a consequence selection in a less seasonal foraging niche acts on those individuals that invest in fewer, but fitter young per breeding attempt. Increased reserves mean that a bird will be in better condition to buffer the physiological and behavioural costs of breeding (e.g., Norris & Evans 2000), because breeding is energetically demanding (Bryant 1988) and has physiological costs such as a reduction in immunity to disease (Sheldon and Verhulst 1996, Norris and Evans 2000) and the release of testosterone which increases aggression (Dufty Jr 1989), both of which reduce immediate and long-term survival. An increased investment in self-maintenance may increase survival because it gives a bird more flexibility in time and space as to when it can forage, allowing it to avoid periods of increased predation risk (Lilliendahl 1998), as well as buffering fluctuations in foraging conditions and so reducing the risk of starvation (Rogers 1987, Houston and McNamara 1993). However, being fat is costly (Witter and Cuthill 1993, Gosler et al. 1995), and so how a bird maximises its fitness between the costs and benefits of carrying increased reserves provides insights into life history evolution.

Those species that experience increased seasonality (*r* selected) will have more food available during breeding and so their breeding strategy is likely to be limited more by factors such as competition for nesting space or nest predation. Therefore despite relatively large clutch sizes and consequently increased energetic expenditure foraging remains predictable and so species do not need to store large amounts of reserves against an increased starvation risk (i.e. low mass response). An increase in breeding effort is traded-off against adult survival (reviewed in Bennett & Owens 2002). Therefore within the same environment the scale of the interrupted foraging response during breeding acts as an index of life history strategy.

## **Mass variation during moult; tropical savannahs as model systems**

Birds adaptively manage their mass during life history activities in order to optimise fitness. Therefore we may expect there to be a mass response during moult, because this is an energetically demanding process with birds needing to spend a greater proportion of time foraging to provide the energy for feather growth (Myrcha and Pinowski 1970). A bird in moult may have one of three mass responses: it may decrease its mass in order to compensate for increased wing loading due to wing-area reductions and so be able to escape more rapidly from predators (mass-dependent response; Swaddle & Witter 1997; Senar, Domenech & Uribe 2002); or it may increase its reserves because the increased demand for food, coupled with the reduced escape time from predators means that foraging predictability is reduced, therefore increased reserves allow birds to forage only during periods of reduced predation risk (interrupted foraging response; Lind, Gustin & Sorace 2004); or a bird may optimise its moult strategy so that there is no discernible effect on mass (Lind 2001). Where food becomes limiting such as with the onset of winter in the Northern hemisphere, Great tits *Parus major* have been shown to arrest their greater covert moult due to direct protein stress or a correlate of protein stress (Gosler 1991), and so a bird's mass has direct implications for moult strategy.

In the tropics the speed of moult is both species and individual specific and tends to be slower than in the Northern hemisphere (e.g., McGregor, Ottosson & Cresswell 2007; Stevens 2010). Predictable foraging in the non-breeding season in tropical savannahs probably allows individuals to reduce the costs of moult by replacing feathers at a slower rate, which results in smaller gaps in the wing, and consequently has a reduced effect on flight performance (Swaddle and Witter 1997). Longer moulting periods will also reduce protein stress on flight muscles, and subsequently there is likely to be a reduced mass response (Gosler 1991). The diversity of moult strategies, extended moult periods and predictable foraging in the non-breeding season make tropical savannahs model systems for studying mass variation during moult in birds. Throughout this thesis I controlled for whether a bird was in active wing moult or not in all models and did not find an effect of moult on mass. This suggests that species may have evolved an optimal moult strategy so that moult does not affect mass. However more detailed study is probably required.

Some tropical birds have been observed to overlap their moult with breeding activities (Fogden 1972, Payne 1972, Foster 1974, Britton 1978, Wilkinson 1983), and this was found



to be common in the savannah birds in Nigeria (Stevens 2010). Moulting is an energetically demanding process and thus species that overlap moulting and breeding, appear to have additional energy available during breeding periods which could be devoted to reproduction but that appears not to be the case (Foster 1974). Organisms that do not utilise all potentially available energy for breeding should presumably be at a selective disadvantage. Therefore those individuals that overlap their moulting with breeding activities may show an increased mass response to compensate for their increased unpredictability of foraging due to higher energy costs. High levels of nest predation in some tropical environments are thought to reduce clutch sizes below the upper limits set by food limitation (Martin 1996), consequently there may be sufficient energy available for a bird to overlap its moulting and breeding. Thus any effect on mass that combining these two costly procedures has will provide further insights into food limitation theory. Further individual level studies into the scale of mass variation in birds which engage in a moulting breeding overlap relative to degrees of nest predation are required.

### **Mass variation as a life history trait**

In conclusion, this thesis shows mass variation to be a clear life history trait because it is a function of environmental seasonality and there are direct trade-offs between it and survival. A bird carrying excess reserves is unlikely to starve, but is more likely to be predated through increased exposure to predators and through reduced escape time. Therefore a bird's mass under a given set of environmental conditions is a trade-off with immediate and longer term survival. Birds trade off increased mass, and consequently condition and their ability to buffer physiological costs during breeding, with increased breeding activities such as clutch sizes, provisioning for chicks, territoriality and aggression. In order to understand the selective pressures that determine behaviour and community structures, limit populations, and act on life history evolution, it is essential to understand how a bird regulates its mass between the risk of starvation and the risk of predation (Abrams 1984, McNamara and Houston 1987, Bolker et al. 2003, Cresswell 2008). This is because the mass of a bird can provide an index of both individual condition and the quality of the foraging environment and therefore survival rates (Sutherland et al. 1996, Lima 1998b, Caro 2005, MacLeod et al. 2007, MacLeod et al. 2008). As such, a bird's mass acts as a bridge between population dynamics, foraging theory and life history.

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