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Survival rates and seasonality  
of tropical birds

By

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to the University of St Andrews

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He is a fool who lets slip a bird in the hand for a bird in the bush

- Plutarch

## Abstract

The paradigm that tropical birds have high survival and low clutch sizes (*K*-selected) and temperate birds have low survival and high clutch size (*r*-selected) is a classic example of how environmental conditions constrain life history trade-offs and are central to life history evolution. This thesis examined how seasonality in a West African tropical savannah influenced life history characteristics in its small bird species by measuring adult survival, body mass variation, moult and residency patterns. Data from this study (adult survival rate  $0.60 \pm 0.05$ ,  $N = 21$ ) combined with existing data worldwide showed that tropical birds lived longer than north temperate congeners ( $0.62 \pm 0.014$ ,  $N = 127$ , versus  $0.54 \pm 0.012$ ,  $N = 78$  adult survival rate). However, adult survival alone was not sufficient to account for small clutch size in tropical birds: first year survival, through extended parental care, was likely to be much higher than in temperate birds to compensate. Life history/body mass trade offs, where smaller north temperate birds compensate for low adult survival through higher fecundity, and larger tropical birds compensate for low clutch size by increasing juvenile survival through increased parental care, suggested that body mass also had important consequences for life history evolution. Body mass variation within species, however, did not vary along a simple seasonal basis across species. Species-specific ecology was likely to be more important than climatic conditions, unlike north temperate birds, suggesting that either food abundance was less uniformly limiting or predation risk was lower in the tropics. Moult period was mostly much longer than in north temperate birds ( $170.6 \pm 9.2$  days for 15/17 species), and so moult probably imposes fewer constraints on flight performance and life history trade-offs. Tropical birds were shown to have a variety of residency and migration patterns, but with partial migration being more common amongst Guinea savannah birds than hitherto thought. Partial migration is a phenotypically plastic response to density dependant factors, which suggested that tropical birds may generally deal with food shortage, when it occurs, by migration rather than body reserves. This, along with the combination of long moult suggested that tropical birds have a conservative response to predation risk, which was supported by higher adult survival. Overall it would appear that tropical birds fit the *K*-selection paradigm, with long conservative lives in the “slow lane”.

## Declaration

I, Ross McGregor, hereby certify that this thesis, which is approximately 42000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in October 2001 and as a candidate for the degree of Doctor of Philosophy in October 2002; the higher study for which this is a record was carried out in the University of St Andrews between 2001 and 2005.

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I hereby certify that the candidate has fulfilled the condition of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and the candidate is qualified to submit this thesis in application for that degree.

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# **Chapter 1: General introduction**

## **1.1 Life history theory**

Life history theory arises directly from natural selection: the “...preservation of favourable variations and the rejection of injurious variations” (Darwin 1859). As competition for resources is fundamental to natural selection, where individuals that gain more resources transmit more of their genes into populations, so those individuals that efficiently manage the resources they acquire will be favoured by natural selection. Key to the management of limited resources to increase fitness is the allocation of resources between the conflicting requirements of survival and reproduction (Horn & Rubenstein 1984). The process of balancing these allocations, or trade offs, results in the life history of an animal (Horn & Rubenstein 1984), which varies enormously across species (Roff 2002). Consequently many traits vary, such as age at maturity, body size, survival rate and age specific fecundity, as a result of adaptation by each organism to optimise the trade offs it needs to make within the environment in which it exists (Lessells 1991).

### **Life history trade offs**

While trade offs may occur between any pair of life history traits the two major trade offs animals must make are between current and future reproduction, or the costs of reproduction (Williams 1966), and the number and fitness of offspring (Lack 1947).

### ***Cost of reproduction***

Current reproduction incurs costs that reduce either future reproductive value or adult survival. These costs may be either physiological or ecological in origin (Calow 1979). Physiological costs include the energy required to produce the offspring and the energy required to provision the offspring (Bryant 1988).

Ecological costs include increased predation risk, e.g. through reduced vigilance during extra foraging to provision young (Magnhagen 1991), or the reduction in mobility of gravid females (Seigel *et al.* 1987).

Empirical evidence for life history trade-offs is extensive (Stearns 1992). For example, the observation of reduced body mass in adults with experimentally increased families suggests that survival may be depressed (Horn & Rubenstein 1984). Artificial selection studies in fruit flies (Fowler & Partridge 1989) and a few other organisms (e.g. see Tallamy & Denno 1982) have shown that increased fecundity does reduce parental survival, but few studies have clearly shown this in birds. There have been, however, many studies on the costs of reproduction in birds that have shown the cost may be transferred to a wide range of traits and that these often differ between the sexes (Lessells 1991). For example, when female collared flycatchers (*Ficedula albicollis*) had their brood size experimentally increased they were shown to reduce their clutch size in the following breeding season, but their survival was not reduced (Gustafsson & Sutherland 1988).

### ***Number and fitness of offspring***

As the number of offspring produced in a single family increases, the amount of energy parents are able to devote to each individual decreases. Consequently there

is a trade off between the number of offspring produced and their fitness (Lack 1947). However, there are some behaviours where family size does not require a division of resources, such as vigilance behaviour (Lazarus & Inglis 1978), or in fact have benefits, such as reduced thermal loss of nestling in larger families (Royama 1966). Despite this, studies have consistently shown that increased family size results in increased mortality and development rate and reduced body size and future fecundity of offspring (see Lessells 1991).

### **Phenotypic and genotypic approaches to the understanding of trade offs**

The analysis of life history evolution has largely followed two courses: the effects of evolution on gene frequencies that determine traits and the effects of selection on phenotypic traits themselves under the assumption that some phenotypic measure of fitness is optimised (Lessells 1991; Roff 2002).

The genetic approach largely examines the rate and direction of change of gene frequencies under selection (Via & Lande 1985; de Jong 1990), whereas the phenotypic approach largely uses optimality modelling to examine predicted and observed trait values and the causes of any differences between these (Lessells 1991). When differences occur they suggest that further selection pressures are acting and so may be used to predict further trait values (Lessells 1991).

### ***Phenotypic plasticity***

Responses by organisms to differing biotic or abiotic environments may invoke different phenotypes from a single genotype, this is termed phenotypic plasticity (Via *et al.* 1995). When this phenotypic plasticity is continuous, the relationship between the phenotype and its environmental pressure is termed the reaction norm

(Stearns 1989). These plastic changes may be reversed when the environmental pressure is removed, or the trait may become fixed (Lessells 1991). It is now generally recognised that many cases of phenotypic plasticity are adaptive and have evolved to maximise fitness in variable environments (Agrawal 2001). To be adaptive, phenotypic plasticity is dependant on the presence of predictable environmental cues (see review in DeWitt *et al.* 1998). However, stochasticity in the environment makes such prediction difficult and may result in further mechanisms to adjust the phenotype, such as has been suggested for the occurrence of asynchronous hatching in birds (Magrath 1989). As parents are unable to predict the availability of food or suitable feeding conditions before they lay a brood they may begin incubation from the laying of the first egg, resulting in a family of varying ages and size (Lack 1954). Under good conditions parents are able to provide for all the chicks, but if feeding conditions are poor, smaller, younger offspring will be out competed by larger, older sibs and so will die, leaving the parents with a brood adjusted appropriately to the level of provision for the current environmental condition – the brood reduction hypothesis (Lack 1954; Ricklefs 1965). However, there have been a great many alternative hypotheses suggested to explain hatching asynchrony and this is still a subject of much debate (see Viñuela 2000).

When a phenotype does not match its environment well it may result in a lower fitness of the individual, and so may be considered as a cost of plasticity. This is likely to occur when stochastic changes in the environment result in a lag between the change and the response (West-Eberhard 1989; Moran 1992; Padilla & Adolph 1996). However, costs are not entirely ecological. Genetic costs may arise

when trade offs are necessary between the degree of plasticity and other fitness enhancing traits (Roff 2002).

### *Optimality modelling*

Optimality modelling has been used to analyse the decision making process that an organism must use to trade off costs and benefits, whether this is daily foraging decisions or longer term decisions such as when to breed and how many offspring to raise (Krebs & Kacelnik 1991). There are three main components to such models: decision variables, currency and constraints (Krebs & Kacelnik 1991). In life history models decision variables refer to the traits themselves and boil down to age specific fecundity and age specific survival (or mortality) (Lessells 1991). The currencies of such models are the rate of increase of a genotype,  $r$  (Charlesworth 1980) and reproductive value, RV (Williams 1966). RV is essentially the number of offspring a female may produce in her lifetime. These two components are related via constraints (Stevens & Krebs 1986). Constraints are either the relationship between fitness and the value of a trait (a fitness curve) or the trade off of resources between two or more traits (a trade off curve) (Lessells 1991). An example of this approach is the study of clutch size.

### *Optimal clutch size*

Lack (1947) first suggested that birds must make a trade off between the number and fitness of offspring by adopting an optimal clutch size. This hypothesis was tested by manipulating family size either up or down by cross fostering either eggs or young chicks between nests (see Lessells 1991). A general pattern emerged that most species produced clutch sizes smaller than the optimal brood size (Lessells 1986; Dijkstra *et al.* 1990). However, these studies did not measure

the longer term survival of offspring from manipulated broods (Lessells 1991). When post-fledging survival was taken into account it was shown that the optimal brood size was equal to clutch size in two species: collared flycatcher *Ficedula albicollis* (Gustafsson & Sutherland 1988) and great tit *Parus major* (Tinbergen & Daan 1990). However, in a further six species tested the clutch size was still lower than optimal brood size (Haartman 1954; Murton *et al.* 1974; Steven 1980; Nur 1984; Lessells 1986; Dijkstra *et al.* 1990). The missing factor appeared to be the cost of reproduction. As there is a cost associated with producing and raising a family, and this cost rises with increasing family size, birds must trade off current reproductive output against future reproductive output. As such it may be more adaptive to produce a smaller than optimal clutch size in any one season (see Stearns 1992).

### **Environmental constraints and life history traits**

A classic example of how environmental constraints may result in general patterns of life history traits across a wide variety of taxa is *r*- and *K*- selection. There is a continuum of life history trade offs from animals living in the “fast lane” and those living in the “slow lane” (Richard *et al.* 2002; Saether *et al.* 2002). Fast lane animals reproduce at a younger age, produce many offspring, grow rapidly, disperse quickly and die young. They have a low environmental sensitivity, which further reduces survival. Slow lane animals reproduce later in life, produce fewer offspring, grow more slowly, and have longer lives. A consequence of this is often high population density (see Horn & Rubenstein 1984). These two extremes are termed *r*- and *K*- selection respectively (Macarthur & Wilson 1967). Across taxa these different life history strategies have been

found to divide between animals of different sizes. Smaller organisms, e.g. insects, tend to be fast lane, *r*-selected, where as larger animals, such as birds and mammals, tend to be slow lane, *K*-selected (Pianka 1970). However, even within taxa this general pattern is true, particularly within groups of plants (see Begon *et al.* 1996)

*r*- and *K*- selected organisms are often associated with particular environmental conditions, constraints or habitats (MacArthur & Wilson 1967) so that in general relatively stable conditions favour *K*- strategies and relatively variable or uncertain conditions favour *r*- strategies (Pianka 1970). While the *r*- and *K*- selection concept has been criticised for not accounting for all aspects of life history evolution (Stearns 1992; Roff 2002), it has been noted that the concept can provide useful insights with the caveat that it cannot embrace the full variety or causes of life history evolution (Boyce 1984). A classic example of this is the influence of climate on life history (see Cardillo 2002).

## **1.2 The influence of seasonal climate on the life history of birds**

Life history theory predicts that in a constant environment a single form, with optimal fitness, will evolve. However, in a predictable environment the evolution of phenotypic plasticity would be expected (Roff 2002). Most birds live in an environment with predictable seasonal changes within and between years. Thus a seasonal environment would be predicted to evolve a suite of phenotypically plastic traits matched to predictable seasonal environments (i.e. a reaction norm) that maximises overall fitness. These reaction norms would then vary depending on the characteristic of the seasonal environments that birds face.

The most important influence of season on an ecosystem is the effect on primary productivity (Bourliere & Hadley 1970). Seasonal variation of primary productivity results in seasonal variation in food abundance for birds, whether this is directly on those species feeding on plants or plant products (seeds, fruit, nectar etc), or indirectly on birds feeding on higher trophic levels that are ultimately dependant on primary productivity in the environment. It may be predicted that birds will time their most energetically costly decisions to coincide with the period of highest food abundance, as this would minimise the costs of trading off their own maintenance, such as moult and maintaining body reserves, with that of other activities such as reproduction, moult, migration and avoiding predation.

### **Reproduction**

Arguably, the most energetically costly event in the annual cycle of a bird is reproduction. Thus seasonal food abundance should result in seasonal bouts of breeding. Birds may be predicted to time breeding events to trade off the costs to themselves with the benefits to their offspring. This means making decisions about the predicted timing of the most important period of the breeding cycle to coincide with the most appropriate period of food abundance. Birds have been found to time the feeding of dependant young with peaks in food abundance, e.g. great tits (*Parus major*) time the nestling phase to coincide with peak caterpillar abundance (van Noordwijk *et al.* 1995), or Eleonora's falcons (*Falco eleonora*) that time their breeding season to coincide with the autumn passage of small birds that are their main prey (Cramp & Perrins 1985). Tropical birds also appear to time their breeding to coincide with peaks in food abundance and so also breed seasonally (Moreau 1950; Skutch 1950; Fogden 1972; Britton 1978; Sinclair

1978; Stiles 1980; Cruz & Andrews 1989; Poulin *et al.* 1992). So, within these seasonal restrictions to breeding, birds have to decide whether to produce many offspring, with lower fitness, at a cost to their own survival, or to produce few offspring, with greater fitness, with a lower cost to their survival.

## **Moult**

For birds, one of the highest costs of maintenance is the replacement of old feathers through moult (Ginn & Melville 1983). As old feathers wear out they must be replaced to maintain their flight and thermal properties. There are many different moulting strategies, but birds must manage this process by minimising the costs of moulting (Jenni & Winkler 1994). Moulting costs include the energy required to grow new feathers (Lindstrom *et al.* 1998), reduction in thermal value of plumage during moult (Nilsson & Svensson 1996), reduction in flight performance increasing predation risk and the combination of reduced flight performance with the need to increase energy intake that moult requires increasing mortality risk (Lind 2001). In addition, birds often have to time their moult to minimise the overlap with other costly processes such as breeding, or to complete it before more extreme changes in food abundance, climate or the need to migrate (Franklin *et al.* 1999). Thus birds must trade off the need to moult with other important life history processes within seasonal constraints such that fitness is not compromised (Hemborg *et al.* 2001).

## **Migration**

For some birds the effects of a seasonal environment may be such that they must move to another location in order to minimise the mortality risks associated with some environmental extreme, i.e. migrate. While migration may be a strategy to

reduce the costs of surviving environmental extremes, it has its own costs.

Migration requires a great deal of energy to fuel the movement itself (Alerstam & Lindstrom 1990), and there is an increase in the risk of mortality to birds fuelling for migration (Lind *et al.* 1999). So birds must trade off the costs and benefits of remaining in an environment that may be harsh against the costs and benefits of migrating (Milinski & Parker 1991). In some species all individuals migrate seasonally, while in others there are no individuals that migrate. However, there are some species that have partial migration, where some individuals migrate but others are sedentary (Berthold 1988). This would appear to be a case of phenotypic plasticity with two very different traits evolving with the same fitness outcomes (Milinski & Parker 1991).

### **Body reserves and risk of predation**

In order to maintain themselves birds must find food and forage to prevent starvation. However, foraging reduces vigilance (Lima 1986), which in turn increases the risk of being depredated (Witter & Cuthill 1993). Birds must therefore trade off the risk of starvation against the risk of predation (Lima 1986). Seasonality in the environment may result in changes to both sides of these trade offs. During periods of food limitation, caused by seasonal climate, the risk of starvation may increase such that birds must accept a higher level of predation risk, or make changes to compensate (Houston & McNamara 1993). In many cases a reduction in body mass may reduce predation risk, but also increases starvation risk (Blem 1990). Thus during periods of food limitation it may be predicted that birds will increase their body mass by carrying a reserve of energy as body fat to reduce their starvation risk (Houston *et al.* 1993). Therefore, when

food is not limiting, birds may be predicted to lose body mass and thus reduce predation risk (Lima 1986). Indeed, this is the pattern that has been shown in blackbirds (*Turdus merula*) that increase in body mass in winter when starvation risk is greater, at the expense of greater predation risk, but lose mass in the summer when starvation risk is lower (Macleod *et al.* 2005). A seasonal climate may also influence body mass regulation within a day, with different strategies during periods of low food abundance and/or temperatures, when overnight maintenance is higher, foraging is less predictable and so starvation risk is higher (Cresswell 1998).

Thus in order to maximise fitness in seasonal climates birds must make trade offs in a variety of life history traits that fundamentally influence their survival. General patterns in seasonality and other climatic characteristics therefore tend to result in general patterns of life history traits. This is particularly obvious when comparing the characteristics of birds in tropical and temperate climates.

### **1.3 Life history in tropical birds**

As I have argued above, a useful starting point to understand life history traits in animals is to understand the environmental constraints (or climate) in which they live.

#### **Seasonal climate in the tropics.**

Climate is largely determined by latitude or altitude. Annual changes in the tilt of the earth's axis in relation to the sun result in changes to the climate on a seasonal basis. Temperatures are different between equatorial and polar regions due to the

angle at which solar radiation strikes these areas. In polar regions this angle is relatively acute, and becomes more or less acute as tilt of the earth's axis changes the angle. However, in equatorial regions this angle is always close to  $90^\circ$  so temperature varies little. This concentration of solar radiation at the equator results in warmer, rising air that cools as it rises. As colder air does not hold as much moisture as warmer air, the moisture condenses and rain is produced. Eventually this rising air spreads out to the north and south of the equator and eventually cools and falls, at approximately  $30^\circ$  north and south. The air that is displaced upwards by convection causes air to be drawn in from the north and south. These air movements are deflected by the Coriolis force of the earth's rotation resulting in them being displaced westwards to the north and eastwards to the south. These north-easterly and south-easterly "trade winds" meet in a low pressure area around the equator, where they rise. This area is known as the Inter-Tropical Convergence Zone (ITCZ), typified by low atmospheric pressure and high rainfall. The ITCZ moves north and south with the tilt of the earth's axis as the area receiving the highest solar radiation moves north and south of the equator. This creates seasonal peaks in rainfall north and south of the equator, with a double peak at the equator. The result is the strong seasonal pattern of dry season and rainy season across most of the tropics. This seasonality becomes more acute with increasing latitude as the ITCZ is over these latitudes for less of the year (Perry & Walker 1977; Tyson 1986; see Osborne 2000)

Tropical climates do not only vary seasonally but can be very variable between years. The most dramatic influence on intra-annual climate is caused by the El Niño Southern Oscillation (ENSO). This phenomenon is caused by a switching of

oceanic currents in the Pacific resulting in warmer than normal waters off the Peruvian coast, and cooler than normal waters around Indonesia, resulting in a shifting of atmospheric pressure between these two areas (Glantz 1987). ENSO events occur every four to five years and can last for up to two years (Trenberth & Hoar 1996). These events vary in intensity and can cause massive changes in global climate, often causing droughts in some parts of the seasonal tropics, such as southern Africa and eastern Australia (Ropelewski & Halpert 1987), and stormy wet weather along the eastern Pacific coast (see Osborne 2000).

Clearly, the tropics are not the benign, stable aseasonal climate they are often assumed to be. There are strong seasonal elements to tropical climates that are dominated by differences in rainfall, unlike the strong seasonal effect of temperature on higher, temperate latitudes.

### **The influence of seasonal climate on tropical ecosystems**

While it has often been assumed that the tropics are models of stable, aseasonal climates it has been shown that almost all tropical forests (van Schaik *et al.* 1993; Wikelski *et al.* 2000) and savannahs (Bourliere & Hadley 1970; de Bie *et al.* 1998) have strongly seasonal phenologies.

The main cause of these changes in plant phenologies with season are due to seasonal changes in levels of solar irradiance and water in tropical forests (van Schaik *et al.* 1993) and water in savannahs (Bourliere & Hadley 1970). The phenologies influenced by these factors are mainly community growth rate, germination, flowering, fruiting and dormancy. As was discussed above the causes in the changes in rain and solar irradiance are due to seasonal shifts in the

earth's axis and the consequent shift in the ITCZ. The seasonal changes in these phenologies has been shown to change with latitude following the track of the sun, which is followed by the track of the ITCZ (van Schaik *et al.* 1993).

As latitude increases within the tropics there is an increase in the seasonal pattern of climate as the ITCZ arrives increasingly later and departs increasingly earlier. Thus as latitude increases the duration, predictability and intensity of the rainy season decreases (de Bie *et al.* 1998) and the changes in seasonal phenology of plants increases (Osborne 2000). Thus this variation in seasonal climate, along with soil type and nutrients, largely determine the plant communities and so animal communities that can be supported (Osborne 2000), with general life history trade-offs, such as *r*- and *K*- strategies, also varying along these gradients in a systematic way, so that particular strategies are associated with particular climatic zones (Dobzhansky 1950).

### **Life history traits of tropical birds**

Consistent differences in the life histories of birds have been found between the tropics and north temperate climatic regions (Russell *et al.* 2004). It was originally noted that clutch size varied with latitude as tropical passerines tended to have two or three eggs (Moreau 1944), temperate passerines had four or five, and high arctic birds five to seven eggs (Ricklefs 1969). However, this latitudinal gradient in clutch size seems to only occur in a northward direction from the equator as south temperate birds are similar to tropical birds in their clutch size (Yom-Tov *et al.* 1994). This consistently smaller clutch size was thought to be a response to higher nest predation rates in the tropics (Skutch 1949). However, this was at odds with the thought that incubation and fledging periods were longer in

the tropics (Skutch 1949; Ricklefs 1968; Skutch 1985; Woinarski 1985), which would increase the exposure time of nests to predators. However, this was recently reviewed, with large sample sizes, and it was found that there was little or no difference in incubation and fledging periods between north temperate and tropical passerines (Geffen & Yom-Tov 2000). The evidence of higher nest predation rates in the tropics was also weak (Martin 1996).

The combined assumptions of a high nest predation rate and a lack of climatic seasonality resulting in a longer breeding season led to the thought that tropical birds must raise more broods per year and could have many more re-nesting attempts per brood (Martin 1996). However, there is evidence that this may not be the case. *Parulid* warblers were found to be single brooded in both north and central America (Skutch 1954) and African races of stonechats (*Saxicola torquata*) have only one brood per year compared with multiple broods in stonechat subspecies in temperate regions (Dittami & Gwinner 1985). More extensive studies of breeding birds in the tropics found that successful pairs did not raise a second brood and suggested that this was due to long period of parental care after fledging (Fogden 1972; Jullien & Thiollay 1998). However, this difference had not been formally tested with a large sample size using phylogenetically independent methods until recently. Russell *et al.* (2004) found that a wide range of tropical and south temperate passerines had significantly longer period of post fledging care and a longer period within the parental territory after nutritional independence than north temperate birds. This extended parental care was predicted to increase juvenile survival, especially in saturated habitats with few vacant territories (Martin 1996).

There have been very few studies of juvenile survival in the tropics but Covas *et al.* (2004) found that juvenile sociable weavers (*Philetairus socius*) had a survival rate very similar to that of adults. They also showed prolonged parental care and delayed dispersal. Schaefer *et al.* (2004) also found that two African *Sylvia* warblers (*Sylvia lugens* and *S. boehmi*) had high juvenile survival, long periods of parental care and delayed dispersal. These traits are not confined to African passerines because red-winged fairy wrens (*Malurus elegans*) in Australia also show similar traits (Russell & Rowley 2000).

All of the traits so far shown in tropical birds (low reproductive rate and high parental investment in offspring) suggested that tropical birds may be *K*-selected organisms and so we may predict high adult survival. Indeed, it has been thought for a long time that tropical birds did have a high adult survival after the finding of an 82% annual return rate of white-bearded manakins (*Manacus manacus*) in Trinidad (Snow 1962), and a minimum annual survival rate of 86% of birds from Borneo (Fogden 1972). However, this was questioned by Karr *et al.* (1990) who found no difference in adult survival rates between a sample of common bird species trapped in Panama with a sample trapped in Maryland, U.S.A. Their study was widely criticised for not controlling for transients in the population, which may bias survival rates downwards as birds that were never re-trapped were assumed to die, when it was more likely that they left the trapping area (Pradel *et al.* 1997). However, subsequent re-analysis of these data did not substantially change their conclusions that tropical birds do not have uniformly high survival rates (Brawn *et al.* 1999). Since Karr's (Karr *et al.* 1990) study high survival rates

were found in Puerto Rico (Faaborg & Arendt 1995), Trinidad (Johnston *et al.* 1997), Peru (Francis *et al.* 1999) and Malawi (Peach *et al.* 2001).

The smaller clutch size of tropical birds does appear to be a uniform observation across tropical and south temperate regions, and this has led to research examining other important life history traits that may help to explain this. High adult survival appears to have become an accepted consequence of lower fecundity in tropical species, despite survival rates having only been measured from a small sample of species from five sites in the tropics, one of which stated that survival was not as high as previously assumed (Karr *et al.* 1990; Brawn *et al.* 1999). Nest predation does not seem to be an adequate explanation, as it has been shown to vary widely across the neo-tropics despite constantly small clutch sizes (Skutch 1985). A prediction of longer development time was predicted from high predation rates and small clutch size (Martin 1996), but was rejected by Geffen & Yom-Tov (2000). It does appear that tropical birds do invest more heavily in older chicks (Russell *et al.* 2004), and there are tantalising indications that this may indeed increase juvenile survival (Covas *et al.* 2004; Schaefer *et al.* 2004). So, while temperate passerines commonly show large clutch sizes, multiple broods per year, short periods of post-fledging care and low adult survival (a typical *r*-selected suite of traits), it has yet to be demonstrated that tropical birds are typical *K*-selected species as further research is needed to establish general patterns across many of their life history traits, not least adult and juvenile survival, nest predation rates, and number of broods per season.

## **1.4 This study**

This study investigates how life history traits in birds have arisen as a consequence of the environmental conditions in an area of the tropics and seeks to address the lack of empirical information on the values of life history variables in the tropics.

### **The climate and habitats of West Africa**

This study was undertaken in the tropics of West Africa, which lies largely between 5° and 20° north of the equator. The seasonal movement of the ITCZ resulting in a rainy season during the boreal summer and a dry season during the boreal winter dominates the climate. There is a general pattern of increasing length of the dry season and decreasing annual rainfall with increasing latitude. Thus the dry season is only three or four months in the south but maybe as long as seven months in the north, where the rains are erratic in timing, amount and distribution both within and between years. This wide range of climatic conditions results in a wide variety of habitats, from humid tropical rainforest in the south, to the dry, hot Sahara desert in the north. (see Elgood *et al.* 1994 and de Bie *et al.* 1998).

The study site of this thesis was located in the savannah of Nigeria within West Africa. The savannahs of West Africa lie between the forest zone and the desert. The boundary between each of these is not sharply defined but change gradually, largely on a north – south axis. However, the boundary of the savannah has been extended south through human activity as the forests have been cleared into a zone of ‘derived’ savannah (Bourliere & Hadley 1970). Within the derived

savannah there are large areas of agriculture interspersed with scrub, but some relict patches of forest do occur. There is therefore a mix of savannah and forest birds, though few forest birds are found in the more savannah like habitats (Elgood *et al.* 1994). From the forest 'boundary' northwards into the savannahs there is a gradual decrease in tree cover and height and an increase in the cover of grasses and herbs.

The savannah can be sub-divided into three zones: Guinea savannah; sudan savannah; sahel savannah. The sahel savannah lies immediately south of the Sahara and is very dry with only short scattered trees, mostly *Acacias*, *Salvadora persica* and *Commiphora africana*. The sudan savannah zone, south of the sahel, is still dominated by *Acacia* tree species, but *Ziziphus* species are also common. Further south still in the Guinea savannah zone the dominant tree species are *Burkea africana*, *Anogeissus leiocarpus*, *Lophira lanceolata* and *Terminalia* species that can grow up to 15m high (Osborne 2000), though human disturbance has resulted in the economically important *Daniella oliveri*, *Vitellaria paradoxa* and *Parkia biglobosa* becoming relatively more common (Elgood *et al.* 1994). In the more northern Guinea savannah *Isoberlinia doka* is often dominant giving rise to very characteristic, miombo like woodlands (Elgood *et al.* 1994). The grasses between the trees can grow up to 2 metres high when undisturbed and are mainly of the *Andropogon* and *Hyparrhenia* genera. Gallery forests are common in riparian strips where mahogany *Khaya senegalensis*, *Raphia sudanica* and the bamboo *Oxytenanthera abyssinica* dominate (Elgood *et al.* 1994).

Due to the pattern of occurrence of the ITCZ to the savannahs rainfall is highly seasonal and this is reflected in the highly seasonal growth of grasses and the top

growth of woody plants, thus there is a highly seasonal peak of food for primary consumers in the ecosystem (de Bie *et al.* 1998). There is also an increase in the number of plants in flower through the rainy season, with a peak in the mid-rains (Bourliere & Hadley 1970). But despite this seasonality the productivity of African savannahs is very high and is able to support high diversity and huge numbers of large mammals. The African savannahs are also well known for their diversity of birds, with 708 species recorded, considerably more than the savannahs of South America (521 species) and Australia (227 species) (Osborne 2000). The combination of these factors makes the Guinea savannah of West Africa an ideal location to study the seasonality and life history of tropical birds.

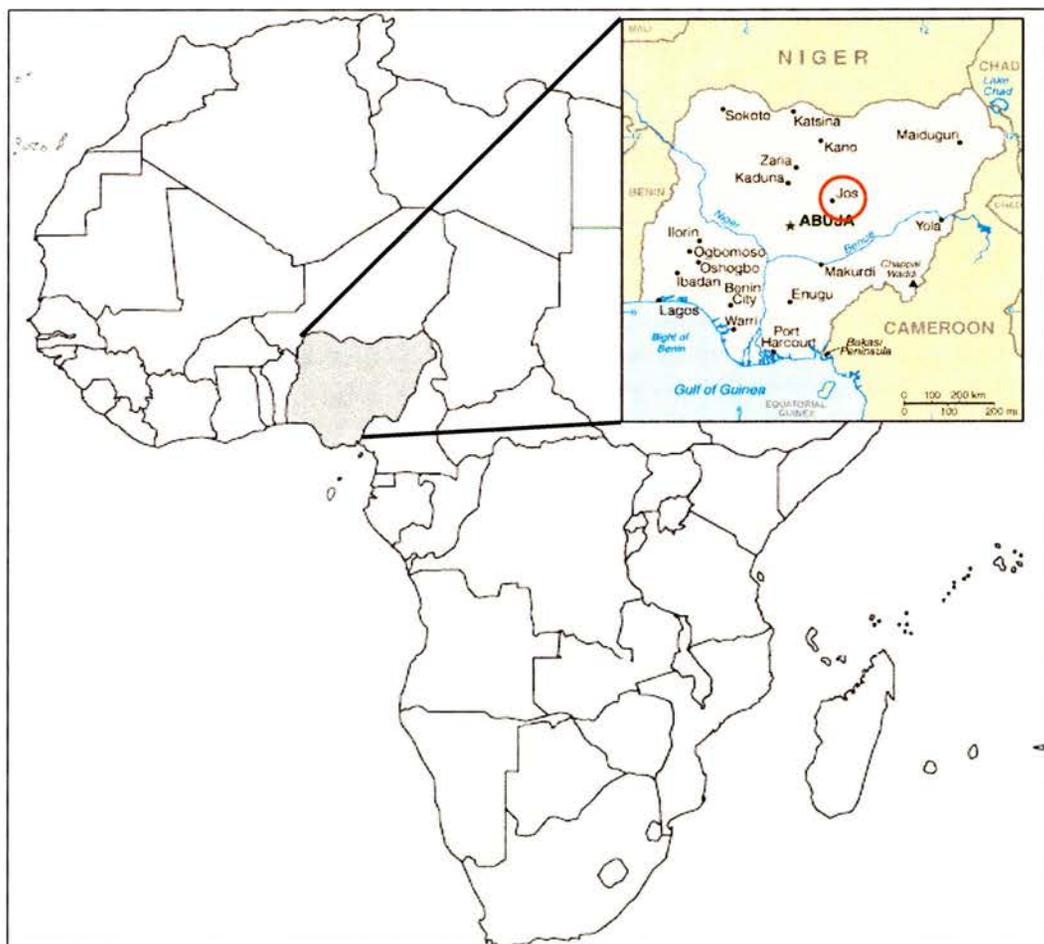


Figure 1.1: Location of study site in Nigeria, West Africa.

This study was conducted in an area of Guinea savannah woodland on the Jos Plateau in central Nigeria (N 09° 52', E 08° 58'), approximately in the middle of the Guinea savannah zone (Figure 1.1). The study site was in degraded woodland scrub in the newly created Amurum Community Forest Reserve. A more detailed description of the site is given in Chapter 6.

### **Hypotheses to be tested**

Recent publications researching the life history of tropical birds have raised many important questions. The aims of this study were to investigate important aspects of the life history of tropical birds in the context of a seasonal environment.

#### ***1. Empirical measures of adult survival***

There is a clear need for further study of adult survival in hitherto un-measured species in locations not so far considered. The questioning of the long held paradigm of high adult survival in tropical birds by Karr *et al.* (1990), followed by the criticism of that study by subsequent researchers and their findings of high adult survival, means that the tropical high – temperate low adult survival paradigm is far from clear. In addition, new models designed to incorporate re-sightings of marked animals (Barker 1999) into models designed only for re-captures of animals (Lebreton *et al.* 1993) can now be used to improve the accuracy of survival estimates. The null hypotheses were:

1. There was no difference in survival rates between West African and north temperate adult resident birds.

2. There was no difference in survival rates of adult resident birds between West Africa and other sites in the tropics

## ***2. Trade-offs of life history traits with survival***

If the accepted paradigm of high adult survival compensating for low clutch size in the tropics was found not to be true it was predicted that other life history trade offs would differ between tropical and north temperate climates. In order to maintain stable populations, in the absence of higher adult survival, there must be compensatory differences in the number of broods per year a pair raise, or the likelihood of nest predation, or the levels of parental care afforded by the parents in order to increase juvenile survival, or some combination of these factors. The null hypotheses were:

1. There was no difference in the number of broods raised per year between tropical and north temperate birds
2. There was no difference in nest predation rates between tropical and north temperate birds
3. There was no difference in duration of parental care between tropical and north temperate birds
4. There was no difference in juvenile survival between tropical and north temperate birds

### ***3. Life history body mass trade offs***

The observation that there may not be a relationship between adult survival and body mass in tropical birds (Francis *et al.* 1999) differed from the clear relationship shown in British birds (Dobson 1990). In north temperate climates this relationship may be driven by energetic effects caused by low winter temperatures (Walsberg 1983), which are absent in tropical climates. As adult survival was measured in West Africa in this study the relationship could be tested for new data along with published estimates of adult survival from other sites in the tropics. The observation of no relationship between survival and body mass also suggested that there might be differences between tropical and north temperate birds in the relationship between other life history traits and body mass, such as fecundity, nest predation, juvenile survival and parental care. The null hypotheses were:

1. That any positive relationship between body mass and survival is less strong, or absent, in tropical regions that lack strong selection against small body size because of energetic considerations
2. If mass correlates positively with survival in temperate regions, but does not in tropical regions, then there will be a negative relationship between mass and: (i) fecundity and/or (ii) nest survival and/or (iii) juvenile survival and/or (iv) parental care in temperate regions to compensate for increased mortality at low mass, but not in tropical regions.

#### **4. Molt**

Molt is an extremely important part of the annual cycle of a bird. It has significant energetic (Nilsson & Svensson 1996; Lindstrom *et al.* 1998) and predation risk costs (Swaddle & Witter 1997) associated with it, which means that birds must manage this cost within the other important, costly stages of the annual cycle, such as breeding and / or migration (Jenni & Winkler 1994). Despite the importance of molt, very little is known about the molt of tropical birds and how different species manage molt in the context of other important life history traits. Molt was measured during this study to determine its timing and duration in a seasonal tropical environment. The null hypotheses were:

1. There was no difference in molt duration between tropical and north temperate passerines
2. Molt timing was not seasonal.

#### **5. Body reserves (mass)**

North temperate birds were known to trade off the costs of maintaining energy reserves against predation risk, and that this trade off varied with season and time of day (Houston *et al.* 1993). While it was known that the tropical environment was seasonal (Osborne 2000) it was not known whether this might result in birds adjusting their body mass to compensate for seasonal changes in food abundance and/or predation risk, and whether any diurnal patterns would also arise. It was predicted that the seasonal environment would result in body mass changes and that these would be timed diurnally and seasonally, with other priorities that affect

the starvation/predation risk trade off, such as moult, affecting any diurnal or seasonal patterns of body mass change. The null hypotheses were:

1. Mass does not increase or decrease during the day in a pattern that is a response to predation risk and starvation risk.
2. Body mass will not increase or decrease seasonally and there will not be a difference in body mass between dry and rainy seasons.
3. Body mass will not differ between moult period and the rest of the year.

#### ***6. Seasonal abundance***

At any one site the abundance of a species may change seasonally for a variety of reasons. Birds may be migrants such that they were seasonally absent for part of the year. Some species are partial migrants, with some individuals, or populations, being migrants and others not. It was known that some species were seasonal long distance migrants to West Africa, either from elsewhere in Africa or from the palearctic (Elgood *et al.* 1994). Previous studies had shown seasonal migration within West Africa, but only for a few species (Elgood *et al.* 1973). Here seasonal abundance was estimated at a previously unstudied site, using modern methods. The null hypotheses were:

1. There was no change in the abundance of a species with season.

2. There was no seasonal change in abundance within the period of occurrence for known migrant species.

### **This thesis**

Each of these hypotheses were tested in the chapters to follow. Chapter Two introduces the new estimates of survival from Nigeria and a new analysis of published survival rates of tropical birds. A simple model is built to examine whether these general survival rates were sufficient to account for the observed low clutch size of tropical birds using published estimates of clutch size, nest survival, post-fledging or first year survival, and number of broods per year. Chapter Three expands upon the survival findings and examines the trade offs in relation to body mass. Differences between climates in the adult survival and body mass relationship are used to make and test predictions on the body mass relationships with other life history parameters: annual fecundity, nest survival, juvenile survival, and fledging period. In Chapter Four the moult of tropical birds in West Africa is measured and compared with moult strategies in similar north temperate species and the differences between climates discussed. Chapter Five discusses moult and its duration and seasonal occurrence. Chapter Six investigates the effects of the seasonal climate of African savannah ecosystems on the abundance of birds at the study site through timing of breeding and migration to provide further background to understand the environmental constraints on life history traits. Finally, Chapter Seven summarises the subjects researched in this thesis and how these subjects relate to one another to create an overview of tropical bird life history evolution.

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## **Chapter 2: Survival rates and its relation to clutch size, number of broods and parental care**

### **Summary**

The long established paradigm of low clutch size in tropical birds being accounted for by high survival was tested. Adult survival rates were measured for 21 species from West Africa. These survival data and survival data from published studies in the tropics were compared with data obtained from published studies of north temperate birds. Comparisons were also made using Phylogenetically Independent Contrasts. Adult survival was found to be higher in tropical birds than north temperate birds, but survival was also very variable between species and sites. Survival also varied significantly within some species between sites. Modelling of demographic parameters showed that adult survival in the tropics was insufficient to account for low clutch size in the tropics. Alternative trade offs must therefore exist. The levels of nest predation, length of the breeding season and extended parental care required to maintain stable populations were explored within the model.

### **Introduction**

Do tropical birds live longer than their north temperate congeners? Life history theory suggests that tropical birds may trade off low clutch size through higher adult survival (Martin 1996). Small clutch size amongst tropical passerines has been long established (Moreau 1944; Yom-Tov 1994) and the finding that White-

bearded Manikins in Trinidad had an 82% return rate each year to their leks (Snow 1962) seemed to suggest that tropical birds were indeed long lived. This became the established paradigm until it was recently questioned by Karr *et al* (1990) who found no difference in survival rates of forest birds between Panama and North America. However, subsequent studies found survival rates to be higher in the tropics than in the north temperate region (Faaborg & Arendt 1995; Johnston *et al.* 1997; Francis *et al.* 1999; Jullien & Clobert 2000; Sandercock *et al.* 2000; de Swardt & Peach 2001; Peach *et al.* 2001; Ghalambor & Martin 2001) so once again the paradigm of high survival balancing small clutch size in the tropics was re-established.

Here new data from West Africa are presented and a more rigorous analysis of published data that broadly confirm the established survival vs. adult clutch size paradigm. However, this study also shows that adult survival may be variable and low in the tropics and that the established difference in average adult survival rate is not sufficient to compensate for the reduced fecundity because of lower clutch size. Therefore it was evaluated which life history traits were more likely to balance low adult survival where clutch size remains low: more breeding attempts and therefore broods per year (Lack & Moreau 1965); greater nest predation (Martin *et al.* 2000); and extended parental care (Russell *et al.* 2004a).

## **Methods**

### **Survival analysis**

Survival rates were estimated for adult birds on the Jos Plateau in central Nigeria using methods that account for transience and trap shyness. Methods were

designed to meet the assumptions of Cormack-Jolly-Seber models (Lebreton *et al.* 1992) and Barker's (1999) model. Sufficient data were obtained to model survival rates for 21 species. The addition of colour-ring re-sightings allowed survival to be modelled according to Barker (1999), thus accounting for trap shyness.

Birds were trapped in mist nets at Amurum Community Forest Reserve (09°52' N, 08°58' E), a small 120 ha reserve of Guinea savannah scrub with small patches of relict gallery forest along streams. The surrounding habitat is degraded scrub and subsistence farming.

Fourteen mist nets totalling 178m in length were placed in fixed 'net rides' for 14 days every four months from 2001-2004. Nets were opened at dawn (0600) each day for 5 hours (until 1100). All birds were marked with individually numbered metal rings from the British Trust for Ornithology and where possible fitted with three additional coloured plastic rings in a unique combination in order to allow individual recognition in the field. Re-sightings of colour ringed individuals were made *between* each four month capture period. These re-sightings included standardised observations made on timed transects through the CES site and surrounding habitat and opportunistic observations made at any time *between* capture periods. Barker's (1999) model makes no assumption regarding equal probability of re-sighting individuals during the re-sighting period.

Trapped birds were identified, wherever possible, as either juveniles or adults. Birds trapped as juveniles were excluded from the analysis in order to minimise any effects of higher juvenile mortality and dispersal.

Estimates of survival were made using Barker's (1999) models which allowed the simultaneous analysis of both re-captures and re-sightings. These models were fitted using the computer software Program MARK (White & Burnham 1999). In order to account for small variations in the interval between each capture 'session' (a 14 day trapping period) the proportion of time between each session was calculated relative to the *shortest* interval and entered into the modelling software (Table 2.1). As many species were trapped in very small numbers, initially only those species with at least 10 individuals that had been trapped more than once were considered. To each species the same four models were built with combinations of time variation allowed in both survival probabilities and recapture probabilities. All other model parameters were fixed to be constant with time.

Table 2.1: Time between constant effort mist-netting sessions

SESSIONS	DAYS BETWEEN SESSIONS	PROPORTION OF TIME BETWEEN SESSIONS
01-Feb	124	1.31
02-Mar	95	1
03-Apr	156	1.64
04-May	108	1.14
05-Jun	163	1.72
06-Jul	159	1.67
MEAN	134.17	
S.E.	11.9	

Goodness of fit was tested on each fully parameterised model using parametric bootstrapping in a two stage process. In each case the deviance of the fitted model was compared with 100 randomly generated deviance values using parameter estimates from the model with all of the assumptions held true. If the proportion of generated values larger than the observed values was  $> 0.2$  then no further simulations were required and it was concluded that the model adequately fit the

data (White & Burnham 1999). If this proportion was  $< 0.2$  the deviance of the fitted model was compared with 1000 bootstrap simulations. If the proportion of generated values larger than the observed values was  $< 0.05$  the model did not fit the data well, so was rejected (White & Burnham 1999). In all cases the goodness of fit testing showed that the model did fit the data (Table 2.2).

Table 2.2: Goodness of fit statistics and sample sizes for survival models

species	GOF p-value	$\hat{c}$	total individuals trapped	total recaptures & resightings
<i>Turtur abyssinicus</i>	0.66	0.88	28	6
<i>Colius striatus</i>	0.5	1.04	53	11
<i>Lybius vieilloti</i>	0.09	1.52	16	4
<i>Chlorocichla flavicollis</i>	0.62	0.93	12	8
<i>Pycnonotus barbatus</i>	0.87	0.89	125	42
<i>Camaroptera brachyura</i>	0.96	0.76	40	24
<i>Platysteira cyanea</i>	0.99	0.78	23	17
<i>Cyanomitra verticalis</i>	0.85	0.83	42	18
<i>Chalcomitra senegalensis</i>	0.79	0.86	48	16
<i>Cinnyris venusta</i>	0.72	0.87	16	4
<i>Zosterops senegalensis</i>	0.86	0.78	48	14
<i>Tchagra senegala</i>	0.82	0.83	11	8
<i>Sporopipes frontalis</i>	0.8	0.84	65	11
<i>Ploceus nigricollis</i>	0.63	0.97	30	14
<i>Ploceus luteolus</i>	0.33	1.16	14	3
<i>Ploceus vitellinus</i>	0.18	1.54	16	5
<i>Lagonosticta rufopicta</i>	0.39	1.21	17	9
<i>Lagonosticta senegala</i>	0.71	0.81	86	10
<i>Lagonosticta sanguinodorsalis</i>	0.95	0.69	33	17
<i>Estrilda caerulescens</i>	1	0.64	72	48
<i>Uraeginthus bengalus</i>	0.96	0.63	128	44

As goodness of fit proportions of  $< 0.2$  may suggest some evidence of a lack of fit the over dispersion in the model was measured by dividing the observed model deviance by the mean of the deviance of the simulated data. This is the Variance Inflation Factor,  $\hat{c}$  (Lebreton *et al.* 1992). If  $\hat{c} = 1$  the model fits the data perfectly but any value of  $\hat{c} > 1$  suggests that there is some over dispersion in the model and values of  $\hat{c} > 3$  suggest that over-dispersion may be problematic (Lebreton *et al.*

1992). No models for any species were so badly over dispersed (Table 2.2).

Program MARK allows small amounts over dispersion to be compensated for by entering the value of  $\hat{c}$  into the program. So while some species had goodness of fit values that were low enough to indicate some lack of fit the level of over dispersion was also low and taken into account (Table 2.2).

To select between the 4 models two techniques were used. Initially model selection used Akaike's Information Criterion (AICc) where the model with the lowest AIC value uses the fewest parameters that still fitted the data. However, if the difference between two models was less than 2 units, AIC was not a good method to select between these models (Burnham & Anderson 1998). If this was the case then Likelihood Ratio Tests were carried out on all possible nested model pairs to determine which of the models provided the best fit with the fewest parameters.

With the best model selected, the model parameters were examined for boundary estimates. This was caused by the logit link function in the model constraining parameters to be within the range 0 – 1. Any parameters approaching or at 0 or 1 had their confidence intervals recalculated using Profile Likelihood, which used a log-likelihood function. Thus it was possible to determine if the parameter was identifiable and estimable. Thus only species where the goodness of fit tests were  $> 0.05$  and where  $\hat{c}$  was  $< 3$  and where the parameters of interest were identifiable and estimable were considered to have appropriate data to measure apparent survival probability.

For each species the model that provided the best fit was the fully time independent model and thus the model parameter output from Program MARK provided the survival rate over the period of the shortest trapping interval (i.e. the period with the proportion constrained to 1; see Table 2.1). It was therefore necessary to adjust this to an annual survival rate. To do this the proportion of shortest interval to a year was calculated and the parameter value was raised to the power of this value. A Taylor Series Expansion (or delta method) was used to recalculate the standard error of the estimate (Seber 1982).

### **Meta-analysis**

Data from six additional studies was analysed (Karr *et al.* 1990; Faaborg & Arendt 1995; Johnston *et al.* 1997; Francis *et al.* 1999; Jullien & Clobert 2000; Peach *et al.* 2001) and compared with data from Nigeria and with data of north temperate passerines used by Peach *et al.* (2001), Johnston *et al.* (1997) and Martin & Li (1992). Data from north temperate migrant species that over winter in the tropics were excluded from the analysis so that comparisons were only made between resident north temperate and resident tropical species. Global analyses used here improved on those carried out previously by excluding species that occur in both temperate and tropical areas and by controlling for phylogenetic effects in all cases.

### ***Phylogenetically independent contrasts***

Closely related species may share characters through common descent and are therefore not statistically independent points (Harvey & Pagel 1991). In order to overcome this statistical non-independence of related species we used phylogenetically independent contrasts (PIC's) to compare survival rates between

sites. The computer software Comparative Analysis by Independent Contrasts (CAIC) (Purvis & Rambaut 1995) was used to test whether changes in phylogeny between sites were associated with changes in survival. Phylogeny was based on Sibley and Ahlquist (1990). Independent contrasts were then compared using t-tests to determine if the mean value of the contrasts differed significantly from zero (Sokal & Rohlf 1995).

### **Population model**

A simple population model based on a life table approach (see Appendix 5.1) was used to predict what average adult survival values balance fecundity and so predict population stability in temperate and tropical regions, using best available data for clutch size, nest survival, and post-fledging or first year survival, and a variable number of broods per year. The model was simply:

Yearly mortality = Number of recruits per year

Where:            Yearly mortality = starting population \* (1-survival rate))

Number of recruits = clutch size \* nest survival rate \* number of breeding attempts \* first year survival

The model was set up with the following assumptions: mean clutch size (2.26 for tropics and 3.90 for the north temperate region – based on means of species used in Martin *et al* (2000) which control for phylogenetic differences by choosing similar species in north temperate and tropical regions); nest survival of 0.35, the mean of 0.39 for tropics and 0.31 for north temperate regions from Martin *et al.* (2000) assuming a 32 day incubation and nestling period combined based on Geffen & Yom-Tov (2000); post-fledging survival in the first year of  $0.33 \pm 0.03$ ,

based only on north temperate studies (Ringsby *et al.* 1998; Bradbury *et al.* 2000; Sillett & Holmes 2002; McGowan *et al.* 2003; Reid *et al.* 2003). The maximum number of broods was systematically varied (up to a maximum of three – an individual bird that could have three broods would not attempt to breed again in any year) as this has a major effect on the magnitude of the predictions.

## Results and discussion

### Adult survival

Sufficient data were obtained to model apparent adult annual survival rates for 21 species at Amurum, Jos (Table 2.3). Estimates had a wide range across species with no clear phylogenetic pattern with large variation in survival even within families (Table 2.3). The apparent adult annual survival rates from Nigeria were compared with values from other studies' (Table 2.4).

Table 2.3. Adult survival rates estimated using Barker's model (Barker 1999) for birds in Nigeria estimated from trapping and colour ring resightings.

Species	adult survival rate (over 95 days)	standard error	annual adult survival rate	taylor series standard error
<i>Turtur abyssinicus</i>	0.9741	0.0148	0.9041	0.0526
<i>Colius striatus</i>	0.6525	0.1680	0.1939	0.1918
<i>Lybius vieilloti</i>	0.9725	0.0237	0.8984	0.084
<i>Chlorocichla flavicollis</i>	0.8105	0.1240	0.446	0.2622
<i>Pycnonotus barbatus</i>	0.7658	0.0469	0.3588	0.0844
<i>Camaroptera brachyura</i>	0.8174	0.0519	0.4609	0.1125
<i>Platysteira cyanea</i>	0.9198	0.0504	0.7252	0.1528
<i>Cyanomitra verticalis</i>	0.8750	0.0905	0.5987	0.2379
<i>Chalcomitra senegalensis</i>	0.7806	0.0980	0.386	0.1862
<i>Cinnyris venusta</i>	0.9888	0.0075	0.9575	0.0278
<i>Zosterops senegalensis</i>	0.7547	0.0984	0.3391	0.1699
<i>Tchagra senegala</i>	0.8115	0.1118	0.4481	0.2371
<i>Sporopipes frontalis</i>	0.7988	0.1215	0.4219	0.2465
<i>Ploceus luteolus</i>	0.8457	0.2109	0.5251	0.5031
<i>Ploceus nigricollis</i>	0.8254	0.0727	0.4784	0.162
<i>Ploceus vitellinus</i>	0.9629	0.0260	0.8648	0.0899
<i>Lagonosticta rufopicta</i>	0.9273	0.0344	0.7484	0.1066
<i>Lagonosticta senegala</i>	0.9687	0.1112	0.8851	0.3903
<i>Lagonosticta sanguinodorsalis</i>	0.8967	0.0651	0.6578	0.1835
<i>Estrilda caerulescens</i>	0.9038	0.0449	0.6781	0.1295
<i>Uraeginthus bengalus</i>	0.8489	0.0839	0.5328	0.2023
mean	0.8620	0.0194	0.5957	0.048

Table 2.4. Phylogenetically Independent Contrasts of survival rates between sites. P values where a significant difference in survival rates exists, even when phylogeny is taken into account, are shown in italics. Data for each location was obtained from the following studies: Malawi - (Peach *et al.* 2001); Panama - (Karr *et al.* 1990); Trinidad - (Johnston *et al.* 1997); French Guiana - (Jullien & Clobert 2000); Peru - (Francis *et al.* 1999); Puerto Rico - (Faaborg & Arendt 1995)

	<b>N. temperate</b>	<b>Nigeria</b>	<b>Malawi</b>	<b>Panama</b>	<b>Trinidad</b>	<b>French Guiana</b>	<b>Peru</b>
	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>
<b>Nigeria</b>	0.5924						
<b>Malawi</b>	<b><i>0.0009</i></b>	0.4940					
<b>Panama</b>	0.5239	0.6164	0.2177				
<b>Trinidad</b>	<b><i>0.0057</i></b>	0.6266	0.1132	<b><i>0.0387</i></b>			
<b>French Guiana</b>	0.3419	0.0828	0.2402	0.2289	0.3124		
<b>Peru</b>	0.1857	0.2230	0.3476	<b><i>0.0258</i></b>	0.5950	<b><i>0.0214</i></b>	
<b>Puerto Rico</b>	0.1103	0.2976	0.3366	0.1325	0.1395	0.1563	0.1170

Survival on average is significantly greater in the tropical ( $0.62 \pm 0.014$ , N=127) compared to north temperate zones ( $0.54 \pm 0.012$ , N=78):  $t_{200.8} = 4.7$ ,  $P < 0.001$ , using all available single species estimates.

In addition, survival clearly varies within (Table 2.3) and between (Table 2.4) studies and also within species between sites. Across the seven tropical studies compared, survival was estimated more than once in thirteen species and five of these species had survival rates that were significantly different between sites (Table 2.5). There was greater variation in survival of African species than neo-tropical species (mean difference in survival: Africa =  $0.448 \pm 0.06$ ; neo-tropics =  $0.129 \pm 0.02$ ; t-test:  $t_{18} = 6.234$ ,  $p < 0.001$ ).

Table 2.5. Survival rates of species with more than one estimate. Standard error of the survival estimate was not calculated for *Coereba flaveola* in Puerto Rico (Faaborg & Arendt 1995). Significance levels for the t statistic assumed infinite degrees of freedom.

species	location 1	location 2	location 1		location 2		s.e.d.	t	p
			survival	s.e.	survival	s.e.			
<i>Pycnonotus barbatus</i>	Nigeria	Malawi	0.359	0.084	0.743	0.038	0.092	4.165	<0.001
<i>Camaroptera brachyura</i>	Nigeria	Malawi	0.461	0.133	0.735	0.062	0.147	1.867	ns
<i>Chalcomitra senegalensis</i>	Nigeria	Malawi	0.39	0.186	0.903	0.081	0.203	2.529	<0.001
<i>Cinnyris venusta</i>	Nigeria	Malawi	0.958	0.028	0.549	0.078	0.083	4.935	<0.001
<i>Lagonosticta senegala</i>	Nigeria	Malawi	0.885	0.39	0.228	0.101	0.403	1.631	ns
<i>Xiphorhynchus pardalotus</i>	French Guiana	Trinidad	0.87	0.049	0.757	0.075	0.090	1.261	ns
<i>Turdus albicollis</i>	French Guiana	Trinidad	0.34	0.074	0.585	0.067	0.100	2.454	0.05
<i>Myrmotherula axillaris</i>	French Guiana	Trinidad	0.87	0.053	0.7	0.11	0.122	1.392	ns
<i>Thamnomanes ardesiacus</i>	French Guiana	Peru	0.71	0.045	0.73	0.007	0.046	0.439	ns
<i>Myrmotherula axillaris</i>	French Guiana	Peru	0.87	0.053	0.7	0.11	0.122	1.392	ns
<i>Formicarius analis</i>	French Guiana	Peru	0.42	0.051	0.56	0.12	0.130	1.074	ns
<i>Myrmotherula axillaris</i>	French Guiana	Panama	0.87	0.053	0.6	0.05	0.073	3.706	<0.001
<i>Formicarius analis</i>	French Guiana	Panama	0.42	0.051	0.42	0.07	0.087	0.000	ns
<i>Mionectes oleaginea</i>	Panama	Trinidad	0.51	0.04	0.627	0.073	0.083	1.406	ns
<i>Dendrocincla fuliginosa</i>	Panama	Trinidad	0.69	0.05	0.787	0.033	0.060	1.619	ns
<i>Myrmotherula axillaris</i>	Panama	Trinidad	0.6	0.05	0.7	0.11	0.121	0.828	ns
<i>Myrmotherula axillaris</i>	Peru	Trinidad	0.7	0.11	0.845	0.054	0.123	1.183	ns
<i>Myrmotherula axillaris</i>	Peru	Panama	0.7	0.11	0.6	0.05	0.121	0.828	ns
<i>Formicarius analis</i>	Peru	Panama	0.56	0.12	0.42	0.07	0.139	1.008	ns
<i>Coereba flaveola</i>	Puerto Rico	Trinidad	0.51	?	0.647	0.042		?	?

### Life history trade-offs with adult survival

The difference within adult survival predicted from the models for population stability with one brood per year in both regions was 0.09 rising to 0.28 with three broods per year (Figure 2.1). As broods per year in tropical areas may be as low as one per year (Fogden 1972; König & Gwinner 1995; Jullien & Thiollay 1998), then predicted adult survival rate is 0.87 (0.25 higher than observed): the results suggest that adult survival alone on average cannot account for lower clutch size in the tropics. In north temperate regions the number of breeding attempts per year is thought to be approximately 1.5 (Martin 1995) to 1.8 (Cramp & Perrins 1985), then predicted survival rate is 0.66 to 0.59 respectively (0.12 – 0.05 higher than observed). The observed value of 0.54 for north temperate birds is met with approximately two broods per year (Figure 2.1).

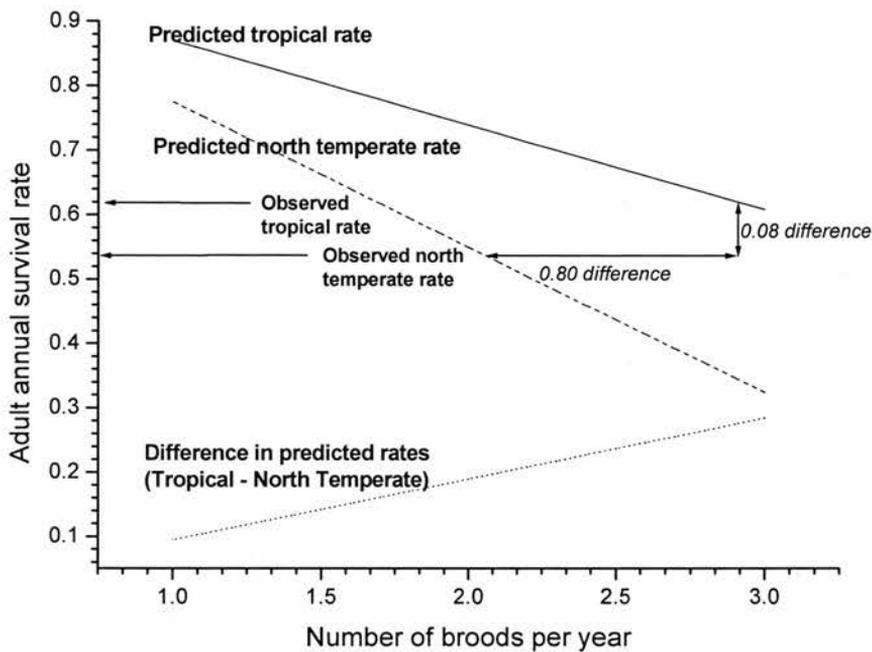


Figure 2.1: Results of a simple model to predict how adult survival would vary so that it balanced yearly recruits into the breeding so that the population remained stable, over a range of number of broods per year, for both north temperate and tropical birds. See text for model assumptions.

If survival rates are not sufficiently high or indeed not uniformly high across the tropics but smaller clutch sizes are (as they appear to be Yom-Tov 1994; Geffen & Yom-Tov 2000) then other life history traits or factors must compensate. These might be:

***1: Variable nest predation.***

Within climatic zones, nest predation is a good explanatory variable for clutch size (Martin *et al.* 2000) suggesting that if adult survival rates and clutch size are low in the tropics then this may be balanced by lower nest predation. Using the same modelling approach and assumptions as above, but using observed north temperate (0.54) and tropical (0.62) survival rates to predict nest survival, the difference in nest survival between tropical and north temperate regions was

predicted to vary from 0.30 with one brood per year in both regions, decreasing to 0.10 with three broods per year (Figure 2.2).

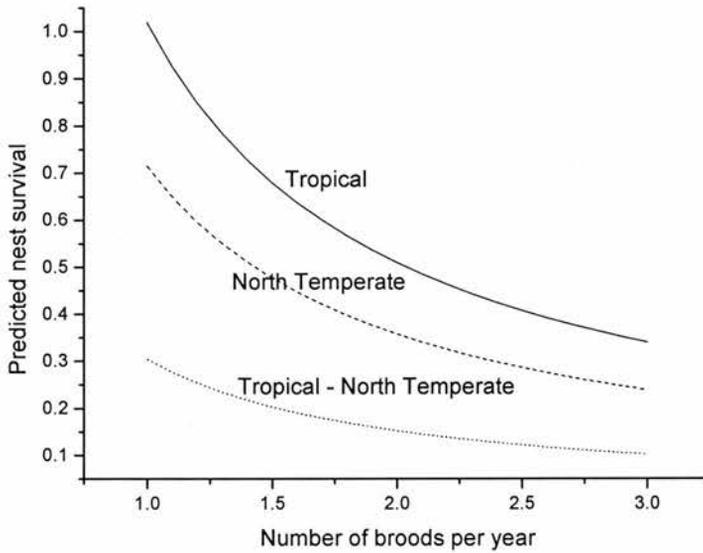


Figure 2.2: Results of a simple model to predict how nest survival would vary so that it balanced yearly recruits into the breeding population so that the population remained stable, over a range of number of broods per year, for both north temperate and tropical birds. Assumptions as in Figure 2.1, except using adult survival of 0.62 for tropics and 0.54 for north temperate birds (see text).

Therefore, if nest survival is to compensate for the lower clutch size, given the observed adult survival rates, then nest survival must be significantly higher in the tropics on average. A study by Martin *et al.* (2000), however, found that tropical and north temperate daily nest survival was not significantly different (mean =  $0.033 \pm 0.003$ ,  $N = 16$  phylogenetically matched pairs, resulting in an average nest survival for a combined average incubation and nestling period of 32 days (Geffen & Yom-Tov 2000) of  $0.35 \pm 0.04$ ). It is interesting to note that although nest survival was found not to be significantly different in Martin *et al.*'s (2000)

study, the values of nest survival were  $0.39 \pm 0.05$  for tropics and  $0.31 \pm 0.04$  for temperate regions: if these values represent the true difference and the lack of a difference is a Type II error because of limited power, then nest survival rate may also partly compensate for the discrepancy between adult survival and clutch size in tropical regions (0.05 difference in predicted adult survival rate for one brood per year rising to 0.16 for three broods per year).

Furthermore *if* higher nest predation for a species in the tropics was balanced by increased clutch size there should be a negative relationship between clutch size and adult survival in the tropics. Although Ghalambor & Martin (2001) found a direct negative relationship between clutch size and adult survival both within and between their north temperate and south temperate samples, we found no significant relationship between clutch size and adult survival for our sample from Nigeria ( $\text{Adj } R^2 = 0.003, p = 0.317$ ) or for 56 neo-tropical species from the six studies described previously ( $\text{Adj } R^2 = -0.02, p = 0.793$ ). However, we did find that there was a significant negative relationship with data from Malawi ( $\text{Adj } R^2 = 0.26, p = 0.004$ ) (Peach *et al.* 2001). There was also no significant relationship within our temperate sample ( $\text{Adj } R^2 = 0.02, p = 0.22$ ). So, it would appear that nest predation rates are not a general factor explaining variation in clutch size between climatic zones.

## ***2: Longer nesting season.***

Repeated breeding resulting in more than one brood within a year may offset low clutch size. The assumption that tropical habitats endure less seasonal extremes in climate than north temperate habitats has resulted in the suggestion that the duration of the nesting season may be greater in the tropics (Wyndham 1986;

Magrath *et al.* 2000) and therefore birds are able to produce multiple broods within a breeding season. Using the same modelling approach and assumptions as for adult survival, but using the observed values for adult survival of 0.54 for north temperate and 0.62 for tropical birds, and 1.8 as the number of broods per year for north temperate birds, tropical birds must make 0.80 attempts more per year on average to compensate for the lower clutch size (Figure 2.1). However, number of broods per year does not appear to differ much between tropical and north temperate zones (Martin 1996). Indeed, it may be smaller (Fogden 1972; Konig & Gwinner 1995; Jullien & Thiollay 1998).

### ***3: Extended parental care.***

Low clutch size may be offset by increased parental investment through extended parental care (here delayed natal dispersal was included as a form of parental care), so that parents invest more during the post-fledging stage and beyond the nutritional independence of their offspring. Using the same modelling approach as above, the post-fledging survival values that balance observed clutch size and adult survival values, using observed values of nest survival as above, vary from 0.29 with one breeding attempt per year in both regions, decreasing to 0.10 with three breeding attempts (Figure 2.3).

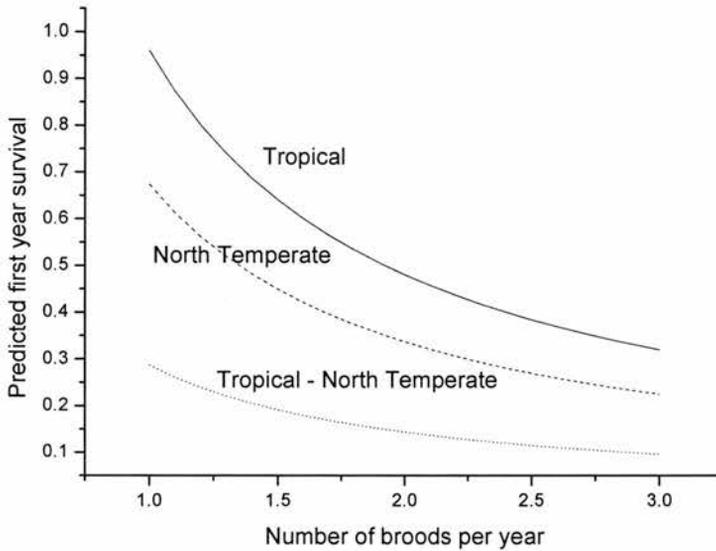


Figure 2.3: Results of a simple model to predict how first year survival would vary so that it balanced yearly recruits into the breeding population so that the population remained stable, over a range of number of broods per year, for both north temperate and tropical birds. Assumptions as in Figure 1, except using adult survival of 0.62 for tropics and 0.54 for temperate birds (see text).

Therefore, if first year survival is to compensate for the lower clutch size, given the observed adult survival rates, then first year survival must be significantly higher in the tropics on average. It was shown very recently (Schaefer *et al.* 2004; Russell *et al.* 2004b) that tropical passerines had longer fledging periods and tolerated their offspring in the natal territory for longer than north temperate species. If parental care is extended then post-juvenile survival rates are likely to be higher. There have been very few measures of survival of juvenile birds in the tropics, either measuring survival to nutritional dependence, or to adulthood. Recently post-fledging survival was measured in two *Sylvia* warblers in Kenya and found to be high: *Sylvia lugens* = 55.4%; *Sylvia boehmi* = 69.2% (Schaefer *et al.* 2004), and survival of juvenile *Philetairus socius* in South Africa did not differ from adult survival at 66% (Covas *et al.* 2004). In north temperate birds post-fledging survival is much lower than this: a mean of  $33.0 \pm 3.0\%$  (Ringsby *et al.*

1998; Bradbury *et al.* 2000; Sillett & Holmes 2002; McGowan *et al.* 2003; Reid *et al.* 2003).

If, on average, tropical species have similar number of broods compared to north temperate species (i.e. around 1.8) then post-fledging care would need to increase survival by 0.16 to 0.53 (Figure 3), approximately a 46% increase above the values known for post-fledging survival in north temperate regions. If tropical species only have one brood per year (Fogden 1972; König & Gwinner 1995; Jullien & Thiollay 1998) then predicted first year survival would have to be as high as 0.96 to maintain a stable population. However, some tropical birds may be raising two or even three broods per year (see review in Martin 1996). Many studies have, however, inferred the number of broods per year, rather than measuring it directly from known pairs of birds (e.g. see Snow & Snow 1963). There is a paucity of data that empirically measures brood frequency in tropical birds and further research is needed.

## **Conclusion**

This study has shown that adult survival rate differences between north temperate and tropical areas are not particularly large or indeed uniform, and cannot compensate solely for the lower productivity associated with lower clutch sizes, and that nest survival and/or number of broods per year and/or first year survival must be higher to compensate. The limited empirical evidence to date, however, only supports extended parental care and first year survival being greater in tropical regions. Therefore the current paradigm, that a higher adult survival rate in the tropics adequately explains the marked difference in clutch size between

north temperate and tropical birds, should be rejected. A paradigm shift is required and it is suggested that further research should continue to examine other life history trade offs in tropical birds, particularly extended parental care, post-fledging survival and juvenile survival.

More data are clearly needed to determine the number of broods on average in tropical birds. While there have been few studies it appears that post-fledging survival may be similar to adult survival (Schaefer *et al.* 2004; Covas *et al.* 2004), suggesting both that first year survival is much higher in tropical birds and that tropical birds must have more than one brood per year on average. These findings agree with the prediction from life history theory that there is a trade off between numbers and fitness of offspring (Lack 1947) and so north temperate birds have reduced juvenile survival as parents provide fewer resources to each individual offspring. To date the only life history traits that have been adequately demonstrated to differ consistently between tropical and north temperate passerines are clutch size and extended parental care.

This study demonstrated that there is sufficient variation in the tropics to better understand life-history trade-offs. Exploring such trade offs in tropical birds should lead to greater insight into how life history processes have evolved in north temperate birds, because processes there may be dominated more by uniform ecological constraints.

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## **Chapter 3: Life history traits and body mass relationships in small tropical and north temperate birds**

### **Summary**

Body size has often been considered a nuisance variable when examining life history trade offs. In studies of tropical birds it has often been controlled for but seldom tested. Differences in climate between the tropics and north temperate regions were predicted to create important differences in the energetic constraints of birds of differing sizes. Body mass correlates across a range of important life history traits in tropical and north temperate birds were examined and the trade offs between them discussed. These relationships were explored using phylogenetically independent methods giving new insights into the evolution of life history trade offs in both tropical and north temperate regions. Results suggested that these trade offs may differ greatly between tropical and north temperate birds and that they have different evolutionary routes. While north temperate birds appeared to be pre-adapted to their environment, tropical birds have adapted their life history to their environment where age specific predation appears to be a major source of selection pressure.

### **Introduction**

Body size will clearly determine many of the energetic considerations of birds and therefore how well they survive at extremes of temperature and when energy is in short supply (Walsberg 1983). Such temperature extremes and periodic energy

shortages occur regularly in northern temperate areas, yet are much less common in both tropical forests and savannahs. Therefore there are likely to be differences in the selection acting on body size and how this influences life history traits in both regions.

Although body size correlates in life history traits have attracted a great deal of attention, they have largely been dismissed as a nuisance variable (Bennett & Owens 2002). However, many of these studies focussed on general patterns across the whole avian taxa. This approach may have swamped finer patterns within lower taxa and differences between climatic regions were lost. The majority of studies have been undertaken in the north temperate climatic zone, and so general principles have been drawn from a relatively small region of the world, with much lower diversity and dominated by the effects of winter climate. By re-examining important life history traits, such as survival, and their relationship with body size in different climatic zones further insights into the evolutions of both systems may be made.

Survival correlates with body mass across a wide range of species (Blueweiss *et al.* 1978) and was shown to be significant in small passerine birds in Britain (Dobson 1990). While this relationship has often been assumed in tropical birds, and included in models comparing survival rates between north temperate and tropical birds (Johnston *et al.* 1997; McCleery *et al.* 1998; Jullien & Clobert 2000; Peach *et al.* 2001; Ghalambor & Martin 2001), it has seldom been tested. Francis *et al.* (1999) showed that there was no relationship between survival and body mass in Peruvian forest birds. They also showed that this was also true in forest birds studied by Johnston *et al.* (1997) in Trinidad.

In this study new data from West Africa was analysed along with 6 previously published studies from the tropics to test the hypotheses that:

1. That any positive relationship between body mass and survival is less strong, or absent, in tropical regions that lack strong selection against small body size because of energetic considerations
2. If mass correlates positively with survival in temperate regions, but does not in tropical regions, then there will be a negative relationship between mass and: (i) fecundity and/or (ii) nest survival and/or (iii) juvenile survival and/or (iv) parental care in temperate regions to compensate for increased mortality at low mass, but not in tropical regions.

## **Methods**

### **Data collection**

Survival rates and body mass data were collected during field work on the Jos plateau in central Nigeria (09°52' N, 08°58' E). Trapping was conducted according to Constant Effort Site (CES) protocols (Bairlein 1995) where nets were placed in fixed positions for 14 days approximately every four months. Nets were operated on each of these days from dawn (0600 hours) to 1100 hours. Every bird trapped was given a unique identifying mark (metal ring with an individual number) and a unique set of colour marks in order to allow individual recognition in the field. Between each trapping session birds were re-sighted and individually identified where possible. Only birds trapped and identified as adults were included in these analyses in order to remove the influence of lower juvenile

survival combined with higher juvenile dispersal producing a low estimate that was not comparable with other studies. These data were then analysed using Barker's model (Barker 1999) in Program MARK (White & Burnham 1999). Apparent adult survival estimates were obtained for 21 species (Table 3.1).

Table 3.1: Mean annual adult survival rates of tropical West African birds measured using mark-recapture with re-sightings and modelled according to (Barker 1999).

Species	Annual adult survival rate	taylor series standard error
<i>Zosterops senegalensis</i>	0.3391	0.1699
<i>Lagonosticta rufopicta</i>	0.7484	0.1066
<i>Turtur abyssinicus</i>	0.9041	0.0526
<i>Tchagra senegala</i>	0.4481	0.2371
<i>Ploceus nigricollis</i>	0.4784	0.1620
<i>Platysteira cyanea</i>	0.7252	0.1528
<i>Pycnonotus barbatus</i>	0.3588	0.0844
<i>Camaroptera brevicaudata</i>	0.4609	0.1125
<i>Nectarinia verticalis</i>	0.5987	0.2379
<i>Estrilda caerulescens</i>	0.6781	0.1295
<i>Ploceus luteolus</i>	0.5251	0.5031
<i>Lagonosticta senegala</i>	0.8851	0.3903
<i>Uraeginthus bengalus</i>	0.5328	0.2023
<i>Lagonosticta sanguinodorsalis</i>	0.6578	0.1835
<i>Nectarinia senegalensis</i>	0.3860	0.1862
<i>Colius striatus</i>	0.1939	0.1918
<i>Sporopipes frontalis</i>	0.4219	0.2465
<i>Nectarinia venusta</i>	0.9575	0.0278
<i>Lybius vieilloti</i>	0.8984	0.0840
<i>Ploceus vitellinus</i>	0.8648	0.0899
<i>Chlorocichla flavicollis</i>	0.4460	0.2622
Mean	0.5957	0.0480

In addition to new data collected in West Africa I analysed published data from Malawi in southern Africa (Peach *et al.* 2001), Trinidad (Johnston *et al.* 1997), Puerto Rico (Faaborg & Arendt 1995), Panama (Brawn *et al.* 1999), French Guiana (Jullien & Clobert 2000) and Peru (Francis *et al.* 1999). The data used by Dobson (1990) which showed a significant positive relationship between survival and body mass in British birds was included in an expanded data set that included

the north temperate data from Peach *et al.* (2001), Johnston *et al.* (1997) and Martin (1995) but with migrant species removed.

Mass data was measured in the field in West Africa using either Pesola spring balances or an Ohaus Scout II electronic balance. Body mass of birds from other studies was collated from a wide variety of sources (Cramp & Perrins 1985; Fry *et al.* 1985; Dunning 1992; Rising 1996; Geffen & Yom-Tov 2000; Conway & Martin 2000; Watson 2003; Iwaniuk & Arnold 2004). All body masses were then log-transformed to normalise the distribution.

Annual fecundity was measured as the mean number of broods raised per year multiplied by the mean clutch size for each species. Clutch size and number of successful broods per year data were collated from various sources (Cramp & Perrins 1985; Fry *et al.* 1985; Geffen & Yom-Tov 2000). However, there was very little data available for brood rate in many tropical species, therefore when the number of broods per year was published as being the same across several species of the same family, it was assumed to be the same for the species in question within this data set.

Nest survival data was collated from many published studies for tropical: (Sargent 1993; Mermoz & Reboreda 1998; Robinson *et al.* 2000; Mezquida & Marone 2001; Seixas & Mourao 2002; Schaefer *et al.* 2004) and temperate birds: (Westmoreland & Best 1985; Tyler 1992; Martin 1993; Post 1995; Mitchell *et al.* 1996; Granfors *et al.* 1996; Winter 1999; Willson & Gende 2000; Brickle *et al.* 2000; Bradbury *et al.* 2000; Stoate & Szczur 2001; McGowan 2001; Kosinski 2001; Doherty & Grubb 2002; Donald *et al.* 2002; Drachmann *et al.* 2002;

Ammer 2003; Knutson *et al.* 2004). Only published data that had measured nest survival using Mayfield's method (Mayfield 1961) were used.

There are surprisingly few published estimates of juvenile survival for north temperate birds: see (Ringsby *et al.* 1998; Bradbury *et al.* 2000; Sillett & Holmes 2002; McGowan *et al.* 2003; Reid *et al.* 2003). There are also very few published studies that have measured juvenile survival in tropical birds: (Zann & Runciman 1994; Russell & Rowley 2000; Schaefer *et al.* 2004; Covas *et al.* 2004). Only four of these studies specifically measured (rather than inferred) juvenile survival in passerine birds from the tropics. Two species, *Sylvia lugens* and *S. boehm* (Schaefer *et al.* 2004), were studied in east Africa but the remaining three species were strictly speaking from south temperate climates. One species was from South Africa, *Philetairus socius* (Covas *et al.* 2004), and two from Australia, *Taenopygia guttata* (Zann & Runciman 1994) and *Malurus elegans* (Russell & Rowley 2000). However, the life history of south temperate passerines has previously been shown to closely match that of tropical species (Yom-Tov 1994; Martin *et al.* 2000).

Extended parental care was measured as the time juvenile birds spent with their parents after leaving the nest (fledging period) using data from (Geffen & Yom-Tov 2000).

## **Analysis**

All statistical analyses were performed using SPSS 11.5 (SPSS for Windows 2002) and according to Sokal & Rohlf (1995). All mass data was log transformed in order to meet assumptions of linearity.

Analyses that use species as statistically independent data are not valid as closely related species may share traits through common ancestry (Harvey & Pagel 1991). It was therefore necessary to control for such effects using Phylogenetically Independent Contrasts (PICs) using Comparative Analysis by Independent Contrasts (CAIC) software (Purvis & Rambaut 1995). Two different procedures were required to, firstly, determine if relationships within climatic zones (tropical or north temperate) were independent of phylogeny, and, secondly, to determine if differences between climatic zones were independent of phylogeny. Each procedure required a different approach within CAIC.

### ***Within climate testing***

For each life history trait each species, its body mass (log transformed) and life history variable was entered into CAIC using phylogeny based on Sibley & Ahlquist (1990). As branch length data was not available a punctuational model of evolution was assumed, with branch lengths being equal in the phylogeny. The predictor variable for each trait was body mass. Using the CRUNCH algorithm, CAIC produced a contrast value across each node in the phylogeny for each variable. These variables were then plotted and were assessed by linear regression forced through the origin. If the relationship between the trait and body mass was true in the absence of phylogenetic effects the gradient of the regression will be significantly different from zero. This was tested statistically using t-tests. The relationships between the contrasts of the various life history traits and the contrasts of the body mass (log transformed) was analysed using linear regressions. Note that the  $R^2$  value for these analyses were included only for comparisons between PIC models. It was not possible to compare  $R^2$  values when

the intercept is forced through the origin with  $R^2$  values of models that include an intercept.

### ***Between climate testing***

For each trait the data from each climate was pooled. The life history variable and body mass (log transformed) for each species was entered into CAIC and the CRUNCH algorithm was again used to provide contrast values for each variable (life history trait and body mass), with body mass as the predictor variable. These contrast values were plotted and the life history trait contrasts were regressed on body mass contrasts with the intercept forced through the origin. The slope of this line was fitted to the plot of the original data (life history trait vs log body mass) and the residuals measured for each species. These residuals were then entered into CAIC and analysed using the BRUNCH algorithm with climatic zone as the dependent (dichotomous) variable. If there were no difference in the trait between each climate half of the contrasts would have been positive and half negative, with the mean being zero. Therefore a t-test was performed to determine if the mean contrast value differed significantly from zero.

## **Results**

### **Within climate testing**

#### ***Adult survival rates***

When the relationship between adult survival rates and body mass was examined for tropical species by study only two sites were found to be significant (Table 3.2). The relationship shown with the Puerto Rico data was weak and was only marginally significant at the 5% level and the sample size was small ( $n = 9$ ). The

data from Panama was also significant at the 5% level, but again this was only marginally, but the sample size was larger ( $n = 25$ ). So it would appear that in tropical birds there is little evidence for a relationship between survival and body mass. Indeed, when the data was pooled across all studies the relationship was not significant (Fig 3.1), or when these data were tested as Phylogenetically Independent Contrasts (PIC) (Fig. 3.2).

Table 3.2: Linear regression of log transformed body mass on adult survival for this study (Nigeria) and 6 other studies of tropical bird survival rates. Regression = equation of linear regression line of best fit;  $R^2$  = coefficient of determination; dof = degrees of freedom, error degrees of freedom; p = probability value for significance of regression line.

Site	Regression	$R^2$	F	dof	p
Nigeria	$y = 0.80 - 0.17x$	0.006	1.12	1, 19	0.30
Malawi	$y = 0.16x + 0.46$	0.003	1.86	1, 26	0.19
Puerto Rico	$y = 0.17x + 0.47$	0.39	6.04	1, 7	0.04
Trinidad	$y = 0.001x + 0.65$	0.07	0.00	1, 15	0.99
French Guiana	$y = 0.85 - 0.18x$	0.009	1.13	1, 14	0.31
Panama	$y = 0.16x + 0.35$	0.13	4.42	1, 23	0.05
Peru	$y = 0.83 - 0.11x$	0.04	1.52	1, 12	0.24

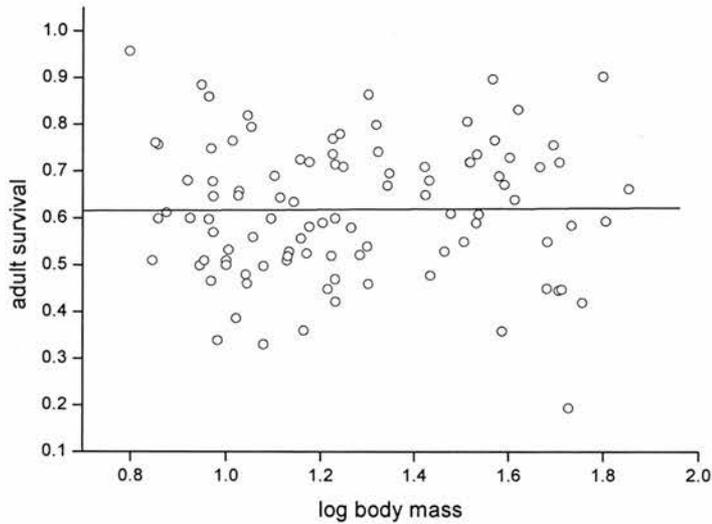


Figure 3.1 Relationship between log transformed body mass and mean annual survival of adults in 100 tropical bird species across 7 studies (including this study) in Africa and the neo-tropics.  $y = 0.006x + 0.61$ ;  $R^2 = 0.01$ ;  $F_{1,98} = 0.014$ ;  $p = 0.91$ .

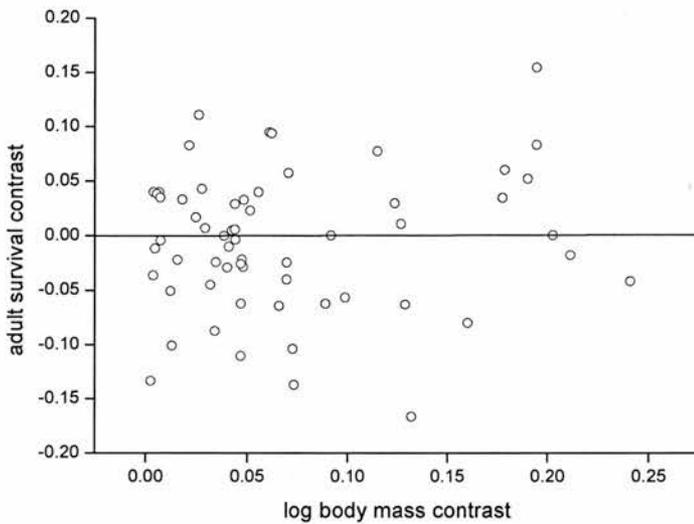


Figure 3.2: Relationship between log transformed body mass contrast values and contrast values of mean annual survival of adults in 100 tropical bird species across 7 studies (including this study) in Africa and the neo-tropics. Linear regression:  $m = 0.005 \pm 0.09$ ;  $R^2 = 0.02$ ;  $F_{1,59} = 0.003$ ;  $p = 0.96$ .

For north temperate species, a significant positive relationship was found in the 78 species analysed (Fig. 3.3) but not when analysed as PICs (Fig 3.4).

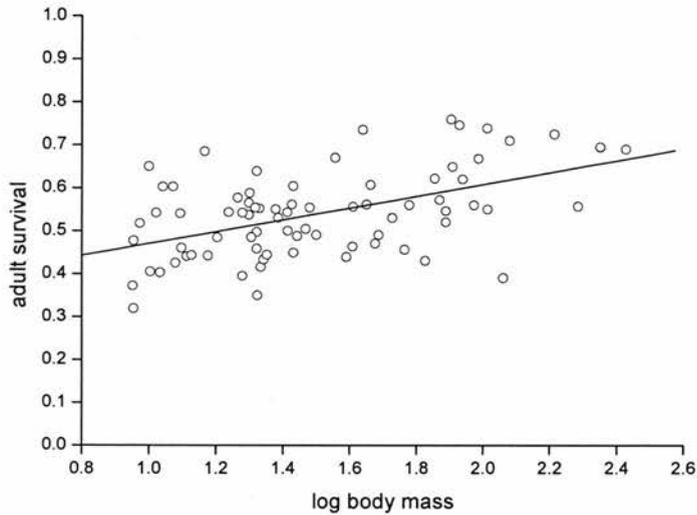


Figure 3.3 - Relationship between log transformed body mass and mean annual survival of adults in 78 north temperate bird species.  $y = 0.14x + 0.33$ ;  $R^2 = 0.26$ ;  $F_{1,77} = 28.06$ ;  $p < 0.001$ .

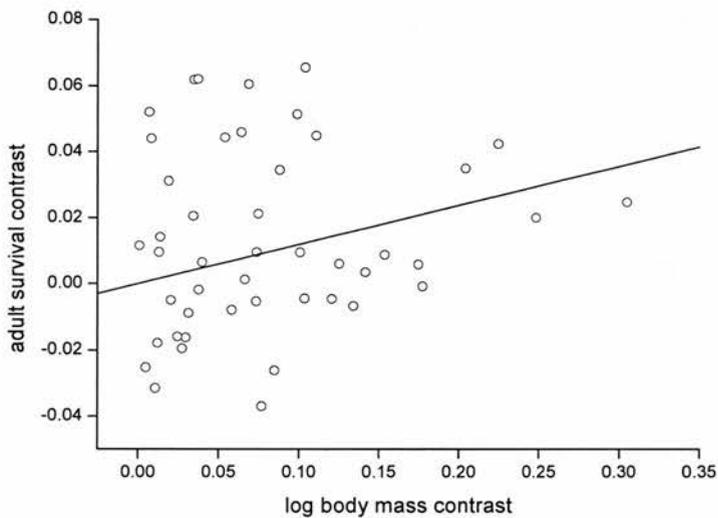


Figure 3.4 - Relationship between log transformed body mass contrast values and contrast values of mean annual survival of adults in 46 contrasts of 78 north temperate bird species. Linear regression:  $m = 0.07 \pm 0.05$ ;  $R^2 = 0.03$ ;  $F_{1,46} = 2.65$ ;  $p = 0.11$

**(i) Fecundity**

From these observations it was predicted that in order to maintain stable populations smaller north temperate birds must have a higher annual fecundity than larger north temperate birds (within the range of body mass sampled here),

but there should be no such relationship in tropical birds. However a significant negative relationship in both north temperate and tropical birds was found (Figure 3.5), although only in tropical but not north temperate birds when phylogeny was controlled (Fig 3.6).

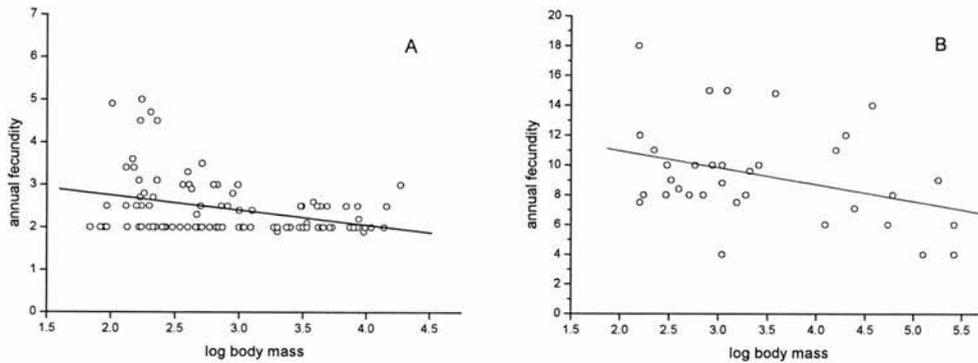


Figure 3.5: Observed relationship between annual fecundity and log transformed body mass for tropical (A) and north temperate (B) birds. Tropical birds (A):  $y = -0.75x + 3.39$ ;  $R^2 = 0.13$ ;  $F_{1,103} = 15.93$ ;  $p < 0.001$ ; north temperate birds (B):  $y = -2.63x + 13.24$ ;  $R^2 = 0.10$ ;  $F_{1,35} = 5.11$ ;  $p = 0.03$ .

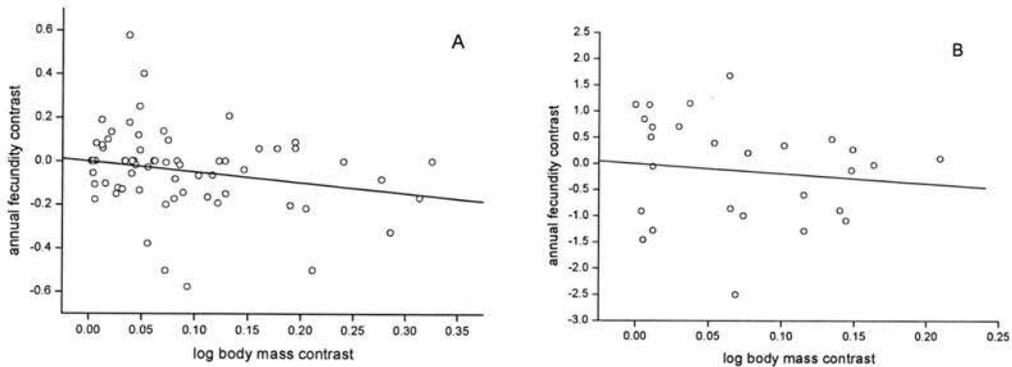


Figure 3.6: Observed relationships between annual fecundity contrast values and log transformed body mass contrast values for tropical (A) and north temperate (B) birds. Tropical birds (A): 65 contrasts of 102 species. Linear regression fit:  $m = -0.49 \pm 0.19$ ;  $R^2 = 0.08$ ;  $F_{1,64} = 6.84$ ;  $p = 0.01$ . North temperate birds (B): 27 contrasts of 35 species. Linear regression:  $m = -1.91 \pm 2.00$ ;  $R^2 = 0.003$ ;  $F_{1,26} = 0.913$ ;  $p = 0.35$ .

### *(ii) Nest survival*

Annual fecundity could only be measured as the mean number of broods raised per year multiplied by the mean clutch size for each species and therefore was an indication of the productivity of chicks, and not the productivity of juvenile birds

potentially able to recruit into the adult population. Survival of both eggs and then dependent young could both potentially influence the annual productivity of adult birds. It was therefore predicted that there would be either a positive relationship between body mass and nest survival or a positive relationship between juvenile survival and body mass, or some combination of the two. Neither tropical nor north temperate birds had a significant relationship (Fig 3.7). When phylogeny was controlled for the relationships remained not significant (Fig 3.8).

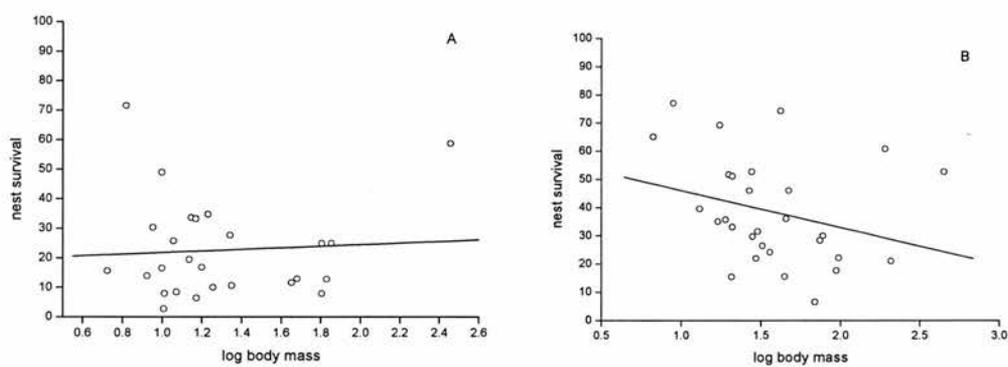


Figure 3.7: Observed relationships between nest survival and log transformed body mass for tropical (A) and north temperate (B) birds. Tropical birds (A): Linear regression:  $y = 1.78x + 19.96$ ;  $R^2 = 0.04$ ;  $F_{1,25} = 0.05$ ;  $p = 0.83$ . North temperate birds (B): Linear regression:  $y = -8.11x + 49.84$ ;  $R^2 = 0.006$ ;  $F_{1,28} = 0.84$ ;  $p = 0.37$ .

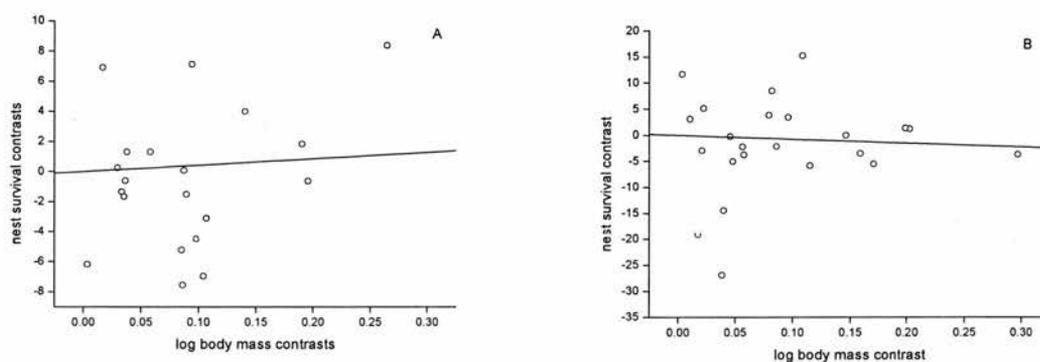


Figure 3.8: Observed relationships between nest survival contrast values and log transformed body mass contrast values for tropical (A) and north temperate (B) birds. Tropical birds (A): 21 contrasts of 26 species. Linear regression fit:  $m = 4.26 \pm 9.21$ ;  $R^2 = 0.04$ ;  $F_{1,19} = 0.21$ ;  $p = 0.65$ . North temperate birds (B): 23 contrasts of 29 species. Linear regression:  $m = -7.52 \pm 16.72$ ;  $R^2 = 0.04$ ;  $F_{1,22} = 0.20$ ;  $p = 0.66$ .

If there is no relationship between mass and overall nest survival in either north temperate or tropical birds then this suggests that there must be a positive relationship between mass and the daily survival rate of nests because larger birds will have longer incubation periods (Drent 1975; Boersma 1982) and chick-rearing periods (Yom-Tov & Hilborn 1981; Walsberg 1983) simply because larger offspring take longer to develop and mature. This was found to be the case when a sample data set was tested (Martin 1995) that contained eight species from Argentina matched phylogenetically with eight species from Arizona in North America. There was a significant positive relationship (Fig. 3.9) between mass and daily survival rate ( $F_{1,13} = 6.0, P = 0.030$ ) controlling for temperate or tropical location as a two level factor ( $F_{1,13} = 2.6, P = 0.13$ ). There was no significant interaction between mass and location ( $F_{1,12} = 0.9, P = 0.37$ ) suggesting that the relationship between mass and daily nest survival rate was the same in temperate and tropical regions.

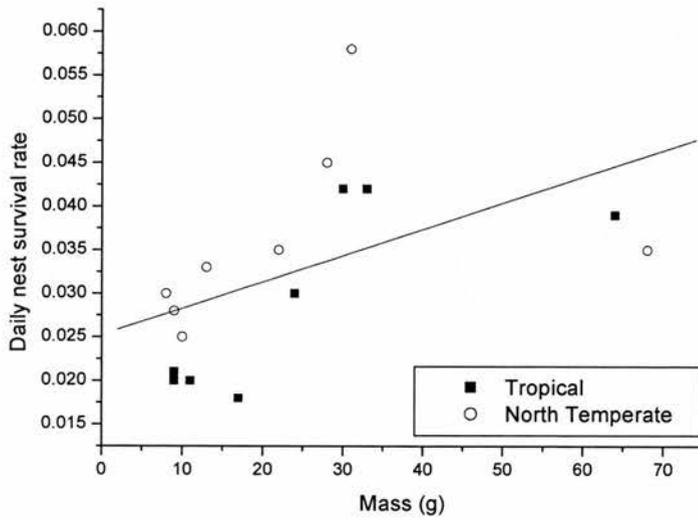


Fig 3.9: Observed relationship between mass and daily nest survival rate.  $y = 0.00030x + 0.025$ ;  $R^2 = 0.22$ ,  $F_{1,15} = 5.2$ ,  $p = 0.039$ .

***(iii) Juvenile survival***

The lack of any relationship between nest survival and body mass suggested that there should be a positive relationship between juvenile survival and body mass in north temperate birds, but not in tropical birds. A weak, non-significant, relationship was found in north temperate but not in tropical species (Fig. 3.10) and also when examined as PICs (Fig 3.11), but sample sizes were very small

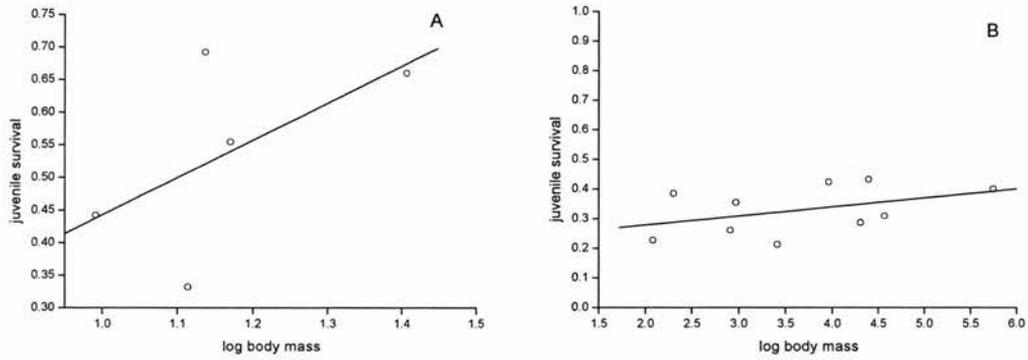


Figure 3.10: Observed relationship between juvenile survival and log transformed body mass for tropical (A) and north temperate (B) passerine birds. Tropical birds (A):  $y = 0.57x - 0.13$ ;  $R^2 = 0.11$ ;  $F_{1,4} = 1.48$ ;  $p = 0.31$ ; north temperate birds (B):  $y = 0.07x + 0.22$ ;  $R^2 = 0.08$ ;  $F_{1,8} = 1.77$ ;  $p = 0.22$ .

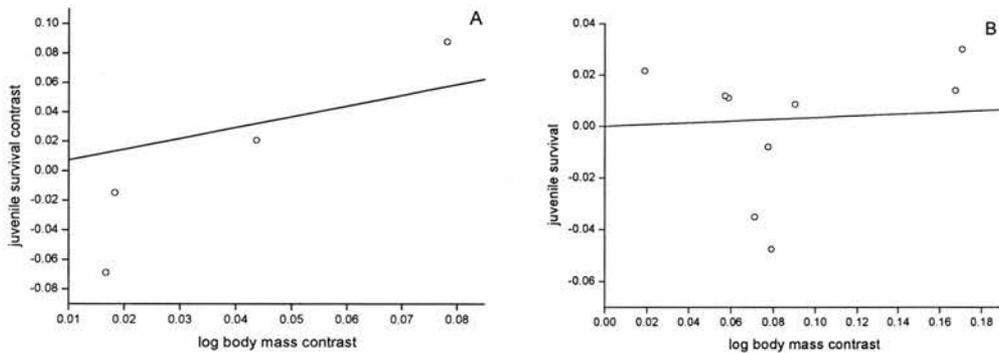


Figure 3.11: Relationship between juvenile survival contrast values and log body mass contrast values for tropical (A) and north temperate (B) birds. Tropical birds (A): 4 contrasts of 5 species. Linear regression fit:  $m = 0.73 \pm 0.57$ ;  $R^2 = 0.14$ ;  $F_{1,19} = 1.64$ ;  $p = 0.29$ . North temperate birds (B): 9 contrasts of 10 species. Linear regression:  $m = 0.03 \pm 0.09$ ;  $R^2 = 0.10$ ;  $F_{1,22} = 0.16$ ;  $p = 0.70$ .

#### (iv) Parental care

Two predictions were made based on two different assumptions of the true relationship between juvenile survival and body mass in tropical birds. If the relationship was assumed to be positive then the mechanism that would assist larger tropical birds to increase the survival of their offspring after fledging could be through extended parental care. However, if it was assumed that there was no

relationship between juvenile survival and body mass in tropical birds then it was predicted that there should also be no relationship between extended parental care and body mass. As it was observed in temperate birds that there was no relationship between juvenile survival and body mass it was predicted that there would be no relationship between extended parental care and body mass. The time juvenile birds spent with their parents after leaving the nest (fledging period) was used as a measure of extended parental care. There was a significant positive relationship between fledging period and body mass in tropical but not in north temperate birds (Figure 3.12).

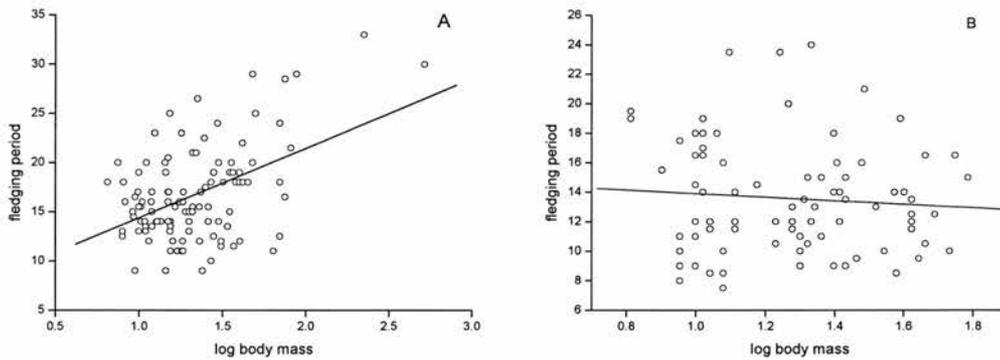


Figure 3.12: Observed relationship between fledging period (days) and log transformed body mass for tropical (A) and north temperate (B) passerine birds. Tropical data (A):  $y = 7.07x + 7.30$ ;  $R^2 = 0.21$ ;  $F_{1,111} = 30.81$ ;  $p < 0.001$ ; temperate data (B):  $y = -1.20x + 15.11$ ;  $R^2 = 0.006$ ;  $F_{1,79} = 0.50$ ;  $p = 0.48$ .

Although the relationship in tropical birds is apparently strong, the data included two species with relatively large body masses and longer fledging periods than most other species (see Fig. 3.13). However, when these outliers were removed the relationship remained positive and significant ( $y = 5.2x + 9.64$ ,  $R^2 = 0.10$ ,  $F_{1,109} = 12.53$ ,  $p = 0.001$ ). In north temperate birds the observed relationship was not significant. Controlling for phylogeny did not change the relationship between

fledging period and body mass in tropical birds, but in north temperate species the relationship was not significant (Fig 3.13).

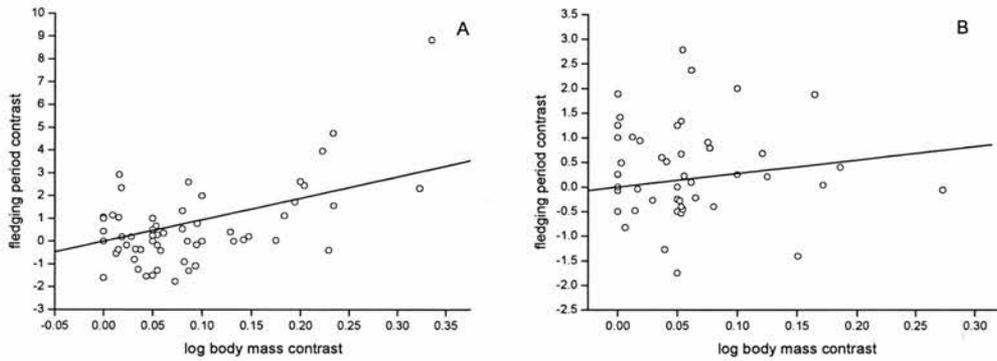


Figure 3.13: Relationships between fledging period contrast values and log transformed body mass contrast values for tropical (A) and north temperate (B) birds. Tropical birds (A): 60 contrasts of 112 species. Linear regression:  $m = 9.50 \pm 1.58$ ;  $R^2 = 0.37$ ;  $F_{1,59} = 36.07$ ;  $p < 0.001$ . North temperate birds (B): 47 contrasts of 159 species. Linear regression fit:  $m = 2.74 \pm 1.77$ ;  $R^2 = 0.03$ ;  $F_{1,46} = 2.40$ ;  $p = 0.13$ .

### Between climate testing

Accounting for phylogeny only changed the pattern of life history traits in north temperate birds. Two relationships were affected by the phylogeny of the species involved; adult survival and body mass and annual fecundity and body mass in north temperate birds (Table 3.3).

Table 3.3: Probability values of each linear regression on the relationship between each life history trait and body mass. Significant values at the 5% level occur in shaded cells. Raw = linear regressions with species as the datum. CAIC = linear regressions with PIC's as the datum.

Trait	TROPICS		NORTH TEMPERATE	
	RAW	CAIC	RAW	CAIC
Adult survival	0.91	0.96	<0.001	0.11
Annual fecundity	<0.001	0.01	0.03	0.35
Nest survival	0.83	0.65	0.37	0.66
Juvenile survival	0.31	0.29	0.22	0.70
Fledging period	<0.001	<0.001	0.48	0.13

However, when differences in each trait between climates were examined (while controlling for body mass) it was found that the observed differences were not significant (Table 3.4). This may have been because any differences were due to phylogenetic effects and not due to independent divergence of the traits themselves, or perhaps more likely, because there were insufficient contrasts in each trait to provide sufficient data for the t-test to have any power.

Table 3.4: Results of t-tests on CAIC contrast values for each life history trait between tropical and north temperate birds. Mean = mean contrast value for the trait, s.e. = standard error of the mean, t = test statistic with test value of 0; d.f. = degrees of freedom, p = probability that mean differs from 0.

Trait	Mean	s.e.	t	d.f.	p
Adult survival	-0.0000013	0.27	0.00	14	1.00
Annual fecundity	0.000022	0.00005	0.44	12	0.67
Nest survival	0.0002	0.00016	1.24	5	0.27
Juvenile survival	-0.01	0.01	-0.98	2	0.43
Fledging period	0.0008	0.0007	1.15	16	0.27

## Discussion

### Pre-adaptation or current life history evolution?

The finding that there was no relationship between body mass and adult survival in tropical birds was surprising as this relationship was known to occur across a

wide range of taxa (Blueweiss *et al.* 1978), including small birds, at least in the north temperate regions (Dobson 1990). While the range of body masses considered in my tropical data set was small, a strong relationship between these variables was found for a similar range of body masses in north temperate birds. The strength of this established relationship in temperate birds (see Dobson 1990) may be however due to non-independence in the data set as the relationship disappears when phylogeny is considered. This presents a problem of interpretation: tests that control for phylogeny inevitably have lower power and so will be prone to Type II errors (accepting the null hypothesis in error). However, when a relationship correctly disappears when phylogeny is controlled for (i.e. there is no true relationship), then this suggests that the presence of any life-history correlations are due to an inherited trait occurring throughout a taxon with many representatives (i.e. at the family level) and not recent adaptation to the current environment. If this is the case here, it would appear that amongst north temperate species the relationship between mass and survival was due to inherited traits and not to recent adaptation of plastic traits (e.g. mass and/or survival) to the current environment.

If the relationship between mass and survival is due to inherited traits and not to recent adaptation of plastic traits in north temperate species then this suggests that north temperate birds have not evolved different life history traits in response to the prevailing environmental conditions, but instead certain taxa with specific life history characteristics were pre-adapted to temperate areas and have colonised and speciated in these areas. It seems likely that the driving environmental force behind this pattern is the winter conditions in the north temperate climate. Low

winter temperatures impose a strong selection pressure on adult survival through higher energy requirements, reduced food availability and predictability and greater predation risk (Rogers 1987; McNamara & Houston 1990; Bednekoff & Houston 1994). All of these pressures are relatively greater on smaller species due to their higher surface area to volume ratio (Walsberg 1983) and a greater number of potential predators (Begon *et al.* 1996).

However this selection perhaps acts so that only those low mass taxa that have high fecundity are able to utilise north temperate areas successfully.

Annual fecundity in tropical species co-varied negatively with body mass, and this was still true when PIC's were examined. Clearly a strong environmental pressure was imposed upon species of different sizes that resulted in local adaptation by those species. In addition to recent adaptation to annual fecundity it appeared that there was also recent adaptation in fledging period. So, amongst tropical birds, and in contrast to north temperate birds, species have adapted to their environment over and above their phylogenetic pre-adaptation.

### **Life history trade-offs with mass in tropical birds**

That there may be no real positive relationship (at least in terms of recent life history evolution) between mass and survival in either tropical or north temperate birds means that there should not be any clear relationships between mass and other life history traits as a consequence: survival variation as a consequence of mass does not need to be compensated for by other life history factors such as fecundity. This was the case for north temperate species. Only survival and fecundity were found to co-vary with body mass in north temperate species, with

lower survival being compensated for by increased fecundity, although these relationships disappeared when controlling for phylogeny. Nevertheless strong relationships, even accounting for phylogeny were found between mass and annual fecundity (negative) and fledging period or extended parental care (positive) in tropical birds (see Table 3.3). That the two relationships should exist together makes sense in the absence of any relationship between mass and adult survival because if birds of higher mass have lower fecundity (in this study clutch size and number of successful broods), then this must be compensated for by increased juvenile survival (in this study fledging period was used as an index of extended parental care). Therefore mass appears to have a more important effect on current life-history trait evolution in tropical birds, compared to temperate birds.

While it appears that smaller north temperate species are being influenced more by their environment than larger species, it may be the opposite in tropical species. Here more intense selection pressure appears to be acting on larger birds, reducing their annual fecundity, resulting in a shift in investment to later in the breeding cycle than smaller species. Larger species may be raising fewer chicks but, if the relationship between juvenile survival and body mass is indeed true, they are able to increase the survival of those few chicks by increasing the period of parental care they provide. The selection pressure resulting in these trade offs may be nest predation. Nest predation (predation of eggs and/or chicks prior to fledging) appears to be higher in the tropics (see Mezquida & Marone 2001), but see also Martin (1996). It was predicted that there would be a positive relationship between nest survival and body mass. However, there was no relationship

between body mass and nest survival. This was perhaps surprising, as small species, by the very nature of their size, should have more predator species able to depredate their smaller eggs and chicks. It may be that across the range of body sizes here there was not a sufficient difference in size to change the predation risk of nests. Tropical birds have been shown to have a very different response to predators at the nest than north temperate species (Ghalambor & Martin 2001). However, it has not been shown whether there is any difference in response to predators across species of different body masses, either in tropical or north temperate species.

However, the costs of nest predation must be greater for birds of higher mass (because they inevitably cannot have as many attempts per year, taking longer for each breeding attempt). The data for number of annual breeding attempts that would show this is very limited however. Although the probability of nest failure may be uniform across bird species of different mass, larger species may be selected to increase juvenile survival by increasing their parental care *when* chicks are successfully raised from the nest because the costs of nest failure increase with mass (see results and Fig. 3.9). This is because larger chicks and eggs must take longer to incubate and develop (Walsberg 1983). This extended parental care, possibly with a longer period to nutritional independence (Russell *et al.* 2004), then means that larger birds *must* inevitably forgo multiple broods per season and have very plastic clutch sizes, so promoting further selection for extended parental care in larger birds. Larger mass birds do not compensate for lower number of breeding attempts per year by breeding for more years because survival does not correlate with mass in tropical birds.

### **Differences between north temperate and tropical birds**

There was no difference between tropical and north temperate climates in any of the relationships tested once phylogeny was accounted for. However, very few contrasts were available, so sample sizes were too small to provide sufficient power to accept the null hypothesis. If the differences observed were truly not significant it may be concluded that these differences were principally due to phylogeny (pre-adaptation) and not recent adaptation to the different environmental conditions between these climatic zones. Unfortunately, the loss of statistical power caused by very few contrasts does not in itself provide any additional information. It may be due to both tropical and temperate birds being clumped together in the phylogeny, or being clumped amongst themselves but separated across the taxonomic tree. It may, of course just be simply a consequence of sampling bias that will be addressed as more bird taxa are sampled.

It was traditionally explained that north temperate bird species lived in the “fast lane”, having high fecundity but low survival, and tropical birds species were in the “slow lane” having lower annual fecundity, but higher adult survival (Skutch 1985; Murray 1985). So, from this study it would appear that ‘fast lane’ species are probably pre-adapted to the environmental conditions that have been imposed by the north temperate climate, rather than have adapted to it. However, ‘slow lane’ species have *adapted* their life history traits involved in breeding to their tropical environment, where age (e.g. nest) specific predation appears to be one of the main agents of selection and therefore evolution of life-history traits.

There is clearly a need for further work to fill the gaps in knowledge, particularly of tropical birds. Further fieldwork is needed to measure juvenile survival across a range of body masses. Juvenile survival is difficult to measure as it is difficult to separate mortality from natal dispersal (Peach *et al.* 2001). Further analysis of the response of adults of different body masses to different predators would also be very valuable. This study also highlights the importance of making useful phylogenetically independent comparisons. The approach here, of collecting data only on common species, has produced too few PICs to analyse with any power. To avoid these problems studies should be designed with phylogeny in mind. This can be achieved by matching species pairs between north temperate and tropical climates (e.g. Martin *et al.* 2000) or studying species within a family that occurs in both climates (e.g. Ricklefs 1997), or choosing to study species that maximise the contrasts within the phylogenetic tree. With these additional measures and considerations a more complete picture of the trade offs between life history traits and body mass in tropical birds would be possible, hopefully providing greater insight to the well studied north temperate 'norm'.

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## **Chapter 4: Moulting of Guinea savannah passerines in West Africa**

### **Summary**

Moulting timing and duration was measured in 17 passerine bird species in the Guinea savannah zone of Nigeria. In 15 species moulting duration was much longer than equivalent north temperate resident passerines. 16 species were found to moult seasonally, with most granivorous species moulting in the dry season. General seasonal patterns in insectivores and nectarivores were not clear.

### **Introduction**

Most passerine birds replace all of their feathers at least once a year in an ordered predictable process termed moulting (Ginn & Melville 1983). This process is costly due to increased energy demands (Lindstrom *et al.* 1998), reduced flight ability (Swaddle & Witter 1997) and reduced insulation (Nilsson & Svensson 1996). Most birds avoid overlapping moulting with other energetically costly processes such as breeding and migration (Jenni & Winkler 1994). Consequently, most passerines time their moulting to occur at the same time of year each year, usually after breeding, in order to manage these costs (Svensson & Hedenstrom 1999). Birds that breed later than others in the same population tend to moult more rapidly in order to avoid a moulting/breeding overlap and still complete their moulting on time (Newton 1966, Morton & Morton 1990). Thus, either the breeding season must be restricted in order to accommodate moulting, or birds must overlap

the two most energetically costly components of their annual cycle (Franklin *et al.* 1999).

Here I describe the moult timing and duration of a sample of passerine birds from the Guinea savannah zone of West Africa. Seasonal patterns of timing are explored and the results discussed in relation to other important aspects of the annual cycle and life history of birds.

## **Methods**

Birds were trapped using mist nets from October 2001 to February 2003 in Guinea savannah woodland at the Amurum Community Forest Reserve, on the Jos Plateau in central Nigeria (N 09° 52', E 08° 58').

Trapped birds undergoing main moult had each primary and secondary feather on one wing measured according to Ginn & Melville (1983). Each feather had its relative growth scored on a scale from 0 (old un-moulted feather) to 5 (new feather completely re-grown) in 6 increments. In most passerines the whole moult process occurs within the time required to moult the primary wing feathers (Ginn & Melville 1983). Consequently, a measure of the timing and duration of the moult of the primary feathers adequately describes the moult of the whole bird. The sum of the scores of the primary wing feathers was calculated and converted to a scale from 0 to 1. There was sufficient data to estimate the moult timing and duration of 17 species of passerines sampled during the study.

This primary moult score was regressed against date of the score with date as the dependant variable (Pimm 1976), thus calculating the average *individual* moult

from the sample population. From the intercept of this regression line with primary moult scores 0 and 1 the mean start and finish date, and thus moult duration, was calculated.

In order to examine the seasonal patterns of moult, species were assigned to guilds and comparisons made in the frequency of species in moult in each month of the year using Kruskal-Wallis tests in SPSS 11.5 (SPSS for Windows 2002).

## Results

Moult duration was variable between species sampled (Table 4.1). Figure 4.1 illustrates that two species (*Cinnyris venusta* & *Emberiza tahapisi*) moulted very rapidly (both in 36 days), but that the remaining species moulted relatively slowly (>100 days: mean ( $\pm$  s.e.) =  $170.6 \pm 9.2$  days). Resident north temperate passerine birds of a similar mass moulted in about 70 days (Ginn & Melville 1983), which was a mean of  $100.6 (\pm 9.2)$  days faster than our sample of slower moulting resident tropical species.

While moult occurred throughout the year timing was seasonally distributed within most species (Table 4.2). All but one species moulted mostly in either the dry season (October to March) or rainy season (April to September). *Zosterops senegalensis*, moulted approximately equally between each season.

Of the species that are mostly insectivorous 2 moulted mostly during the rainy season (*Pycnonotus barbatus*; *Sylvietta brachyura*), and one moulted approximately equally between each season (*Zosterops senegalensis*).

Amongst the nectarivores 2 moulted mostly during the dry season (*Cyanomitra verticalis*; *Chalcomitra senegalensis*) and one (*Cinnyris venustus*) moulted entirely within the rainy season.

Table 4.1: Mould duration of 17 species of passerine in the Guinea Savannah zone of Nigeria. 'n' = number of moult scores used in regression.

Species	Binomial	Duration	s.e.	n
Common Bulbul	<i>Pycnonotus barbatus</i>	179	21.22	18
Northern Crombec	<i>Sylvietta brachyura</i>	184	43.96	5
African Yellow White-eye	<i>Zosterops senegalensis</i>	135	57.51	9
Green-headed Sunbird	<i>Cyanomitra verticalis</i>	181	19.99	24
Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>	246	46.74	10
Variable Sunbird	<i>Cinnyris venustus</i>	36	10.52	42
Speckle-fronted Weaver	<i>Sporopipes frontalis</i>	166	21.26	21
Village Weaver	<i>Ploceus cucullatus</i>	161	43.18	12
Northern Red Bishop	<i>Euplectes franciscanus</i>	148	22.27	7
Lavender Waxbill	<i>Estrilda caerulescens</i>	199	10.54	24
Red-cheeked Cordon Bleu	<i>Uraeginthus bengalus</i>	133	8.52	61
African Quailfinch	<i>Ortygospiza atricollis</i>	118	19.43	14
Red-billed Firefinch	<i>Lagonosticta senegala</i>	203	31.64	11
Rock Firefinch	<i>Lagonosticta sanguinodorsalis</i>	118	23.13	18
Black-bellied Firefinch	<i>Lagonosticta rara</i>	197	21.50	7
Bronze Manikin	<i>Lonchura cucullata</i>	191	19.48	59
Cinnamon-breasted Bunting	<i>Emberiza tahapisi</i>	36	10.97	19

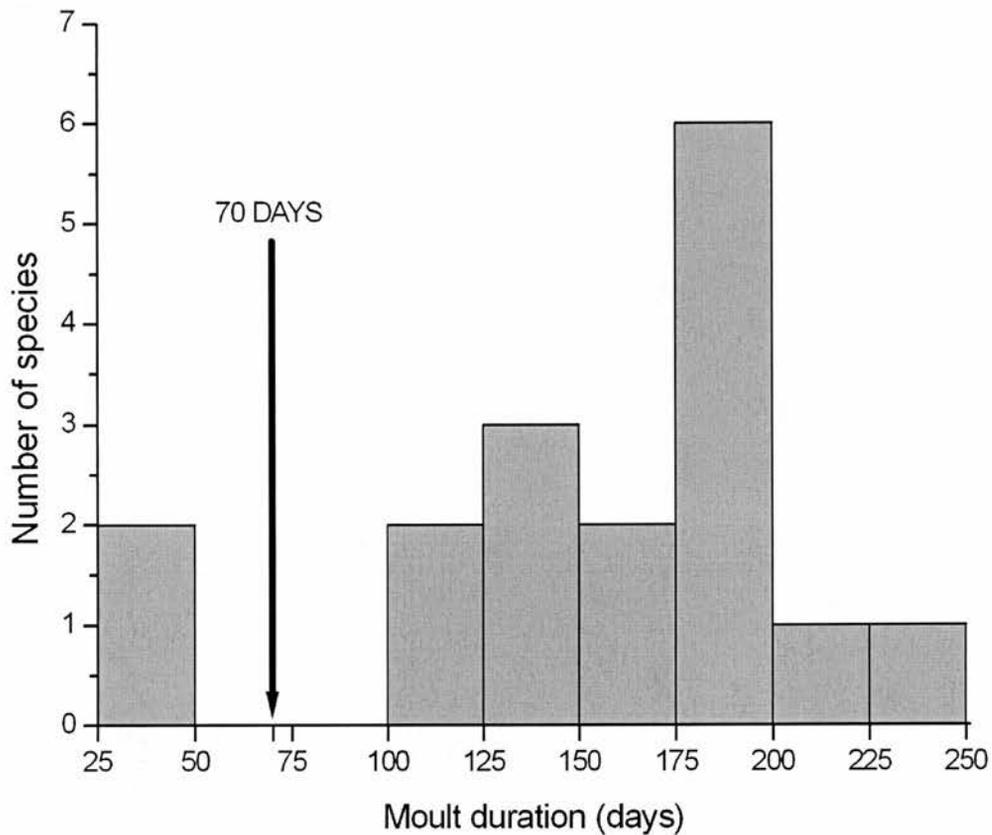


Figure 4.1: Frequency of moult duration amongst species. Arrow indicates 70 days (approximate mean value for similar north temperate passerines).

Table 4.2: Moult timing of 17 species of passerines in the Guinea savannah zone of Nigeria. ‘% Wet’ = proportion of moult during the rainy season (April – September); ‘% Dry’ = proportion of moult during dry season (October – March); ‘n’ = number of moult scores used in regression.

Species	Binomial	Start Date	s.e.	Finish Date	s.e.	% Wet	% Dry	n
Common Bulbul	<i>Pycnonotus barbatus</i>	29-Mar	16.70	28-Sep	13.09	98.9	1.1	18
Northern Crombec	<i>Sylvietta brachyura</i>	23-Apr	32.97	27-Oct	29.07	85.3	14.7	5
African Yellow White-eye	<i>Zosterops senegalensis</i>	26-Jul	54.80	11-Dec	17.44	47.4	52.6	9
Green-headed Sunbird	<i>Cyanomitra verticalis</i>	26-Oct	17.26	27-Apr	10.09	14.4	85.6	24
Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>	27-Jul	39.12	3-Apr	25.57	26.8	73.2	10
Variable Sunbird	<i>Cinnyris venustus</i>	6-Apr	8.14	12-May	6.67	100.0	0.0	42
Speckle-fronted Weaver	<i>Sporopipes frontalis</i>	25-Feb	13.03	11-Aug	16.80	78.3	21.7	21
Village Weaver	<i>Ploceus cucullatus</i>	6-Sep	37.11	17-Feb	22.07	14.9	85.1	12
Northern Red Bishop	<i>Euplectes franciscanus</i>	14-Oct	16.81	12-Mar	14.60	0.0	100.0	7
Lavender Waxbill	<i>Estrilda caerulescens</i>	5-Oct	6.67	24-Apr	8.16	11.6	88.4	24
Red-cheeked Cordon Bleu	<i>Uraeginthus bengalus</i>	9-Dec	7.57	22-Apr	3.93	15.8	84.2	61
African Quailfinch	<i>Ortygospiza atricollis</i>	7-Mar	10.23	5-Jul	16.53	79.7	20.3	14
Red-billed Firefinch	<i>Lagonosticta senegala</i>	22-Feb	18.51	15-Sep	25.66	80.8	19.2	11
Rock Firefinch	<i>Lagonosticta sanguinodorsalis</i>	28-Dec	22.12	26-Apr	6.74	21.2	78.8	18
Black-bellied Firefinch	<i>Lagonosticta rara</i>	14-Oct	19.81	1-May	8.38	15.2	84.8	7
Bronze Manikin	<i>Lonchura cucullata</i>	29-Sep	18.20	10-Apr	6.96	5.2	94.8	59
Cinnamon-breasted Bunting	<i>Emberiza tahapisi</i>	19-Mar	7.89	25-Apr	7.62	66.7	33.3	19

Of the granivorous species 4 moulted mostly during the rainy season (*Sporopipes frontalis*; *Ortygospiza atricollis*; *Lagonosticta senegala*; *Emberiza tahapisi*) and 7 moulted mostly during the dry season (*Ploceus cucullatus*; *Euplectes franciscanus*; *Estrilda caerulescens*; *Uraeginthus bengalus*; *Lagonosticta sanguinodorsalis*; *Lagonosticta rara*; *Lonchura cucullata*).

This pattern of seasonality differed significantly between the granivores and the insectivores (Kruskal-Wallis:  $\text{Chi}^2 = 7.7$ ; d.f. = 1;  $p = 0.005$ ) and between the granivores and nectarivores (Kruskal-Wallis:  $\text{Chi}^2 = 13.4$ , d.f. = 1,  $p < 0.001$ ), but not between the insectivores and nectarivores (Kruskal-Wallis:  $\text{Chi}^2 = 1.6$ , d.f. = 1,  $p = 0.20$ ). However, as there were few species of insectivore and nectarivore sampled there is little power to these tests. Despite this, the pattern of dry season moult amongst the granivores does seem compelling (Figure 4.2).

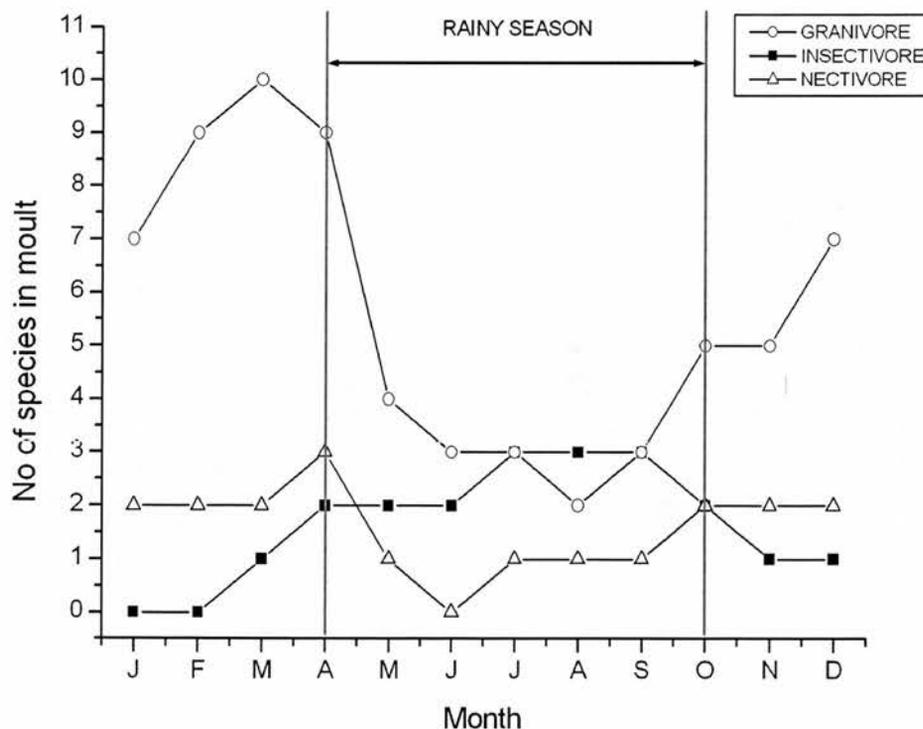


Figure 4.2: Seasonal distribution of moult of species by guild. Rainy season occurs from approximately 01 April to 31 October.

## **Discussion**

### **Moult timing**

The 17 passerines sampled here mostly showed a seasonal pattern to their moult. Granivorous birds mostly moulted during the dry season. Food availability for granivorous birds increases through the late rainy season as grasses complete flowering and set seed. It then decreases through the dry season and reaches a minimum at the start of the rainy season as seeds germinate (Ward 1965). This may explain why in most granivores moult was during the dry season, when food abundance was at its greatest for this guild of species. However, 4 species of granivores moulted during the rainy season. Three of these species also eat insects, in particular termites (Fry & Keith 2004), and so may be able to find sufficient insect food to provide energy to moult. In particular this may help to explain the very rapid moult of *Emberiza tahapisi*.

The seasonal pattern of moult is less clear in both insectivore and granivore guilds, due to small sample sizes. However, the seasonality of moult in most species is similar to findings from Liberia where 3 of 4 species were found to have seasonal moult (Chapman 1995). Further work is required to collect moult data from more species of these guilds.

### **Moult duration**

Moult duration was greater than 100 days for all but two species, which is typical for tropical birds (Craig 1996, Foster 1975, Fogden 1972). Long moult periods are often associated with extensive breeding overlap within the tropics (Franklin *et al.* 1999, Ginn & Melville 1983). This may be facilitated by, though not caused by,

small clutch sizes in tropical birds (Franklin *et al.* 1999) as birds are able to provision fewer offspring and still find sufficient resources to grow new feathers. However, if food availability is seasonally abundant, the extended parental care shown by most tropical birds (Russell *et al.* 2004, Schaefer *et al.* 2004) may *require* birds to overlap breeding and moult in order to complete both during the period of adequate food abundance.

### **Conclusion**

Guinea savannah passerines exhibit a clear seasonal pattern of moult and have long moult duration. However, further work is needed to explore the occurrence and extent of overlap between moult and breeding in Guinea savannah passerines and the consequences of this to their annual cycle and life histories. Data on the breeding phenology of Guinea savannah passerines is currently very limited.

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## **Chapter 5: Body mass variation of birds in a seasonal tropical environment.**

### **Summary**

Body mass variation was species specific amongst thirty three species studied in West Africa despite a strong seasonal change in climate between the dry and rainy seasons. Even amongst those species that did show a seasonal mass change between dry and rainy seasons the direction of this mass change was not necessarily as predicted. Several species showed significant changes in body mass between years where body mass was seen to decline from 2001 to 2004. For all but one species it was thought that changes in the management of the Amurum reserve may have been the cause of the observed pattern. Relatively few species showed significant diurnal mass variation. This may have partly been due to the sampling regime not being designed to examine these patterns. Most of those species that did show diurnal mass variation may have exhibited a bimodal distribution across the day. Some species showed a significant change in body mass between the period of main moult and the rest of the year, but some did not show any significant difference. There did not appear to be a relationship between body mass variation and moult speed. Although further research is clearly needed this study has shown that tropical birds do exhibit body mass variation across a range of temporal scales, and that these patterns do not have a simple seasonal explanation.

## Introduction

Body mass variation in birds has attracted a great deal of both theoretical (Lima 1986; Houston *et al.* 1988; Houston & McNamara 1993; McNamara *et al.* 1994; Bednekoff & Houston 1994a; Bednekoff & Houston 1994b) and empirical (Haftorn 1992; Gosler 1994; Meijer *et al.* 1994; Graedel 1995; Cresswell 1998; Lilliendahl 2002) study over the last 20 years. However, most of this interest has come from a north temperate perspective, with predictions and observation mostly based on the effects of winter or migration on both seasonal and diurnal body mass regulation. There have been no theoretical considerations of body mass regulation in tropical birds and very few field studies measuring either seasonal or diurnal mass variation (Crowe *et al.* 1981; Brown & Bhagabati 1998; Box *et al.* 2002).

However, many of the theoretical models created to explain mass variation in temperate bird species should apply to tropical species. In order to survive, every individual must be able to gain enough energy to maintain itself (Houston *et al.* 1993). However, carrying excess body mass may be costly. A larger body mass is energetically more costly to maintain (Lindström & Rosen 2002) and also requires more energy to move it around (Nudds & Bryant 2000). Increased body mass may also incur a cost through increased predation risk through an increase in time spent foraging while gaining mass and therefore exposed to predation risk (Lima 1986) and through mass-dependent predation risk, where mass reduces acceleration and manoeuvrability during escape from an attack by a predator (Witter & Cuthill 1993). However, as foraging opportunities may be unpredictable, maintaining low energy reserves, and hence body mass, may also

incur a cost – the risk of starvation (Blem 1990). It would therefore appear that birds should maintain as low a body mass as possible. Thus there is a selection pressure on birds to balance these costs by trading off body mass and predation risk (Lima 1986). Empirically, it is clear that birds are able to regulate their own body mass as they usually have a body mass within the potential maximum or minimum possible under physiological or environmental constraints (Lima 1986; Rogers 1987) and so body mass represents a trade-off between the conflicting pressures of predation and starvation.

The relative importance of predation and starvation has been hypothesised to vary both diurnally and seasonally as predictability of foraging opportunities vary (Houston *et al.* 1993). Moulting may also affect body mass as birds require more resources (Myrcha & Pinowski 1970) and also because during wing moulting a reduction in wing area results in an increase in wing loading (Hedenstrom & Sunada 1999) and hence predation risk.

### **Diurnal body mass**

During each night individuals lose body mass as they are unable to forage but still have to maintain metabolic processes (Blem 1990). During the following day individuals then have to regain mass lost overnight. In order to minimise mass-dependent predation risk it is theorised that birds should delay regaining lost mass until as late as possible each day (Houston *et al.* 1988; Houston & McNamara 1993; Houston *et al.* 1993). However, the predictions of such models are dependant on the state of the individual and the relative risks of starvation and predation it faces (Houston *et al.* 1993). If foraging is safe and predictable across

each day the individual should increase mass evenly across the day (Houston *et al.* 1993).

When foraging is safe but is of lower quality models predict that mass should peak early in the day and then decrease across the rest of the day (McNamara *et al.* 1994). If predation risk interrupts foraging, but forage is of high quality, a bimodal pattern of mass gain with increases early in the morning and late in the evening may occur (McNamara *et al.* 1994).

### **Seasonal mass variation**

Unpredictability of foraging opportunities may also arise seasonally. For example in the winter in temperate zones shorter days and cold or freezing temperatures may reduce available foraging time and may make food harder to find, consequently individuals may need increased body reserves as insurance against periods where foraging is more difficult and energy budgets may not be met (Houston *et al.* 1993). Most seasonal mass variation predictions are based on the colder temperatures and shorter days of the north temperate winter having a heavy influence on the predictability of food supply and on metabolic costs of maintenance (Rogers 1987; McNamara & Houston 1990; Bednekoff & Houston 1994b). However, these predictions are simply based on a seasonal environment having an effect on the relative trade offs a bird has to make between starvation and predation risk. As the Guinea savannah of West Africa has a strongly seasonal environment that is very likely to influence the predictability of foraging opportunities (Elgood *et al.* 1994) it may be predicted that there may be a seasonal change in the body mass of birds in this environment also.

## **Moult and mass variation**

During moult birds need increased energy intake as growing new feathers will be costly: as foraging needs increase so does the unpredictability of foraging because intake rate per unit time must increase (Houston *et al.* 1993). Therefore during moult birds may increase in mass as a result of physiologically necessary processes (Myrcha & Pinowski 1970; Dolnik & Gavrilov 1979). Also, main flight feather moult results in the loss of one or more feathers on each wing so reducing the wing area. This reduction in wing area results in an increase in wing loading (Hedenstrom & Sunada 1999) and therefore reduce flight performance, in particular escape flight that may result in an increase in predation risk (Slagsvold & Dale 1996; Swaddle & Lockwood 2003). As a consequence, body mass may be *decreased* during moult (Holmgren *et al.* 1993; Swaddle & Witter 1997a). Again the relative strength of starvation versus predation risk will determine whether mass is gained or lost during moult.

Different species moult at different rates and the number of feathers being simultaneously moulted determines this rate (Jenni & Winkler 1994). Faster moult speeds therefore result in larger gaps in the wing, which has a greater effect on flight performance (Swaddle & Witter 1997b). It could therefore be predicted that birds with more rapid moult would show a greater decrease in body mass between the moult period and the rest of the year.

## **Body mass and fat**

Several studies have found a strong correlation between body mass and fat (Gosler *et al.* 1998). Energy is stored as fat and may be scored by examining the relative amounts of subcutaneous fat visible under the skin (Kaiser 1993). Thus, body mass was a good measure of stored energy levels. As this chapter investigates how body reserves as measured by mass vary in tropical birds it was thought necessary to confirm that, in general, that body mass was indeed an indicator of fat reserves in tropical species. This was found to be the case in 22/26 species where sufficient fat score data were collected (Appendix 5.2).

## **Predictions**

Based on the theoretical models explained above it was possible to make the following predictions of body mass variation in tropical birds.

1. Diurnal mass variation:
  - a. Mass variation may show a bimodal pattern as foraging may be interrupted during the middle of the day by high temperatures.
  - b. Mass may be gained evenly during the day because predation risk is unimportant, or mostly at the end of the day because predation risk is important
  - c. Mass may be gained early in the day because foraging is unpredictable

2. Seasonal mass variation:

- a. Body mass may increase or decrease seasonally because of a strong seasonal change in climate.

3. Moulting and mass variation:

- a. Body mass may differ between moulting period and the rest of the year.
- b. Species that moult more quickly may show a greater mass change during the moulting period than those that moult more slowly, increasing in mass if starvation risk is relatively more important and reducing mass if predation risk is relatively more important.

## **Methods**

### **Data collection**

Bird were captured in mist nets at Amurum Community Forest Reserve on the Jos Plateau in central Nigeria (N 09° 52', E 08° 58'). Most birds trapped had a set of basic biometric measurements recorded that included: wing length, mass, fat score, pectoral muscle score, moult status (whether in active remige moult or not) and the presence or absence of a brood patch. In each case wing length was measured as the flattened, straightened wing chord using a stopped wing rule (Svensson 1992). Mass was measured either using a Pesola spring balance or an Ohaus Scout II electronic balance. When using a Pesola spring balance mass was measured to the nearest 0.1g if using a 100g balance or to the nearest 1g of using a 300g or above balance. When using the electronic balance the measurement was always to the nearest 0.1g. Fat score was estimated according to (Kaiser 1993) but only to the nearest whole number. Pectoral muscle was estimated on a 4 point scale from 0 to 3 according to the ESF Songbird migration manual (Bairlein 1995)

### **Analysis**

Species were chosen for analysis if there were more than twenty individuals with mass measured at initial capture only. Only new captures were used to prevent pseudo-replication and the effects of handling increasing body mass in the short term e.g. (Lilliendahl 1997). The following species had more than twenty independent body mass measurements and so were analysed for mass variation. Common names follow Borrow & Demey (2001) and scientific names follow Sibley & Monroe (1990).

### ***Non-passerines***

Black-billed wood dove *Turtur abyssinicus*  
Yellow-fronted tinkerbird *Pogoniulus chrysoconus*  
Greater honeyguide *Indicator indicator*  
Red-throated bee-eater *Merops bulocki*

### ***Passerines***

#### *African insectivores*

Common wattle-eye *Platysteira cyanea*  
African yellow white-eye *Zosterops senegalensis*  
Snowy-crowned robin chat *Cossypha niveicapilla*  
Common bulbul *Pycnonotus barbatus*  
African thrush *Turdus pelios*  
Grey-backed camaroptera *Camaroptera brevicaudata*

#### *African granivores*

African quailfinch *Ortygospiza atricollis*  
Bronze manikin *Lonchura cucullata*  
Village weaver *Ploceus cucullatus*  
Black-necked weaver *Ploceus nigricollis*  
Vitelline masked weaver *Ploceus vitellinus*  
Speckle-fronted weaver *Sporopipes frontalis*  
Northern red bishop *Euplectes franciscanus*  
Black-winged bishop *Euplectes hordeaceus*  
Red-cheeked cordon bleu *Uraeginthus bengalus*  
Lavender waxbill *Estrilda caerulescens*  
Black-rumped waxbill *Estrilda troglodytes*  
Red-billed firefinch *Lagonosticta senegala*  
Bar-breasted firefinch *Lagonosticta rufopicta*  
Rock firefinch *Lagonosticta sanguinodorsalis*  
Cinnamon-breasted bunting *Emberiza tahapisi*

#### *Sunbirds*

Variable sunbird *Cinnyris venusta*  
Scarlet-chested sunbird *Chalcomitra senegalensis*  
Green-headed sunbird *Cyanomitra verticalis*

#### *Palearctic Migrants*

Whinchat *Saxicola rubetra*  
Pied flycatcher *Ficedula hypoleuca*  
Garden warbler *Sylvia borin*  
Whitethroat *Sylvia communis*  
Willow warbler *Phylloscopus trochilus*

For each species the data was checked visually for outliers by plotting wing length against mass. Any clear outliers, that may have been a result of mistakes

made during measurement or recording, were removed from the data set. In each case a fully parameterised General Linear Model (GLM) was built that included the variables: body mass, wing length, year, time of year, time of day, and observer. Wherever applicable sex and/or age were included in the model. Each model then had two way interactions tested (where applicable) between time of year and sex and age; time of day and sex and age. Any significant interactions remained in the model, along with their appropriate individual variable. Non-significant interactions were removed from the model. At this point if time of day, sex or age were not significant ( $p < 0.05$ ) the variable was removed from the model. Year and observer always remained in the model as these were considered general confounding or “nuisance” variables (i.e. it was necessary to control for these variables but they were not of specific interest).

Table 5.1: Classification of time of year into different seasons.

MONTH	6 SEASON	4 SEASON	2 SEASON
DEC	MID DRY	MID DRY	DRY
JAN			
FEB	LATE DRY	EARLY RAINS	RAINS
MAR			
APR	EARLY RAINS	MID RAINS	RAINS
MAY			
JUN	MID RAINS	EARLY DRY	DRY
JUL			
AUG	LATE RAINS	EARLY DRY	DRY
SEP			
OCT	EARLY DRY	EARLY DRY	DRY
NOV			

For each species a GLM model was built as described above with time of year classified into months. In each case time of year was then reclassified into four seasonal periods (Table 5.1) and the GLM model building process started again. Once this was completed time of year was reclassified into two seasonal periods:

dry and rainy seasons. The dry season was classified as October to March and the rainy season as April to September. The GLM model building process was again restarted. In a few cases the distribution of samples meant that it was possible to improve on the temporal resolution of a four season model by reclassifying time of year into six seasons, or two month blocks (Table 5.1).

### **Examining seasonal mass variation**

For each species with time of year significant in the model the residual mass for each period of the year was examined. Residual mass was examined as this allowed the changes in body mass with time of year to be examined, while accounting for other variables in the model (such as time of day, sex, age etc.).

When time of year had a significant interaction with another variable the residual mass was for each period of the year was examined for each grouping (e.g. if time of year interacted significantly with sex the residual mass for each sex was examined across the year). In each case the mean residual mass and its standard error was plotted with time of year. Every species was also tested with time of year classified into dry and rainy seasons. Examination of residual mass was identical to the method described above, but residual mass for each season was not plotted graphically.

### **Examining diurnal mass variation**

When time of day was a significant variable in the model for a species again the mean residual mass and its standard error was examined. Interactions were examined in the same way as described for seasonal mass variation.

### **Mass variation and moult**

In order to examine the effects of moult on body mass a GLM model was built that included moult coding as a variable. Only birds recorded as being either in main remige moult, or certainly not being in moult of any kind were selected for analysis. Unfortunately, this rigorous data selection resulted in sample sizes being too small for adequate analysis, even for the most numerous recorded species. Consequently, analysis had to be restricted to comparing the period of moult for each species with the rest of the year. This method was less satisfactory as it would include individuals that were not in moult during the moulting period, as they had either not started or had completed their moult when trapped, and would include individuals that were in moult during the non-moult period as they had started or completed moult early or later than the average individual. Time of year was classified into either the period identified as being the period of main moult for that species (see Chapter 4) or the rest of the year out with that period. Again a GLM was built, interactions tested and residual mass variation examined as described for seasonal mass variation.

### **Body mass and fat score**

Body mass was plotted against fat score for each species and the relationship between these two variables tested using linear regression.

### **Examining proportional change in body mass**

Each species analysis was summarised into tables and the changes in residual body mass (whether seasonally, diurnally or with moult season) were calculated with respect to overall body mass. As Lean Body Mass (LBM) was not

calculated, and there were no published estimates for LBM for any of the species examined here, changes in body mass were relative to the lowest mean body mass for the temporal period being examined.

All statistical analyses were processed using SPSS 11.5 (SPSS for Windows 2002).

## Results: species accounts

**Black-billed wood dove: Mean body mass:  $62.0 \pm 0.73\text{g}$  (n = 39), mean wing length:  $112.0 \pm 0.49\text{mm}$  (n = 39)**

Time of year was not a significant variable whether classified by month, four or two seasons (Table 5.2).

Table 5.2: Seasonal mass variation in black-billed wood dove.

Time of year	SS	df	error df	F	p
12 months	51.74	8	24	0.52	0.83
4 seasons	22.82	3	29	0.67	0.58
2 seasons	0.22	1	31	0.02	0.89

**Yellow-fronted tinkerbird: Mean body mass:  $11.0 \pm 0.06\text{g}$  (n = 90), mean wing length:  $56.8 \pm 0.18\text{mm}$  (n = 90).**

While Yellow-fronted tinkerbirds increased their body mass for the first three hours of the morning and possibly during the afternoon it appeared that they did not continue to increase mass across the whole morning. There was no seasonal variation in mass.

Table 5.3: Yellow-fronted tinkerbird. With time of year classified by month the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{month} + \text{observer} (R^2 = 0.29)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	13.59	16	3.20	<0.001
Intercept	0.94	1	3.56	0.06
Time	1.71	1	6.44	0.01
Wing	1.97	1	7.42	0.008
Year	1.35	3	1.70	0.17
Month	5.54	10	2.09	0.04
Obs	0.07	1	0.28	0.60
Error	19.10	72		
Total	10746.77	89		
Corrected Total	32.70	88		

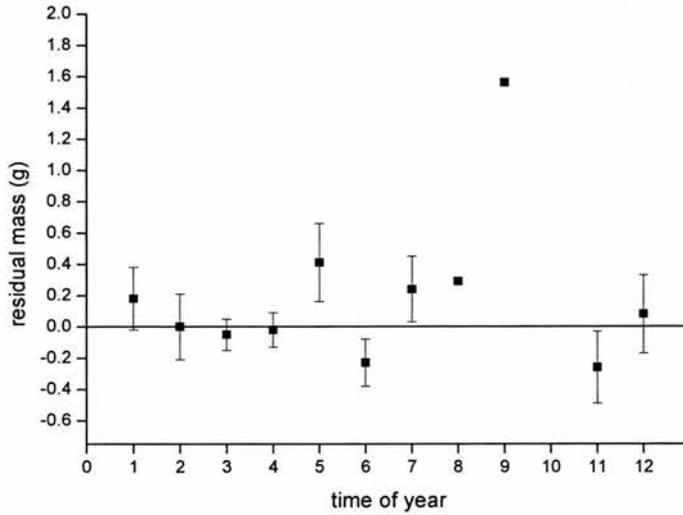


Fig 5.1: Yellow-fronted tinkerbird - residual mass variation with time of year classified by month.

The large body mass in September was due to a single gravid female (figure 5.1). When this datum was removed time of year was no longer a significant variable in the model ( $SS = 2.80$ ,  $df = 9$ , error  $df = 72$ ,  $F = 1.17$ ,  $p = 0.33$ ). Time of day was still significant however ( $SS = 1.71$ ,  $df = 1$ , error  $df = 72$ ,  $F = 6.44$ ,  $p = 0.01$ ) -

Figure 5.2: mass increased until 0900 and then remained stable until 1100.

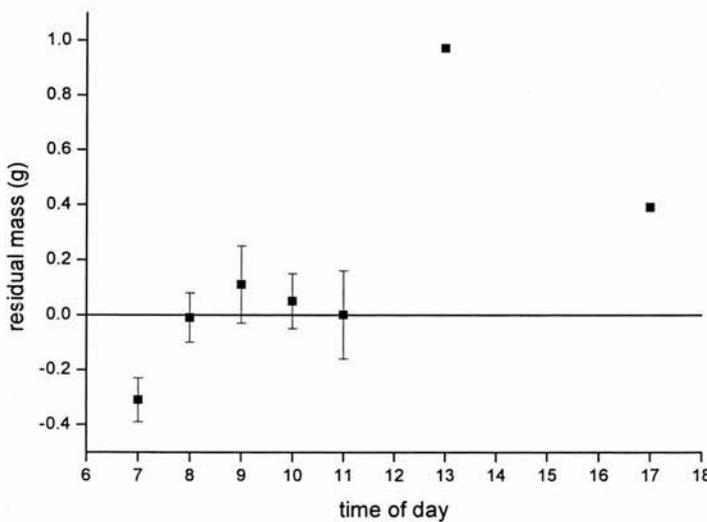


Fig 5.2: Yellow-fronted tinkerbird - residual mass variation with time of day.

When time of year was reclassified into four and two seasons it was not a significant variable (Table 5.4)

Table 5.4: Yellow-fronted tinkerbird – GLM model output for time of year variable when classified into four and two seasons.

<b>Time of year</b>	<b>SS</b>	<b>df</b>	<b>error df</b>	<b>F</b>	<b>p</b>
4 seasons	0.75	3	78	0.93	0.43
2 seasons	2.80	1	72	1.17	0.33

**Greater honeyguide: Mean body mass:  $47.2 \pm 0.71\text{g}$  (n = 24), mean wing length:  $118.0 \pm 0.96\text{mm}$  (n = 24).**

Time of year was not a significant variable whether classified by month, four or two seasons (Table 5.5)

Table 5.5: Greater honeyguide – GLM model output of time of year classified into different periods.

<b>Time of year</b>	<b>SS</b>	<b>df</b>	<b>error df</b>	<b>F</b>	<b>p</b>
12 months	12.54	6	12	0.36	0.89
4 seasons	9.74	3	15	0.67	0.58
2 seasons	0.00	1	17	0.00	0.996

**Red-throated bee-eater: Mean body mass:  $23.9 \pm 0.28\text{g}$  (n = 37), mean wing length:  $99.8 \pm 0.53\text{mm}$  (n = 37)**

Time of year was not significant in any model whether classified by month, four seasons or two seasons (Table 5.6).

Table 5.6: Red-throated bee-eater - GLM model output of time of year classified into different periods.

<b>Time of year</b>	<b>SS</b>	<b>df</b>	<b>error df</b>	<b>F</b>	<b>p</b>
12 months	13.78	6	27	1.06	0.41
4 seasons	7.44	3	30	1.14	0.35
2 seasons	0.21	1	32	0.09	0.76

**Common wattle-eye: Mean body mass:  $14.4 \pm 0.17\text{g}$  ( $n = 35$ ), mean wing length:  $66.9 \pm 0.35\text{mm}$  ( $n = 35$ )**

Table 5.7: Common wattle-eye. With time of year classified by month the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.45)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	21.45	13	3.10	0.01
Intercept	0.07	1	0.12	0.73
Wing	5.40	1	10.14	0.004
Year	6.62	3	4.14	0.02
Month	10.64	8	2.50	0.04
Obs	0.01	1	0.01	0.91
Error	11.18	21		
Total	7241.35	35		
Corrected Total	32.63	34		

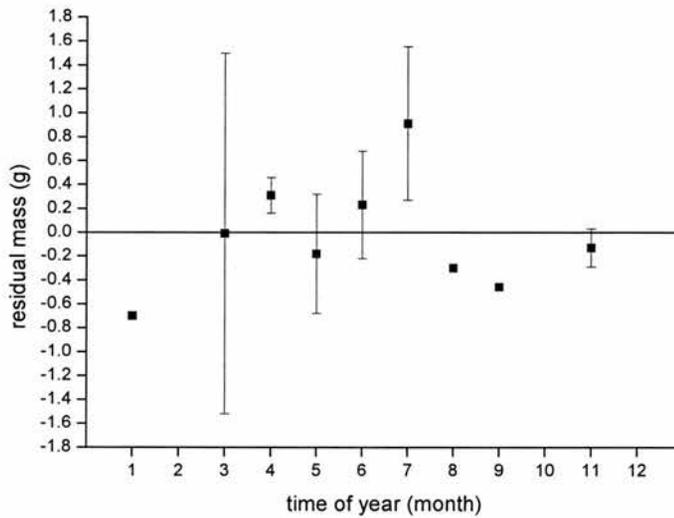


Figure 5.3: Common wattle-eye – variation in residual mass by time of year classified by month.

Data was sparse across all months so time of year was re-classified into four seasonal periods. However, time of year was no longer significant ( $SS=4.19$ ,  $df=3$ , error  $df = 22$ ,  $F=2.06$ ,  $p=0.13$ ). This was also the case when time of year was classified as dry and rainy seasons ( $SS=2.37$ ,  $df=1$ , error  $df = 25$ ,  $F=3.42$ ,

p=0.075). The lack of any consistent pattern of mass variation may be due to a lack of power, as there were relatively few data for this species.

**African yellow white-eye: Mean body mass:  $9.54 \pm 0.06\text{g}$  (n = 103), mean wing length:  $58.2 \pm 0.19\text{mm}$  (n = 101)**

Table 5.8: African yellow white-eye. With time of year was classified by month the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.18)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	11.57	17	2.21	0.01
Intercept	0.03	1	0.10	0.75
Time	1.94	1	6.29	0.01
Wing	5.17	1	16.79	<0.001
Year	0.86	3	0.93	0.43
Month	4.39	11	1.30	0.24
Obs	0.91	1	2.96	0.09
Error	23.73	77		
Total	8778.98	95		
Corrected Total	35.30	94		

There was no variation in body mass with time of year, but time of day was significant.

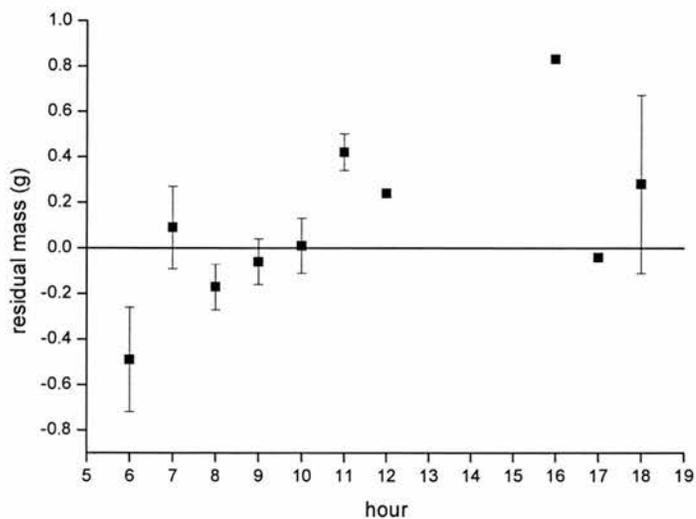


Figure 5.4: African yellow white-eye – variation in residual mass by time of day.

Most of the mass was added in the morning (Figure 5.4). There was a significant increase in mass up to 1200 (Linear regression:  $y = 0.15x - 1.36$ ,  $R^2 = 0.74$ ,  $SS = 1.85$ ,  $df = 1$ , error  $df = 71$ ,  $F = 6.12$ ,  $p = 0.02$ ), but there was insufficient data to draw conclusions about change of mass in the afternoon.

Time of year was not a significant variable whether classified by month, four or two seasons (Table 5.9).

Table 5.9: African yellow white-eye – GLM model output for time of year when classified by month, four seasons and two seasons.

Time of year	SS	df	error df	F	p
12 months	4.39	11	77	1.30	0.24
4 seasons	0.92	3	86	0.94	0.42
2 seasons	0.66	1	88	2.06	0.15

**Snowy-crowned robin chat: Mean body mass:  $36.7 \pm 0.41\text{g}$  ( $n = 57$ ), mean wing length:  $100.5 \pm 0.73\text{mm}$  ( $n = 56$ ).**

Snowy-crowned robin chats increased their body mass from a minimum in the dry season to peak in the late rainy season when they are thought to breed.

Table 5.10: Snowy-crowned robin chat. With time of year classified into two month categories the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.66)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	373.47	7	15.93	0
Intercept	14.76	1	4.41	0.04
Wing	294.49	1	87.94	0
Year	12.34	1	3.68	0.06
Month	61.93	4	4.62	0.003
Obs	15.84	1	4.73	0.04
Error	160.75	48		
Total	76246.59	56		
Corrected Total	534.22	55		

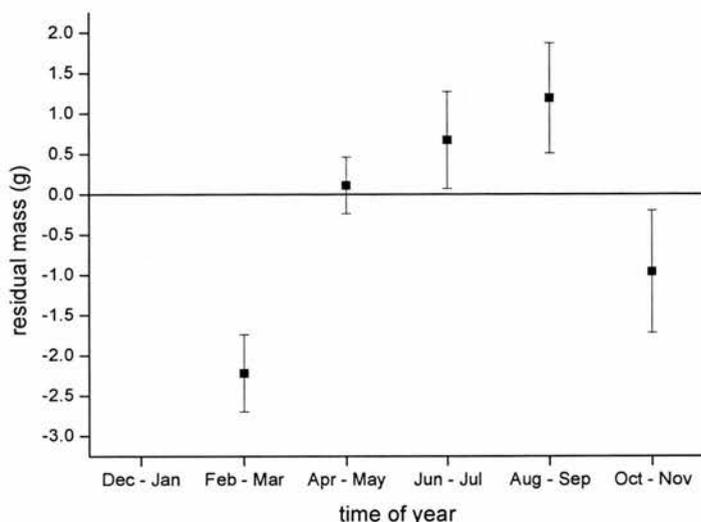


Fig 5.5: Snowy-crowned robin chat – variation in residual mass by time of year classified in two month blocks.

**Common bulbul: Mean body mass:  $38.3 \pm 0.22\text{g}$  (n = 190), mean wing length:  $99.5 \pm 0.29\text{mm}$  (n = 185)**

Mass increased from a minimum in the mid dry season to a peak in the mid-rains before a steady decrease through the rest of the year. The total variation in mass across the year was 1.98g, or 5.2% of mean body mass.

Table 5.11. Common Bulbul. With time of year initially classified into two month blocks the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.32)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	577.15	10	9.37	<0.001
Intercept	3.05	1	0.50	0.48
Wing	409.62	1	66.53	<0.001
Year	29.66	3	1.61	0.19
Time of year	103.77	5	3.37	0.006
Obs	12.78	1	2.08	0.15
Error	1034.42	168		
Total	265089.53	179		
Corrected Total	1611.56	178		

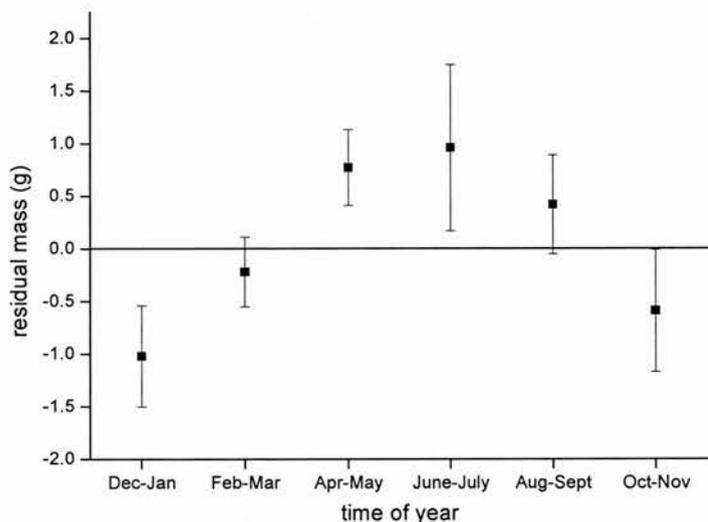


Figure 5.6: Common bulbul – variation in residual body mass with time of year classified into two month blocks.

**African thrush: Mean body mass:  $65.3 \pm 0.37\text{g}$  (n = 126), mean wing length:  $120.0 \pm 0.52\text{mm}$  (n = 124)**

African thrushes showed a peak of mass during December to February and a significantly lower mass March to May.

Table 5.12: African thrush. With time of year classified into 4 seasonal periods the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{time of year} + \text{observer} (R^2 = 0.17)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	461.00	8	4.18	<0.001
Intercept	511.52	1	37.13	<0.001
Wing	122.74	1	8.91	0.003
Year	109.01	3	2.64	0.05
Time of year	192.40	3	4.66	0.004
Obs	19.91	1	1.45	0.23
Error	1556.63	113		
Total	521844.88	122		
Corrected Total	2017.63	121		

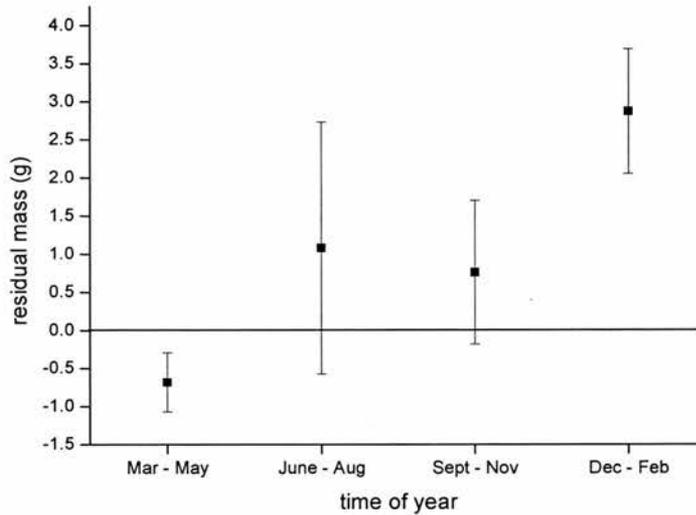


Figure 5.7: African thrush - variation in residual body mass with time of year classified into four seasons.

When time of year was re-classified into two seasons (dry and rainy seasons) the seasonal effect was no longer significant. However, age became significant ( $SS = 66.29$ ,  $df = 1$ , error  $df = 117$ ,  $F = 4.39$ ,  $p = 0.04$ ), despite not being significant in the previous model and not having any significant interaction with time of year (Table 5.13). This difference was only 1.25g, or 1.9% of mean body mass.

Table 5.13: African thrush –difference in residual body mass between adult and immature birds.

	mean residual mass	standard error
Immature	0.88	0.64
Adult	-0.37	0.41

**Grey-backed camaroptera: Mean body mass:  $11.1 \pm 0.11g$  ( $n = 75$ ), mean wing length:  $56.6 \pm 0.33mm$  ( $n = 75$ )**

Individuals generally increased their mass across the day there was no seasonal variation in body mass.

Table 5.14: Grey-backed camaroptera. With time of year classified by month the model was:

$$\text{mass} = \text{time of day} + \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.43)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	33.80	16	4.48	<0.001
Intercept	0.37	1	0.78	0.38
Time of day	2.97	1	6.31	0.015
Wing	17.88	1	37.95	<0.001
Year	0.59	2	0.62	0.54
Month	2.66	10	0.57	0.84
Obs	0.06	1	0.12	0.73
Error	26.86	57		
Total	9202.63	74		
Corrected Total	60.65	73		

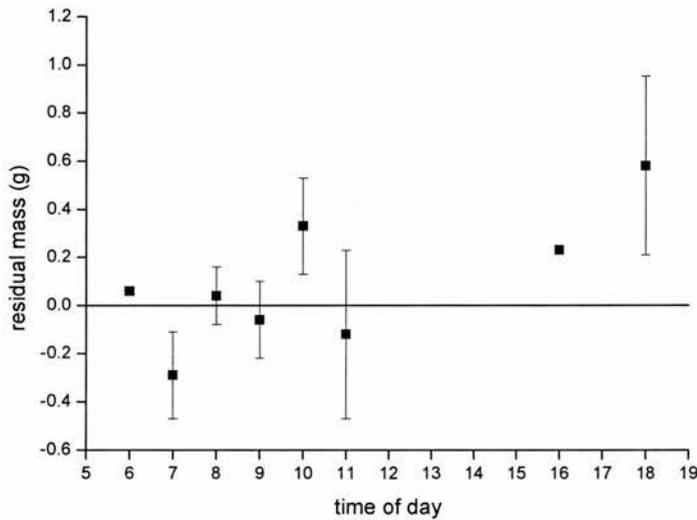


Figure 5.8: Grey-backed camaroptera – variation in residual mass by time of day.

When time of year was reclassified into seasonal periods it was still not a significant variable (table 5.15)

Table 5.15: Grey-backed camaroptera – GLM model output for time of year classified into four and two seasons.

Time of year	SS	df	error df	F	p
4 seasons	1.45	3	64	1.10	0.36
2 seasons	0.12	1	68	0.27	0.61

**African quailfinch: Mean body mass:  $10.7 \pm 0.10\text{g}$  (n = 67), mean wing length:  $55.7 \pm 0.16$  (n = 67)**

Whether classified by month, four seasons or two seasons, time of year was not a significant variable in any model (Table 5.16).

Table 5.16: African quailfinch – GLM model output for time of year classified by month, four and two seasons.

Time of year	SS	df	error df	F	p
Month	3.05	7	46	1.40	0.23
4 seasons	0.03	3	48	0.03	0.993
2 seasons	0.08	1	51	0.26	0.62

However, sex was a significant variable in each of these models (GLM classified by month SS = 2.45, df = 1, error df = 46, F = 7.86, p = 0.01). There was a difference of 0.38g, or 3.6% of mean body mass (Table 5.17).

Table 5.17: African quailfinch - mean residual mass of female and males.

	Mean residual mass	standard error
female	-0.23	0.10
male	0.15	0.09

**Bronze manikin: Mean body mass:  $8.98 \pm 0.04\text{g}$  (n = 265), mean wing length:  $50.7 \pm 0.09\text{mm}$  (n = 256).**

Immature birds maintained a lower body mass than adults in the early dry season, when they would have been very young (< 2 months old). However, immature birds then increased their body mass in the mid-dry season to similar levels to adults. However, immatures then lost more body mass in the early rains than adults. During this period the availability of seeds decreases considerably with germination following the first rains. Adult body mass may be mirroring seed

availability. While there are not data to confirm this it is generally agreed that in African savannah grass seeds are most abundant in the late rains to early dry season (at Jos during September and October) and decline in abundance through the dry season. As the rains progress seed abundance decreases more rapidly as seeds germinate, but now newly grown grasses have yet set seed.

Table 5.18: Bronze manikin – with time of year initially classified into 4 seasons the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{observer} + \text{time of day} + \text{time of year} + \text{age} + \text{time of year*age} + \text{time of day*age} \quad (R^2 = 0.21)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	23.92	12	6.61	<0.001
Intercept	1.04	1	3.45	0.07
Time of day	10.18	1	33.77	<0.001
Wing	2.86	1	9.49	0.002
Year	2.96	2	4.90	0.008
Time of year	2.37	3	2.62	0.05
Obs	0.63	1	2.09	0.15
Age	2.23	1	7.39	0.007
Age*Time of day	1.06	1	3.52	0.06
Time of year*Age	2.10	2	3.48	0.03
Error	71.76	238		
Total	20469.90	251		
Corrected Total	95.68	250		

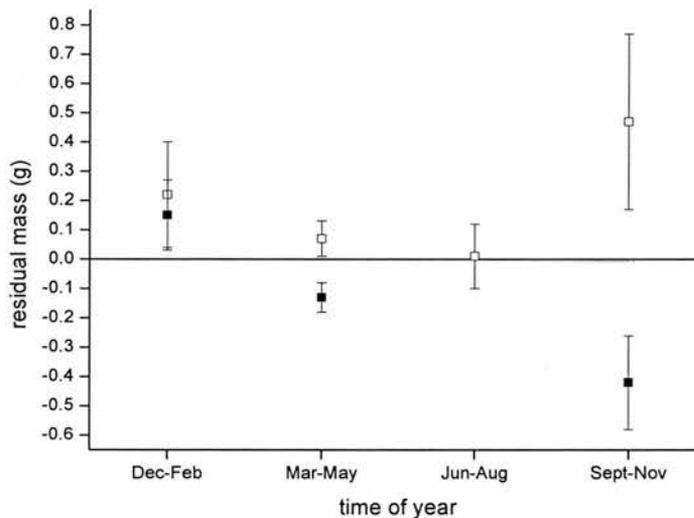


Figure 5.9: Bronze manikin – variation in residual body mass by time of year classified into four seasons for immature ■ and adult birds □.

Adult birds increased mass across the morning until 1000 and then lost the mass gained between 1000 and 1100. As there was only a single datum after 1200 it was not possible to draw conclusions about mass change in the afternoon.

Immature birds started the morning with a much lower body mass but ‘caught up’ with adults by 0800. It appeared that immature birds increased mass much more by late evening, suggesting the need for reserves to endure the night (Figure 5.10).

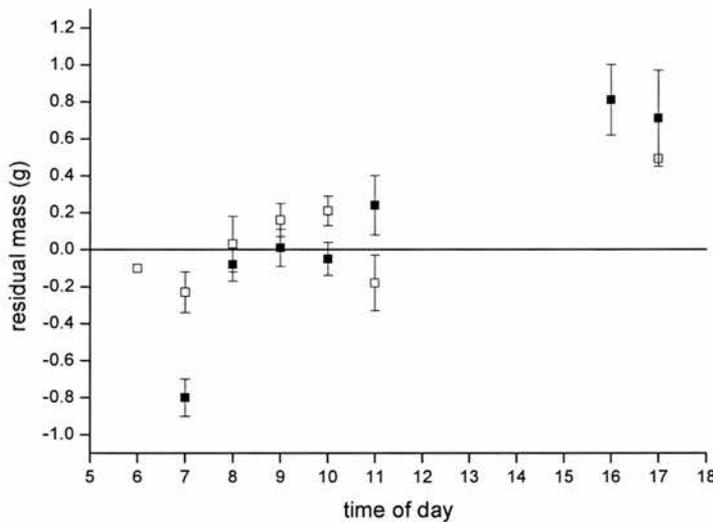


Figure 5.10: Bronze manikin – variation in residual mass by time of day for immature (■) and adult (□) birds.

**Village weaver Mean body mass:  $37.8 \pm 0.50\text{g}$  ( $n = 113$ ), mean wing length:  $87.7 \pm 0.39\text{mm}$  ( $n = 113$ )**

Initial data checking indicated that the sexes were clearly of different sizes (Fig 5.11), but that mistakes had been made in sexing some individuals. This was likely to be adult females and immature males being incorrectly aged and sexed. There were also two data that were either incorrectly weighed or incorrectly recorded (see Fig 5.11). These data were removed from the analysis. Because of the problem with correctly sexing and aging birds, age and sex could not be reliably used as variables in any models.

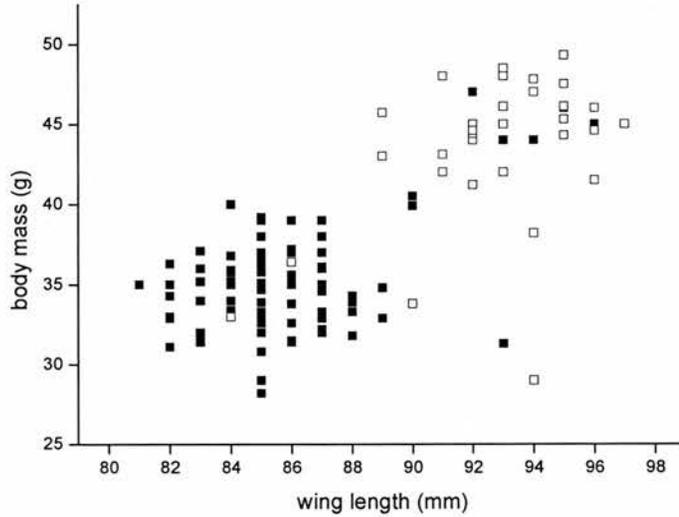


Figure 5.11: Village weaver – body mass (in grams) with wing length (in mm). □ = males; ■ = females.

Table 5.19: Village weaver – with time of year classified by month the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.74)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	2460.81	12	27.32	<0.001
Intercept	316.69	1	42.20	<0.001
Wing	1254.16	1	167.11	<0.001
Year	94.77	3	4.21	0.01
Month	229.67	7	4.37	<0.001
Obs	0.76	1	0.10	0.75
Error	765.51	102		
Total	166169.88	115		
Corrected Total	3226.32	114		

The pattern of mass variation across the year was not very clear (Fig 5.12). It appeared that birds did not change their body mass much until later in the year, during the early to mid dry season.

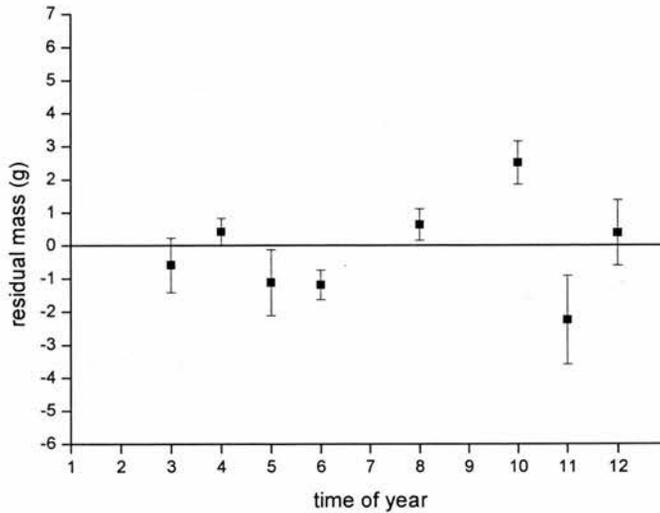


Figure 5.12: Village weaver – variation in residual mass with time of year.

When time of year was reclassified as four seasons or by two seasons it was no longer a significant variable in the model (Table 5.20)

Table 5.20: Village weaver – GLM model output for time of year when classified into four and two month periods.

Time of year	Sum of Squares	df	error df	F	p
4 seasons	10.49	3	103	0.58	0.63
2 seasons	0.13	1	106	0.02	0.89

**Black-necked weaver: Mean body mass:  $27.1 \pm 0.29\text{g}$  (n = 62), mean wing length:  $79.6 \pm 0.39\text{mm}$  (n = 61)**

Patterns of seasonal variation in mass were unclear in black-necked weaver and its significance depended on pooling. Time of year was marginally significant when individual month periods were modelled (Table 5.21). When time of year was classified into four seasonal periods only time of day remained a significant variable in the model (time of year:  $SS=4.32$ ,  $df = 3$ , error  $df = 51$ ,  $F=0.47$ ,  $p=0.70$ ; time of day:  $SS=14.24$ ,  $df=1$ , error  $df = 51$ ,  $F=4.68$ ,  $p=0.04$ ): Fig. 5.13.

Table 5.21: Black-necked weaver - with time of year classified by month the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.53)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	200.92	15	5.43	<0.001
Intercept	30.34	1	12.31	0.001
Time	17.67	1	7.17	0.01
Wing	135.72	1	55.04	<0.001
Year	17.88	3	2.42	0.08
Month	48.41	9	2.18	0.04
Obs	11.30	1	4.58	0.04
Error	110.96	45		
Total	45165.11	61		
Corrected Total	311.88	60		

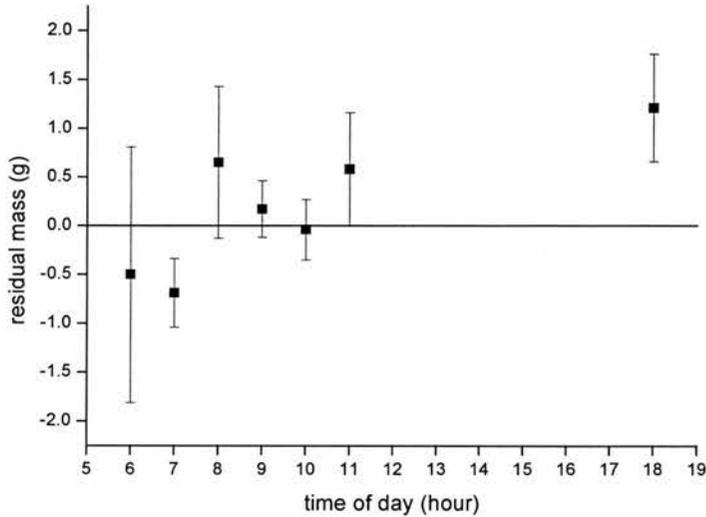


Figure 5.13: Black-necked weaver – variation in residual mass with time of day.

When time of year was classified into dry and rainy seasons it was again a significant variable (SS=17.21, df=1, error df = 52, F=6.74, p=0.01), as was time of day (SS=21.18, df=1, error df = 52, F=8.30, p=0.006) and sex (SS=12.38, df=1, error df = 52, F=4.85, p=0.03). Mass variation between the seasons was only 0.98g, or 3.2% of mean body mass (Table 5.22) and between sexes the difference

was small: 0.65g or 2.4% of mean body mass, although males were always larger than females (Table 5.23).

Table 5.22: Black-necked weaver - difference in residual mass between dry and rainy seasons.

Season	Mean residual mass	standard error
Dry	-0.39	0.3
Rainy	0.49	0.24

Table 5.23: Black-necked weavers - difference in residual body mass between males and females.

Sex	Mean residual mass	standard error
Female	-0.27	0.22
Male	0.38	0.36

**Vitelline masked weaver: Mean body mass:  $20.7 \pm 0.67\text{g}$  (n = 28), mean wing length:  $70.8 \pm 0.55\text{mm}$  (n = 28)**

Mass did not vary at all with any model. Mass was analysed with three models, each with month classified into different periods (Table 5.24).

Table 5.24: Vitelline masked weaver – GLM model output for time of year for three seasonal classifications.

Time of year	SS	df	error df	F	p
12 months	9.33	5	18	0.14	0.98
4 seasons	4.16	2	21	0.18	0.84
2 seasons	5.58	1	22	0.51	0.48

**Speckle-fronted weaver: Mean body mass:  $16.8 \pm 0.22\text{g}$  (n = 52), mean wing length:  $67.6 \pm 0.22\text{mm}$  (n = 49)**

Time of year was not a significant variable when classified by month or into four seasonal periods (Table 5.25)

Table 5.25: Speckle-fronted weaver – GLM model output for time of year variable when classified by month and into four seasons.

Time of year	SS	df	error df	F	p
12 months	18.64	8	34	1.27	0.29
4 seasons	2.79	3	39	0.46	0.71

However, age was significant (model with time of year classified by month: SS=11.68, df=1, error df = 34, F=6.37, p=0.02). The differences between adult and immature birds was 1.55g, or 9.2% of mean body mass (Table 5.26).

Table 5.26: Speckle-fronted weaver – difference in residual mass between immature and adult birds.

Age	Mean residual mass	standard error
Immature	-1.42	0.3
Adult	0.13	0.18

However, time of year was significant when classified into dry and rainy seasons (Table 5.27). The difference between the dry and rainy seasons was small: 0.94g or 5.6% of mean body mass (Fig. 5.14).

Table 5.27: Speckle-fronted weaver - with time of year classified into dry and rainy seasons the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{time of year} + \text{observer} + \text{age} \quad (R^2 = 0.35)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	55.01	7	4.62	0.001
Intercept	0.06	1	0.03	0.86
Wing	3.97	1	2.33	0.13
Year	32.43	3	6.36	0.001
Time of year	11.30	1	6.65	0.01
Obs	0.36	1	0.21	0.65
Age	9.38	1	5.52	0.02
Error	69.73	41		
Total	13947.78	49		
Corrected Total	124.74	48		

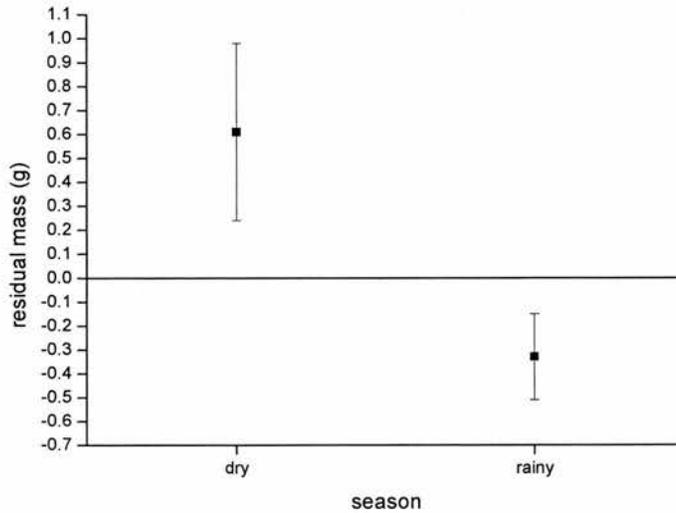


Figure 5.14: Speckle-fronted weaver – difference in residual mass between dry and rainy seasons.

**Northern red bishop: Mean body mass:  $15.5 \pm 0.13\text{g}$  ( $n = 127$ ), mean wing length:  $62.3 \pm 0.28\text{mm}$  ( $n = 127$ ).**

Body mass increased from a minimum in the early rains, when seed availability may be at a minimum, to peak in the mid-dry season when seed availability should be at a maximum (Fig. 5.15). As time of year was very sparsely distributed by month it was initially re-classified into four seasonal periods (Table 5.28).

Table 5.28: Northern red bishop - with time of year classified into four seasonal periods the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{time of year} + \text{sex} \quad (R^2 = 0.61)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	172.64	6	34.06	<0.001
Intercept	1.27	1	1.50	0.22
Wing	24.36	1	28.83	<0.001
Year	2.82	1	3.34	0.07
Time of year	11.84	3	4.67	0.004
Sex	19.22	1	22.76	<0.001
Error	101.37	120		
Total	30739.28	127		
Corrected Total	274.01	126		

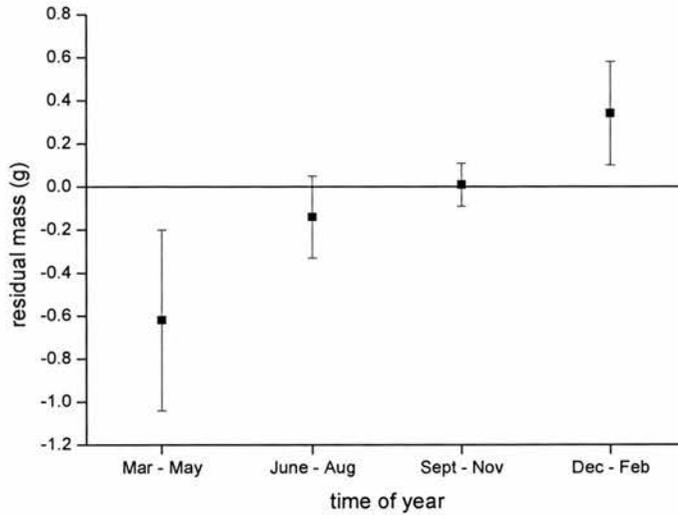


Figure 5.15: Northern red bishop – variation in residual mass with time of year classified into four seasons.

Residual body mass also differed significantly between the sexes in this model (see Table 5.28). This difference was small: 0.47g, or 3.0% of mean body mass (Table 5.29). However, when not a breeding plumage male, this species was very difficult to sex accurately. It is likely therefore that some birds sexed as female were actually juvenile males.

Table 5.29: Northern red bishop – difference in residual body mass between males and females.

Sex	Mean residual mass	standard error
Female	-0.18	0.11
Male	0.29	0.15

**Black-winged bishop: Mean body mass:  $20.5 \pm 0.32\text{g}$  (n = 55), mean wing length:  $74.8 \pm 0.75\text{mm}$  (n = 55).**

When classified by month or into four seasonal periods mass did not vary significantly with time of year (Table 5.30), but varied significantly between dry and rainy seasons (Table 5.31 and Fig. 5.16).

Table 5.30: Black-winged bishop – GLM model out put for time of year variable when classified by month or into four seasonal periods.

Time of year	SS	df	error df	F	p
12 months	19.99	5	49	2.33	0.06
4 seasons	3.14	2	48	0.91	0.41

Table 5.31: Black-winged bishop - with time of year classified into two seasons the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{time of year} + \text{observer} + \text{sex} (R^2 = 0.71)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	217.51	5	27.35	<0.001
Intercept	5.56	1	3.49	0.07
Wing	3.35	1	2.10	0.15
Year	0.04	1	0.02	0.88
Time of year	8.32	1	5.23	0.03
Obs	0.62	1	0.39	0.53
Sex	16.26	1	10.22	0.002
Error	77.93	49		
Total	23409.19	55		
Corrected Total	295.44	54		

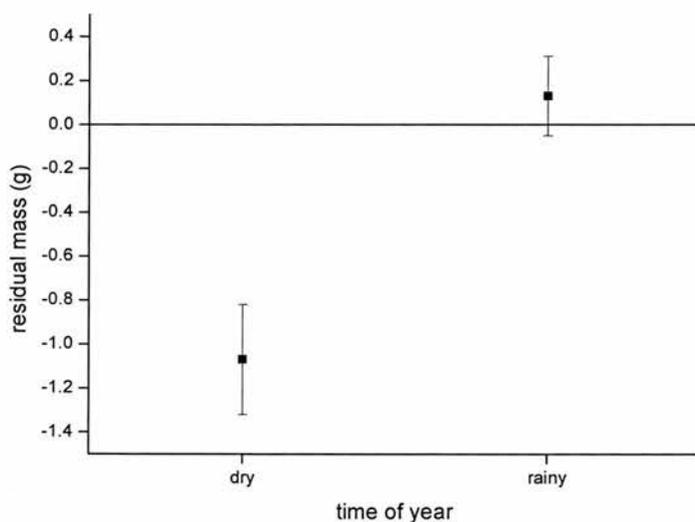


Figure 5.16: Black-winged bishop – difference in residual mass between dry and rainy seasons.

Interestingly, black-winged bishops showed an opposite pattern of seasonal mass variation to northern red bishops. The seasonal change in body mass is also greater: black-winged bishop = 1.2g; northern red bishop = 0.41g. This change

was more than double when expressed as a percentage of mean body mass: black-winged bishop = 5.85%; northern red bishop = 2.65%.

Sex was also a significant variable in the above model (Table 5.32), with a difference of 0.33g or 1.6%. Again this was a difficult species to sex accurately so it was likely that some immature males were incorrectly identified as females.

Table 5.32: Black-winged bishop – difference in residual body mass between males and females.

Sex	Mean residual mass	standard error
Female	-0.16	0.21
Male	0.17	0.29

**Red-cheeked cordon bleu: Mean body mass =  $10.24 \pm 0.05\text{g}$  (n = 238), mean wing length =  $54.4 \pm 0.08\text{mm}$  (n = 238)**

There was significant variation in mass with time of year when classified into four periods dependent on sex (Table 5.33, Fig. 5.17).

Table 5.33: Red-cheeked cordon-bleu - with time of year classified into four seasonal periods the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{time of year} + \text{obs} + \text{sex} + \text{month} * \text{sex} (R^2 = 0.21)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	30.12	12	6.25	<0.001
Intercept	4.25	1	10.59	0.001
Wing	1.63	1	4.06	0.05
Year	0.53	3	0.44	0.72
Month	3.08	3	2.56	0.06
Observer	0.28	1	0.70	0.40
Sex	13.51	1	33.66	<0.001
Month * Sex	13.59	3	11.29	<0.001
Error	90.32	225		
Total	25090.48	238		
Corrected Total	120.44	237		

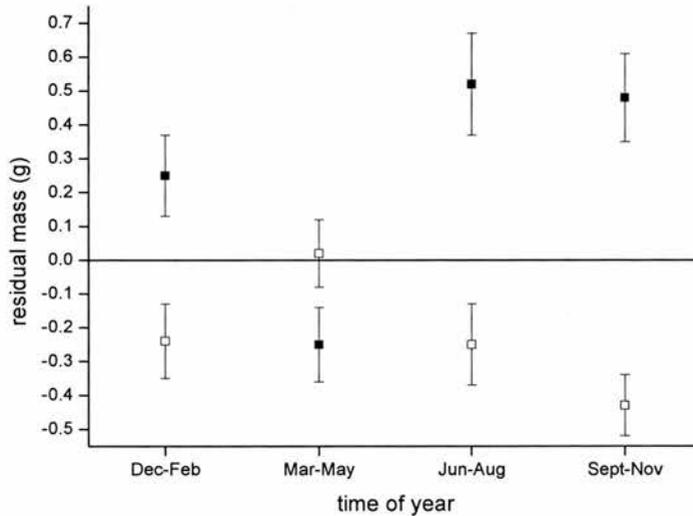


Figure 5.17: Red-cheeked cordon bleu – variation in residual mass by season with sex. □ = male; ■ = female.

Females maintained a significantly higher body mass every season except the early rainy season. During the early rains males significantly increased their body mass compared to the rest of the year. Female body mass declined from a peak in the mid-rains to drop significantly during the early rains.

**Lavender waxbill: Mean body mass =  $9.32 \pm 0.04$ g (n = 195), mean wing length =  $53.4 \pm 0.11$ mm (n = 191).**

Over the course of a year body mass increased from its lowest point during the late dry season to peak in the late rains, when this species is thought to breed (Table 5.34). There was then a decline in mass into the early dry season (Figure 5.18). Time of day increased over the day as a whole. But it appeared that birds increased mass slightly during the morning, but may have begun to lose mass towards mid-day. There was a larger increase in mass during the afternoon towards dusk (Figure 5.19).

Table 5.34: Lavender waxbill – with time of year classified into four seasonal periods the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{time of year} + \text{observer} \quad (R^2 = 0.17)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	11.82	9	5.42	<0.001
Intercept	2.97	1	12.28	0.001
Time	6.48	1	26.77	<0.001
Wing	1.61	1	6.65	0.01
Year	1.88	3	2.58	0.06
Time of year	1.99	3	2.75	0.04
Obs	0.08	1	0.32	0.57
Error	43.83	181		
Total	16707.56	191		
Corrected Total	55.65	190		

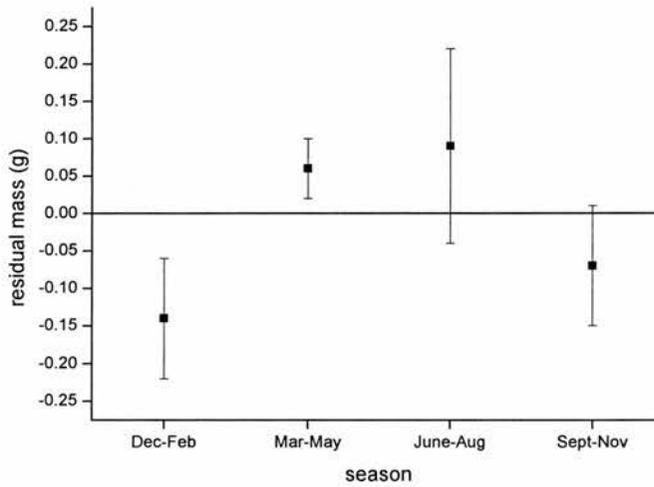


Figure 5.18: Lavender waxbill – variation in residual mass with time of year classified into four seasons.

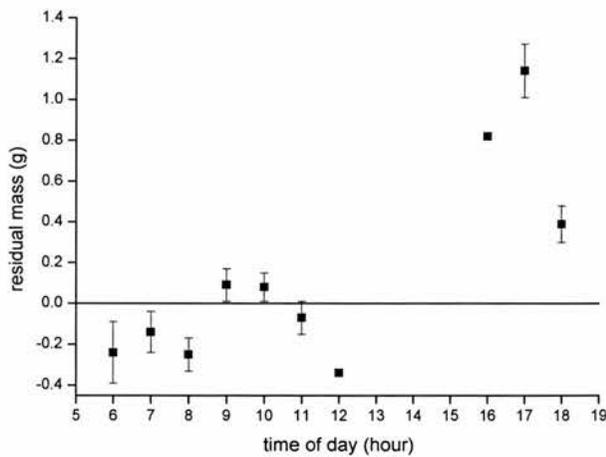


Figure 5.19: Lavender waxbill – variation in residual mass with time of day.

**Black-rumped waxbill: Mean body mass =  $7.42 \pm 0.08\text{g}$  (n = 61), mean wing length =  $50.9 \pm 0.17\text{mm}$  (n = 61).**

There was no variation in mass with any model variable, including time of year (table 5.35) Data was sparsely distributed across the year when classified by month or into four seasonal periods. Consequently it was possible that any existing pattern would not have been detectable. However, as data was evenly distributed between dry and rainy seasons (sample size of 30 and 31 respectively) any difference between these periods should have been detectable.

Table 5.35: Black-rumped waxbill – GLM model output for time of year variable when classified into month, four seasons and two seasons.

<b>Time of year</b>	SS	df	error df	F	p
12 months	1.30	8	49	0.53	0.83
4 seasons	0.74	3	54	0.85	0.47
2 seasons	0.29	1	56	1.03	0.32

**Red-billed firefinch: Mean body mass:  $8.86 \pm 0.04\text{g}$  (n = 259), mean wing length:  $51.9 \pm 0.09\text{mm}$  (n = 254)**

There was significant variation in mass with time of year when classified into four periods dependent on sex (Table 5.33, Fig. 5.20). There was little change in mass over the year until the early dry season when females increased their body mass. Most birds are thought to breed during this season. Males however reduced their body mass at this time of year.

Table 5.33: Red-billed firefinch - with time of year classified into four seasonal periods the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{time of year} + \text{observer} + \text{sex} + \text{time of year} * \text{sex}$$

( $R^2 = 0.15$ )

Source	Sum of Squares	df	F	Sig.
Corrected Model	24.09	12	4.69	<0.001
Intercept	2.32	1	5.42	0.02
Wing	3.15	1	7.37	0.007
Year	3.51	3	2.73	0.05
Time of year	3.18	3	2.48	0.06
Obs	3.15	1	7.37	0.007
Sex	0.24	1	0.57	0.45
Time of year*Sex	6.50	3	5.06	0.002
Error	102.26	239		
Total	19961.09	252		
Corrected Total	126.35	251		

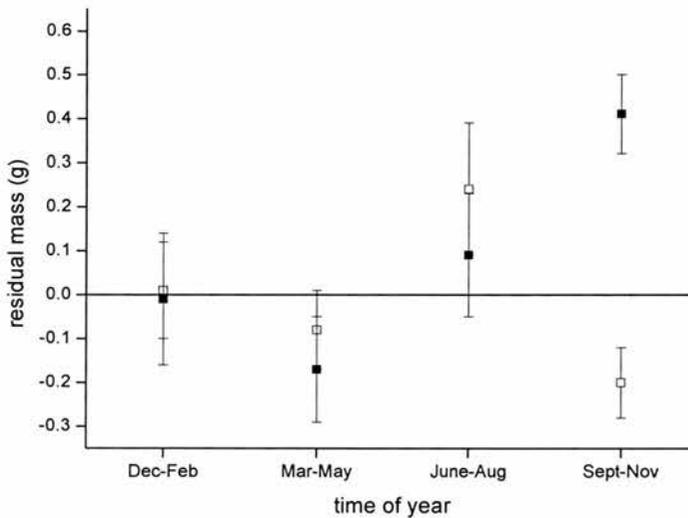


Figure 5.20: Red-billed firefinch – variation in residual mass with season by sex. □ = male, ■ – female.

When the seasonal data was re-classified into 2 seasons the model changed. Time of year was no longer significant, but the interaction between time of day and sex was (Table 5.34): males were lighter in the morning than females (Fig. 5.21).

Table 5.34: Red-billed firefinch - with time of year classified into two seasonal periods the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{observer} + \text{sex} + \text{sex} * \text{time} \quad (R^2 = 0.12)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	18.60	8	5.20	<0.001
Intercept	1.01	1	2.27	0.13
Time	0.25	1	0.57	0.45
Wing	5.52	1	12.34	0.001
Year	10.85	3	8.08	<0.001
Obs	3.46	1	7.73	0.006
Sex	4.13	1	9.23	0.003
Sex * Time	3.14	1	7.01	0.009
Error	109.63	245		
Total	20085.91	254		
Corrected Total	128.22	253		

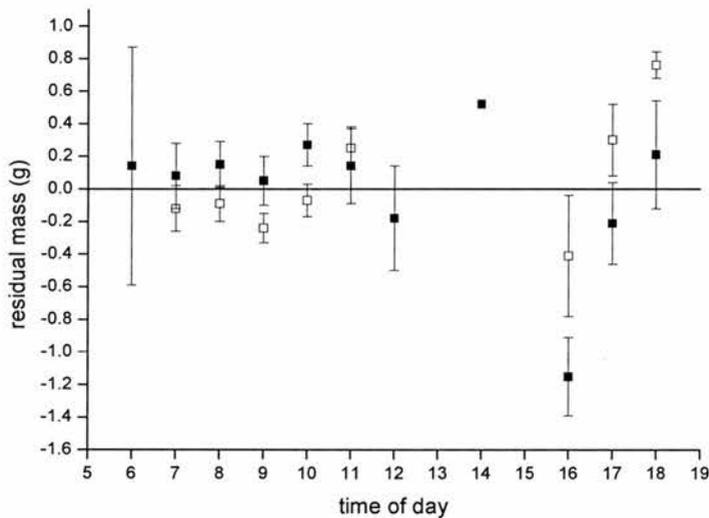


Figure 5.21: Red-billed firefinch – variation in residual mass with time of day by sex. □ = male, ■ = female.

Figure 5.21 suggests that there was a different pattern of mass variation in the morning and afternoon. So, each period was examined separately (Figs. 5.22 & 23). From the pattern of variation shown in figure 5.22 it would appear that there is no significant variation in mass of females across the morning, but that males increase mass during the morning, with most of this increase occurring from 1000 – 1100. From the pattern of variation shown in figure 5.23 it would appear that

both sexes increased mass before dusk. The body mass of males was always higher than females but females increased in mass at a slightly higher rate. Males increased in mass by 1.17g, or 13.2% of mean body mass, in the three hours to dusk. Over this same period females increased body mass by 1.36g, or 15.3% of mean body mass.

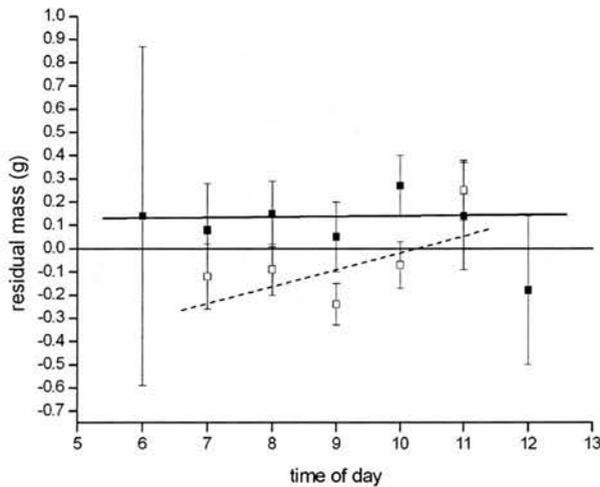


Figure 5.22: Red-billed firefinch – variation in residual mass with time of day by sex (morning only). □ = male, ■ = female. Linear regression female (solid line):  $y = 0.002x + 0.12$ ,  $r^2 = 0.00075$ . Linear regression male (dashed line):  $y = 0.07x - 0.75$ ,  $r^2 = 0.34$ .

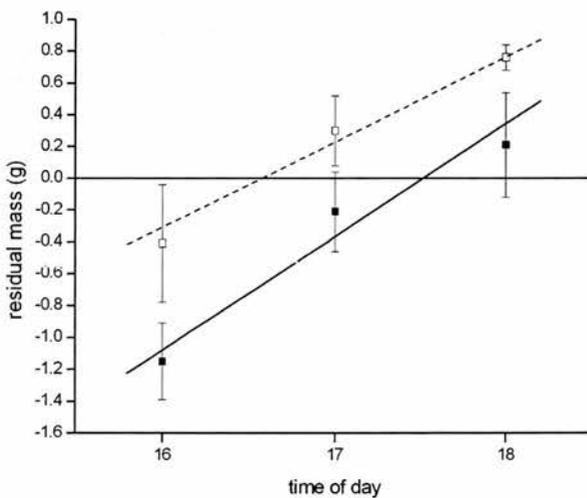


Figure 5.23: Red-billed firefinch – variation in residual mass with time of day by sex (afternoon only). □ = male, ■ = female. Linear regression female (solid line):  $y = 0.71x - 12.5$ ,  $r^2 = 0.95$ . Linear regression male (dotted line):  $y = 0.54x - 8.89$ ,  $r^2 = 0.99$ .

**Bar-breasted firefinch: Mean body mass:  $51.6 \pm 0.25\text{g}$  (n = 38), mean wing length:  $9.3 \pm 0.08\text{mm}$  (n = 39)**

Mass was tested against time of year classified by month, 4 seasons and 2 seasons. None was significant (Table 5.24). Data was perhaps too sparsely distributed across the year to detect any pattern in mass variation. However, samples were approximately equally distributed between dry and rainy seasons (n was 18 and 20 respectively), and so should have been able to detect any difference present.

Table 5.24: Bar-breasted firefinch – GLM model output for time of year variable when classified by month, four seasons and two seasons.

<b>Time of year</b>	<b>SS</b>	<b>df</b>	<b>error df</b>	<b>F</b>	<b>p</b>
12 months	2.09	7	25	1.16	0.36
4 seasons	0.49	3	28	0.57	0.64
2 seasons	0.006	1	31	0.02	0.89

**Rock firefinch: Mean body mass:  $10.5 \pm 0.07\text{g}$  (n = 116), mean wing length:  $52.5 \pm 0.13\text{mm}$  (n = 115).**

Body mass increased significantly from the lowest point in the mid-dry season (Table 5.25, Fig. 5.24). It would appear for this species that the reduction of seeds at the start of the rains does not have a significant impact on body mass. Mass peaked in the late rains and early dry season, which is when rock firefinches are thought to breed at this site.

Table 5.25: Rock firefinch – with time of year was classified into four seasonal periods the model was:

$$\text{mass} = \text{time of day} + \text{wing} + \text{year} + \text{time of year} + \text{observer} \quad (R^2 = 0.17)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	16.23	9	3.61	0.001
Intercept	2.02	1	4.06	0.05
Time of day	2.15	1	4.30	0.04
Wing	1.22	1	2.44	0.12
Year	0.58	3	0.39	0.76
Time of year	5.44	3	3.64	0.02
Obs	0.00	1	0.01	0.94
Error	52.41	105		
Total	12850.50	115		
Corrected Total	68.64	114		

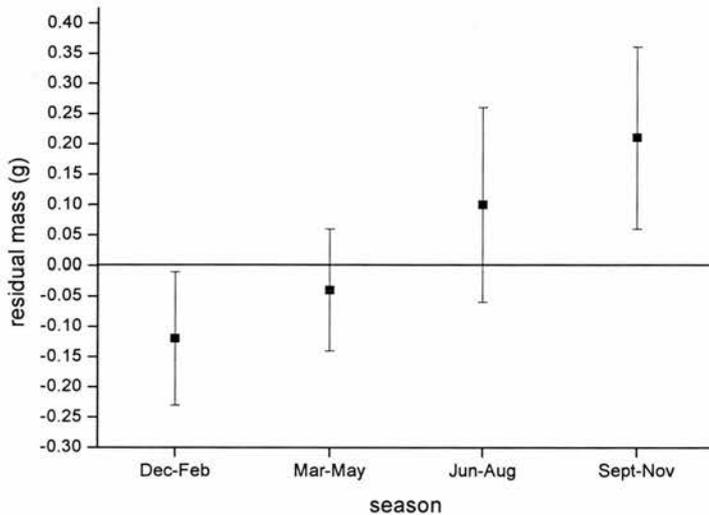


Figure 5.24: Rock firefinch – variation in residual mass with time of year classified into four seasons.

Body mass increased significantly with time of day, but a different pattern of mass variation was apparent in the morning than in the afternoon (Fig. 5.25). During the morning mass increased for the first three hours after dawn but decreased during the two hours after that. In the afternoon there was clearly a greater variation in body mass, but sample size was small. The difference in body mass between morning (0700 – 1100) and afternoon (1500 – 1800) was not

significant ( $t = 1.81$ ,  $df = 113$ ,  $p = 0.07$ ), but this was likely due to insufficient power.

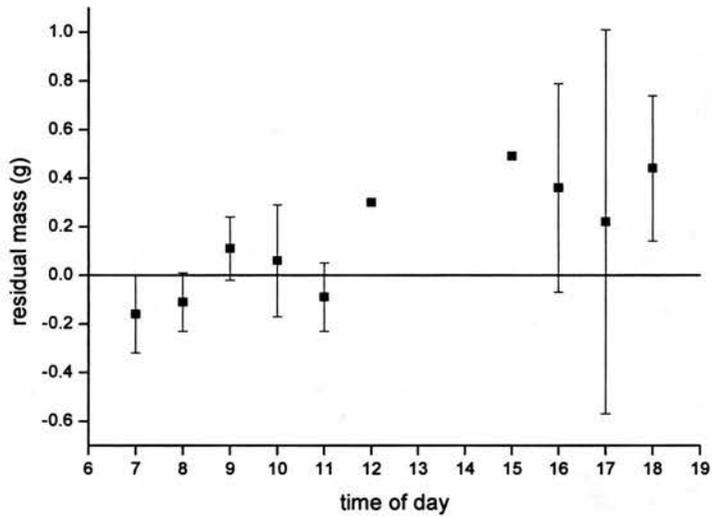


Figure 5.25: Rock firefinch – variation in residual mass with time of day.

Time of year was no longer significant when classified into two seasons ( $SS=0.20$ ,  $df=1$ , error  $df = 115$ ,  $F=0.39$ ,  $p=0.54$ ).

**Cinnamon-breasted bunting: Mean body mass:  $13.7 \pm 0.13\text{g}$  (n = 94), mean wing length:  $75.2 \pm 0.29\text{mm}$  (n = 94).**

Mass was tested against time of year classified by month, four seasons and two seasons. None was significant (Table 5.27).

Table 5.27: Cinnamon-breasted bunting – GLM model output for time of year variable classified by month, four seasons and two seasons.

Time of year	SS	df	error df	F	p
12 months	13.85	8	78	1.64	0.13
4 seasons	6.01	3	82	1.80	0.15
2 seasons	0.895	1	76	0.78	0.38

However, mass varied significantly with time of day (Table 5.28). Birds increased body mass across the whole day (Fig. 5.26). However, as there was no data from the middle of the day it was not possible to say if birds maintained, or lost mass across this period.

Table 5.28: Cinnamon-breasted bunting - with time of year classified by month the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{month} + \text{observer} (R^2 = 0.32)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	60.06	14	4.08	<0.001
Intercept	2.40	1	2.28	0.135
Time	28.30	1	26.92	<0.001
Wing	5.13	1	4.88	0.03
Year	6.11	3	1.94	0.13
Month	6.09	8	0.72	0.67
Obs	0.71	1	0.68	0.414
Error	82.01	78		
Total	17455.05	93		
Corrected Total	142.07	92		

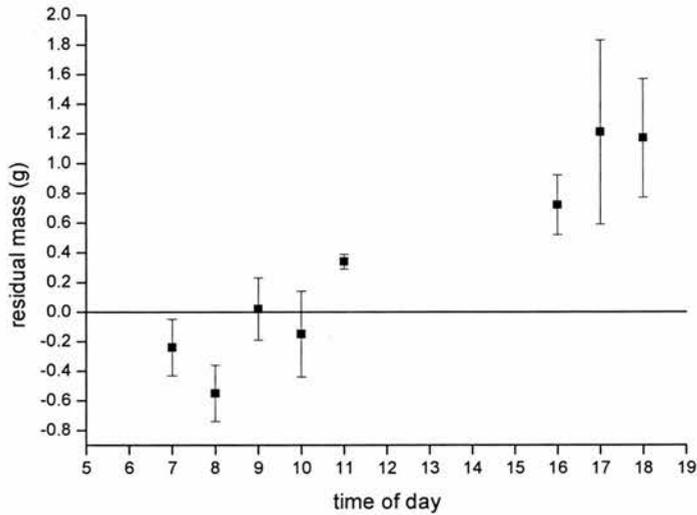


Figure 5.26: Cinnamon-breasted bunting – variation in residual mass with time of day.

**Variable sunbird: Mean body mass:  $6.29 \pm 0.05\text{g}$  (n = 148), mean wing length:  $50.9 \pm 0.19\text{mm}$  (n = 148)**

Body mass was significantly lower December to January (the dry season): (Table 5.29, Fig. 5.27). Mass varied with time dependent on sex (Fig. 5.28).

Table 5.29: Variable sunbird - with time of year classified into two month periods the model was:

$$\text{mass} = \text{time of day} + \text{wing} + \text{year} + \text{time of year} + \text{observer} + \text{sex} + \text{sex} * \text{time of day} \quad (R^2 = 0.49)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	24.65	13	11.66	<0.001
Intercept	0.91	1	5.57	0.02
Time	0.13	1	0.78	0.38
Wing	10.23	1	62.89	<0.001
Year	2.00	3	4.10	0.008
Time of year	4.84	5	5.95	<0.001
Obs	0.06	1	0.35	0.56
Sex	0.99	1	6.06	0.02
Sex * Time of day	0.90	1	5.55	0.02
Error	21.79	134		
Total	5897.90	148		
Corrected Total	46.44	147		

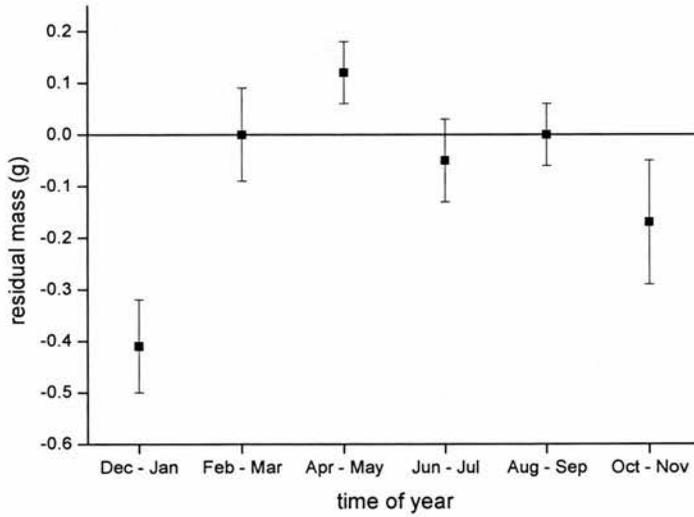


Figure 5.27: Variable sunbird –variation in residual mass with time of year classified into two month blocks.

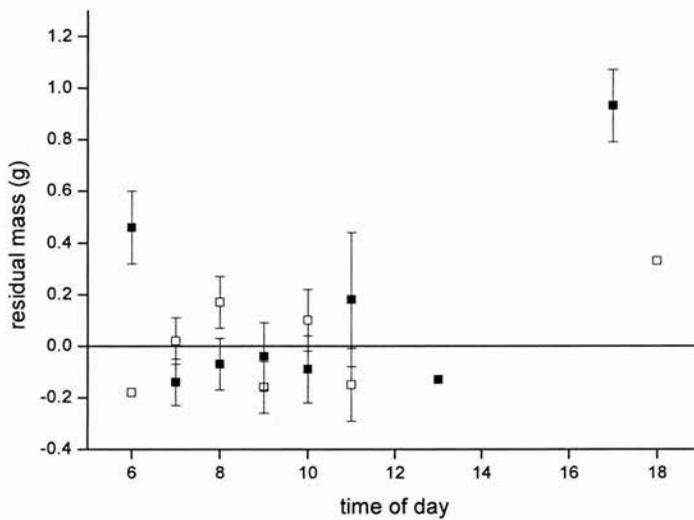


Figure 5.28: Variable sunbird - variation in residual mass with time of day by sex. □ = male; ■ = female.

The pattern of daily mass variation illustrated in figure 5.28 showed that both sexes maintained an approximately similar and constant body mass through most of the morning. Female however, had a higher body mass at 0600. There was very limited data from later in the day, but it did suggest that birds were increasing mass greatly towards dusk.

**Scarlet-chested sunbird: mean body mass:  $10.5 \pm 0.09\text{g}$  (n = 112), mean wing length:  $65.7 \pm 0.35\text{mm}$  (n = 111)**

Time of year was not significant predictor of mass whether classified by month, four seasons or two seasons (Table 5.30).

Table 5.30: Scarlet-chested sunbird – GLM model output for time of year classified by month, four seasons and two seasons.

<b>Time of year</b>	<b>SS</b>	<b>df</b>	<b>error df</b>	<b>F</b>	<b>p</b>
Month	5.11	8	97	1.52	0.16
4 seasons	1.50	3	102	1.15	0.33
2 seasons	0.61	1	105	1.05	0.31

However, sex was significant in each model (e.g. with time of year classified by month: SS = 3.61, df = 1, error df = 97, F = 8.61, p = 0.004). The difference in residual mass between the sexes was 0.23g, or 2.2% of mean body mass (Table 5.31).

Table 5.31: Scarlet-chested sunbird – difference in residual mass between males and females.

<b>Sex</b>	<b>Mean residual mass</b>	<b>standard error</b>
Female	-0.13	0.11
Male	0.10	0.08

**Green-headed sunbird: Mean body mass:  $12.4 \pm 0.15\text{g}$  (n = 55), mean wing length:  $65.0 \pm 0.34\text{mm}$  (n = 55)**

The pattern of mass variation was best defined when time of year was classified into four seasonal periods (Table 5.32). Body mass declined from a peak in the late rainy season to minimum in the early rainy season. There was no significant variation in body mass through the dry season (Figure 5.29).

Table 5.32: Green-headed sunbird. With time of year classified into four seasonal periods the model was:

$$\text{mass} = \text{time} + \text{wing} + \text{year} + \text{month} + \text{sex} \quad (R^2 = 0.78)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	55.46	9	21.78	<0.001
Intercept	1.16	1	4.10	0.05
Time	1.90	1	6.72	0.01
Wing	8.10	1	28.63	<0.001
Year	3.44	3	4.05	0.01
Month	5.11	3	6.03	0.002
Sex	1.90	1	6.71	0.01
Error	12.73	45		
Total	8472.99	55		
Corrected Total	68.19	54		

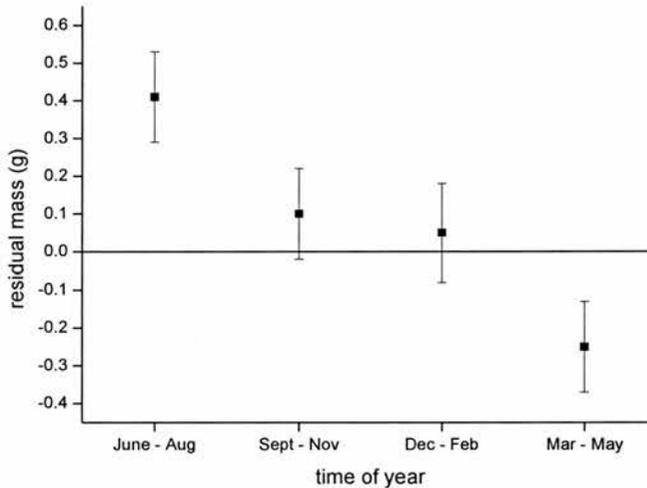


Figure 5.29: Green-headed sunbird – variation in residual mass with time of year classified into four seasons. (SS = 5.11, df = 3, F = 6.03, p = 0.002).

There was also a significant difference in body mass between the sexes. However this difference was only 0.21g, or 1.7% of mean body mass (Table 5.33).

Table 5.33: Green-headed sunbird – difference in residual body mass between females and males.

	Mean	Standard Error
Female	-0.12	0.09
Male	0.09	0.1

Time of day was also a significant in the model (Table 5.32). Body mass increased steadily across the morning, however, data was only available from the period 0600 to 1100 (Fig. 5.30).

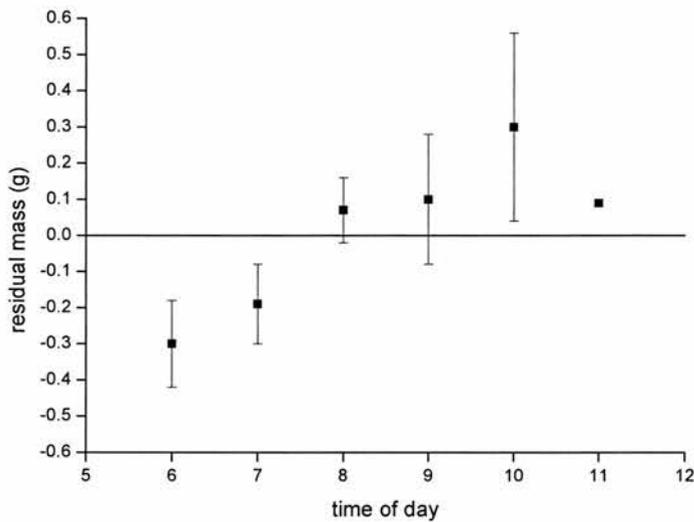


Figure 5.30: Green-headed sunbird – variation in residual mass by time of day.

**Whinchat: Mean body mass:  $18.6 \pm 0.40\text{g}$  ( $n = 71$ ), mean wing length:  $77.3 \pm 0.24\text{mm}$  ( $n = 70$ ).**

As whinchat is a highly seasonal migrant, time of year was re-classified into autumn (October to December) and spring (April to May). There was significant seasonal variation in mass and variation in mass by sex, and the sex difference did not change with season (Table 5.44). Whinchats had significantly higher mass in the spring compared to the autumn (Fig. 5.31). Males were significantly larger than females (Fig. 5.32).

Table 5.44: Whinchat – with season classified into two seasons the model was:  
 $\text{mass} = \text{wing} + \text{year} + \text{season} + \text{observer} + \text{sex}$  ( $R^2 = 0.5$ )

Source	Sum of Squares	df	F	Sig.
Corrected Model	421.70	6	12.41	<0.001
Intercept	2.51	1	0.44	0.51
Wing	21.13	1	3.73	0.06
Year	75.89	2	6.70	0.002
Season	326.31	1	57.63	<0.001
Obs	0.18	1	0.03	0.86
Sex	37.88	1	6.69	0.01
Error	356.71	63		
Total	24895.27	70		
Corrected Total	778.41	69		

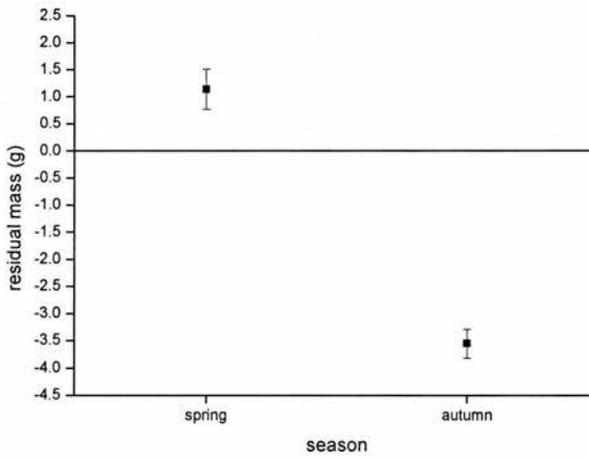


Figure 5.31: Whinchat – difference in residual body mass between autumn and spring.

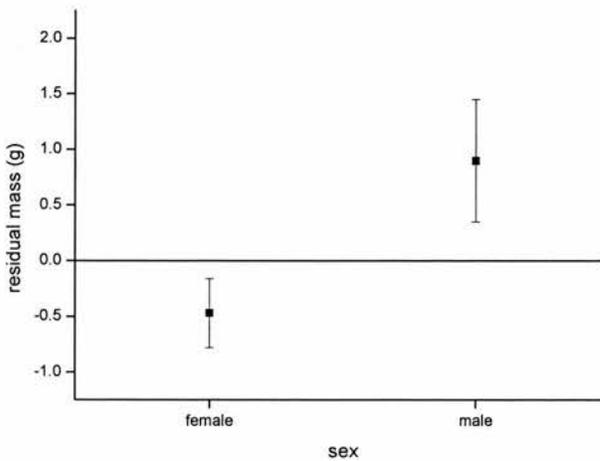


Figure 5.32: Whinchat – difference in residual body mass between males and females.

**Pied flycatcher: Mean body mass:  $13.3 \pm 0.48\text{g}$  ( $n = 29$ ), mean wing length:  $80.8 \pm 0.25\text{mm}$  ( $n = 28$ )**

Birds that were arriving in autumn had a significantly lower body mass than other seasons (Table 5.33, Fig. 5.33). Few birds winter at this site, so birds must not be dispersing far as they do not appear to be fattening for further migration. Winter mass is higher than arrival mass as birds regain condition. In spring there was an increase in body mass due to pre-migratory fattening.

Table 5.33: Pied flycatcher – with time of year was classified into three seasons: autumn, winter, spring the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{season} + \text{observer} \quad (R^2 = 0.48)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	110.14	6	4.83	0.004
Intercept	5.83	1	1.53	0.23
Wing	10.92	1	2.87	0.11
Year	12.33	2	1.62	0.22
Season	39.06	1	10.28	0.005
Obs	1.64	1	0.43	0.52
Error	72.17	19		
Total	4842.83	26		
Corrected Total	182.31	25		

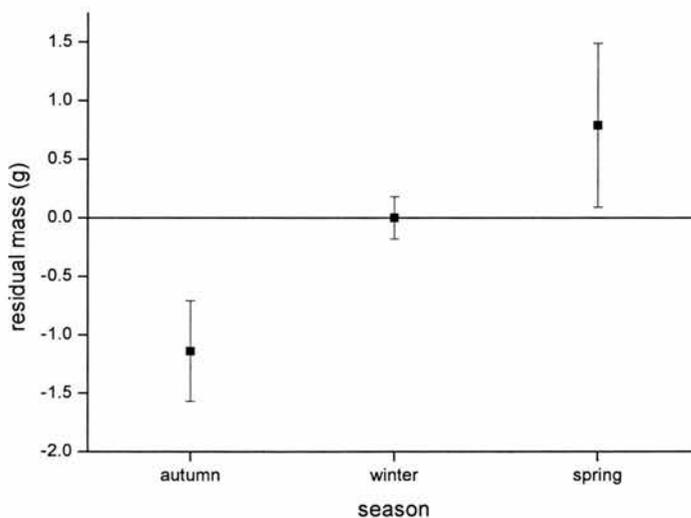


Figure 5.33: Pied flycatcher – residual mass variation across 3 seasons.

**Garden warbler: Mean body mass:  $20.5 \pm 0.17\text{g}$  ( $n = 324$ ), mean wing length:  $81.7 \pm 0.13\text{mm}$  ( $n = 321$ )**

There was significant variation in mass by month (Table 5.34). Birds arrived in September having migrated from Europe. Bird then increased body mass through the autumn as they deposited fat as migratory fuel (Fig. 5.34).

Table 5.34: Garden warbler - with time of year classified by month the model was:

$$\text{mass} = \text{wing} + \text{year} + \text{month} + \text{observer} \quad (R^2 = 0.26)$$

Source	Sum of Squares	df	F	Sig.
Corrected Model	850.8	11	11.09	<0.001
Intercept	4	1	0.57	0.45
Wing	36.4	1	5.22	0.02
Year	40.2	3	1.92	0.13
Month	641.7	6	15.33	<0.001
Obs	7.1	1	1.02	0.32
Error	2106.4	302		
Total	135227.5	314		
Corrected Total	2957.2	313		

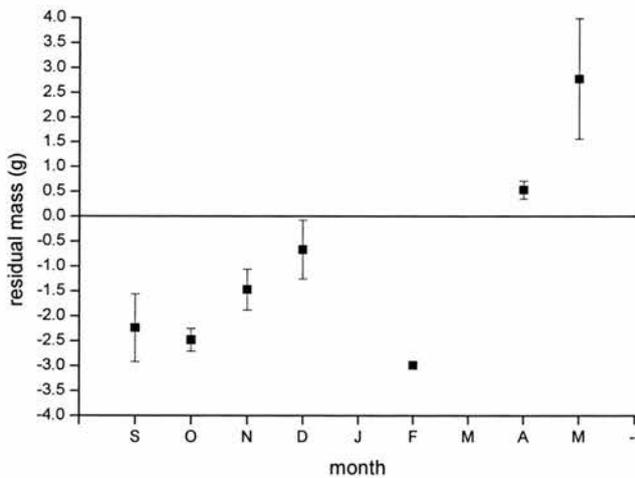


Figure 5.34: Garden warbler – variation in residual mass with time of year.

Few birds wintered at this site (*pers obs*) and the single capture in February suggested that they maintained a lower body mass when resident for the winter. During spring passage birds were arriving and rapidly increasing mass as they again deposited fat to fuel their return migration north. The difference between spring and autumn was examined by reclassifying seasonal data into two periods, spring and autumn. The model was the same and time of year was still significant (SS=553.92, df=1, error df = 313, F=78.64,  $p < 0.001$ ): Fig. 5.35.

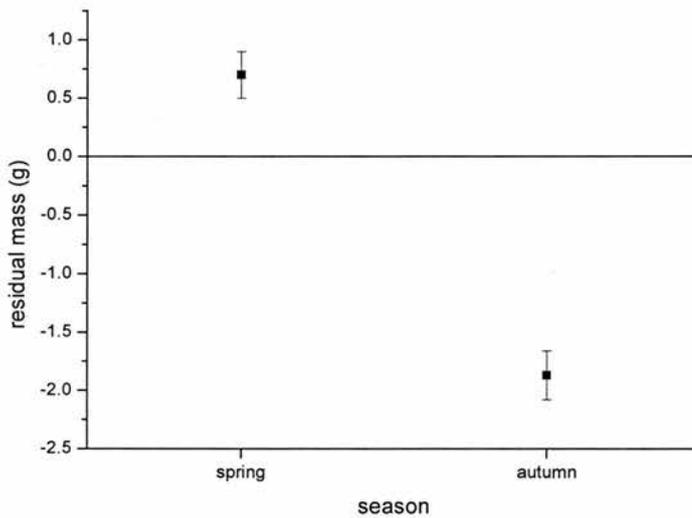


Fig 5.35: Garden warbler – difference in residual mass between spring and autumn.

So, while birds in autumn were fuelling for continuing migration, they did not deposit as much fat as they did for the northward spring migration. It was likely that birds continuing south in autumn were not migrating as far as they were in spring. Alternatively, birds continuing south perhaps did not have to cross such harsh ecological barriers (such as the Sahara desert) and so did not have to gain extra fat as ‘insurance’ against poor conditions for migration. Further analysis of Garden warbler mass variation may be found in the appendix.

**Whitethroat: Mean body mass:  $15.1 \pm 0.15\text{g}$  ( $n = 141$ ), mean wing length:  $79.0 \pm 0.14\text{mm}$  ( $n = 141$ )**

There was significant variation in mass by month dependent on sex (Table 5.35, Fig. 5.36).

Table 5.35: Whitethroat - with time of year classified by month the model was: mass = wing + year + month + observer + sex + month\*sex ( $R^2 = 0.25$ )

Source	Sum of Squares	df	F	Sig.
Corrected Model	135.28	15	3.75	<0.001
Intercept	7.28	1	3.03	0.085
Wing	0.66	1	0.27	0.60
Year	28.60	3	3.96	0.01
Month	96.94	6	6.71	<0.001
Obs	0.00	1	0.00	0.97
Sex	0.45	1	0.19	0.67
Month * Sex	22.63	3	3.13	0.03
Error	269.63	112		
Total	29617.37	128		
Corrected Total	404.90	127		

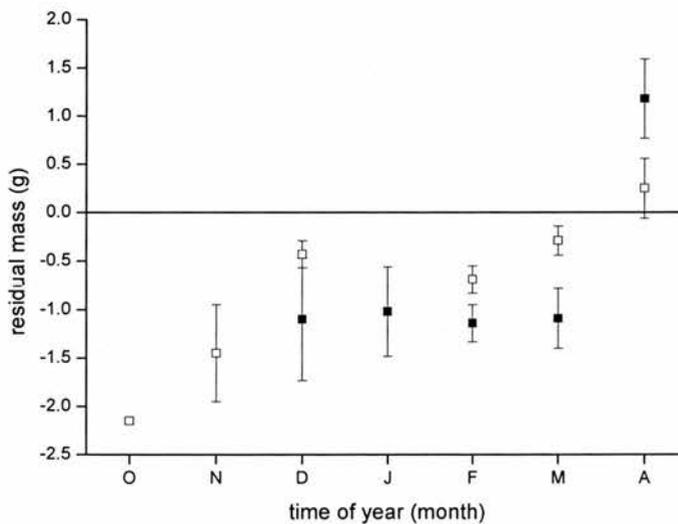


Figure 5.36: Whitethroat - residual mass with time of year by sex.  $\square$  = male;  $\blacksquare$  = female.

The pattern of variation in Figure 5.36 suggests that there were different fattening and migration strategies for each sex. In spring males increased mass earlier than females. Males may have been departing earlier and with less mass than females that were mostly departing in April and with a higher fuel load. As early departing males had a lower body mass (i.e. less fuel load) they should have been travelling a shorter distance north, perhaps only to the sahel. In the early autumn males were arriving earlier and with less body mass than females. However, males increased body mass through the early winter (November & December), which suggests that males may be staging in Jos and continuing further south. However, females arrived later and did not change mass suggesting that they were over wintering in the Jos area.

**Willow warbler: Mean body mass:  $8.4 \pm 0.22\text{g}$  (n = 66), mean wing length:  $65.6 \pm 0.36\text{mm}$  (n = 66)**

There was significant variation in mass with month (Table 5.36, Fig. 5.37).

Table 5.36: Willow warbler - with time of year classified by month the model was:

mass = wing + year + month + observer ( $R^2 = 0.572$ )

Source	Sum of Squares	df	F	Sig.
Corrected Model	131.48	7	13.39	<0.001
Intercept	8.18	1	5.83	0.02
Wing	30.39	1	21.65	<0.001
Year	3.59	1	2.56	0.12
Month	17.06	4	3.04	0.02
Obs	26.44	1	18.84	<0.001
Error	81.39	58		
Total	4837.97	66		
Corrected Total	212.88	65		

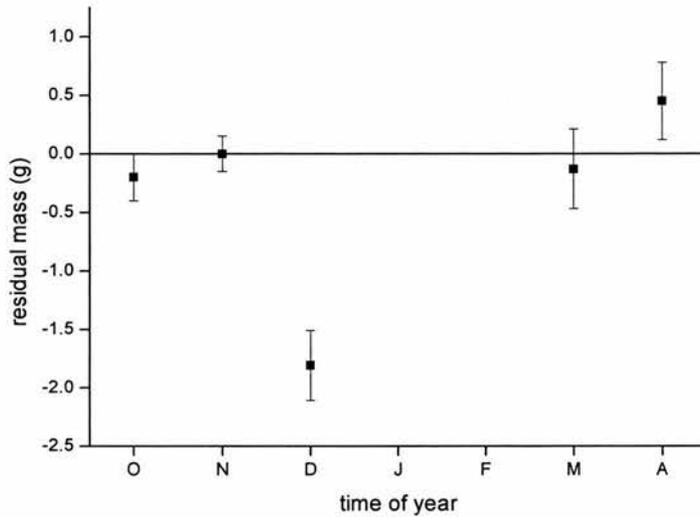


Figure 5.37: Willow warbler – variation in residual body mass with time of year classified by month.

The pattern in figure 5.37 appears to show that birds in autumn had a higher body mass than those, relatively few, birds that over winter at this site. This would suggest that many of the birds trapped in autumn were passing through this site and continuing further south. This is supported by the relatively similar body mass of birds in spring compared to year. The slightly higher body mass of spring birds while not significant is interesting as it suggests that they were fuelling for a longer journey than those in autumn.

## **Results: Across species summaries**

### **Seasonal mass variation**

The GLM model results for the time of year variable by its different classifications are summarized in table 5.38. Of the thirty-three species tested twelve did not show a significant variation in body mass with time of year. The remaining twenty-one species had a significant relationship between body mass and time of year with at least one classification. Five species were found to have a significant interaction between time of year and either age or sex.

When each species was tested with time of year classified into dry and rainy seasons, only nine showed a significant relationship (Table 5.39). Six species were found to increase body mass during the rains (snowy-crowned robin chat; common bulbul; black-necked weaver; black-winged bishop; variable sunbird; green-headed sunbird), one species decreased body mass during the rains (speckle-fronted weaver) and in one species (northern red bishop) females increased in body mass during the rains but males decreased in body mass. However, none of these species showed a large relative change in body mass (maximum change was 6.2%).

Eight species showed a significant relationship between body mass and year (see Appendix 5.2).

Table 5.38: Summary of GLM model results examining body mass variation with time of year and time of day. n = sample size.

species	time of year					year	time of day	sex	age	interactions	p	n
	12 months	2 month blocks	four seasons	two seasons	ns							
non-passerine	ns	-	ns	ns	ns	ns	ns	-	ns			39
black-billed wood dove	ns	-	ns	ns	ns	ns	ns	-	ns			90
yellow-fronted tinkerbird	ns	-	ns	ns	ns	ns	ns	-	ns			24
greater honeyguide	ns	-	ns	ns	ns	ns	ns	-	ns			37
red-throated bee-eater	ns	-	ns	ns	ns	ns	ns	-	ns			35
African insectivores	*	-	ns	ns	**	ns	ns	-	ns			103
common wattle-eye	ns	-	ns	ns	ns	ns	ns	-	ns			57
african yellow white-eye	***	-	ns	****	ns	ns	ns	-	ns			190
snowy-crowned robin-chat	***	***	ns	***	ns	ns	ns	-	ns			126
common bulbul	***	***	ns	***	ns	ns	ns	-	*			75
african thrush	***	-	ns	ns	ns	ns	ns	-	ns			67
grey-backed camaroptera	ns	-	ns	ns	ns	ns	ns	-	ns			67
African quailfinch	ns	-	ns	ns	ns	ns	ns	-	ns			67
bronze mannikin	****	-	ns	ns	****	ns	ns	-	time of year* age			67
village weaver	****	-	ns	ns	****	ns	ns	-	time of day* age			113
black-necked weaver	*	-	ns	**	ns	**	*	-	ns			62
vitelline masked weaver	ns	-	ns	ns	ns	ns	ns	-	ns			28
speckle-fronted weaver	ns	-	ns	**	ns	ns	ns	-	*			52
northern red bishop	***	-	ns	****	ns	ns	ns	-	ns			127
black-winged bishop	ns	-	ns	*	ns	ns	ns	-	ns			55
red-cheeked cordon bleu	interaction	-	ns	ns	ns	ns	ns	-	time of year*sex			238
lavender waxbill	interaction	-	*	ns	ns	****	ns	-	time of year*age			195
black-rumped waxbill	ns	-	ns	ns	ns	****	ns	-	ns			61
red-billed firefinch	*	-	ns	ns	ns	ns	ns	-	time of year*sex			259
bar-breasted firefinch	ns	-	ns	ns	ns	ns	ns	-	time of day*sex			38
rock firefinch	*	-	ns	ns	ns	*	*	-	ns			116
cinnamon-breasted bunting	ns	-	ns	ns	ns	****	ns	-	ns			94
sun birds	****	****	****	****	****	****	****	-	time of day*sex			148
variable sunbird	****	-	ns	****	ns	ns	ns	-	ns			112
scarlet-chested sunbird	ns	-	ns	ns	ns	ns	ns	-	ns			55
green-headed sunbird	****	-	****	*	****	****	****	-	ns			71
whinchat	-	-	-	-	****	****	ns	-	ns			29
pied flycatcher	-	-	-	-	****	****	ns	-	ns			324
garden warbler	****	-	-	-	****	****	ns	-	ns			141
whitethroat	interaction	-	-	-	****	****	ns	-	time of year*sex			66
willow warbler	*	-	-	-	****	****	ns	-	ns			66

symbol	p
*	0.05 - 0.02
**	0.01 - 0.02
***	0.01 - 0.001
****	< 0.001

Table 5.39: Body mass variation between dry and rainy seasons.

	species	two seasons	residual body mass			min body	
			dry season	rainy season	difference	mass	%
non-passerine	black-billed wood dove	ns					
	yellow-fronted tinkerbird	ns					
	greater honeyguide	ns					
	red-throated bee-eater	ns					
African insectivores	common wattle-eye	ns					
	african yellow white-eye	ns					
	snowy-crowned robin-chat	****	-1.7	0.46	2.16	35.73	6.0
	common bulbul	***	-0.53	0.69	1.22	38.03	3.2
	african thrush	ns					
	grey-backed camaroptera	ns					
African granivores	African quailfinch	ns					
	bronze mannikin	ns					
	village weaver	ns					
	black-necked weaver	**	-0.39	0.49	0.88	27.10	3.2
	vitelline masked weaver	ns					
	speckle-fronted weaver	**	0.61	-0.33	0.94	16.51	5.7
	northern red bishop (female)	****	-0.28	-0.01	0.27	15.92	1.7
	northern red bishop (male)	****	0.55	-0.36	0.91	14.56	6.2
	black-winged bishop	*	-1.07	0.13	1.2	20.44	5.9
	red-cheeked cordon bleu	ns					
	lavender waxbill	ns					
	black-rumped waxbill	ns					
	red-billed firefinch	ns					
	bar-breasted firefinch	ns					
rock firefinch	ns						
cinnamon-breasted bunting	ns						
sun birds	variable sunbird	***	-0.17	0.06	0.23	6.21	3.7
	scarlet-chested sunbird	ns					
	green-headed sunbird	*	-0.18	0.12	0.3	12.01	2.5

### Diurnal body mass variation

Eleven species were found to have a significant relationship between body mass and time of day (Table 5.40). Three species also had a significant interaction between time of day and either age or sex. The change in residual body mass between morning and evening was calculated relative to minimum body mass (Table 5.40). This was not possible for two species (yellow-fronted tinkerbird and green-headed sunbird). Mass change over the morning only was calculated for these species. Relative change in residual body mass was very variable, from 0.8 to 17.3% of minimum body mass.

Table 5.40: Diurnal mass variation amongst thirty three species tested. Time of day column represents the level of significance of this variable in the GLM. Any significant interactions are shown with an indication of their significance (\* -  $p = 0.02-0.05$ ; \*\*\* -  $p = 0.001$ ). The earliest and latest time of day where there was a mean residual body mass value is shown in columns am and pm respectively. n = sample size . Two species in which there was insufficient data to examine the effect across the whole day were examined across the morning only. These species' results were shown in italics.

	species	time of day	interactions	p	residual body mass			min body mass	s.e.	%	n		
					am	pm	change						
non-passerine	black-billed wood dove	ns									39		
	yellow-fronted tinkerbird	**			0700 - 1100		-0.31 - 0.39	-	0.31	10.61	0.1	2.9	90
	greater honeyguide	ns											24
	red-throated bee-eater	ns											37
African insectivores	common wattle-eye	ns											35
	african yellow white-eye	**			0600	1800	-0.49	0.28	0.31	9.2	0.26	3.4	103
	snowy-crowned robin-chat	ns											57
	common bulbul	ns											190
	african thrush	ns											126
	grey-backed camaroptera	**			0700	1800	-0.29	0.58	0.87	10.82	0.27	8.0	75
African granivores	African quailfinch	ns											67
	bronze mannikin (immature)		interaction	time of day*age *	0700	1700	-0.23	0.49	0.72	8.05	0.12	8.9	106
	bronze mannikin (adult)				0700	1700	-0.8	0.71	1.51	8.72	0.1	17.3	156
	village weaver	ns											113
	black-necked weaver	**			0600	1800	-0.5	1.21	1.71	26.15	0.75	6.5	62
	vitelline masked weaver	ns											28
	speckle-fronted weaver	ns											52
	northern red bishop	ns											127
	black-winged bishop	ns											55
	red-cheeked cordon bleu	ns											238
	lavender waxbill	****			0600	1800	-0.24	0.39	0.63	9	0.12	7.0	195
	black-rumped waxbill	ns											61
	red-billed firefinch (male)				0700	1800	-0.12	0.76	0.88	8.72	0.09	10.1	140
	red-billed firefinch (female)		interaction	time of day*sex ***	0600	1800	0.14	0.21	0.07	8.79	0.16	0.8	119
	bar-breasted firefinch	ns											38
	rock firefinch	*			0700	1800	-0.16	0.44	0.6	10.39	0.12	5.8	116
cinnamon-breasted bunting	****			0700	1800	-0.24	1.17	1.41	13.08	0.29	10.8	94	
sun birds	variable sunbird (male)		interaction	time of day*sex *	0600	1700	0.08	0.91	0.83	6.38	0.24	13.0	70
	variable sunbird (female)				0600	1800	0.25	0.4	0.15	5.92	0.09	2.5	78
	scarlet-chested sunbird	ns											112
	green-headed sunbird	**			0600 - 1000		-0.3 - 0.3	-	0.6	12.09	0.21	5.0	55
palearctic migrants	whinchat	ns											71
	pie'd flycatcher	ns											29
	garden warbler	ns											324
	whitethroat	ns											141
	willow warbler	ns											66

## Body mass and moult

Moult period information was only available for fifteen of the thirty-three species studied. Of these fifteen only seven had a significantly different mass between the moult period and the rest of the year (Table 5.41). In two species (red-cheeked cordon bleu and red-billed firefinch) there was a significant interaction between time of year (classified into moult and not moult periods) and sex. Changes in residual body mass between these two periods were small: 2 to 5.2% of minimum body mass.

Table 5.41: Body mass difference between moult and non-moult periods for fifteen species with measured main moult period. Species with shaded data showed a statistically significant difference in body mass between moult periods and the rest of the year.

	species	GLM model output for time of year				residual body mass			min body mass	direction of change	moult period (days)				
		SS	df	error df	F	p	non-moult period	s.e.				difference			
non-passerine	black-billed wood dove														
	yellow-fronted tinkerbird														
African insectivores	greater honeyguide														
	red-throated bee-eater														
	common wattle-eye														
	african yellow white-eye	0.10	1	84	0.03	0.86	-0.10	0.08	0.10	0.07	0.20	9.49	2.1	135	
	snowy-crowned robin-chat														
	common bulbul	<b>84.92</b>	<b>1</b>	<b>172</b>	<b>13.87</b>	<b>&lt;0.001</b>	<b>-0.77</b>	<b>0.36</b>	<b>0.40</b>	<b>0.21</b>	<b>1.17</b>	<b>38.00</b>	<b>3.1</b>	<b>increase</b>	<b>179</b>
	african thrush														
	grey-backed camaroptera														
	African quailfinch	0.64	1	44	1.99	0.17	0.16	0.16	-0.05	0.08	0.21	10.61	2.0		118
	bronze mannikin	<b>1.68</b>	<b>1</b>	<b>144</b>	<b>5.02</b>	<b>0.03</b>	<b>-0.19</b>	<b>0.10</b>	<b>0.04</b>	<b>0.05</b>	<b>0.23</b>	<b>8.97</b>	<b>2.6</b>	<b>increase</b>	<b>191</b>
village weaver	0.78	1	105	0.13	0.72	0.02	0.23	-0.20	0.81	0.22	36.89	0.6		161	
black-necked weaver															
vitelline masked weaver															
speckle-fronted weaver	1.46	1	42	0.69	0.41	0.33	0.46	-0.08	0.22	0.41	16.65	2.5		166	
northern red bishop	<b>9.63</b>	<b>1</b>	<b>121</b>	<b>11.31</b>	<b>0.001</b>	<b>-0.31</b>	<b>0.17</b>	<b>0.10</b>	<b>0.09</b>	<b>0.41</b>	<b>15.06</b>	<b>2.7</b>	<b>increase</b>	<b>148</b>	
black-winged bishop															
red-cheeked cordon bleu (male)	<b>8.75</b>	<b>1</b>	<b>229</b>	<b>20.91</b>	<b>&lt;0.001</b>	<b>-0.30</b>	<b>0.07</b>	<b>-0.06</b>	<b>0.09</b>	<b>0.24</b>	<b>9.96</b>	<b>2.4</b>	<b>increase</b>	<b>133</b>	
red-cheeked cordon bleu (female)						<b>0.45</b>	<b>0.08</b>	<b>-0.08</b>	<b>0.10</b>	<b>0.53</b>	<b>10.13</b>	<b>5.2</b>	<b>decrease</b>		
lavender waxbill	0.055	1	119	0.21	0.65	0.00	0.22	0.00	0.04	0.00	9.22	0.0		199	
black-rumped waxbill															
red-billed firefinch (male)	<b>5.52</b>	<b>1</b>	<b>183</b>	<b>12.53</b>	<b>0.001</b>	<b>-0.19</b>	<b>0.08</b>	<b>0.03</b>	<b>0.10</b>	<b>0.22</b>	<b>8.74</b>	<b>2.5</b>	<b>increase</b>	<b>203</b>	
red-billed firefinch (female)						<b>0.35</b>	<b>0.10</b>	<b>-0.10</b>	<b>0.09</b>	<b>0.45</b>	<b>8.69</b>	<b>5.2</b>	<b>decrease</b>		
bar-breasted firefinch															
rock firefinch	<b>2.3</b>	<b>1</b>	<b>92</b>	<b>4.19</b>	<b>0.04</b>	<b>0.14</b>	<b>0.14</b>	<b>-0.07</b>	<b>0.09</b>	<b>0.21</b>	<b>10.32</b>	<b>2</b>	<b>decrease</b>	<b>118</b>	
cinnamon-breasted bunting	0.75	1	73	0.72	0.40	-0.10	0.13	0.09	0.17	0.19	13.63	1.4		36	
variable sunbird	0.00	1	141	0.00	0.98	0.00	0.09	0.00	0.04	0.00	6.21	0.0		36	
scarlet-chested sunbird	0.21	1	103	0.50	0.48	-0.12	0.17	0.01	0.06	0.13	10.53	1.2		246	
green-headed sunbird	<b>2.35</b>	<b>1</b>	<b>46</b>	<b>8.36</b>	<b>0.006</b>	<b>0.21</b>	<b>0.09</b>	<b>-0.11</b>	<b>0.09</b>	<b>0.32</b>	<b>12.29</b>	<b>2.6</b>	<b>decrease</b>	<b>181</b>	
whinchat															
pied flycatcher															
garden warbler															
whitethroat															
willow warbler															

## **Discussion**

### **Body mass and energy reserves**

Most studies of body mass variation in birds have been conducted in north temperate climates. Other studies have shown that birds store energy as body fat and that there was a close correlation between body mass and body fat e.g. (Witter & Cuthill 1993; Gosler *et al.* 1998). Consequently many studies assume that variation in body mass was due to a variation on fat stores. However, when this was tested for the twenty-eight resident tropical species studied here there was only a relationship between body mass and fat score in four species (see Figure A5.1 in Appendix 5.2 and Table A5.2.1). Two species always had a score of zero, so no sub-cutaneous fat was ever recorded for these species (black-billed wood dove and common wattle-eye). An additional four species had fat scores of 00 or 10. It was not possible to measure fat on greater honeyguide as their skin is too thick to see the fat underneath. The highest fat score reliably measured on a tropical species was 30. In contrast the five palearctic migrant species all had a strong correlation between fat and body mass and had fat measured over a much wider range (up to score 80). In these species fat is used to fuel migration (Blem 1990) rather than as an insurance against starvation.

The lack of a correlation between body mass and fat score suggests that most tropical species are not increasing in mass due to energy stored as fat. Body mass change must therefore be due to change in body tissues or in the alimentary canal. In particular the change in body mass due to water intake and storage may be particularly important for species living in a hot and seasonally dry climate.

Three species appeared to show a decline in body mass at fat scores of 30, this may be due to less fit individuals, that may be smaller, having to carry more body fat as insurance against starvation when they cannot compete for food resources with larger congeners. Alternatively the counter-intuitive negative relationship between mass and fat may provide further support that other sources of variation in mass such as water balance may have a relatively much greater effect.

### **Seasonal mass variation**

There is a large seasonal weather difference in the Guinea savannah of West Africa. There is a prolonged dry season from October to March each year followed by a period of increasingly predictable rains from March onwards (Elgood *et al.* 1994). From this it was predicted that there would be a strong seasonal effect to food availability for the birds studied and this would be reflected in changes in body mass resulting in a seasonal peak of mass coinciding with the time of greatest unpredictability of foraging opportunities.

These analyses showed that this prediction of a simple seasonal effect was not uniformly met. It appeared that species could be classified into three groups:

1. those species that shown no seasonal change in body mass.
2. those species that do show a significant difference in body mass between dry and rainy seasons, with some species increasing in body mass during the rains and some species decreasing body mass during the rains.

3. those species that show a significant seasonal variation in body mass but not between a simple dry season rainy season classification.

The species that show no seasonal variation in body mass (Table 5.38 & 5.39) were found across a range of families, foraging groups and body masses. This would suggest that there was not a simple overall explanation for this effect. The effect was also not due to low sample size as some species showed strong effects with small sample sizes. Within each of these species several hypotheses may explain the observed lack of variation:

1. birds always maintained a minimum body mass as food availability was always predictable
2. birds always maintained a minimum body mass as predation risk was always high.
3. birds always maintained a maximum body mass as food availability was always unpredictable
4. birds always maintained a maximum body mass as predation risk was always low.

It was also possible that birds were trading off food availability and predation risk but that there was either no seasonal change in both of these factors, or that changes in the factors always balanced. In the absence of considerably more information on food availability and its seasonal abundance, predators and their seasonal abundance and environmental factors such as temperature and rainfall it

was not possible to make conclusions about the causes of the observed constant body mass.

***Dry and rainy seasons.***

Amongst those species that did show a significant change in body mass between dry and rainy seasons six species reduced mass during the dry season, one increased mass during the dry season and in one (northern red bishop) the sexes changed mass in opposite directions. These species were from four families (Muscicapidae, Pycnonotidae, Passeridae and Nectarinidae) and did not have uniformly higher sample sizes, so it was unlikely that results were due to phylogeny or sample size.

As most species lost mass during the dry season, it would suggest that either food was more available or that predation risk was lower. However, food availability seems an unlikely explanation, as the different seasons should act differently on different foraging groups. Insect abundance increases during the rains (Wolda 1977; Janzen 1980) therefore food should be more predictable for insectivorous birds, thus they should lose, not gain mass during the rainy season. Seed abundance should also vary seasonally. Seed abundance should be highest at the end of the rains, after grasses have set seed, and then reduce through the dry season as seeds are consumed by granivores themselves, consumed by insects, and lost to fire (Crowley & Garnett 1999). At the start of the rains seed abundance should reduce rapidly due to germination and decay (de Bie *et al.* 1998), though there should also be an increase in insect food and a slow increase in seeds as grasses flower and set seed. However, not all granivores reduced mass during the dry season, when food abundance should be higher than during the rains. It is

more intriguing that body mass in male and female northern red bishops changed in opposite directions between the seasons. It was possible that other sexual differences amongst the granivores were not detected due to sample size or species being sexually monomorphic such that they were not sexed at time of capture.

While sunbirds were classed as nectarivores most species are largely insectivorous (Fry *et al.* 2000). As insect abundance and availability of flowering plants should have been higher during the rains (Hopkins 1968; Janzen 1980) it was predicted that sunbirds should have a lower mass during the rains than during the dry season. However, scarlet-chested sunbirds showed no seasonal mass change and both variable sunbirds and green-headed sunbirds changed mass opposite to this prediction. A possible explanation for the observed pattern in variable and green-headed sunbird was that as foraging opportunities are perhaps more restricted, more time had to be spent foraging in habitats with less cover and so exposed to greater predation risk than during the rainy season, as a result low mass was dictated primarily by predation risk (Houston *et al.* 1993).

Finally, eight species did not show a significant difference in mass between the dry and rainy seasons but did have significant mass variation across the year when examined at different temporal scales. When the mass variation of each species was examined it was clear that there was not one simple pattern of mass variation suggesting that there was not a single simple explanatory factor governing mass regulation in these species.

Clearly the pattern of seasonal mass variation in tropical birds is much more complicated than in those north temperate birds studied so far. Small north temperate birds that have been studied show a relatively simple change of mass between summers characterised by relatively mild temperatures and high food abundance with low body mass in birds and winters with low temperatures and unpredictable food supply and higher body masses (Haftorn 1989; Kullberg 1998; Cresswell 1998; Macleod *et al.* 2005). Despite a clear seasonal difference in climate between the rainy and dry seasons in the Guinea savannah of West Africa (Elgood *et al.* 1994) it appears that season was insufficient to explain mass variation in many tropical species. This study has highlighted that seasonal body mass variation may occur in tropical birds but it is not an invariable pattern and that there was not a simple explanation for the observed mass variation. Seasonal body mass variation may be species specific as it was difficult to find simple patterns even within very similar closely related species. A great deal more information on basic natural history, ecology and seasonality of tropical birds is needed to begin understanding how they trade off energy reserves and predation risks.

### **Inter-annual mass variation**

The observed negative relationship between body mass and year in seven of the eight species that showed a significant relationship between body mass and year may be due to the introduction of conservation management to the study site. The removal of intensive grazing changed the grass sward from one of very short cropped grass to a very tall, dense grass sward. This change may have had two effects: change in food abundance and change in cover from predators. The

increase in grass sward surviving to seeding may have increased food abundance for granivores. The increase in the available green herb layer may also have increased insect abundance. However, an increase in abundance may have increased the number of insects foraging on seeds. The increased sward height and a reduction of burning at the site may have reduced the availability of seeds to some granivores (Crowley & Garnett 1999). The increase in cover within the habitat may have either reduced predation risk, as birds were able to find refuge from predators, or it may have increased predation risk, as snakes and spiders may be less detectable to birds. That common wattle-eye did not show a similar pattern, was not surprising as it was largely restricted to the canopy of gallery forest and so was isolated from changes to the herb layer. Without more information on *which* predators were important, whether their abundance changed in response to management and whether food availability changed it was not possible to draw any firm conclusions from the observed variation. The results with respect to inter-annual variation are interesting however because they suggest that habitat characteristics may be one of the most important factors in determining how mass in tropical birds reflects the trade-off between starvation and predation risk, and that seasonal changes within a habitat type are not.

### **Diurnal mass variation.**

Significant diurnal mass variation was spread across eight families so phylogenetic effects were excluded. From the observed patterns of mass variation it appeared that there was a bimodal distribution in diurnal body mass of birds in this study. However, as this study was not specifically designed to look for such patterns there was a gap in data for the middle of the day (logistically and

ethically there are problems in mist-netting during the middle of the day in tropical areas). There was also very little data in the afternoon for many of the species illustrated. This may be why relatively few species appeared to show a significant variation in diurnal body mass: biologically birds must lose mass overnight while they cannot forage and therefore must gain mass during the following day or they will starve. The significant gaps in data across the whole of the daylight period meant that the observed bimodality was, at best, speculative. It was also possible that mass variation was simply a linear function.

If observed pattern was genuinely bimodal it suggests that birds were maintaining a low body mass during the day and only increasing body mass later in the afternoon in order to compensate for the overnight period when energy is being expended for metabolic process but not being gained through foraging. Such a pattern would suggest that birds were experiencing significant predation risk through the day and so must maintain a low body mass (McNamara *et al.* 1994). However, if body mass increased linearly across the whole day it would suggest that birds were not having to trade off body mass against predation risk (Houston *et al.* 1993). It was also possible that some species were following the former pattern and some the latter pattern. What this study does show clearly however is that there were interesting diurnal mass variation patterns in tropical birds that warrant further investigation.

Further data from mid-day onwards would be required to establish the true pattern of diurnal mass gain. To date there are no published studies examining diurnal mass variation in tropical birds. This may be due to the logistical problem of trapping through the middle of the day. High mid-day temperatures would subject

trapped birds to heat stress that may prove fatal for a significant proportion of the sample trapped. Activity of small birds was also low during the middle of the day (*pers. obs.*), so it may be difficult to gain adequate sample sizes from this period.

### **Seasonal body mass variation and moult**

The lack of a consistent pattern in mass change due to moult was not surprising. There have been several studies that have shown different patterns of mass variation due to moult, both between and within species (see Lind *et al.* 2004). As species with significant and not significant relationships between mass and time of year classified by moult period were spread across several families it was unlikely that this was a phylogenetic effect.

It has been predicted that main flight feather moult may influence body mass as wing loading is changed (Lind & Jakobsson 2001), this may influence a birds ability to successfully escape predators (Slagsvold & Dale 1996; Swaddle & Witter 1997a). Thus, if predation risk was important, birds should reduce their body mass to compensate for reduced flight ability during moult as was shown in *Passer montanus* (Lind & Jakobsson 2001), *Calidris alpina* (Holmgren *et al.* 1993), *Archilochus colubris* (Chai 1997) and *Sturnus vulgaris* (Swaddle & Witter 1997a).

The analysis here suggested that some species were unaffected by moult and did not have to change body mass at all to compensate for a theoretical change in flight performance. Some species did indeed show a reduction in body mass between the moult period and the rest of the year. These species may have been reducing body mass as predicted; to mitigate the effects of reduced flight

performance. However, several species did not change body mass as predicted; they increased body mass. Amongst these species predation risk may have been negligible, so the increase in body mass was simple due to physiological processes associated with moult; higher body water content and an increased blood volume in the actively growing feathers (Myrcha & Pinowski 1970; Dolnik & Gavrilov 1979).

It was also predicted that birds with faster moult would exhibit a greater change in body mass between the moult period and the rest of the year. However, the species that moulted most rapidly (cinnamon-breasted bunting and variable sunbird) did not show any difference in mass between moult period and the rest of the year. Most species studied had very slow moults (see Chapter 4) and consequently were likely to have only very small gaps in the wing, which may not have reduced flight performance enough to influence mass change. Amongst these slower moulting species there was no obvious pattern between moult speed and change in body mass. Indeed, two species with slow moults (red-cheeked cordon bleu and red-billed firefinch) showed opposite changes in body mass between the sexes.

However, this analysis only classified birds into two broad temporal categories (moult period and the rest of the year) *not* into birds recorded as being in active moult and birds recorded as not being in active moult. Thus the comparison may not have been valid. Moult speed and period was measured for the *average* individual and so did not account for individual variability. It was therefore possible that some individuals classified as being in moult by time of year alone were not actually in active moult. While analysis would have been improved by

including moult status (in moult or not in moult) as a variable in the GLM model, and determining if moult is related to mass, while controlling for time of year, sample sizes were too small.

## **Conclusion**

The overwhelming effect of season on body mass regulation seen in temperate birds (Rogers 1987) was not found here in tropical birds. While temperature and day length is the main effect of season in temperate regions, in the tropics the main seasonal effect is rainfall (Osborne 2000). Despite the strong seasonal effect of rainfall on the environment body mass regulation did not follow simple seasonal patterns across all species. In order to find what, if any, general processes influence body mass regulation in tropical birds further research should concentrate on processes important to individual species. Better knowledge of each species ecology, their predators and their ecology and phenology is needed. This study has shown that body mass regulation does occur in tropical birds, that it is variable and that it is clearly not a simple reaction to seasonal climate. This variability suggests that further research into body mass regulation in tropical birds may provide new insights into the processes driving such regulation.

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## **Chapter 6: Seasonal abundance of Guinea savannah birds in central Nigeria**

### **Summary**

The seasonal environment of the Guinea savannah has a strong effect on plant growth and so affects the abundance of food available to birds. This seasonal food abundance was predicted to have an effect on the seasonal abundance of birds through migration, dispersal, breeding and behaviour. Previous studies of the general status and migratory patterns of birds in Nigeria allowed predictions to be made about the likely peaks in abundance and the migratory status of the species studied. Densities were estimated using Distance methods and comparisons made between four seasonal periods. More species varied in abundance with season than predicted. While several reasons for this were suggested it may be that hitherto undetected altitudinal migration was occurring in some species.

### **Introduction**

The tropical environment is often equated with humid, largely aseasonal, rainforest. However, even within the humid tropical rainforests the environment is seasonal, even on and around the equator (Osborne 2000). This seasonal pattern is caused by the displacement of the Intertropical Convergence Zone (ITCZ). The ITCZ bring rains northwards from the equator during the boreal summer and southwards from the equator during the austral summer (Wallace & Hobbs 1977). In West Africa this results in a wet season during the boreal “summer” months and a dry season during the “winter” (Elgood *et al.* 1973). Within West Africa as

latitude increases the “rainy season” becomes shorter and drier resulting in a cline of vegetation types from the rainforests in the south to the sahel in the north (Elgood *et al.* 1994). However, these changes in habitats can be classified into approximate bands of different zones lying across approximately east-west across the region. From south to north these vegetation zones are: rainforest; derived savannah; Guinea savannah; sudan savannah; sahel savannah.

This seasonal rainfall pattern dominates the primary productivity of the savannah regions which in turn dominates the ecology of these ecosystems in West Africa (Bourliere & Hadley 1970). Primary productivity ultimately influences the abundance of food for bird populations and as such has an influence on the seasonality of various important life history traits, such as breeding season, moult and migration. These may then impact upon abundance of individuals in a seasonal manner. The relative importance will then vary with latitude as the duration and intensity of the rainy season varies. Indeed it may be expected that seasonality patterns will be at their most extreme at the highest and lowest latitudes in sub-Saharan West Africa as the ITCZ has its lowest and highest effects at these latitudes respectively.

This study was conducted in the Guinea savannah in Nigeria, so it was likely that bird populations would vary in abundance seasonally. Nigerian birds have been studied relatively well compared with other West African countries. Records of birds from across Nigeria were collated and interpreted by Elgood *et al.* (1994) to give an overview of the range, status and breeding periods of most Nigerian species. In addition to this there have been several studies, particularly general mist netting studies, that have provided limited data on seasonal changes in

numbers and occurrences of bird at various sites across Nigeria. These studies mostly tried to establish migration patterns of African species and were summarised by Elgood *et al.* (1973)

Seasonal abundance of common bird species were estimated at Amurum Community Forest Reserve on the Jos plateau (09°52' N, 08°58' E) in central Nigeria. Once analysis identified reliable density estimates of species, the pattern of seasonal change in these densities was compared with predictions of seasonal abundance from Elgood *et al.* (1994) and Elgood *et al.* (1973). Comparisons were then made between the predicted pattern of seasonal abundance and that observed from this study, the aims of which were therefore to:

1. establish base-line densities of species at the study site and to accurately quantify how these vary seasonally where possible
2. to relate seasonal changes in abundance to previously established residency patterns, climatic variation and phenology.

## **Methods**

### **Study site**

The entire study was carried out within the 120 hectare Amurum Community Forest Reserve, an area of recently protected Guinea savannah within the Jos plateau forest-grassland mosaic ecoregion (White 1983). While the site was approximately 1300m Above Sea Level (ASL) it was not a montane habitat, as this generally occurs above 1700m ASL in West Africa (Elgood *et al.* 1994). The

topography was varied, with 100m high inselberg rock outcrops, and deep (10m) erosion gullies within narrow strips of gallery forest. Between the inselbergs and gallery forests there were patches of relatively flat mixed scrub interspersed with patches of open grassland (Fig 6.1).

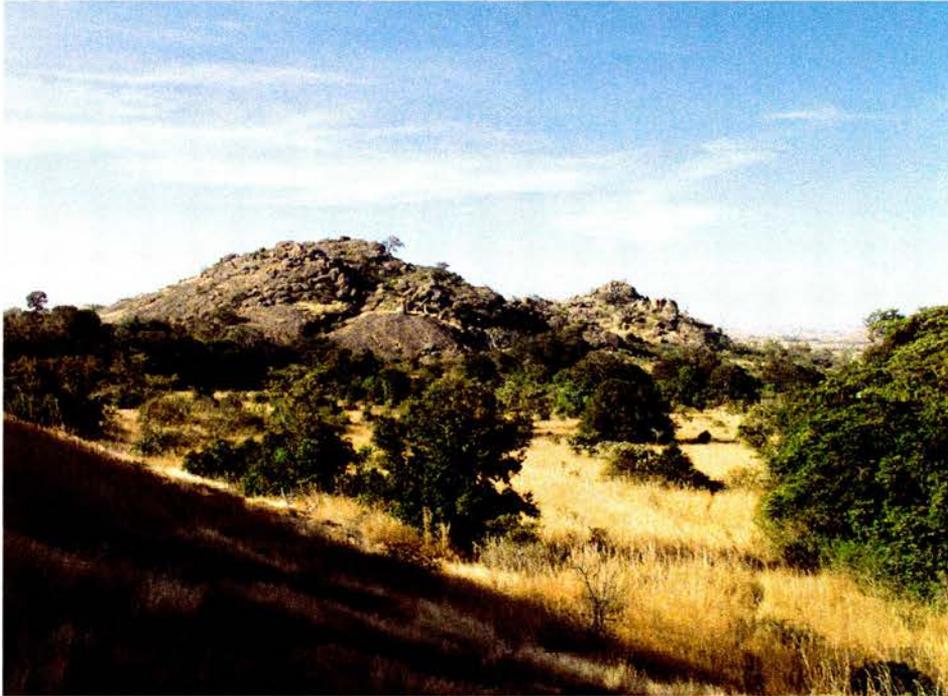


Figure 6.1: Habitat mosaic in Amurum Community Forest Reserve, Jos plateau.

### **Density estimates**

In order to estimate density, Distance (Thomas *et al.* 2003) methodology was employed. Due to the difficult topography it was not possible to use line transects, as in order to fit 100m long transects into the relatively small area it would have been necessary to deliberately place them in accessible positions, thus violating important assumptions of the method. Consequently, circular point counts were used as these could be placed anywhere within the reserve, with accessibility either being less of a problem, or used to eliminate points that were completely inaccessible. During the first field season twenty points were established and repeated twice. In subsequent field visits 48 additional point counts were

established on a randomly placed grid with a spacing of 110m. This spacing ensured that, with the potential error in GPS receivers, each point remained statistically independent. Points were then grouped together such that each point in each group could be visited during three hours fieldwork from dawn until 0900. Limiting observations to this period reduced possible bias from changes in activity due to time of day. Points were placed in one of four groups and each group was visited twice every three to four months. In total 644 point counts were carried out between May 2002 and January 2004.

At each point a timed five minute count was carried out after a one minute 'settling period'. During those five minutes every bird seen within 100m of the point was identified and the radial distance to the bird measured to the nearest metre using a laser rangefinder. Any birds that were not specifically identified during the count were found and identified after the count.

In order to make comparisons between seasons the year was divided into four: March to May - early rainy season; June to August - late rainy season; September to November - early dry season; December to February - late dry season. These divisions provided a good trade off between temporal resolution and sample size within each period.

To estimate density using Distance 4.1 (Thomas *et al.* 2003) the data was initially considered without any temporal stratification. For each species the software produced a frequency histogram of number of sightings with distance. This histogram was manipulated manually so that the observed distribution of detection probability was similar to the distribution of a model distribution – in

this case a model with a half-normal key function and a cosine series expansion. Once this distribution was fixed, a series of model distributions with different key functions and series expansions were compared with the observed distribution. The model that provided the best overall fit with the fewest parameters was assessed using Akaike's Information Criterion (AIC). Where difference in AIC's values was greater than three there was sufficient difference to reject the model with the higher AIC value. When more than one model had an AIC value within three of the lowest AIC value a visual inspection was used to select the model that proved the best fit to the observed distribution. Particular attention was paid to the difference in distributions at or near 0 metres. Once the best model distribution was selected the distance records were stratified by season. The detectability function was also stratified by season, by modelling the detection function for each season separately, thus accounting for any seasonal change in the pattern of detectability.

Comparisons between each season for each species were made by calculating a t-statistic and degrees of freedom according to Buckland *et al.* (2001) and comparing these against published statistical tables (Rohlf & Sokal 1995).

## **Results and discussion**

Of the thirty four species analysed (i.e. those that had sufficient records to calculate meaningful densities), twenty one varied significantly between seasons. These twenty one species included three migrant species that were completely absent from the study site during some part of the year. The remaining eighteen species were always present. Five of these peaked in abundance during the dry

season, eleven during the rainy season and two did not peak at all, but had one period that was significant lower during the year (table 6.1).

Table 6.1: Seasonal variation in density (birds per hectare) with season. Darkest rectangles indicate the season with the highest density shading to the lightest rectangles that represent the season with the lowest density.

SPECIES	DRY	RAINS		DRY	Max density	Min density	sig diff
	Dec – Feb	Mar – May	Jun – Aug	Sep - Nov			
common bulbul	0.29	0.27	0.14	0.11	late dry	early dry	sig
black-crowned tchagra	0.03	0.02	0.01	0.005	late dry	early dry	sig
lavender waxbill	0.23	0.19	0.03	0.006	late dry	early dry	sig
red-cheeked cordon bleu	0.03	0.17	0.11	0.22	early dry	late dry	sig
cinnamon-breasted bunting	0.08	0.03	0.02	0.06	late dry	late rains	sig
Adamawa turtle dove	0.05	0.07	0.03	0.02	early rains	early dry	sig
western grey plantain eater	0.008	0.01	0.004	0.01	early rains	late rains	sig
red-throated bee-eater	0.01	0.06	0.04	0.04	early rains	late dry	sig
yellow-throated leaflove	0.04	0.10	0.03	0.01	early rains	early dry	sig
familiar chat	0.01	0.05	0.02	0.03	early rains	late dry	sig
African thrush	0.02	0.03	0.02	0.007	early rains	early dry	sig
rock-loving cisticola	0.02	0.05	0.06	0.02	late rains	dry	sig
grey-backed camaroptera	0.05	0.20	0.19	0.08	early rains	late dry	sig
common wattle-eye	0.03	0.07	0.10	0.04	late rains	late dry	sig
scarlet-chested sunbird	0.03	0.14	0.15	0.04	late rains	late dry	sig
rock firefinch	0.13	0.19	0.02	0.16	early rains	late rains	sig
speckled mousebird	0.09	0.09	0.05	0.03	-	early dry	sig
laughing dove	0.03	0.03	0.007	0.03	-	late rains	sig
stone partridge	0.04	0.01	0	0.05	early dry	late rains	ns
yellow-fronted tinkerbird	0.03	0.03	0.02	0.02	-	-	ns
sun lark	0.009	0.01	0.007	0.02	early dry	late rains	ns
sulphur-breasted bush shrike	0.03	0.005	0.02	0.02	late dry	early rains	ns
village weaver	0.12	0.04	0.007	0.4	early dry	late rains	ns
bronze manikin	0.55	0.25	0.04	0.06	late dry	late rains	ns
black-billed wood dove	0.01	0.01	0.03	0.02	late rains	late dry - early rains	ns
grey hornbill	0.008	0.01	0.004	0.009	early rains	late rains	ns
snowy-crowned robin chat	0.007	0.03	0.07	0.007	late rains	dry	ns
mocking cliff-chat	0.02	0.05	0.03	0.02	early rains	dry	ns
yellow-crowned gonolek	0.02	0.05	0.02	0.01	early rains	early dry	ns
green-headed sunbird	0.05	0.18	0.18	0.07	rains	late dry	ns
variable sunbird	0.20	0.34	0.25	0.24	early rains	late dry	ns

Only three (cinnamon-breasted bunting, African thrush, and scarlet-chested sunbird) of these twenty one species were previously known to be migrants within Nigeria while the remaining eighteen were described as being resident by Elgood *et al.* (1973) (Table 6.2).

Table 6.2: comparison between the observed peak in abundance from this study with that predicted from Elgood *et al.* (1973).

SPECIES	Study peak	sig diff	Elgood prediction	Elgood peak
common bulbul	dry	sig	resident	none
black-crowned tchagra	dry	sig	resident	none
lavender waxbill	dry	sig	resident	none
red-cheeked cordon bleu	dry	sig	resident	none
cinnamon-breasted bunting	dry	sig	<b>mig in Nigeria</b>	dry
Adamawa turtle dove	rains	sig	resident	none
western grey plantain eater	rains	sig	resident	none
red-throated bee-eater	rains	sig	resident	none
yellow-throated leaflove	rains	sig	resident	none
familiar chat	rains	sig	resident	none
African thrush	rains	sig	<b>mig in Nigeria</b>	rains
rock-loving cisticola	rains	sig	resident	none
grey-backed camaroptera	rains	sig	resident	none
common wattle-eye	rains	sig	resident	none
scarlet-chested sunbird	rains	sig	<b>mig in Nigeria</b>	rains
rock firefinch	rains	sig	-	-
laughing dove	none	sig	resident	none
speckled mousebird	none	sig	resident	none
stone partridge	dry	ns	resident	none
sun lark	dry	ns	<b>mig in Nigeria</b>	rains
sulphur-breasted bush shrike	dry	ns	<b>mig in Nigeria</b>	rains
village weaver	dry	ns	resident	none
bronze manikin	dry	ns	resident	none
black-billed wood dove	rains	ns	resident	none
grey hornbill	rains	ns	<b>mig in Nigeria</b>	twin
snowy-crowned robin chat	rains	ns	<b>mig in Nigeria</b>	rains
mocking cliff-chat	rains	ns	resident	none
yellow-crowned gonolek	rains	ns	resident	none
green-headed sunbird	rains	ns	resident	none
variable sunbird	rains	ns	<b>mig in Nigeria</b>	rains
yellow-fronted tinkerbird	none	ns	resident	none

However, five species were not found to vary seasonally in this study but were described as migratory by Elgood *et al.* (1973) (Fig. 6.2). Two of these species (sun lark and grey-hornbill) occurred at very low densities, so it was unlikely that any significant seasonal variation could be detected, as sightings were too few. It also appeared that the migration pattern of these species was less pronounced on the Jos plateau than on the lower lying Guinea savannah plains (pers. obs.). The remaining three species were all predicted to peak in abundance during the rainy

season. Despite the lack of any significant difference between each seasonal period it was noted that the observed highest densities followed this pattern for all but one species; sulphur-breasted bush-shrike.

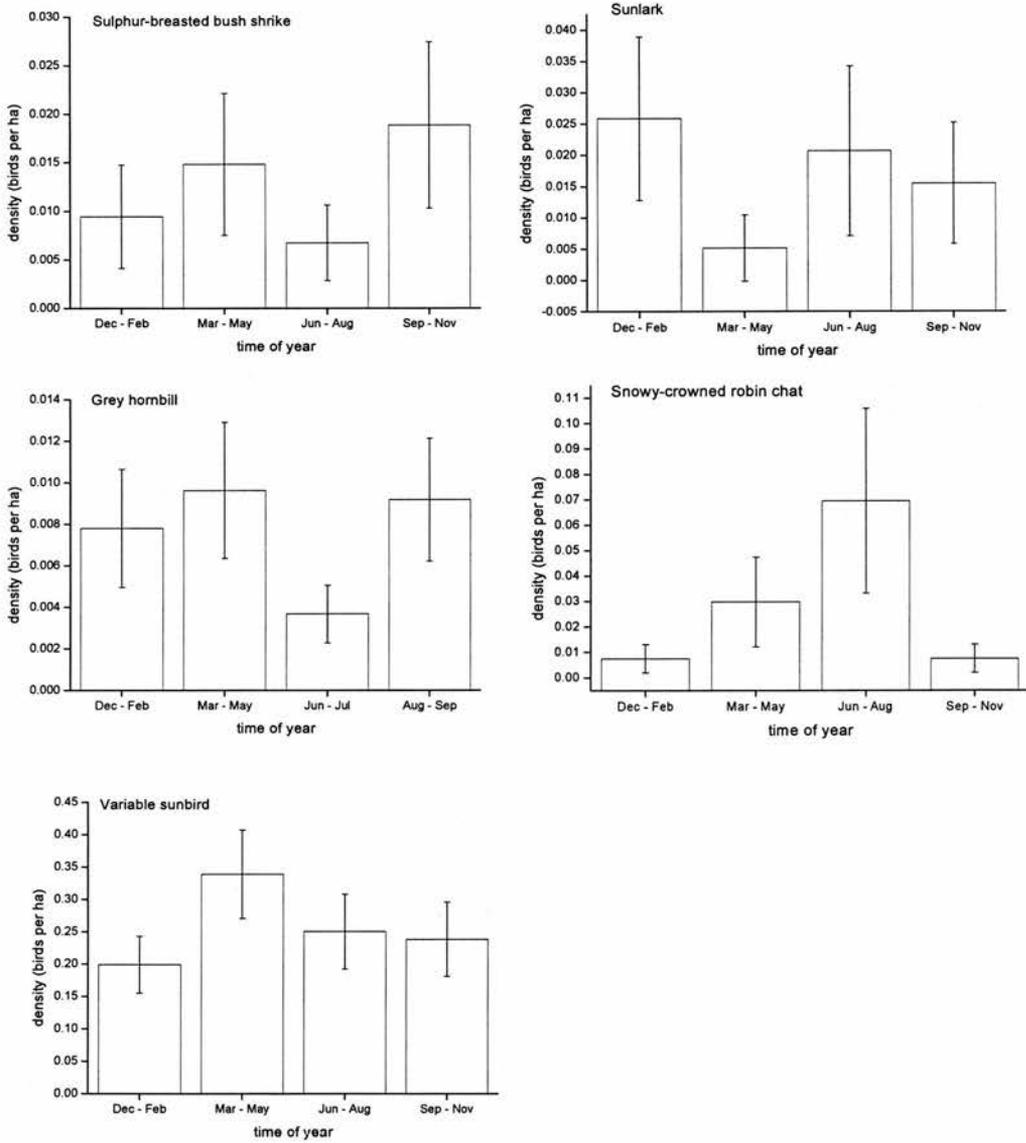


Figure 6.2: Seasonal density ( $\pm$  s.e.) estimates of African migrant species with no significant variation in abundance

### Dry season peak abundance

Five species peaked in the dry season (Fig 6.3).

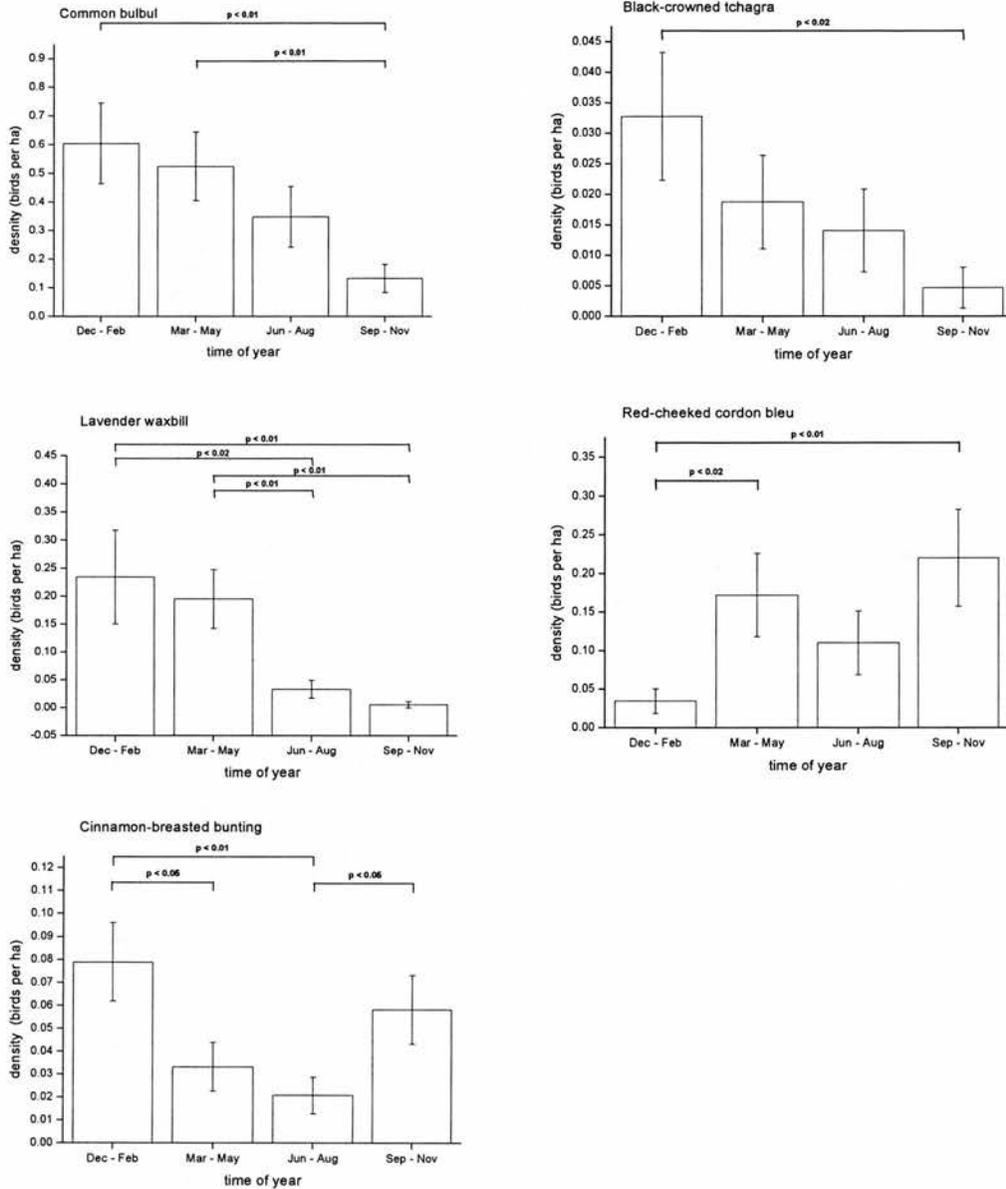


Figure 6.3: Seasonal density ( $\pm$  s.e.) estimates of species with abundance peaking in the dry season. Statistically significant difference between seasons shown by horizontal lines and appropriate level of significance.

Of the five species that were more common in the dry season only one, cinnamon-breasted bunting, was previously described as an intra-African migrant. This pattern was as predicted. This species is resident across much of its range in Nigeria but is a rainy season migrant to the northern Sudan and Sahel zones. There are very few records of this species south of the rivers Niger and Benue (Elgood

*et al.* 1994), so it was likely that the peak in abundance in the dry season was due to northern breeding birds joining the resident breeding birds on the Jos plateau.

Of the other four species, three (common bulbul, black-crowned tchagra, and lavender waxbill) showed a similar pattern: a peak in the late dry season, with a steady decrease through the rains to a minimum in the early dry season. None of these species were known to be intra-African migrants, so it was predicted that their populations should remain reasonably stable across the year. This pattern may have occurred in lavender waxbill as it is a solitary breeder that forms flocks at other times of the year (Fry & Keith 2004). It breeds in Nigeria from the late rains through the early dry season (Fry & Keith 2004), when abundance was observed as being at its lowest. After this period birds may form family groups that may aggregate at times, thus explaining the observed higher abundance during the late dry season and early rains.

The pattern observed for common bulbul and black-crowned tchagra was more difficult to explain. These species were resident, not undergoing any migrations, although local movements were considered possible by Fry *et al.* (2000). While both have been recorded breeding over a wide range of dates (Elgood *et al.* 1994) it would appear that the peak breeding period was the mid-rains. Therefore any peak in abundance may be predicted to be during the period following this, as adults may be joined by immature birds. It would therefore be predicted that abundance should peak in the late rains or early dry season, but neither species showed this pattern, indeed this period had the lowest abundance. It may be that when these species have dependent young they are much more skulking and inconspicuous. This would also coincide with the vegetation being at its most

lush, following a full season of growth, and birds were therefore harder to detect, although in theory the Distance methodology of modelling separate detectability functions for each season should deal with this. However, in the late dry season, the vegetation was noticeably less lush and dense, especially the herb layer (pers. obs.). This would increase the likelihood that individuals were counted more than once (which Distance cannot deal with), combined with the presence of juvenile birds, that may remain in the natal territory for some months (Geffen & Yom-Tov 2000).

Red-cheeked cordon bleu had a different pattern. There was a significant difference in abundance between the peak in the early dry season to a minimum in the late dry season. The peak in the early dry season may be explained by the presence of young birds in the population, as this species breeds in the late rains and early dry season in Nigeria (Fry & Keith 2004). The following drop in abundance suggested that birds were undergoing local movement away from the study site, perhaps to find food or water. However, food was likely to be abundant at this time of the year for this granivorous species. More information about the ecology of this species on the Jos plateau is needed to explain the observed pattern.

### **Rainy season peak abundance**

Eleven species showed a significant variation in seasonal abundance that peaked during the rainy season (Fig. 6.4). Only two species, African thrush and scarlet-chested sunbird, were described as migrants by Elgood *et al.* (1973).

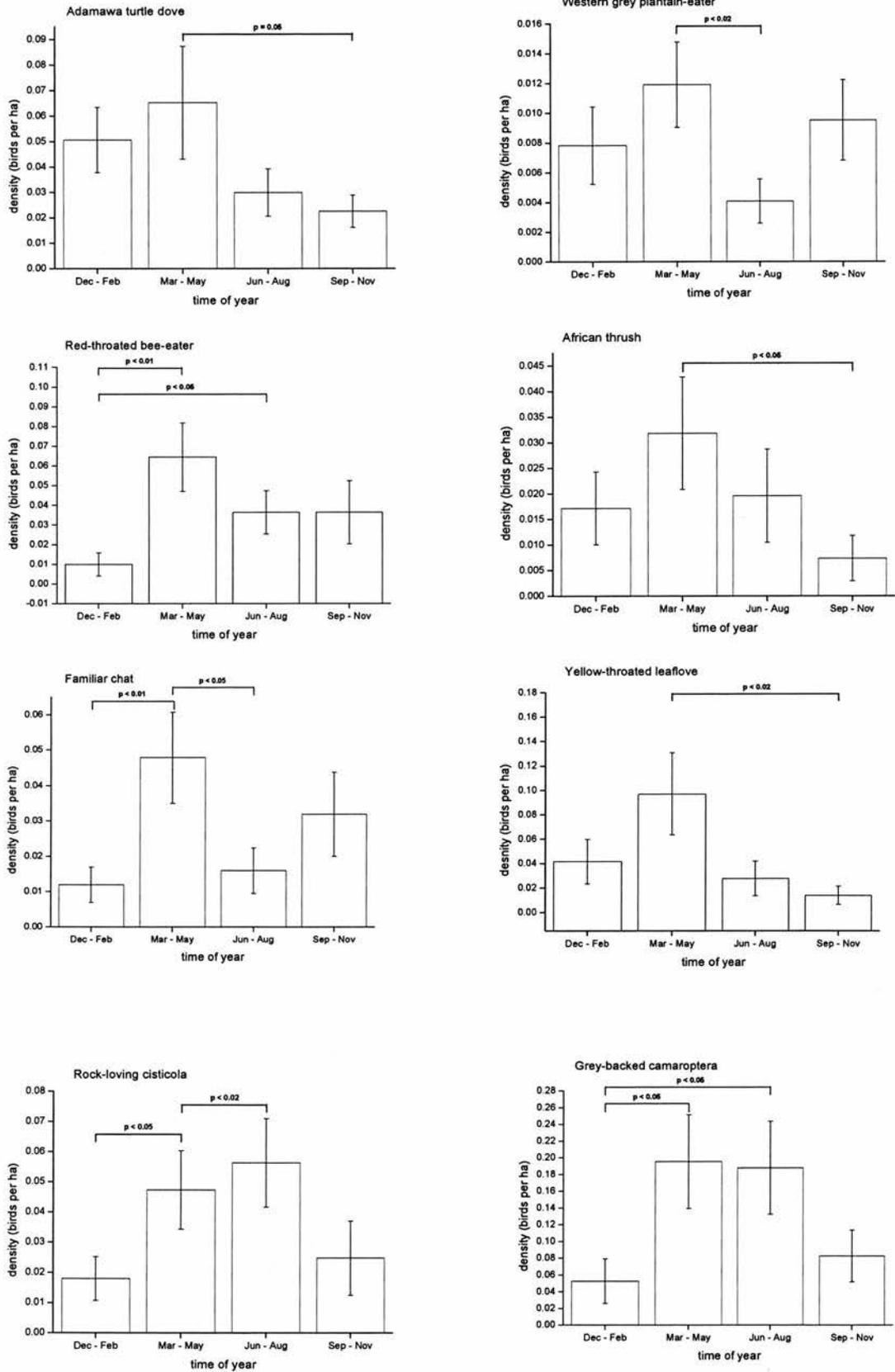


Figure 6.4: (see next page for rest of figure)

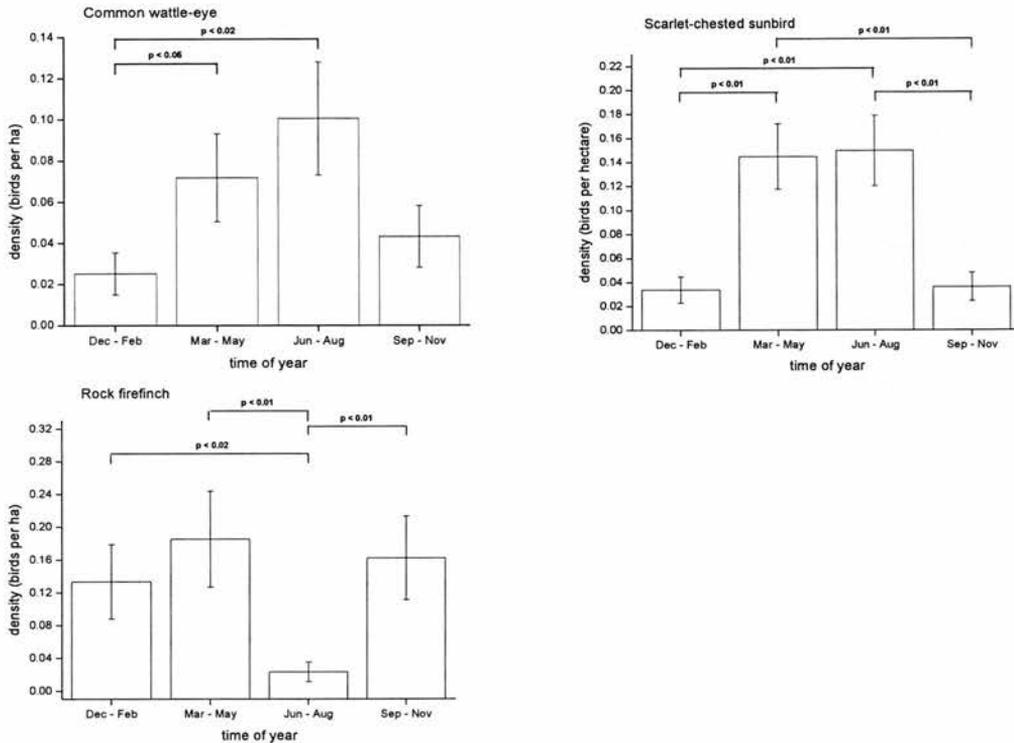


Figure 6.4 (continued): Seasonal density ( $\pm$  s.e.) estimates of species with abundance peaking in the rainy season. Statistically significant difference between seasons shown by horizontal lines and appropriate level of significance.

African thrush was described as peaking in Zaria and Kano (to the north of this study site) during the rains and flocks were also noted from Ibadan (to the south) during the dry season (Elgood *et al.* 1994). They were present all year as far north as Kano and even the sahel of Tchad. This pattern of continuous year round occurrence was also found during this study, as was the pattern of an increase during the rains (Fig 6.4)

The pattern of seasonal abundance of scarlet-chested sunbird noted here (Fig. 6.4) was the same as previously recorded at two other sites, both in the northern Guinea savannah, where birds were more scarce in the dry season (Elgood *et al.* 1973). So these data agree with Elgood *et al.* (1973) that this species is a partial migrant, moving north to breed during the rainy season.

The remaining nine species were described by Elgood *et al.* (1994) as resident. This suggested that changes in abundance found here may have been due to an increase in population size due to breeding, which would subsequently decline with young birds dispersing from their natal territory. However, it was also possible that some species were undertaking migrations, or short distance seasonal movements, hitherto undetected.

While Elgood *et al.* (1994) stated that Adamawa turtle doves were resident, there was some indication that they may be short distance migrants (Fig. 6.4). Birds were only noted from the sahel in Maiduguri during the rainy season and from the Mambilla plateau during the dry season, which was described as local movement. On the Jos plateau more birds occurred during the rainy season, when they bred at the site. This was contrary to the predicted pattern and suggested that this stenotopic, upland species was undertaking local seasonal movements.

Western grey plantain-eater was seasonally less abundant in the late rainy season compared with the early rainy season (Fig. 6.4). However, this large species occurred at very low densities and the change in density was absolutely small. Indeed these differences equated to only a single bird, so the significant difference was likely due to chance. The species was described as resident by Elgood *et al.* (1994), as were the other turaco species. So, while the pattern was not as predicted there was no strong evidence that this species was not sedentary.

Red-throated bee-eater was intensively studied in Nigeria and is known to be sedentary except at the extremes of its range. However, they are known to disperse away from colony sites after breeding (Elgood *et al.* 1973). This species

breeds in Nigeria from December to March, when the observed abundance was at its lowest here (Fig. 6.4). It would appear that abundance was low in the late dry season as birds were closely tied to their breeding sites, then dispersing locally from the breeding colonies, explaining the observed peak in the early rainy season.

Yellow-throated leaflove was described as being non-migratory (Elgood *et al.* 1994), so any seasonal changes in abundance may be due to changes in behaviour or the presence of juveniles in the population. In this study there was a peak in abundance during the early rains (Fig. 6.4), suggesting that the significant variation in abundance was due to a change in behaviour (e.g. more mobility leading to double counting) rather than the presence of juveniles, as this species breeds from May to August in Nigeria (Elgood *et al.* 1994).

The distinct, statistically significant, peak in abundance of familiar chats (Fig. 6.4) suggested the occurrence of an early rains passage of birds through the study site. While, this was contrary to predictions of this resident species they were recorded as occurring only during the rainy season in the sahel at 15° N in Mali (Keith *et al.* 1992), suggesting that some populations do migrate.

While considered a resident species by Elgood *et al.* (1994) rock-loving cisticola is known to undertake short distance movements in southern Africa (Urban *et al.* 1997). The significant increase in abundance during the rains (Fig. 6.4) suggested that birds on this site might be moving from the site during the dry season to find more suitable habitat. This may be due to the lack of standing water in the preferred habitat, rocky inselbergs, during the dry season. So, while the presence

of significant seasonal abundance was against predictions, it was likely that movements of this stenotopic species were only local.

A large difference in densities of grey-backed camaroptera was observed between both periods of the rainy season and the late dry season (Fig. 6.4). Elgood *et al.* (1973) recorded that grey-backed camaropteras were more commonly trapped in “spring” compared to “winter” at Zaria, in the northern Guinea savannah, suggesting that there was a “shift in the centre of gravity of [the] population” (Urban *et al.* 1997). However, it was also known to be sedentary further north in its range at Malamfatori in the sahel. The pattern of abundance found here suggested that there was a movement of birds to the study site during the rainy season. Therefore, the populations that do migrate during the year appear to be much further south than previously thought, against the prediction that this was a sedentary species.

The observation that common wattle-eye was more abundant during the rains than the dry season suggested that birds were leaving the study site during the dry season (Fig. 6.4). While this is contrary to the predictions from Elgood *et al.* (1973) it does lend weight to Bannerman’s view (cited in Elgood *et al.* 1973) that this species moves south when the rains are over.

Scarlet-chested Sunbird was not generally thought to be a migrant, though Elgood *et al.* (1973) suggested that it may be a partial migrant as they were less abundant in the dry season at Shaganu, in the west of Nigeria but a similar latitude to Jos, and more abundant during the rainy season in Zaria, 130 km north west of Jos. The seasonal changes in abundance found here also followed this pattern (Fig.

6.4), so this species was clearly a partial seasonal migrant, at least in the Guinea savannah zones.

Rock Firefinch was only recently described to science (Payne 1998) so nothing was known of its population range and status, residency patterns, or ecology. A single study of the population density of this species was carried out in May – June 2002 at the same site (Wright & Jones 2005). Densities were found to be higher both within the Amurum Reserve (0.79 birds/ha; 95% CL 0.51 – 1.21) and in the surrounding habitat (0.55 birds/ha; 95% CL 0.38 – 0.82) than at any period during this study. However, Wright & Jones (2005) surveyed more areas of preferred habitat (bare rock outcrops) than this study. Little was known about its breeding season other than two juvenile birds less than three months old were trapped when the holotype was trapped, at the same site as this study, in November 1995. During this study seven juvenile birds were trapped in November 2001 and 2002, thus agreeing with the observations of Payne (1998) that this species breeds at the end of the rainy season and the start of the dry season. It was during the early part of this period that abundance was significantly lower than the rest of the year (Fig. 6.4). Given that this is a stenotopic, endemic species, it seems likely that it is resident, and non-migratory. The observed reduction in abundance during the late rains may be due to a change in behaviour, possibly linked to greater secrecy and reduction of range during nesting, reducing their chance of being double counted.

#### **Aseasonal variation in abundance**

Two species were found to vary in abundance in a pattern that did not fit with the seasonal climate: speckled mousebird and laughing dove (Fig. 6.5). Both species

were considered by Elgood *et al.* (1994) as non-migratory, so the changes observed here was against predictions.

Speckled mousebird reduced in abundance from the late dry season, through the rains to a minimum in the early dry season, though there was only a statistically significant difference between the early rains and early dry season (Fig. 6.5). This species was described as resident by Elgood *et al.* (1994) and “highly sedentary, but some erratic local (seasonal) movements.” by Fry *et al.* (1988). The pattern of abundance found here did not suggest sudden and erratic seasonal fluctuations in abundance, even though there was a significant change in abundance with season. The lower abundance of birds in the late rains and early dry season may be due to the tendency of this species to form larger aggregations when conditions are harsh. They also do not cope well with cold conditions, roosting in tight groups and in severe cold, entering torpor (Fry *et al.* 1988). During the latter half of the rainy season on the Jos plateau the percentage of daily cloud cover was often very high, with foggy mornings and long periods of moderate rainfall. Due to the altitude (1100 – 1300m ASL) this resulted in periods of cool weather lasting many days. These conditions may have resulted in further aggregations of mousebirds, which were less likely to be encountered, combined with an altitudinal movement from the high plateau. While overnight temperatures reached a minimum in the late dry season, when speckled mousebird abundance was at its greatest, temperatures quickly increased during the morning, thus birds only had to cope with cold conditions for relatively short periods. This species breeds on the Jos plateau in the early rains (Elgood *et al.* 1994), so if birds were

leaving in the late rains they may be expected to return before they breed, thus accounting for the peak in abundance during the late dry season.

The significantly lower abundance found in laughing dove during the late rains was possibly due to chance (Fig. 6.5). The density of this species was very low, so the absence of only a few individuals would have been enough to account for the observed seasonal dip. This species was considered “probably sedentary” by Elgood *et al.* (1994), but they noted that there was some seasonal change in numbers in some areas (although they did not state which areas). However, in southern Africa it was known to be a partial migrant, thought to move west during the rains (Fry *et al.* 1988). The seasonal pattern shown here, with a marked decline during only one period, the late rains, was consistent with this pattern, but there was no evidence of where birds may be going.

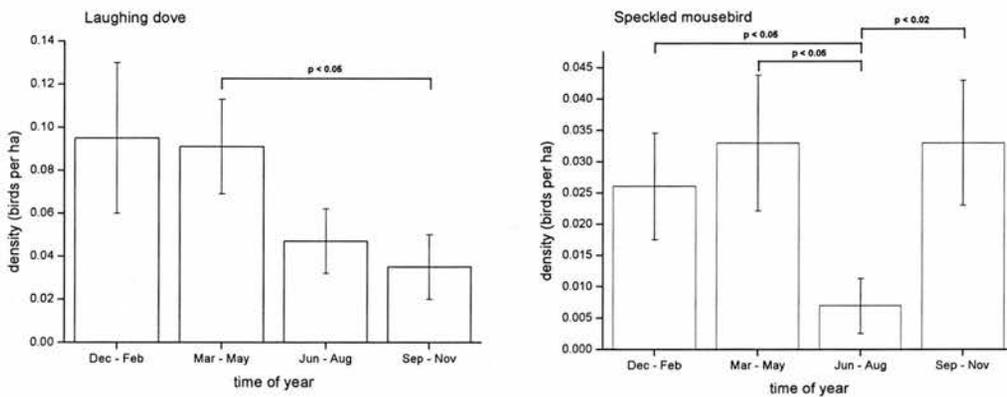


Figure 6.5: Seasonal density ( $\pm$  s.e.) estimates of species with abundance varying aseasonally. Statistically significant difference between seasons shown by horizontal lines and appropriate level of significance.

## Seasonal migrants

Three species were known to be seasonal migrants that completely left the study area during part of the year. All three of these species showed significant variation within the period (Table 6.3).

Table 6.3: Monthly variation in densities (number of birds per hectare) of seasonal migrants. Darkest rectangles indicate the season with the highest density shading to the lightest rectangles that represent the season with the lowest density, white rectangles indicate no birds recorded (i.e. density = 0).

SPECIES	Time of year							Max density	Min density	sig diff
	November	January	March	May	June	July	August			
fanti saw-wing				0.043	0.046	0.007	<b>0.099</b>	August	July	sig
violet-backed starling			<b>0.027</b>	0.008	0.009	0.002	0.023	March	July	sig
whitethroat	0.003	0.045	<b>0.078</b>					March	November	sig

Two species were intra-African migrants (fanti saw-wing, violet-backed starling) that migrated to the Guinea savannah from the forest zone during the rainy season in order to breed (Elgood *et al.* 1994). Both species showed a peak in abundance at the end of the rainy season (Fig. 6.6), though this was only significant in fanti saw-wing. This peak was likely due to the presence of juveniles in the population combined with pre-migratory aggregations. Violet-backed starling also had a significant peak at the beginning of the rainy season, presumably due to the presence of birds on passage through the study site.

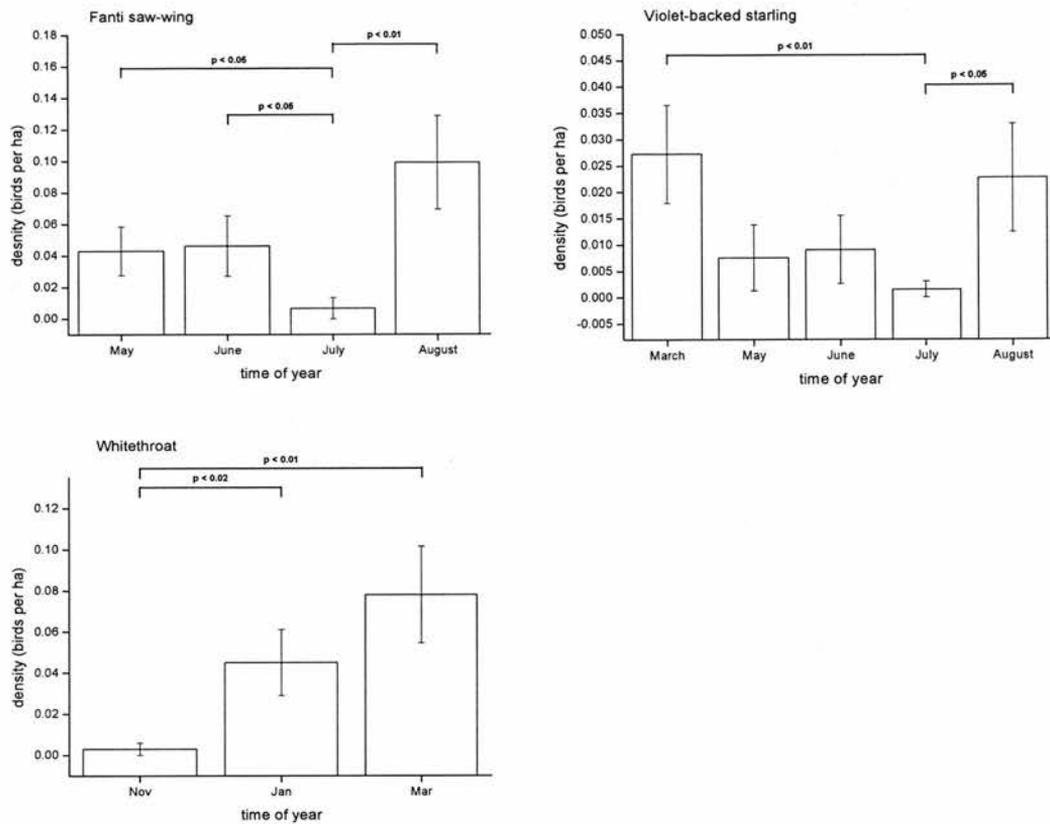


Figure 6.6: Seasonal density ( $\pm$  s.e.) estimates of intra-African migrant species. Statistically significant difference between seasons shown by horizontal lines and appropriate level of significance.

Only one palearctic migrant, whitethroat, was encountered in sufficient numbers to estimate its density. It occurred at increasing density through the dry season to peak in the early rains when there were likely to be many passage birds that wintered further south (Fig 6.6). The increase from November to January suggested that birds were continuing to arrive through the dry season. Birds may be arriving from the north as the sahel becomes increasingly hot, dry and harsh.

### Concluding discussion

The Guinea savannah of West Africa is a highly seasonal environment where the effects of seasonal rainfall on primary production has an overwhelming effect on

the ecology of the whole ecosystem, similar to the effects of low winter temperatures on north temperate ecosystems (Bourliere & Hadley 1970). This effect on primary production changes the food availability of all the bird species in the Guinea savannah, with different feeding guilds experiencing different seasonal peaks in food availability. Consequently it was expected that different bird species with different food requirements and breeding seasons would show seasonal peaks in abundance and that these peaks would be variable but seasonally dependent. It was expected that seasonal abundance would vary due to seasonal movements of birds, seasonal population increases due to breeding and seasonal changes in behaviour influencing the estimates of abundance.

While some species migrated completely from the study site, most species were always represented by some individuals throughout the year. Twenty one species studied here (61.8% of the total) were found to have some statistically significant change in their abundance between two or more seasons. However, only three of these species were already known to be migrants. The causes of seasonal changes in abundance for the remaining eighteen species were variable.

### **Behavioural changes**

Seven species were likely to have changed their behaviour during breeding and so changed the likelihood that they were counted more than once during each period (i.e. moved between points during counts so increasing their probability of being double counted). Although point counts should ideally be instantaneous to reduce the problem of double counting, in reality, and indeed in this study, this is impossible. Therefore mobile and conspicuous species, and indeed any species that may react to the presence of the observer by moving after being initially

counted are more likely to be recorded in more than one point. Two of these species, common bulbul and black-crowned tchagra, may have become more tied to nest sites and become more skulking thus *reducing* the likelihood that they were counted more than once. Four species, red-throated bee-eater, lavender waxbill, red-cheeked cordon bleu and rock firefinch, formed flocks when not breeding and so were more likely to be counted more than once during these periods compared to the breeding period. Finally, yellow-throated leaflove was more likely to be counted more than once during the breeding season as they became more active and vocal. During breeding this normally skulking species foraged more widely in scrub surrounding their preferred habitat of gallery forest. Also, males displayed by chasing females conspicuously around their territory (Keith *et al.* 1992). Both of these changes in behaviour may have increased the likelihood that they were counted at more than once each day, which may explain the increase in abundance during the early rains that was observed here.

### **Partial Migration**

Seven species showed patterns that suggested that they may undertake some sort of local movement or partial migration. Two of these species (Adamawa turtle dove and grey-backed camaroptera) were tentatively suggested as having some migratory populations within Nigeria (Elgood *et al.* 1973; Elgood *et al.* 1994). The patterns in seasonal abundance shown here confirm this. Three species, familiar chat, rock-loving cisticola and laughing dove, had populations elsewhere in Africa that were either migratory or underwent seasonal changes in habitat (Fry *et al.* 1985) that may explain the changes in abundance observed here. However, laughing dove densities were very low and changes between seasons may have

been due to chance. This was also the likely explanation for seasonal changes in densities of the large, non-migratory, western grey plantain-eater. Common wattle-eye was suggested as a partial rains migrant to the savannah zones by Bannerman, but Elgood *et al.* (1973) found no indication to agree with this pattern. However, the finding here of lower densities during the dry season agreed with the comments of Bannerman. While speckled mousebird was known to occasionally move erratically, the pattern of seasonal abundance found here suggested that they may move more regularly from the Jos plateau, in response to the relatively cool period in the late rains. This likely altitudinal migration has not been described for this species from elsewhere in Africa (Fry *et al.* 1988).

### **Sedentary 'migrants'**

The absence of any significant difference between seasonal densities of five species described as migratory by Elgood *et al.* (1973) was partly due to sample size. Three of these species, sunlark, sulphur-breasted bush shrike and grey hornbill, occurred at low densities, so the lack of statistically significant change may simply have been due to chance. However, sulphur-breasted bush shrike was on the edge of its dry season range on the Jos plateau and was absent from Zaria (130km north) during the dry season (Elgood *et al.* 1973), consequently the peak in the late dry season may be due to migrants from further north 'over wintering' at the study site. Snowy-crowed robin chat had a pattern of abundance that agreed with its status as a partial rains migrant to the Guinea savannah, but the differences in abundance between seasons were not statistically significant. This was most likely a result of small sample sizes, as this species was often very skulking. However, the lack of any change in densities of variable sunbirds across

the year appeared to be genuine, suggesting that the population breeding on the Jos plateau was sedentary. A slight, non-significant, peak in abundance in the early rains may have been evidence of passage birds from further north migrating south after breeding in the dry season. However, it was also possible that this was due to the presence of fledged young in the population. Grey hornbills are thought to be a classic example of a seasonal tropical migrant and so it was somewhat surprising that there was no significant change in abundance across the year.

While densities were low, the obvious visual migration of this species in the early rains and late dry season was not seen on the Jos plateau when it was obvious on the Guinea savannah plains elsewhere at the same latitude (pers. obs.) The lack of a difference between the dry and rainy seasons combined with the lack of passage birds suggested that birds were resident and sedentary on the Jos plateau and that birds on migration avoided flying over the plateau, presumably migrating around to the west and east. As the migration of this species is at very low altitude (tree top height) (Elgood *et al.* 1973), the Jos plateau may indeed act a barrier to migration.

### **Migrants**

Only three species that were seasonally absent occurred in sufficient number to have their densities estimated. Both fanti saw-wing and violet-backed starling were intra-African migrants that came from further south in Nigeria to breed in the Guinea savannah. The only palearctic migrant was whitethroat, which was absent in the rainy season. This species winters largely in the sahel (Cramp & Perrins 1992) but the increase in numbers from November to January found here suggested that they moved further south, into the Guinea savannah, through the

dry season as conditions became harsher further north (Lack 1986). This agreed with the finding that densities of whitethroats in the Nigerian sahel increased from mid-winter to spring (Wilson 2005). The first whitethroats arrived at the study site in early September but were at very low densities at that time so, by chance, were not recorded during point counts in that period (pers. obs.). While whitethroats have been recorded as far south as Ibadan, approximately 7° N (Elgood *et al.* 1994), it was notable that they were not trapped during five years of mist netting at Vom on the Jos Plateau, (only 45km south west of this study site) during the 1960's (V Smith pers. comm.). It would seem that the current wintering population in Jos was a relatively recent phenomenon, likely due to an increase in desertification due to drought and habitat destruction in the sahel (Gonzalez 2001).

### **Sedentary residents**

The remaining eight species that occurred in adequate numbers to estimate densities did not show any statistically significant difference in density between the seasons, but this was predicted as these species were described as resident by Elgood *et al.* (1994).

### **Conclusion**

More species were found to vary significantly in abundance than predicted from Elgood *et al.* (1973) and Elgood *et al.* (1994). When species with seasonal abundance due to factors other than migration were excluded, then the number of apparently migratory species was still much higher than predicted. This suggested that some species were making seasonal movements to and from the study site despite never having shown any seasonal movements elsewhere in Nigeria. That

the study site was at 1300m ASL may have resulted in seasonal altitudinal migration in some species despite the general assertion that the Jos plateau was too low to be considered montane (Elgood *et al.* 1994). Indeed, even in the truly montane habitats in Nigeria (the Obudu and Mambilla plateau's - which are part of the Cameroon highlands) only two species (mountain wagtail and northern double-collared sunbird) are known to be altitudinal migrants (Elgood *et al.* 1973). However, there have been no formal studies in these areas that may establish whether other species are partial migrants as shown here. Even with the limited data from other studies as a reference, this study clearly shows that the altitudinal anomaly of the Jos plateau has an additional influence on several species that were hitherto thought to be sedentary or migratory.

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## **Chapter 7: Concluding discussion**

In order to be successful in the “struggle for life” an animal tries to produce as many viable offspring as possible (Darwin 1859). However, an animal will be constrained in doing this by the environment in which it lives and the constraints on resource availability it imposes. Because resources are limited, an animal must trade off its own survival to continue reproducing against the numbers of viable offspring (i.e. grandchildren) it can produce at any one time (see review in Lessells 1991). These types of trade-offs are known as life history traits (Ricklefs & Wikelski 2002) and are a fundamental part of any animal’s maximisation of lifetime reproductive success (Stearns 1992; Roff 2002).

In this study the trade off birds have to make between their own survival and the clutch size they produce was examined in the context of the seasonal environment in which they occur. The constraints placed on survival and clutch size, along with other important life history traits such as maintenance of body reserves (body mass) and flight condition (moult) were also explored.

The environmental constraints imposed by a seasonal environment that varied in food availability and the different life-history traits interacted in a complex way to produce the pattern of life histories that were observed. This study was particularly concerned with the effects of climate, and its seasonality, and used north temperate and tropical regions as two different climatic areas to compare so that life history traits could be more easily interpreted as consequences of environmental conditions. Seasonality had different effects in each climate, but in

each resulted in constraints to food abundance and the energetics of birds, which in turn had fundamental influences on the trade offs birds in each region made.

## **Survival**

One of the previously well established (and indeed “classic”) examples of how environmental constraints affect life-history traits is the relationship between latitude and adult survival and clutch size. Tropical environments are thought to be under less environmental constraint in terms of climatic variation, leading to a more predictable environment and as a consequence the opportunity for the evolution of high adult survival (Dobzhansky 1950). Adult survival was then thought to offer a simple explanation for the observed differences in clutch size between tropical and temperate climates (Moreau 1944; Snow & Lill 1974; Skutch 1985; Yom-Tov 1994; Martin 1996): if adult survival is high then fecundity does not need to be high for the population to increase.

While this study made clear that adult survival was indeed higher in tropical birds than in north temperate birds it was also clear that there was not a simple trade off with clutch size to compensate. Adult survival was shown not to be uniform in the tropics with variation within and between sites, as well as variation within species between sites. This made it clear that further constraints were in place and so further trade offs must be occurring to account for the anomaly between adult survival not being sufficiently high to balance the low clutch size. There were several other predicted constraints that may explain why adult survival was insufficient to compensate for low clutch size in tropical birds: nest predation, length of the breeding season, and extended parental care. Modelling of these

variables suggested one, or other, or a combination of increased nest survival, more broods per year and higher juvenile survival was necessary to account for the gap between adult survival and clutch size.

Empirical evidence for nest survival and the number of broods raised per year in tropical birds is, however, equivocal. Indeed it was often assumed that nest predation was *higher* in the tropics (Skutch 1949; Foster 1975; Robinson *et al.* 2000), but some studies have shown it be variable in the tropics (Skutch 1985), and perhaps no different to nest survival in north temperate regions (Martin *et al.* 2000). Another often assumed trait in tropical birds that may compensate for low clutch size was multiple broods per year (Skutch 1985; Karr *et al.* 1990). But, limited empirical evidence suggests that tropical birds only have one successful brood per year (Fogden 1972; König & Gwinner 1995; Jullien & Thiollay 1998) and so this would not compensate for lower clutch size in tropical birds.

The rejection of nest survival and multi-brooding as compensation for low clutch size leaves only higher juvenile survival as a possible explanation. Again empirical evidence for higher juvenile survival in the tropics is limited but published studies do suggest that juvenile survival is indeed higher (but see Zann & Runciman 1994; Russell & Rowley 2000; Covas *et al.* 2004; Schaefer *et al.* 2004). But, how do adult tropical birds trade off low clutch size through higher juvenile survival?

It would appear that higher juvenile survival is achieved by increasing parental care after offspring have fledged, and indirectly by allowing them to remain in the natal territory after they are nutritionally independent (Russell *et al.* 2004).

Investing in fewer offspring with higher parental care rather than many offspring with lower parental care appears to be an adaptation to maximise fitness in tropical birds. If this is indeed the compensatory mechanism used by tropical birds to trade off their own survival against reproductive value why is it so different from north temperate birds? It may be an adaptation to higher nest predation, but strong evidence for this is lacking. However, it may also be an adaptation to habitat saturation (Russell & Rowley 2000). Higher survival of adult birds would result in lower turn over of territories, thus resulting in greater competition for space for juvenile birds recruiting into the population (Kokko & Lundberg 2001). The extended parental care afforded by tropical birds to their offspring may be an adaptation to increase their likelihood of successfully finding and establishing a territory for themselves.

That tropical birds are able to provide higher levels of extended parental care to their offspring must be, to a certain degree, a consequence of their environment. The lack of seasonality severe enough to cause *severe* food limitation (as occurs in north temperate winters) in the tropics may mean that tropical birds have the opportunity to provide this level and value of care to their offspring – i.e. they are not constrained by seasonal climate. It was already established that tropical environments are indeed seasonal (Osborne 2000) and in the African savannahs at least this does result in a seasonal change in food abundance (de Bie *et al.* 1998). So, it may be predicted that there would be a differences in the level and duration of extended parental care across regions with differing levels of seasonality. Specifically in West Africa we may expect a clinal change from south to north as seasonal rainfall declines. In addition, as seasonal rainfall is likely to cause

differences between feeding guilds in the patterns of seasonal food abundance it may be predicted that there would be differences in the phenology of breeding and extended parental care of species from different guilds (Poulin *et al.* 1992). This would be dependant on food being limited seasonally, and this is another aspect of tropical bird ecology that has yet to be established, so for these predictions to be examined the presence and levels of food limitation would also have to be investigated.

Unfortunately there is a paucity of data to fully determine the life history trade offs undertaken by tropical birds, particularly juvenile survival. Further research into age specific survival rates is needed, but with recent models able to determine survival rates from colour ring re-sightings (Barker 1999) this has not only become easier but more robust.

## **Size**

While trade offs may occur between adult survival and clutch size it would appear that additional constraints are induced by size, and that these constraints are different in tropical and temperate areas because of the differing environmental conditions there. Adult survival was shown to be constrained by body mass in north temperate birds from Britain (Dobson 1990), but it was shown not to be the case in tropical birds from Peru and Trinidad (Francis *et al.* 1999). This study examined a wider range of tropical sites and species and found that there was also no relationship between adult survival and body mass. This difference between life history constraints in tropical and north temperate birds suggested that there may be other differences in trade offs or constraints in reproductive variables. By

examining the relationships between body mass and annual fecundity, nest survival, juvenile survival and fledging period for both tropical and north temperate birds stark differences were found. North temperate birds only showed a relationship between annual fecundity and body mass (in addition to adult survival) and tropical birds had a body mass relationship with annual fecundity and extended parental care (though data was lacking for juvenile survival). These relationships seemed to show that small temperate birds were able to trade off their lower adult survival with higher annual fecundity, whereas in the tropics larger birds traded off lower fecundity with greater extended parental care.

When phylogenetic effects were considered, however, it appeared that north temperate birds had the relationship between survival and fecundity as a consequence of their ancestry, with taxa already having the traits necessary to exist in a north temperate climate, where the greater energetic constraints that winter climate imposes on smaller birds means that only those species already with high annual fecundity were able to endure the lower adult survival. In contrast, the significant relationships shown in tropical birds remained when phylogeny was accounted for, perhaps indicating that these species had evolved these characters relatively recently. Tropical birds seem to be more variable in life history traits within taxa, suggesting more and possibly more recent adaptation to their environment. This plasticity is underlined by the difference in species that either occur in both climates, or species that have been introduced from one climate to another: tropical stonechats (*Saxicola torquata*) have higher adult survival and lower clutch size than north temperate stonechats (Konig & Gwinner

1995) and birds introduced to New Zealand from Britain have a lower clutch size (Duncan *et al.* 1999).

This study has shown that body mass is an important constraint on life history trade offs, and that differences in these trade offs between climates do exist, so future studies should be aware of these differing effects and not merely control for body size, but use it to better understand life history trade offs. That body mass appears to be constraining the life history of birds of different sizes in north temperate and tropical regions suggests that the different climates in these areas have different effects on birds of different body masses.

Birds in north temperate climates were known to trade off the two constraints of starvation and predation risk (Lima 1986). Individuals can increase their body mass and hence reduce their starvation risk, but this is at the expense of an increase in predation risk as heavier birds are slower and less manoeuvrable and so are more likely to be predated (Witter & Cuthill 1993). North temperate birds face an increased starvation risk during the winter as food becomes less abundant and less predictable so must increase their body mass, despite the increased cost of higher predation risk (Houston & McNamara 1993). Thus seasonal climate has a great influence on important life history trade offs in temperate birds.

But as the climate is so different in the tropics do birds face the same trade offs and if so is it to the same degree? As already discussed much of the tropics has a seasonal climate, in particular the African savannahs, where rather than being dominated by seasonal temperature differences the seasons are dominated by rainfall differences which affect plant growth, and thus food abundance through

the ecosystem (Bourliere & Hadley 1970; de Bie *et al.* 1998; Osborne 2000). So, it was predicted that birds would have to regulate their body mass seasonally. Some birds were indeed found to change their body mass with season but others did not and some did change body mass but not on a clearly seasonal basis. Consequently it appeared that there was no single overall explanation for seasonal mass variation equivalent to the “fat in winter” temperate explanation.

The lack of a uniform single explanation for seasonal mass variation is perhaps not surprising as rainfall may be predicted to have a different effect on different foraging guilds, with peaks in food abundance being different for granivores, frugivores, nectivores and insectivores (Poulin *et al.* 1992). However, classifying the tropical birds that were measured into such guilds also failed to provide an overall explanation for the patterns of mass variation observed. It would therefore appear that body mass regulation is more species specific in tropical birds than amongst those north temperate birds studied so far. This would suggest that starvation risk/predation risk trade offs are likely to be more complex in the tropics. If absolute food abundance is largely not limiting for some species, and birds are relatively long lived they may adopt a more conservative daily, seasonal and annual cycle to limit predation risk, indeed it has been shown that tropical birds with eggs or dependant young responded to reduce predation risk to themselves even at greater risk to their offspring, while north temperate birds responded to reduce mortality of their offspring, even at greater mortality risk to themselves (Ghalambor & Martin 2001).

## Moult

That tropical birds have a more conservative approach to predation risk as a consequence of environmental conditions, resulting in (or as a consequence of the survival/clutch size trade-off) higher adult survival and a “slow” breeding strategy, is further supported by the data on moult patterns in this study. Moult is a necessary life history trait in all birds that may have strong consequences for survival (Nilsson & Svensson 1996), breeding (Franklin *et al.* 1999), body mass regulation (Myrcha & Pinowski 1970) and migration (Jenni & Winkler 1994). It is an energetically costly process that requires additional food intake (Lindstrom *et al.* 1998) while at the same time reducing flight performance (Swaddle & Witter 1997), both of which may increase the risk of mortality through predation (Lind 2001).

Due to the high costs of moult birds try to minimise the overlap between the period in which they moult with the period in which they breed, as this is also energetically costly and has increased mortality risks associated with it (Jenni & Winkler 1994). A physiological consequence of moult is an increase in water content (Dolnik & Gavrilo 1979) which increases body mass. Birds may then compensate by reducing their body mass but increasing starvation risk (Lind *et al.* 2004). This is also combined with the reduced flight performance adding to the predation risk. For those species that have to migrate, there may be a temporal constraint on moult period, which may need to be squeezed in between breeding and migration, this is particularly the case for tropical-temperate migrants (Jenni & Winkler 1994).

As the results of this study with respect to survival and size suggest that tropical birds are experiencing variable constraints, and so have different life history trade offs, it may be predicted that they will have very variable moult strategies. However, they may still be limited by the food abundance consequences of a seasonal climate and seasonal breeding. Moult was measured across a range of species in West Africa and found to be very slow in comparison with similar north temperate birds for all but two species. However, moult was largely seasonal in nature, particularly for granivorous birds, that moulted mostly during the dry season. This was likely to be a period of high food abundance for this feeding guild of birds, suggesting that it was both energetically costly, and that food was sufficiently limiting during the rainy season to preclude moulting during that period. However, it may be that food was not limiting and birds were simply moulting when they had finished breeding and that breeding was more costly and so was timed for peak food abundance towards the end of the rains.

The very slow moult shown by most species is further evidence of a very conservative life cycle. Slower moult results in smaller gaps in the wing, which would minimise the reduction in flight performance (e.g. see Swaddle & Witter 1997). This strategy would therefore minimise the mortality risk due to moult and so fits with both the conservative approach to predation risk and the higher adult survival shown in tropical birds, that allows a slow breeding strategy.

## **Residency**

Variation in environmental conditions, such as climatic seasonality in the Guinea savannah was predicted to have important consequences for seasonal abundance

of birds. Again the less severe seasonality (e.g. at least with respect to cold temperatures) may have resulted in variable patterns of abundance in tropical birds, for the same reason that life history trade-offs appear to be more variable. The seasonal change in food abundance was likely to provide periods where costs of gaining energy would be at their lowest. The regularity of the seasonal movement of the ITCZ was likely to result in the peak of food abundance being relatively predictable. Thus it was predicted that abundance would change seasonally due to movements of birds, population increases due to breeding and changes in behaviour influencing estimates of abundance.

As with body mass and moult it was found that there was a wide variety of patterns shown across species. Some species were shown not to change in abundance between seasons when it was predicted that they would (e.g. variable sunbird *Cinnyris venusta*), others changed seasonally when it was predicted that they would not (e.g. speckled mousebird *Colius striatus*), some species did match their predictions, either by not changing in abundance or changing in abundance seasonally. Overall, more species changed in abundance than was predicted and for many species the changes were consistent with partial migration. It was suggested that many of these partial migrants were making altitudinal movements to and from the high Jos plateau.

These findings have important implications for the study of life history evolution in these birds. While long distance migration is known to have many costs (Alerstam & Lindstrom 1990), the costs of short distance migration are less well known. However, short distance migration would clearly need some fuelling, in the form of body fat, so there will be costs associated with it (both energetic and

predation risk). However, birds make these costly choices to maximise fitness. Birds trade off the costs of remaining in a single territory, which may become less optimal due to seasonality, with costs of migrating. Clearly this trait is advantageous for some birds but not for others. Partial migration was shown to be controlled by genetic polymorphism in many species such that both migrants and residents in a population have equal fitness (see Berthold 1988). The causes of this are likely to be competition for limited resources during some part of the year. As competition increases, the fitness of a bird that migrates will increase, thus the fitness value of a resident will be density dependent and so it would be expected that there would be an ideal free distribution of birds between residency and migration (see review in Milinski & Parker 1991). Thus the seasonal environment in the tropics is producing a more complicated pattern of life history trade offs than previously thought. There is however a need for further work to clarify the causes of seasonal abundance changes, whether there is food limitation due to climate and how this affects the choices that birds have to make.

## **Synthesis**

Overall this study can be synthesised into three inter-related subjects: the differences in life history evolution between tropical and north temperate birds; individual decision making processes in tropical birds; and abiotic influences on climate and their effects on seasonality. Within each of these subjects there are interactions between the abiotic and biotic environments which influence the decision making that individual birds make in order to maximise both their own survival and their lifetime reproductive success. An overview of the interactions

studied in this thesis is shown in Figure 7.1.

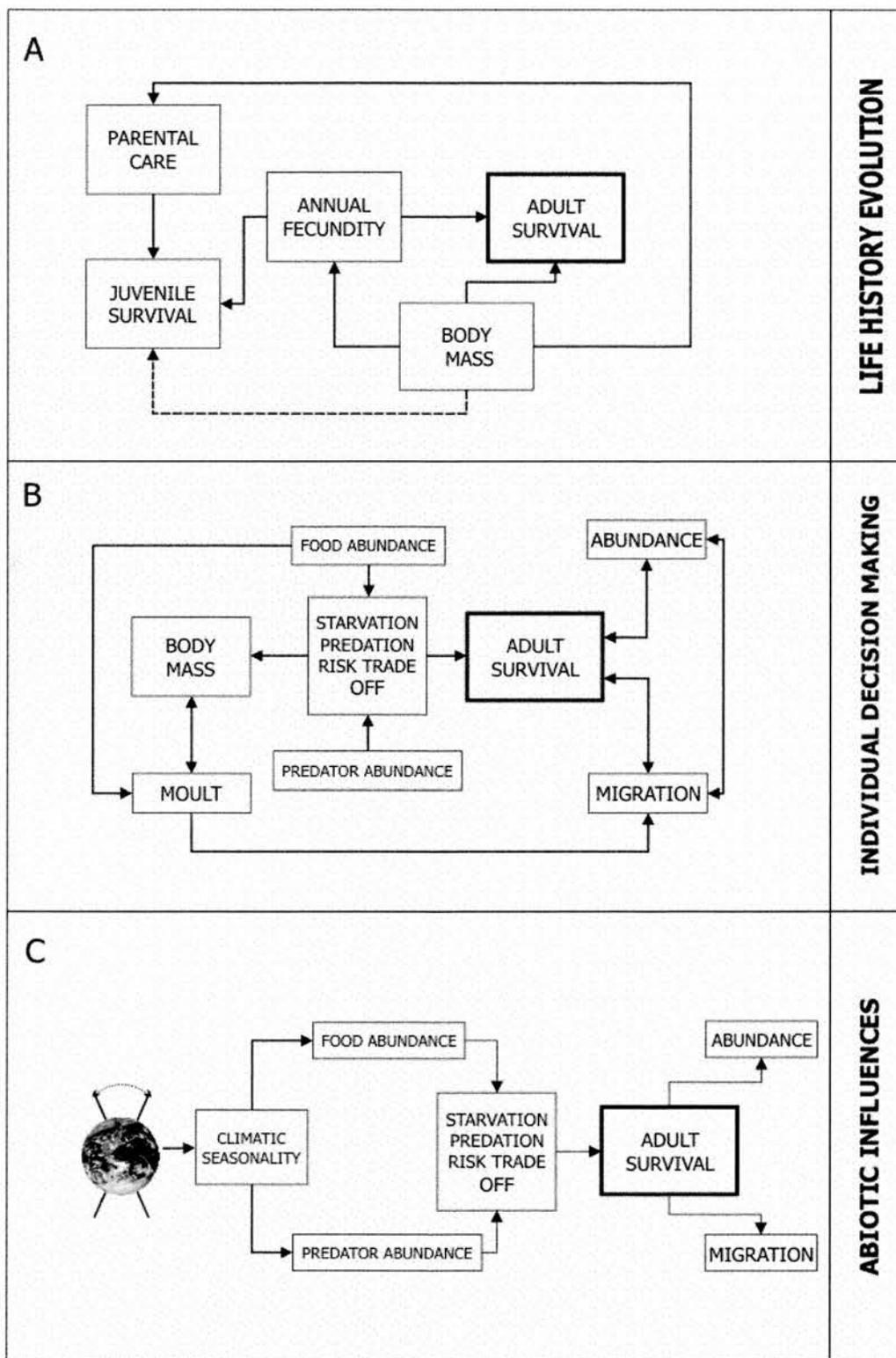


Figure 7.1: Interactions between life history traits, individual constraints and abiotic factors.

As most of these interactions are dealt with in detail within other chapters they will not be repeated here. However these diagrams bring up some interesting further questions. Figure 7.1A illustrates the life history trade offs studied in Chapters Two and Three, centred on the most important trade off between survival and reproduction. This study identified juvenile survival as a very important trait within life history evolution in tropical birds. It was suggested that tropical birds achieved higher juvenile survival by increasing the parental care afforded to offspring after fledging. The high adult survival shown in tropical birds that make this additional investment suggests that costs associated with such a trait are small.

So, why do north temperate birds not make a similar investment? The costs of making such an investment must be too high for temperate birds otherwise such a trait would have evolved. The lack of costs to tropical birds may be a consequence of high food abundance (suggested by the lack of body mass change in Chapter Five). If competition with their own offspring for food after nutritional independence is low then the costs of allowing them to remain in the natal territory will also be low, with benefits to the parents of increased juvenile survival, making this a 'cheap' means of increasing lifetime reproductive success. However, north temperate birds must be faced with competition for food from their own offspring after nutritional independence, either directly through costs to their own survival, or indirectly by costs to other offspring in subsequent broods that are being provided for by the parents. Thus the trade off north temperate birds make must be influenced by different patterns of seasonal food abundance and age dependent mortality risks than tropical birds. Higher probability of starving in

the following winter and perhaps higher predation risk overall may mean simply that increased parental care after fledging is not worth it for temperate birds: most offspring will die regardless of the post fledging investment. Further research into this aspect of life history trade offs in tropical birds is still needed.

Juvenile survival is clearly an important factor in the demography of tropical birds (Figure 7.1) but data are lacking to test this. For example, it was not possible to establish a significant relationship between body mass and juvenile survival, though one was predicted (Chapter Three): hence the dashed line in Figure 7.1A. It was also not possible to establish if the observed juvenile survival of tropical birds was sufficient to compensate for the discrepancy between adult survival and clutch size in tropical birds (Chapter Two). Further research into juvenile survival in relation to adult survival in the tropics is currently the single biggest area of research needed to better understand life history traits in tropical birds.

Another important finding illustrated by Figure 7.1A is the influence of body mass on life history trade offs (Chapter Three). Rather than being a “nuisance” variable, it was found that there were clear differences between tropical and north temperate birds in the effects of body mass on trade offs. It was also found that the causes of these patterns were possibly through different evolutionary routes, although it was clear that further research into the effects of body mass on life history of birds in the tropics is needed.

Body mass was also an important aspect of the individual decision making processes (as illustrated in Figure 7.1B). Body mass regulation was found to be largely species specific and simple seasonal patterns were difficult to establish.

Although the individual contributions of starvation and predation risk to the mass of the birds studied were not measured by this study, many birds did appear to be regulating their body mass as if starvation risk was not a major consideration and with a priority on minimising predation risk. High adult survival in any case suggests that predation risk is minimised by tropical birds by their behaviour, as was shown by Ghalambor and Martin (2001). Alternatively predation risk for tropical birds may simply be much less than in temperate areas. The wide variety of body mass regulation strategies that tropical birds appeared to be using suggests that further research on this topic would yield interesting results, but field measurements of food and predator abundance would be required to determine how tropical birds are making this trade off.

This study provides some much needed estimates of moult period and duration of tropical birds (Chapter 4), and suggests that the costs of moult are different in the life history trade offs in tropical birds compared to temperate birds. It is difficult to say, however, whether the slower or longer moult in tropical birds means that moult is now a relatively minor cost, or that moult is so slow because it is a relatively major cost. Unfortunately data were not sufficient to examine the relationship between body mass and moult with any confidence, so the importance of moult in the trade-offs illustrated in Figure 7.1 is not clear. The suggestion from this study is that moult is now a relatively minor cost to tropical birds because the lower seasonality means that it can be spread over a longer period. But, further research to truly establish if moult does not affect the starvation/predation risk trade off in tropical birds is needed.

Finally, the importance (or lack of importance) of competition (e.g. abundance) and mechanisms to reduce that competition (e.g. migration) are also illustrated in Figure 7.1. Tropical birds were shown to have a variety of residency and migration patterns and with some general patterns emerging, such as between the rainy and dry seasons. Some species have responded to seasonal opportunity by adopting migration and so are constrained by the need to acquire fat reserves, to carry out moult at non-migration times and possibly to shorter breeding seasons, at least through shorter periods of extended parental care. In this respect, tropical migrants may be very similar to temperate migrants. A direct prediction from this study might then be that those species that are intra-African migrants have higher clutch sizes, higher nest survival or higher adult survival to compensate for the lack of first year survival because they cannot have extended periods of parental care.

The starvation/predation risk trade off is determined by the relative abundance of food and predators, which are in turn affected by the seasonal climate (Fig 7.1C). The differences in this seasonality between tropical and north temperate climates has very different effects on the individual decision making and life history trade offs that tropical birds have to make in comparison to their north temperate congeners. It was shown by this study that tropical birds appear to be *K*-selected animals with high survival but low annual productivity, unlike *r*-selected north temperate species that exhibit low survival but very high annual productivity (Dobzhansky 1950). Adult survival was a major focus of this thesis and was shown to be higher in tropical than north temperate birds, but that this difference was not uniform between sites and species, and even within species. So while the

*r/K*-selection hypothesis was again shown to be useful it was again not able to provide a complete understanding of different life history traits and trade offs (Boyce 1984). Climate and seasonality clearly have a strong influence on tropical ecosystems, as they do in north temperate ecosystems, but much work is needed to understand these effects more clearly and how they constrain life history evolution in tropical birds. There is still a great deal to learn about the biology of tropical birds, but this study has added to not only the understanding of tropical birds but has illustrated that by understanding tropical systems further insights into north temperate systems are possible.

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# APPENDIX

## Appendix 5.1: Population model life tables.

Table A5.1.1: Predicted adult survival from simple population model for north temperate birds. Assumed values of life history traits are in grey (see text).

predicted adult survival rate	starting population	annual population mortality	clutch size	nest survival	fledglings per pair	annual brood rate	1st year survival	number of recruits	population change
0.775	100	22.52	3.9	0.35	68.25	1	0.33	22.52	0
0.752	100	24.77	3.9	0.35	75.08	1.1	0.33	24.77	0
0.730	100	27.03	3.9	0.35	81.90	1.2	0.33	27.03	0
0.707	100	29.28	3.9	0.35	88.73	1.3	0.33	29.28	0
0.685	100	31.53	3.9	0.35	95.55	1.4	0.33	31.53	0
0.662	100	33.78	3.9	0.35	102.38	1.5	0.33	33.78	0
0.640	100	36.04	3.9	0.35	109.20	1.6	0.33	36.04	0
0.617	100	38.29	3.9	0.35	116.03	1.7	0.33	38.29	0
0.595	100	40.54	3.9	0.35	122.85	1.8	0.33	40.54	0
0.572	100	42.79	3.9	0.35	129.68	1.9	0.33	42.79	0
0.550	100	45.05	3.9	0.35	136.50	2	0.33	45.05	0
0.527	100	47.30	3.9	0.35	143.33	2.1	0.33	47.30	0
0.505	100	49.55	3.9	0.35	150.15	2.2	0.33	49.55	0
0.482	100	51.80	3.9	0.35	156.98	2.3	0.33	51.80	0
0.459	100	54.05	3.9	0.35	163.80	2.4	0.33	54.05	0
0.437	100	56.31	3.9	0.35	170.63	2.5	0.33	56.31	0
0.414	100	58.56	3.9	0.35	177.45	2.6	0.33	58.56	0
0.392	100	60.81	3.9	0.35	184.28	2.7	0.33	60.81	0
0.369	100	63.06	3.9	0.35	191.10	2.8	0.33	63.06	0
0.347	100	65.32	3.9	0.35	197.93	2.9	0.33	65.32	0
0.324	100	67.57	3.9	0.35	204.75	3	0.33	67.57	0

Table A5.1.2: Predicted adult survival from simple population model for tropical birds. Assumed values of life history traits are in grey (see text).

predicted adult survival rate	starting population	annual population mortality	clutch size	nest survival	fledglings per pair	annual brood rate	1st year survival	number of recruits	population change
0.869	100	13.05	2.26	0.35	39.55	1	0.33	13.05	0
0.856	100	14.36	2.26	0.35	43.51	1.1	0.33	14.36	0
0.843	100	15.66	2.26	0.35	47.46	1.2	0.33	15.66	0
0.830	100	16.97	2.26	0.35	51.42	1.3	0.33	16.97	0
0.817	100	18.27	2.26	0.35	55.37	1.4	0.33	18.27	0
0.804	100	19.58	2.26	0.35	59.33	1.5	0.33	19.58	0
0.791	100	20.88	2.26	0.35	63.28	1.6	0.33	20.88	0
0.778	100	22.19	2.26	0.35	67.24	1.7	0.33	22.19	0
0.765	100	23.49	2.26	0.35	71.19	1.8	0.33	23.49	0
0.752	100	24.80	2.26	0.35	75.15	1.9	0.33	24.80	0
0.739	100	26.10	2.26	0.35	79.10	2	0.33	26.10	0
0.726	100	27.41	2.26	0.35	83.06	2.1	0.33	27.41	0
0.713	100	28.71	2.26	0.35	87.01	2.2	0.33	28.71	0
0.700	100	30.02	2.26	0.35	90.97	2.3	0.33	30.02	0
0.687	100	31.32	2.26	0.35	94.92	2.4	0.33	31.32	0
0.674	100	32.63	2.26	0.35	98.88	2.5	0.33	32.63	0
0.661	100	33.93	2.26	0.35	102.83	2.6	0.33	33.93	0
0.648	100	35.24	2.26	0.35	106.79	2.7	0.33	35.24	0
0.635	100	36.54	2.26	0.35	110.74	2.8	0.33	36.54	0
0.622	100	37.85	2.26	0.35	114.70	2.9	0.33	37.85	0
0.608	100	39.15	2.26	0.35	118.65	3	0.33	39.15	0

Table A5.1.3: Predicted overall nest survival from simple population model for north temperate birds. Assumed values of life history traits are in grey (see text).

adult survival rate	starting population	annual population mortality	clutch size	predicted nest survival	fledglings per pair	annual brood rate	1st year survival	number of recruits	population change
0.54	100	46	3.9	0.715	139.39	1	0.33	46	0
0.54	100	46	3.9	0.650	139.39	1.1	0.33	46	0
0.54	100	46	3.9	0.596	139.39	1.2	0.33	46	0
0.54	100	46	3.9	0.550	139.39	1.3	0.33	46	0
0.54	100	46	3.9	0.511	139.39	1.4	0.33	46	0
0.54	100	46	3.9	0.477	139.39	1.5	0.33	46	0
0.54	100	46	3.9	0.447	139.39	1.6	0.33	46	0
0.54	100	46	3.9	0.420	139.39	1.7	0.33	46	0
0.54	100	46	3.9	0.397	139.39	1.8	0.33	46	0
0.54	100	46	3.9	0.376	139.39	1.9	0.33	46	0
0.54	100	46	3.9	0.357	139.39	2	0.33	46	0
0.54	100	46	3.9	0.340	139.39	2.1	0.33	46	0
0.54	100	46	3.9	0.325	139.39	2.2	0.33	46	0
0.54	100	46	3.9	0.311	139.39	2.3	0.33	46	0
0.54	100	46	3.9	0.298	139.39	2.4	0.33	46	0
0.54	100	46	3.9	0.286	139.39	2.5	0.33	46	0
0.54	100	46	3.9	0.275	139.39	2.6	0.33	46	0
0.54	100	46	3.9	0.265	139.39	2.7	0.33	46	0
0.54	100	46	3.9	0.255	139.39	2.8	0.33	46	0
0.54	100	46	3.9	0.246	139.39	2.9	0.33	46	0
0.54	100	46	3.9	0.238	139.39	3	0.33	46	0

Table A5.1.4: Predicted overall nest survival from simple population model for tropical birds. Assumed values of life history traits are in grey (see text).

adult survival rate	starting population	annual population mortality	clutch size	predicted nest survival	fledglings per pair	annual brood rate	1st year survival	number of recruits	population change
0.62	100	38	2.26	1.019	115.15	1	0.33	38	0
0.62	100	38	2.26	0.926	115.15	1.1	0.33	38	0
0.62	100	38	2.26	0.849	115.15	1.2	0.33	38	0
0.62	100	38	2.26	0.784	115.15	1.3	0.33	38	0
0.62	100	38	2.26	0.728	115.15	1.4	0.33	38	0
0.62	100	38	2.26	0.679	115.15	1.5	0.33	38	0
0.62	100	38	2.26	0.637	115.15	1.6	0.33	38	0
0.62	100	38	2.26	0.599	115.15	1.7	0.33	38	0
0.62	100	38	2.26	0.566	115.15	1.8	0.33	38	0
0.62	100	38	2.26	0.536	115.15	1.9	0.33	38	0
0.62	100	38	2.26	0.510	115.15	2	0.33	38	0
0.62	100	38	2.26	0.485	115.15	2.1	0.33	38	0
0.62	100	38	2.26	0.463	115.15	2.2	0.33	38	0
0.62	100	38	2.26	0.443	115.15	2.3	0.33	38	0
0.62	100	38	2.26	0.425	115.15	2.4	0.33	38	0
0.62	100	38	2.26	0.408	115.15	2.5	0.33	38	0
0.62	100	38	2.26	0.392	115.15	2.6	0.33	38	0
0.62	100	38	2.26	0.377	115.15	2.7	0.33	38	0
0.62	100	38	2.26	0.364	115.15	2.8	0.33	38	0
0.62	100	38	2.26	0.351	115.15	2.9	0.33	38	0
0.62	100	38	2.26	0.340	115.15	3	0.33	38	0

Table A5.1.5: Predicted first year nest survival from simple population model for north temperate birds. Assumed values of life history traits are in grey (see text).

adult survival rate	starting population	annual population mortality	clutch size	nest survival	fledglings per pair	annual brood rate	predicted 1st year survival	number of recruits	population change
0.54	100	46	3.9	0.35	68.25	1	0.674	46	0
0.54	100	46	3.9	0.35	75.08	1.1	0.613	46	0
0.54	100	46	3.9	0.35	81.90	1.2	0.562	46	0
0.54	100	46	3.9	0.35	88.73	1.3	0.518	46	0
0.54	100	46	3.9	0.35	95.55	1.4	0.481	46	0
0.54	100	46	3.9	0.35	102.38	1.5	0.449	46	0
0.54	100	46	3.9	0.35	109.20	1.6	0.421	46	0
0.54	100	46	3.9	0.35	116.03	1.7	0.396	46	0
0.54	100	46	3.9	0.35	122.85	1.8	0.374	46	0
0.54	100	46	3.9	0.35	129.68	1.9	0.355	46	0
0.54	100	46	3.9	0.35	136.50	2	0.337	46	0
0.54	100	46	3.9	0.35	143.33	2.1	0.321	46	0
0.54	100	46	3.9	0.35	150.15	2.2	0.306	46	0
0.54	100	46	3.9	0.35	156.98	2.3	0.293	46	0
0.54	100	46	3.9	0.35	163.80	2.4	0.281	46	0
0.54	100	46	3.9	0.35	170.63	2.5	0.270	46	0
0.54	100	46	3.9	0.35	177.45	2.6	0.259	46	0
0.54	100	46	3.9	0.35	184.28	2.7	0.250	46	0
0.54	100	46	3.9	0.35	191.10	2.8	0.241	46	0
0.54	100	46	3.9	0.35	197.93	2.9	0.232	46	0
0.54	100	46	3.9	0.35	204.75	3	0.225	46	0

Table A5.1.6: Predicted first year nest survival from simple population model for tropical birds. Assumed values of life history traits are in grey (see text).

adult survival rate	starting population	annual population mortality	clutch size	nest survival	fledglings per pair	annual brood rate	predicted 1st year survival	number of recruits	population change
0.62	100	38	2.26	0.35	39.55	1	0.961	38	0
0.62	100	38	2.26	0.35	43.51	1.1	0.873	38	0
0.62	100	38	2.26	0.35	47.46	1.2	0.801	38	0
0.62	100	38	2.26	0.35	51.42	1.3	0.739	38	0
0.62	100	38	2.26	0.35	55.37	1.4	0.686	38	0
0.62	100	38	2.26	0.35	59.33	1.5	0.641	38	0
0.62	100	38	2.26	0.35	63.28	1.6	0.601	38	0
0.62	100	38	2.26	0.35	67.24	1.7	0.565	38	0
0.62	100	38	2.26	0.35	71.19	1.8	0.534	38	0
0.62	100	38	2.26	0.35	75.15	1.9	0.506	38	0
0.62	100	38	2.26	0.35	79.10	2	0.480	38	0
0.62	100	38	2.26	0.35	83.06	2.1	0.458	38	0
0.62	100	38	2.26	0.35	87.01	2.2	0.437	38	0
0.62	100	38	2.26	0.35	90.97	2.3	0.418	38	0
0.62	100	38	2.26	0.35	94.92	2.4	0.400	38	0
0.62	100	38	2.26	0.35	98.88	2.5	0.384	38	0
0.62	100	38	2.26	0.35	102.83	2.6	0.370	38	0
0.62	100	38	2.26	0.35	106.79	2.7	0.356	38	0
0.62	100	38	2.26	0.35	110.74	2.8	0.343	38	0
0.62	100	38	2.26	0.35	114.70	2.9	0.331	38	0
0.62	100	38	2.26	0.35	118.65	3	0.320	38	0

## Appendix 5.2: Body mass and fat score

Table A5.2.1: Results of linear regression between fat score and body mass.  $m$  = slope of regression,  $s.e.$  = standard error,  $n$  = sample size. Shaded results showed a significant relationship. The darker the shading the smaller the  $p$  value (see legend below).

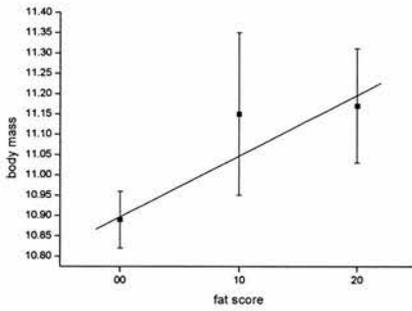
	species	linear regression						n	
		m	s.e.	intercept	s.e.	r <sup>2</sup>	p		
non-passerine	black-billed wood dove	all fat scores 00						39	
	yellow-fronted tinkerbird		0.15	0.04	10.75	0.07	0.92	0.18	90
	greater honeyguide	cannot be measured							24
	red-throated bee-eater	only fat scores 00 and 10							37
African insectivores	common wattle-eye	all fat scores 00							35
	african yellow white-eye		0.09	0.08	9.43	0.10	0.59	0.44	103
	snowy-crowned robin-chat		-0.12	0.76	36.87	0.88	0.02	0.90	57
	common bulbul	only fat scores 00 and 10							190
	african thrush		1.98	0.10	63.12	0.12	0.997	0.03	126
	grey-backed camaroptera		-0.11	0.20	11.22	0.32	0.13	0.64	75
African granivores	African quailfinch		-0.05	0.45	11.02	0.89	0.01	0.93	67
	bronze mannikin		0.11	0.05	8.85	0.14	0.71	0.16	67
	village weaver		-0.54	0.63	38.58	1.17	0.27	0.48	113
	black-necked weaver		1.08	0.03	25.78	0.06	0.999	0.02	62
	vitelline masked weaver		0.63	0.64	18.84	1.39	0.33	0.42	28
	speckle-fronted weaver	only fat scores 00 and 10							52
	northern red bishop		0.07	0.12	15.36	0.23	0.15	0.61	127
	black-winged bishop		0.21	0.51	20.05	0.76	0.08	0.72	55
	red-cheeked cordon bleu		0.00	0.00	10.38	0.07	0.22	0.69	238
	lavender waxbill		0.27	0.02	8.99	0.04	0.990	0.005	195
	black-rumped waxbill		0.14	0.10	7.24	0.21	0.67	0.39	61
	red-billed firefinch		0.17	0.09	8.65	0.15	0.64	0.20	259
	bar-breasted firefinch		0.19	0.11	9.04	0.13	0.60	0.22	38
	rock firefinch		0.08	0.05	10.44	0.08	0.68	0.38	116
cinnamon-breasted bunting		0.39	0.03	13.11	0.04	0.994	0.05	94	
sun birds	variable sunbird		0.17	0.15	6.06	0.21	0.55	0.47	148
	scarlet-chested sunbird		0.11	0.26	10.40	0.71	0.08	0.72	112
	green-headed sunbird	only fat scores 00 and 10							55
paleartic migrants	whinchat		1.67	0.35	10.80	1.44	0.824	0.005	71
	pie flycatcher		0.13	0.02	10.46	0.76	0.937	0.002	29
	garden warbler		1.28	0.20	15.35	0.73	0.893	0.001	324
	whitethroat		0.63	0.13	13.41	0.36	0.819	0.005	141
	willow warbler		0.59	0.13	6.30	0.26	0.809	0.006	66

symbol	p
*	0.05 - 0.02
**	0.01 - 0.02
***	0.01 - 0.001
****	< 0.001

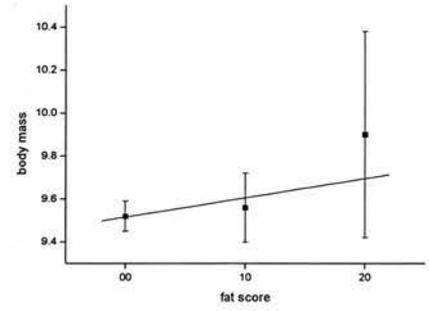
When the relationship between body mass and fat score was examined it was found that for most tropical species there was not a significant relationship

between the two variables (Table A5.2.1). However, four tropical species did show significant, positive relationships between body mass and fat score. All five of the palearctic migrants tested showed a strong positive relationship between body mass and fat score (Table A5.2.1).

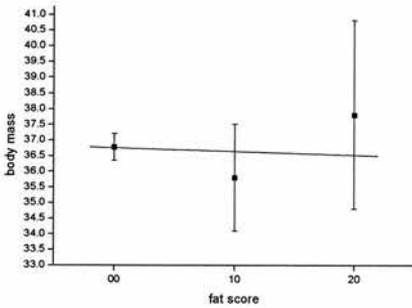
Figure A5.1: Graphs illustrating the relationship between fat score and body mass relationship between fat score and body mass (in grams) for 26 species with three or more fat scores.



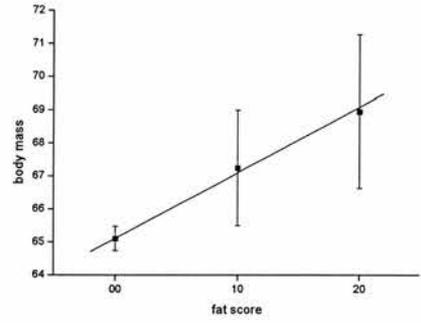
yellow-fronted tinkerbird



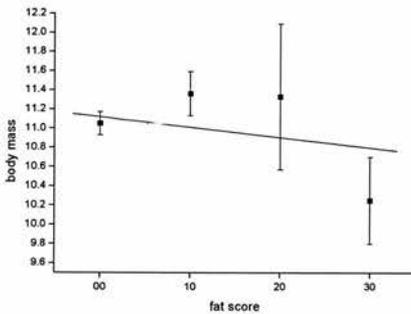
African yellow white-eye



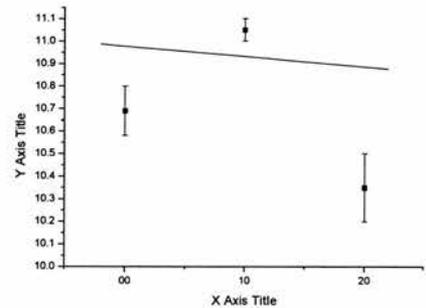
snowy-crowned robin chat



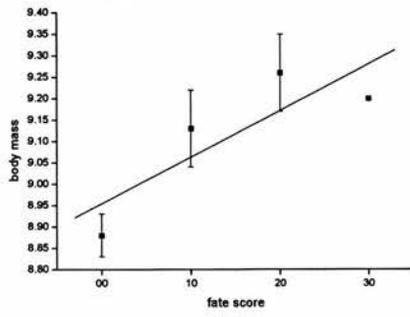
African thrush



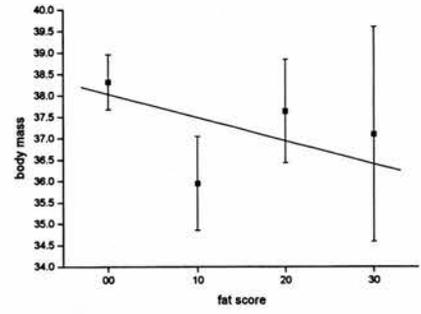
grey-backed camaroptera



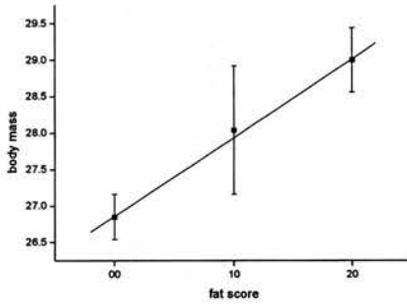
African quailfinch



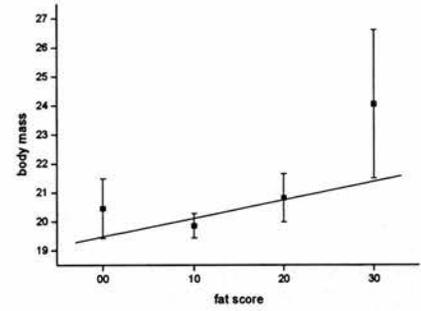
bronze manikin



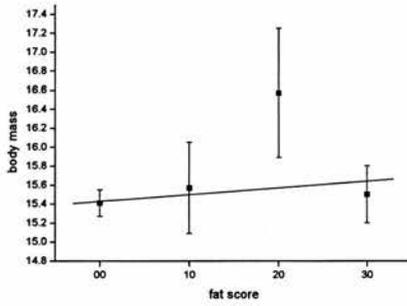
village weaver



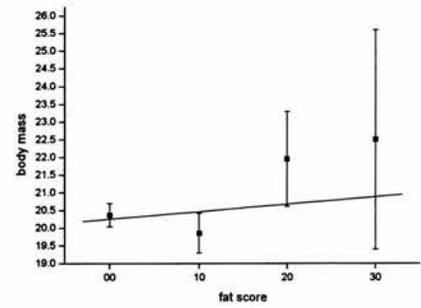
black-necked weaver



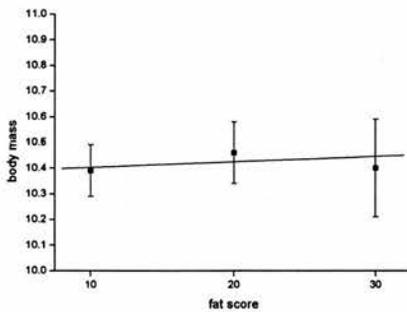
vitelline masked weaver



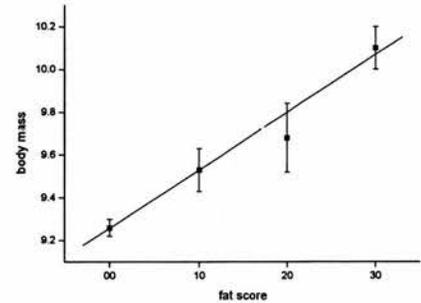
northern red bishop



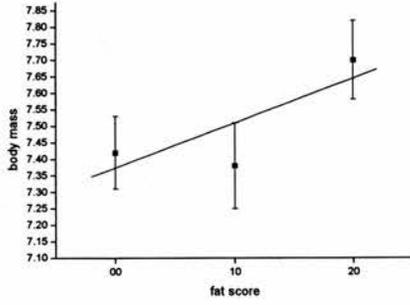
black-winged bishop



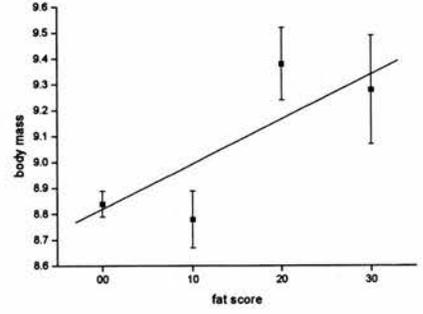
red-cheeked cordon-bleu



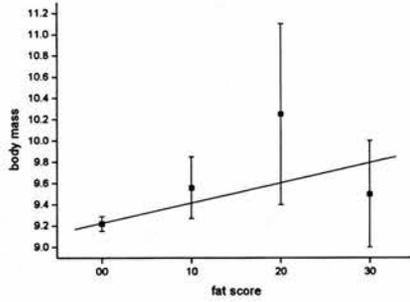
lavender waxbill



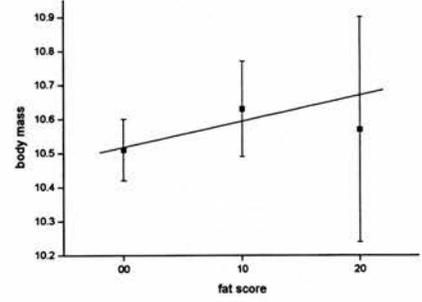
black-rumped waxbill



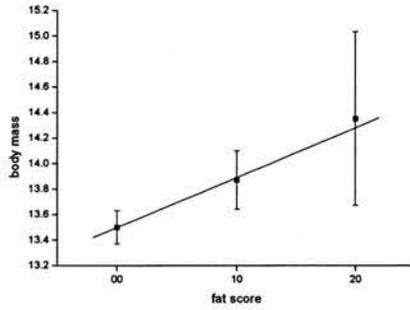
red-billed firefinch



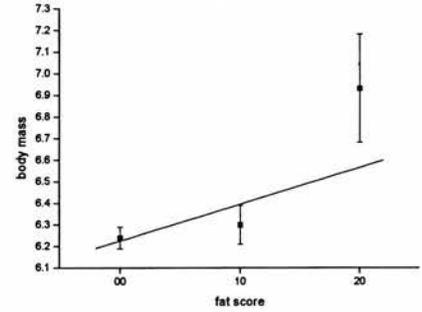
bar-breasted firefinch



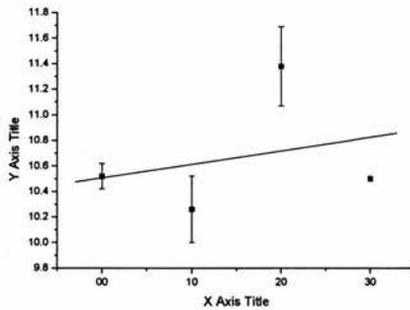
rock firefinch



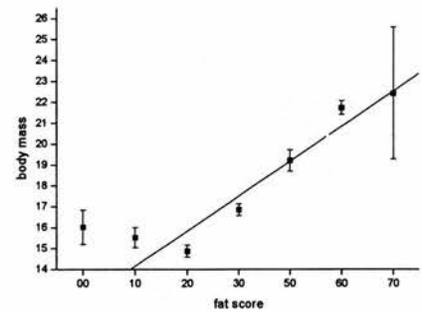
cinnamon-breasted bunting



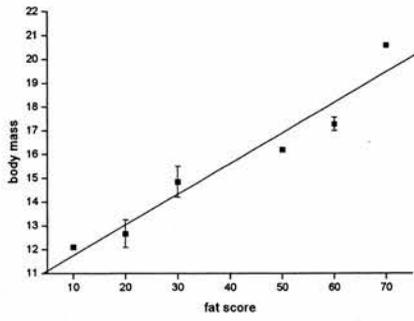
variable sunbird



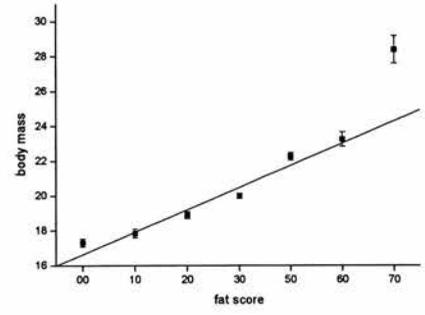
scarlet-chested sunbird



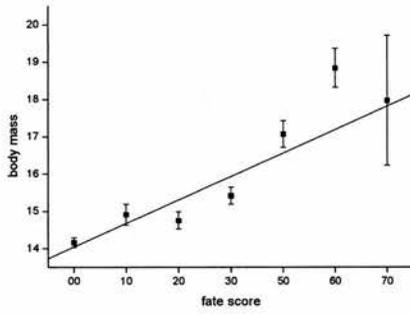
whinchat



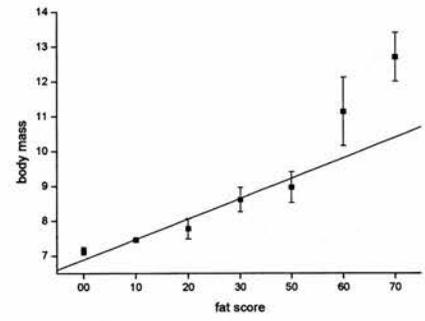
pied flycatcher



garden warbler



whitethroat



willow warbler

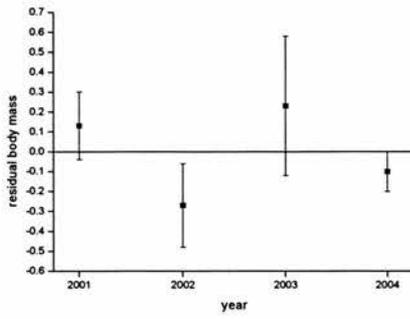
## **Appendix 5.2: Annual variation in mass**

Eight species showed a significant relationship between body mass and year.

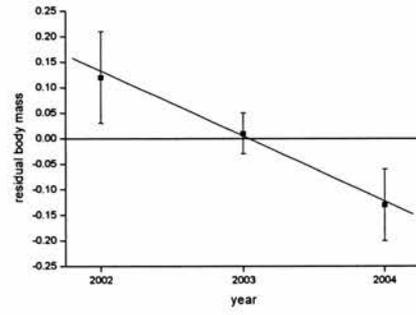
While this was considered a nuisance variable the relationship between residual body mass and year was plotted (Figure A5.2 on next page) for each of species.

This was to determine if there was a consistent pattern in mass change across all years. Figure A5.2 showed that seven species declined in mass across the years.

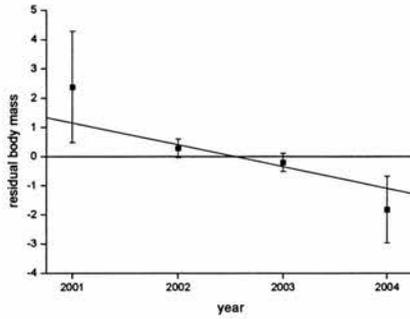
One species, common wattle-eye, did not show a consistent trend.



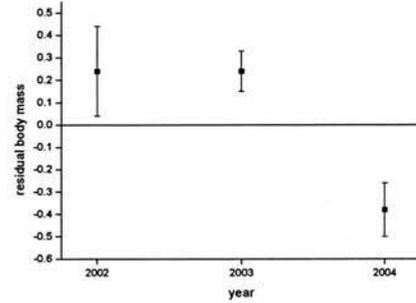
common wattle-eye



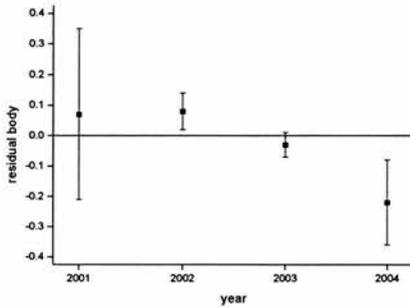
bronze mannikin



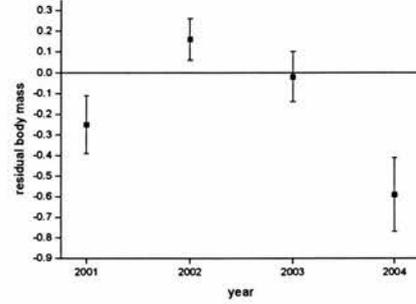
village weaver



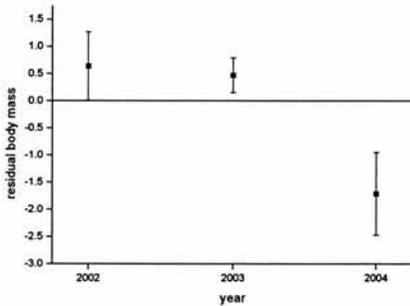
black-rumped waxbill



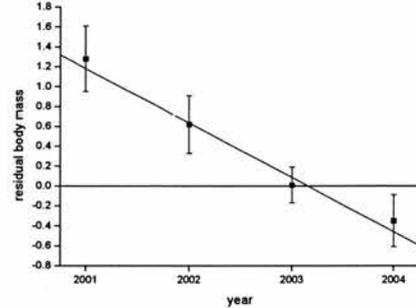
variable sunbird



green-headed sunbird



whinchat



whitethroat

Figure A5.2: Inter-annual variation in body mass for those species in which year was a significant variable in the model.