LIFE HISTORY TRADE-OFFS BETWEEN SURVIVAL, MOULT AND BREEDING IN A TROPICAL SEASON ENVIRONMENT

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Life history trade-offs between survival, moult and breeding in a tropical season environment

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Submitted for the degree of Doctor of Philosophy
to the University of St Andrews

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February 2010

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Abstract

The trade-off between current and future investment in reproduction lies at the heart of life history theory. The need to differentially allocate resources between these two options arises generally as a result of environmental pressures. Higher risk of mortality in adults is linked with increased investment in current reproduction, whereas the opposite is true where adults are long-lived (the *r*- *K* selection paradigm). Perhaps the most obvious factors influencing the environment stem from seasonality of the climate, since rainfall and temperature affect food availability, resulting in a higher risk of mortality. The available trade-offs that an organism can make will therefore be constrained by environmental variability potentially resulting in general adaptation and so ultimately influencing evolution of biome-specific life-history traits. In this thesis, I examine how the seasonality of a West African tropical savannah environment influences moult and breeding timing and duration, and survival in West African tropical savannah bird species. I show that moult in tropical birds follows the same basic descendant pattern through the wing feathers, but is a much lengthier process than for temperate species (mean = 131 ± 11 days, N = 29 species), and that it frequently overlaps with breeding activities. This suggests either that either the feathers of tropical species take longer to grow; that it is a relatively low-cost activity and has little influence on life history trade-offs; or that individuals further aim to reduce mortality risk by attempting to maintain high flight capability at all times. Breeding also occurred over a longer season than for temperate species, although an obvious peak in occurrence was identified to coincide with the food-abundant period of the late rains and early dry season. Lengthy breeding seasons may indicate an increased tendency to renest (possibly as a result of higher nest predation levels), and we also identified a prolonged immature plumage phase – potentially indicating an extended duration of parental care. Survival rates were calculated from mark-recapture models based on mist-netting data. Previous work has focussed on the use of incorporating mark-resighting data alongside that obtained by standard mark-recapture techniques. Here, I assess the models applied in those methods, identify problems associated with over-paramaterisation, goodness of fit and the generation of biologically unrealistic estimates, and so provide suggestions on how to improve the protocol. Average survival from my study (40 species: 0.63 ± 0.02) was higher than previous estimates obtained from this site and were comparable with estimates from other Afrotropical and Neotropical areas, although rates varied greatly between species. Juvenile survival (13 species) was similar or possibly lower than adult survival. I then used my empirically derived estimates of moult, breeding and survival life history traits to identify potential trade-offs between traits. Overall I was unable to identify significant relationships between any of the life history trait estimates, other than between adult survival and clutch size. In this, the results followed those of previous researchers in identifying a pattern of lower investment in current reproduction (clutch size) and maximisation of adult survival in tropical species. My study, however, demonstrates for the first time how moult and breeding duration are likely to be less constrained in tropical environments.

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Chapter 1: General introduction

Life history theory

Darwin's (1859) theory of evolution by natural selection rests on five propositions. These state that (1) all individuals vary; (2) part of this variation is heritable; (3) that all populations have the potential to populate the earth; (4) ancestors leave differing numbers of descendants; and (5) that the numbers of descendants left depends on the interaction between the characteristics of the individual and the environment. Essentially, individuals that are better adapted to their environments are more likely to survive and pass on their heritable characteristics to their descendants. Evolution by natural selection is therefore the change in heritable characteristics of a population over generations. The cumulative adaptation through inheritance, mutation and natural selection enables individuals of a species to more efficiently deal with environmental constraints.

One of these constraints is the availability of resources. Efficient use of limited resources is therefore a key component in the evolutionary process and provides a means by which individuals vary and how well they compete. This efficiency relates to the way that resources are allocated between the different activities which promote fitness (i.e. maximise their production of descendants), and this differential allocation of energy to an organism's traits such as growth, survival, storage and reproduction, and the trade-offs involved, results in its life history (Horn & Rubenstein 1984; Bennett & Owens 2002). Life history analysis is therefore the study of how variation in life history traits leads to variation in the fitness of individuals (Stearns 1992) and aims at identifying the causative factors behind species' allocation of resources differentially between the various life history components (Lack 1968; Horn & Rubenstein 1984; Roff 1992; Charlesworth 1994). Traditionally, only age-specific values of fecundity and mortality were considered true life history traits (Cole 1954; Partridge & Harvey 1988) since an increase in one, whilst holding the other constant, increases fitness. Now however, a suite of other traits (such as longevity, parity, age of first breeding, incubation period, growth rate, offspring size, size at maturity and sex ratio of offspring) are included within the life history framework (see e.g. Lack 1968; Gadgil & Bossert 1970; Rahn & Ar 1974; Horn 1978**;** Stearns & Koella 1986; Stearns 1992; Starck & Ricklefs 1998). This has prompted further questions regarding the independence or co-variation of each of these traits i.e. is there a selective response for each of these factors independently or are they a function of a combination of traits (Bennett & Owens 2002).

Life history trade-offs

Natural selection is presumed to optimise the investment of resources in growth, reproduction and survival according to the constraints placed upon it by the environment (Lack 1954, 1968; Williams 1966a; Gadgil & Bossert 1970; Charnov & Krebs 1974; Stearns 1976; Bell 1980; Charlesworth 1994). Investing resources solely into growth, survival or reproduction is not possible at all ages and increasing investment in one generally results in a decrease in the resources available for the other (i.e. growth affects reproduction and reproduction is costly and therefore affects survival) (Bennett & Owens 2002). The range of values of one trait will therefore frequently influence the potential range of values for a second trait. This lack of independence between many life history traits may result in difficulties identifying the effect of an experimental manipulation on a target trait because of covariation with others (e.g. see Bell & Koufopanou 1986; Lessells *et al.* 1989; Lessells 1991).

Of all life history trade-offs perhaps the most important (and certainly the most frequently studied) are those dealing with the costs of current reproduction in relation to future survival or growth (Lack 1947; Williams 1966a; Charnov & Krebs 1974; Reznick 1985). Gilman & Crawley (1990) demonstrated the trade-off between reproductive investment and survival in the ragwort (*Senecio jacobaea*) where only those individuals that invested least in reproduction survived the winter. Individuals that delayed reproduction or reduced it to a level below the maximum appeared to grow faster, larger and have increased resources available for future reproductive attempts. In animals, such trade-offs may occur through increased predation risk, reduced time available for comfort and maintenance behaviours and immunosuppression as a result of the extra foraging necessary to provision young (Magnhagen 1991), reduced parental survival (Hõrak 2003) or investment during future breeding attempts (Parejo & Danchin 2006). A trade-off also exists between the number of offspring and their individual fitness (e.g. Werner & Platt 1976; Montague et al. 1981; Stearns 1992; Sinervo 1990; Begon et al. 1996). Should a parent invest in a small number of high-quality (larger, stronger, better developed) young, or in a greater number of young that are inferior (smaller, weaker, more dependent)? Often this trade-off occurs prior to the young being laid/born (e.g. in the size of the egg) (e.g. Rahn *et al.* 1975; Alisauskas 1986) or takes the form of variable levels of parental care (i.e. a larger number of individuals results in each receiving proportionally less than individuals in smaller broods – e.g. Ricklefs 1984). For example, experimental reduction of yolk size resulted in offspring of the lizard *Scleroporus occidentalis* having a slower sprint speed than those from unmanipulated eggs (Sinervo 1990). Reduced fitness, expressed as a reduced ability to avoid predators, is likely to occur in larger broods since the greater division of maternal resources results in smaller eggs. This is a general theme among such studies with offspring of larger broods suffering increased mortality, reduced size and lower future fecundity (Lessells 1991).

Overall then, there is a general presumption that natural selection favours those individuals whose life histories balance the trade-offs in a manner that maximises lifetime reproductive output (Krebs & Davies 1993).

Influence of environment

The habitat in which an organism lives will inevitably have an impact on the ‘decisions’ it makes with regard to managing resources, avoiding predation, investing in reproduction etc. Abiotic factors, such as changes between harsh and favourable weather conditions (e.g. Tammaru & Hõrak 1999), or the interaction with other biotic factors in an organism's surroundings, e.g. food limitation (e.g. Martin 1987) or nest predation (Kulesza 1990; Sieving 1992) should both influence the life histories of individuals, populations and species. As a consequence, one would expect particular environmental conditions to result in similar life history strategies for similar organisms. This has indeed been found to be the case as comparisons of interactions between combinations of life history traits have shown (Sibly & Calow 1983; Begon *et al.* 1996). In general, habitats can be considered as having either a high or low cost of reproduction (MacArthur & Wilson 1967). Habitats with high reproductive costs are generally unpredictable and have variable adult and juvenile mortality. In contrast, habitats with more strongly defined and predictable patterns usually have low reproductive costs and low levels of adult mortality. In response, organisms in the former habitat tend to be small, achieve sexual maturity earlier, produce many offspring but die younger, and those in the latter habitat are large, slow-growing, produce fewer offspring and have longer lifespans. These two scenarios (corresponding to the '*r*- and *K*-selection' of MacArthur & Wilson (1967) and Pianka (1970)) are the extremes of a wide continuum of life history trade-offs (Saether et al. 2002) which follow a general latitudinal gradient in environmental conditions – variable northern areas favouring *r*-selected organisms, to less variable tropical areas (favouring *K*-selected organisms). It is these variations in environmental conditions that are believed to be the main factor behind the life histories if species in these areas (Fischer 1960; Pianka 1966; Rohde 1992; Rosenzweig 1995; Gaston 2000; Cardillo 2002).

Where the environment is variable but predictable certain individuals may also show considerable plasticity in their life histories (Levins 1963; Lessells 1991; Gabriel & Lynch 1992; Via *et al.* 1995). This phenotypic plasticity may eventually result in the trait becoming fixed, leading to further life history variation between species or, if further changes in environmental conditions cause a reduction in fitness, reversion back to its original state.

Avian life histories

The diversity of life history strategies in avian systems has achieved more attention than any other group of organisms most likely because of both the relative ease by which birds can be studied and the consistency of their general life cycle (Bennett & Owens 2002). Alongside these there is also great diversity in avian life history traits (see also Bennett 1986; Owens & Bennett 1995; Arnold & Owens 1998) for example, in a sample of 200 species Bennett & Owens (2002) describe size differences of 40000 times, egg weight differences of 6000 times, development times of 25 times and mortality rates of almost five times. Such diversity provides considerable opportunities for exploration of life history variation especially since there are still no wholly supported ecological explanations for the broad diversity in contemporary avian life histories (see Partridge & Harvey 1988; Charnov 1993; Owens & Bennett 1995) - though it is clear that competition and predation/mortality must play significant roles (Lack 1947, 1968; Cole 1954; Martin 1987; Charlesworth 1994).

Much of the recent interest in the variation in life history strategies stems from publication of Lack’s hypotheses (Lack 1947, 1948a, 1948b) relating to clutch size variation in birds. He proposed that clutch size evolved through natural selection such that the maximum number of young may be produced and that the most productive clutch size would also be the most common since it must be the most suitably adapted. This hypothesis was further extended with the suggestion that individual birds phenotypically adjust their clutch sizes according to environmental conditions (Perrins & Moss 1975; Drent & Daan 1980; Högstedt 1980). Numerous studies have failed to find evidence in support Lack’s hypothesis, the majority instead finding that the largest broods were the most productive in terms of the number of young fledged (Perrins 1964; Cavé 1968; Perrins & Moss 1975; Hegner & Wingfield 1987; Tarburton 1987) or alive after a given time (e.g. 3 months, Nur 1984). Brood manipulation experiments (e.g. Parejo & Danchin 2006) have found that although parents are able to increase provisioning rates and successfully raise the experimentally increased brood to fledging there are often intragenerational costs to be borne (e.g. reduced time spent in comfort behaviours (Parejo & Danchin 2006), and reduced condition of adults(Lessells 1986), or the reduced likelihood of laying a second clutch (Sanz & Tinbergen 1999)). Numerous studies have since shown both positive (Tinbergen 1987; Moreno et al. 1995; Jacobsen et al. 1995; Fargallo & Merino 1999; Roulin et al. 1999; Sanz & Tinbergen 1999; Tinbergen & Both 1999; Klemp 2000; Rytkönen & Orell 2001; Hõrak 2003) and negative or non-existent (Harris 1966; Boyce & Perrins 1987; Korpimäki 1988; Orell & Koivula 1988; Røskaft 1985; Verhulst 1995; Roulin et al. 1999; Klemp 2000) relationships between parental effort (clutch size) and inter-generational costs (e.g. offspring recruitment rate, quality or future fitness) and it is therefore still unclear as to the extent of any effect. It is perhaps likely that other costs such as the incidence of non-breeding or the timing and duration of moult may play important roles, however these have yet to be extensively investigated. The failure to breed in any particular season (or during any available nesting period for species having multiple broods) represents a considerable loss, in particular for short-lived species, and the 'decision' to disperse or migrate instead may be a result of costs incurred from previous attempts.

Tropical versus temperate life histories

Of particular interest in contemporary avian life history studies is the apparent 'slow-fast' continuum between tropical and north temperate bird species (i.e. low reproductive rates and high adult survival in tropical species compared with high investment in reproduction and low survival in temperate species), which is thought to arise because of differential environmental constraints operating in the two areas. (e.g. Ekman & Askenmo 1986; Bennett & Harvey 1988; Saether 1988; Martin 1995, 1996, McGregor 2005). Birds in the tropics have been found to have small clutch sizes compared to phylogenetically similar species occurring in north temperate areas (e.g. Moreau 1944; Woinarski 1985; Yom-Tov 1987; Rowley & Russell 1991; Young 1994; Willson et al. 1996). A number of theories have been proposed to account for this striking difference: higher levels of nest predation (Skutch 1949; Lima 1987), renesting capability (Lack & Moreau 1965; Karr *et al.* 1990; Rowley *et al.* 1991), aseasonality of tropical climates (Ashmole 1963b; Cody 1966; MacArthur 1972), food limitation (Lack 1948b; Orell 1983; Järvinen 1989), and higher adult survival / lower predation rates (Curio 1988; Dale *et al.* 1996; Sandercock *et al.* 2000).

Nest predation and renesting capability

It is unlikely that either nest predation or renesting capability play significant roles in the differences between the life histories of tropical and temperate species. There is a lack of consistent variation between nest predation rates at different latitudes (Skutch 1985; Martin 1996) and a number of studies (e.g. Skutch 1949; Snow & Snow 1963) have shown that tropical species still have smaller clutches when compared with temperate species that suffer similar levels of nest predation. Rather, reduced provisioning rates in tropical species (one of the supposed links with nest predation) may be more an attempt to reduce adult mortality than to counter the threat of increased nest predation (Ghalambor & Martin 2001). Similarly, increased renesting capability in tropical species cannot account for the variation in clutch size because many north temperate species (of families such as the Turdidae, Fringillidae and Emberizinae) are recorded to produce similar numbers of broods (2-3) and make similar numbers of renesting attempts (4-5) yet still maintain higher clutch sizes and shorter nesting periods (Martin 1995).

Aseasonality of the climate

Reduced seasonality in tropical areas is thought to allow populations to stay near carrying capacity, creates habitat limitation and therefore greater competition (Ashmole 1963a; Cody 1966; MacArthur 1972). Populations near carrying capacity may favour higher adult survival particularly as reproductive effort is decreased through smaller clutch sizes (Cody 1966; MacArthur & Wilson 1967; Pianka 1970, 1972; MacArthur 1972). Similarly, allowing longer development times for offspring may permit enhanced development of the immune system thereby increasing juvenile and adult survival probabilities

(Ricklefs 1992). Since tropical species face higher exposure to parasites than temperate counterparts (Moller & Erritzoe 1996; Moller et al. 2001) this lengthened development period may have considerable fitness benefits. This theory has since been contradicted (Palacios & Martin 2006) by studies showing a decreased immune response from species with increased development time – possibly as a result of retarded development of immune systems through prolonged time spent at sub-optimal temperatures (from reduced nest attentiveness). Longer development time therefore appears to be a result of other factors (e.g. reduced attentiveness and provisioning) rather than a selected response to increase fitness.

Food limitation

If food is more difficult to obtain in the tropics then both smaller clutch sizes and increased offspring development times may result (Lack 1948b; Dyrcz 1974; Ricklefs 1976; Boag 1987). A number of factors such as reduced seasonality and increased prey diversity (Ashmole 1963b; Cody 1966; Thiollay 1988), reduced available foraging time (e.g. because of rain - Willis 1967; Skutch 1985), and increased competition (Ashmole 1963a; Cody 1966; Ricklefs 1980) may cause food to be limiting in tropical areas. There is still disagreement whether food is limiting in the tropics and if so, the extent to which it influences avian life histories (Skutch 1949; Dittami & Gwinner 1985; Thiollay 1988; König & Gwinner 1995). Until the relative quantities of food being delivered to young have been assessed determination of the extent of food limitation will remain difficult.

Increased adult survival/reduced predation

Increased adult survival resulting from reduced reproductive effort may be sufficient to compensate for the low reproductive rates of many tropical species. Furthermore, lower extrinsic adult mortality should select for lower effort and lower risk-taking (for themselves) in tropical areas since the fitness benefits of their avoiding predation (and being able to renest) far outweigh those of withholding parental care (Curio 1988; Charlesworth 1994; Dale et al.

1996; Williams 1966b; Martin 2002). This mechanism would also help to explain smaller clutches, lower nest attentiveness, longer incubation periods, higher adult survival and increased incidence of co-operative breeding compared with northern regions (Rowley & Russell 1991; Arnold & Owens 1999; Martin *et al.* 2000; Sandercock et al. 2000; Ghalambor & Martin 2001; Sanz 2001; Martin 2002).

Most studies of tropical bird mortality have 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, but see Karr *et al.* 1990). Despite these elevated rates McGregor (2005) found that survival rates in West African passerines (compared with neotropical and north temperate species) were insufficiently high to compensate for low reproductive effort. His data also suggested that neither nest predation nor number of broods per year could account for smaller clutch sizes. Perhaps a more likely mechanism compensating for the small clutch size in tropical birds is the combined effect of both elevated adult and juvenile survival (possibly as a result of extended parental care).

The reason for higher survival rates in tropical birds is still subject to debate but may indicate reduced seasonal starvation and predation risk (Rogers & Heath-Coss 2003; Brandt & Cresswell 2009). Because of their extrinsic nature, both of these factors can be effectively decoupled from the covarying traits listed above and may themselves prove to be the most significant drivers behind the tropical system. Alongside the reduced mortality of adults in tropical areas, elevated levels of post-fledging survival compared to those of temperate species, would also help compensate for small clutch sizes. More focus on determining the causes of both extrinsic and intrinsic mortality and measuring first-year survival are necessary before further advances in understanding the differences in life history traits can be made (Martin 2004).

The role of moult in the life histories of birds

Although many factors have been discussed above relating to the impact of various life history traits, one factor frequently excluded from such studies, particularly for passerines, is the influence of moult (Langston & Rohwer 1996; Rohwer 1999; Filardi & Rohwer 2001). Wear and abrasion of feathers along with damage by UV exposure, fungi, bacteria and ectoparasites means that feathers show a decreasing functional effectiveness with time and may occasionally also become irreparably damaged or lost. Efficient maintenance and replacement is therefore imperative and can be achieved either through comfort behaviours (e.g. preening, anting, dust-bathing) or moult.

Moult represents perhaps the single highest cost of maintenance for birds and requires a major allocation of resources. Complete replacement and maintenance of full functionality of the plumage is generally a lengthy process. This is not surprising given the physiological demands required to adjust metabolism (i.e. switch from protein to amino acid metabolism (Murphy et al. 1990; Murphy & King 1991) and double basal metabolic rate (Lindström *et al.* 1993)), increase peripheral blood flow (Dietz et al. 1992)) and meet the increased energetic requirements (Murphy & King 1992). Loss of feathers also affects thermoregulation through reduced insulation (Lustick 1970; Pohl 1971; Dietz et al. 1992; Lind 2001) and greater heat loss through increased blood flow near the surface of the skin (King 1980). Alongside these are the numerous ecological consequences that must be overcome (e.g. reduced manoeuvrability which results in increased predation risk and reduced foraging capability (e.g. Pennycuick 1989; Chai 1997; Chai & Dudley 1999). Such impacts generally result in modifications to behaviour such that individuals become quieter and more skulking (e.g. Newton 1966; Haukioja 1971). The costs of moult must therefore be balanced against other aspects of a bird’s life and considerable potential exists for the timing, frequency and duration of moult to have a major influence on other life history traits.

To fit efficiently into the life of a bird the moult strategy must balance a number of important considerations – how quickly do the feathers degrade and how significantly is flight affected? Which feathers should be replaced? How much energy is there available for feather replacement (and therefore how quickly can moult occur)? When is the most suitable time to moult (without impinging on other activities e.g. breeding or migrating, or during times of food stress)? How quickly should moult be undertaken? (Franklin et al. 1999). The identification of the most suitable time to moult must therefore be traded off with other significant life history processes (Hemborg et al. 2001) as the energetic costs of simultaneously moulting and breeding/migrating are considered too great in many cases (e.g. Payne 1972; Ricklefs 1974).

In most north temperate resident passerine species moult generally occurs during distinct and predictable periods each year during a window between other significant life history processes (usually a complete moult immediately after nesting (Dwight 1900, Pyle et al. 1987; Mulvihill & Rimmer 1997). Most studies of tropical species have shown that moult here tends to occur over much longer periods, possibly as a result of a less predictable climate (e.g. Stresemann & Stresemann 1966; Bloesch et al. 1977; Sutter 1980; Edelstam 1984; Zann 1985). As a result greater overlap with other significant life history events (such as breeding) is reported in tropical species (Fogden 1972; Payne 1972; Foster 1974; Britton 1978; Wilkinson 1983). Tropical species are recorded to interrupt moult more readily than temperate species in order to accommodate the unpredictable timing of breeding opportunities (e.g. Snow 1966; Keast 1968; Serventy 1971; Zann 1985; Thompson 1988) often resulting in significant differences in the timing of moult of individuals within a species (e.g. Oschadleus & Underhill 2006. In tropical areas where climate is marked by well-defined ‘seasons’ birds seem more prone to adopt a more regular, synchronised and well-timed moult (e.g. Dowsett & Dowsett-Lemaire 1984).

The timing of moult appears to be partly controllable by the individual (Dhondt & Smith 1980; Morton & Morton 1990) with fine-tuning occurring as a result of perceived future environmental conditions such as food availability, temperature, social cues and factors which influence moult once it has started (e.g. poor weather) (Palmer 1972; Payne 1972; Hahn et al. 1992). Recent work by Dawson (2005) however suggests that prolactin secretion controls the instigation of moult. Photoperiodicity is known to control prolactin secretion, however breeding activity also serves to enhance this and this may provide a means by which moult can be timed to coincide as near as possible with the end of breeding in temperate species. Hemborg et al. (1999) suggests that delayed moult may be one of the mechanisms regulating investment in reproduction in birds. The physiological mechanism for over-riding this and allowing for the moult-breeding overlap (often seen in tropical species) is yet to be determined. In general then, it is as important for tropical species to carefully schedule moult such that fitness is not compromised as it is for temperate species (Hemborg *et al.* 2001) and the seemingly more variable nature of moult in tropical species may reflect the reduced predictability of tropical environments.

This study

Considerable diversity in avian life history strategies exists along with an ever-expanding literature relating to possible theories and interrelationships between the various traits. In spite of this, relatively few empirical studies have yet been undertaken in tropical areas, and particularly in Africa, to fully examine the tropical-temperate ‘slow-fast’ paradigm, assess its validity and determine whether or not it is actually a result of differing patterns of environmental constraint and consequent patterns of natural selection. Potential key factors such as the role of age-related mortality, the interspecific variations in timing of moult and its possible influence on the scheduling and energetics of breeding, and potential differences in predation rates between geographical areas, have yet to be thoroughly evaluated from field data (Felsenstein 1985; Harvey & Pagel 1991; Martin & Li 1992; Martin 1995; Martin & Clobert 1996). Alongside this, the work by Karr *et al.* (1990), which raised doubts about the validity of the assumption of higher survival in tropical species, also implies that the assumption of higher survival in tropical areas itself needs further consideration. The overall aims of this study were therefore to produce empirical data on the important life history processes of tropical bird species and use these to assess how these relate to one another in a seasonal tropical environment.

It is important to consider phylogeny of species before interpreting comparisons of data between species, and between groups of species between regions. Common ancestry may result in species sharing life history traits thereby making assumptions of statistical independence of species in data analyses invalid (Harvey & Pagel 1991). Previous analyses by McGregor (2004) (using Phylogenetically Independent Contrasts on species common to this study) however, revealed no significant relationships between life history traits and the comparisons of life history data between species were performed with this in mind.

In assessing the relationships between life history traits I also examine the extent to which various life history parameters vary within and between trophic guilds (i.e. the grouping of species according to diet and foraging method). Given that food limitation is hypothesised to be an important factor in determining life history traits and their variation between tropical and temperate areas (e.g. Skutch 1949, Konig & Gwinner 1995), then assessment of life history characteristics by trophic guilds may provide a useful insight into any differences that exist between species. A number of studies have shown strong divisions and variation in timing of aspects of reproduction and moult between different trophic guilds (e.g. Skutch 1950, Snow & Snow 1964, McGregor 2005) whereas others have identified either limited or no relationship (e.g. Marini & Duraes 2001). Assessment of life history characteristics according to guild membership may therefore also permit improved interpretation of the relevant importance of environmental variation (e.g. rainfall and subsequent water availability linked to seed availability and digestibility, (Ward 1965) and insect emergence (Wolda 1977)) in tropical species.

Study area

The fieldwork for this study was undertaken in the savannahs of Nigeria in tropical West Africa. These lie midway along a gradient in vegetative cover from the dense rainforested areas in the south to the open grasslands and deserts in the north. This latitudinal change in vegetation is strongly linked to the effects of the Inter-Tropical Convergence Zone (ITCZ), a seasonally fluctuating zone of low pressure formed by the meeting of winds from high-pressure belts to the north and south. During the northern summer (between late April and September) the ITCZ is centred to the north of the equator and the climate of the region is then dominated by moisture-laden southwesterly winds resulting in a rainy season. With the sun tracking south of the equator from October onwards, the low pressure of the ITCZ draws northeasterly winds from across the Sahara (Jones 1998). These winds, known as Harmattan, are hot, dry and dusty, and result in a dry season. Across the region rainfall decreases with latitude and the dry season varies in duration from 3 months in the south to almost seven in the north. Significant annual variation in duration, extent and distribution of rainfall are common in the north and in upland areas such as the Jos Plateau, in central Nigeria.

The primary study site for this work was located at the 120 hectare Amurum Community Forest Reserve on the Jos Plateau (9.87^{o}N 8.98^{o}E), approximately 12km from the city of Jos. Although centred in the savannah zone, the study area is slightly atypical of the habitat at similar latitudes in the remainder of Nigeria because of its altitude. Lying at around 1300m, the plateau receives more rainfall than areas of similar latitudes in the rest of the country and as a consequence has a shorter dry season (3-4 months) and greater range of habitats (isolated relict forests fragments are present alongside savannahs) (Elgood *et al.* 1994).

Figure 1. Location of the four study sites (Amurum, Gwafan, Pankshin and Yankari) within Nigeria

The habitat at Amurum was characterised by patches of scrub savannah, gallery forests, rocky outcrops (inselbergs) and mixed farmland. Although subject to degradation, the site still contains areas of climax vegetation typical of the Guinea savannah zone with small patches of 13-17m high broadleaved woodlands and gallery forests (of *Brachystegia eurycoma*, *Parkia biglobosa*, *Vitellaria paradoxa*, *Terminalia* spp.). The majority of the site however is dominated by lower growing scrub of *Combretum* spp. occasional *Acacia* spp. and large areas of grasslands dominated by species such as *Andropogon* spp. and *Hyparrhenia* spp. (White 1983; Elgood *et al.* 1994). As with elsewhere in Nigeria (Geomatics International 1998), the habitat at Amurum has changed during the course of the study primarily as a result of a growing local human population. Unofficial settlement has resulted in increasing encroachment of small arable farms and high levels of cattle and goat grazing around the periphery of the reserve. A similar increase in the rate of loss of standing timber through fuelwood collection has also occurred along with the more frequent setting of illegal fires. A number of community outreach programmes and initiatives aimed at reinstating areas of habitat (through the transplanting of nursery trees) have been instigated however and it is hoped that the rate of degradation can be slowed.

Figure 2. View west across Amurum Community Forest Reserve showing the progressive decline in habitat quality beyond the reserve boundary.

This habitat degradation is especially noticeable along the boundaries of the Reserve with the savannah giving way to more open and heavily degraded grazing and arable land. Outside of the reserve the habitat more closely resembles plains grassland. Here there is a much lower mean vegetation height and fewer bushes and trees (generally restricted to mango orchards, plantations of non-native species such as *Eucalyptus* and much smaller patches of remnant gallery forest). The contrast in habitat quality on-site with that of surrounding areas may therefore result in the reserve acting as an island, potentially resulting in reduced dispersal and increased site fidelity. Such characteristics may enhance any assessments of annual survival.

Despite the anthropogenic influences operating at the study site, bird diversity remains high and around 280 species have been recorded within the study site. The seasonal variation of the climate results in seasonal peaks in vegetative growth (de Bie *et al.* 1998; Osborne 2000), flowering of plants (usually through the rainy season) (Bourliere & Hadley 1970) and a consequent seasonality in food abundance. As a result, the bird species composition at the site is also seasonally variable and the large number of resident species (196) are supplemented by up to 46 migrant Palearctic species between September and May, and a further 38 species of intra-African migrants at other times of the year. And, as noted by McGregor (2005), it is precisely this climatic variation and species diversity which makes this an ideal location to examine the life history of birds in tropical seasonal environments.

Data from two other sites in Plateau state (Gwafan, Jos - N 09° 52’, E 08° 58’, and Pankshin - N 09° 20’, E 09° 26’) and one from the neighbouring state of Bauchi (at Yankari Game Park - N 09° 45’, E 10° 30’) were also used in this study. The habitat in all three of these additional sites is structurally similar to that of Amurum (Gwafan and Pankshin are more degraded) although Yankari comprises Sudan, rather than Guinea, savannah and therefore has some differences in floral composition. Yankari has also benefited from longer periods of protection and the habitat quality is therefore markedly better than the other three sites used in this study.

Aims of this study and hypotheses to be tested

1. Assessment of timing and duration of moult

The replacement of feathers is a costly process both physiologically (Payne 1972; King 1981) and behaviourally (Swaddle & Witter 1997) and the sequence of feather replacement, its scheduling, and the time-taken for its completion, will all impact upon other life history traits, such as breeding and long-term survival (Langston & Rohwer 1996). Because of the apparently reduced contrast between seasons in tropical areas it is expected that birds in such areas are less constrained to moult during specific periods and are more opportunistic, fitting moult around other aspects of the annual cycle. As yet however, there are comparatively few studies of how tropical species manage the scheduling of feather replacement alongside other life history activities or more particularly, how the choices made in timing of moult impact upon the success of these other activities. We investigate the characteristics of moult in a selection of common West African bird species in Chapter two and used these results (in Chapter six) to examine the relationships between different life history traits in tropical species. The hypotheses tested were:

1. That sequence of moult in the wing and tail feathers will be similar between tropical and temperate species.

2. Reduced seasonal constraints should result in tropical species taking longer to complete moult than similar temperate species.

3. Reduced seasonality in tropical areas should lead to timing and duration of moult being variable and unpredictable between individuals and years.

4. Because larger feathers take longer to produce, speed of moult will be determined by size and taxonomy.

2. Assessment of the scheduling and duration of breeding periods

As arguably the most important of all life history traits, the need for an individual to determine the optimal time to breed is essential if the attempt is to be successful. Timing of breeding in temperate areas is strictly regulated by a strongly seasonal climate (Murton & Westwood 1977; Stutchbury & Morton 2001) and most authors have found this also to be the case for species in the tropics (Skutch 1950; Snow & Snow 1964; Fogden 1972; Dowsett 1985). Despite this, the scheduling of activities by animals in the tropics and the methods by which this is achieved is still poorly understood (Gwinner & Dittami 1985; Bronson 1987; Wingfield *et al.* 1992; Hau 2001) although food availability is believed to be the main factor (Moreau 1950; Snow & Snow 1964; Stiles 1980; Poulin *et al.* 1992), mediated by a seasonal variation in rainfall (Leigh *et al.* 1996). We examine the timing and duration of breeding birds in West African birds in Chapter three with the aim of relating this to the scheduling of other life history traits (Chapter six).

The aims of chapter three were therefore to:

1. Produce baseline data on the timing and duration of breeding of a range of common West African bird species.

2. Compare our estimates with those of previously published data for tropical savannah bird species.

We also tested the hypotheses that:

1. The occurrence of juveniles and immatures in mist net samples provides a suitable means of assessing timing and duration of breeding.

2. Timing of breeding is not seasonal.

3. There is no difference in timing of breeding between different guilds and families.

3. Empirical measures of survival

Annual survival of adult tropical species has long been considered to be much higher than that for similar north temperate species (e.g. Rowley & Russell 1991; Faaborg & Arendt 1995; Johnston *et al.* 1997; Martin 2004). Indeed this, alongside a latitudinal difference in clutch size, prompted much of the early discussion and theorising about avian life history evolution (Moreau 1944; Lack 1948b; Skutch 1949; Partridge & Harvey 1988; Martin 2004). Although an increasing number of studies have supplemented our knowledge of survival in tropical species, relatively few of these have been carried out in afrotropical regions (e.g. Yom-Tov *et al.* 1994; Peach *et al.* 2001; McGregor *et al.* 2007). Only when reliable estimates from a range of tropical systems are available will meaningful comparisons between tropical and temperate systems be possible. Recent work by McGregor *et al.* (2007) supplemented our knowledge of survival in African birds with the aid of models incorporating resightings but, whilst useful, many of the estimates derived were affected by small sample sizes. We used similar techniques to those employed by McGregor *et al.* (2007) to generate estimates for a greater range of species for both adult and juveniles. In chapter three our aims were therefore to:

1. Update and improve the accuracy of the survival estimates previously generated in this study area with a further four years' worth of data.

2. Produce preliminary estimates of juvenile survival and compare these with adult rates.

3. Compare our estimates with other published data for tropical species.

4. Assessment of current mark-recapture approaches

The use of survival estimates in the study of variation in life history traits is only of value if the derived estimates are reasonably robust. Our study centres on the use of a long-running dataset (now in its ninth year) generated according to a fixed protocol. Because we encountered problems in applying the modelling approach used in earlier analyses of data from this site (McGregor *et al*. 2007) we adopted an alternative, less parameterised approach. In chapter four we assess the validity of this approach, performing a quantitative appraisal comparing the two approaches. We also attempt to identify the reasons behind the difficulties encountered in applying the original approach to our larger dataset, and discuss the potential for improving the field methodology. The aims of this chapter therefore, were to:

1. Identify the key factors and optimum characteristics in applying survival rate analysis to CES data from a methodological perspective, with regard to:
    a. Variable catch rates
    b. Trap shyness, and
    c. Resighting rates

2. Identify the key factors affecting the analytical approaches in applying survival rate analysis techniques to CES data, addressing in particular:
    a. Goodness of fit of models
    b. Reduction in parameters
    c. Model selection
    d. Identification of biologically realistic models, and
    e. Overall recapture rates.

These general results were then applied to the long running ringing scheme that is the basis of this study to create recommendations to improve the methodology of the study so that future years' efforts could be carried out more efficiently to improve our estimates of survival rate.

5. Interrelationships between moult, breeding and survival

The life cycles of birds broadly consist of three key activities, those associated with reproduction, maintenance of condition, or the avoidance of predation or starvation. Life history theory however predicts that it is not possible to maximise fitness in all of these activities since investment in one results in reduced availability of resources for the others. The higher predictability of tropical environments is believed to result in individuals having reduced mortality than temperate species and therefore investing less in current reproduction. In chapter six we used our empirically derived estimates to examine the potential trade-offs between moult, breeding and survival in savannah birds, specifically:

1. Breeding period timing and duration
2. Moult duration, timing and variability in timing
3. Overlap of moult and breeding
4. Duration of the immature plumage phase
5. Adult and juvenile survival

The results of the testing of the covariation between these life history traits were then used to test a general prediction of life history theory:

6. that investment in clutch size, duration of breeding, moult or the immature phase covaries with adult survival

Chapter 6 therefore links the different measure of life history covered in this study and finishes with a discussion of the general implications of my findings to life history theory

Chapter 2: Timing, duration and variability of moult in tropical savannah birds

Summary

The annual scheduling of the replacement of flight feathers, and the length of time it takes, is generally well defined and predictable in resident, temperate bird species. In most cases, moult starts towards the end of the breeding season and must be completed before impending deterioration in local environmental conditions. This results in a moult duration (in smaller species) of <100 days and is usually finished in time to allow diversion of resources for improving body condition. In a tropical environment with reduced seasonality, these temporal constraints may be less severe allowing for an increase in the variation in order, timing and duration of moult.

I investigated the patterns of moult in a range of tropical African birds in order to make general comparisons with those of temperate species. All 44 of the species assessed followed the same basic order of moult through the flight feathers as seen for temperate species. The level of coincidental moult between wing feather tracts was much higher for tropical species, with up to five tracts moulting simultaneously in some species. This was considered to be a result of the length of time taken to complete moult, which averaged 131 ± 11 days across the 29 species assessed here and overall ranged from one to nine months.

Active remex moult was recorded in all months of the year highlighting the reduction in constraints for tropical species. Although the level of synchrony was high for certain groups (Ploceidae), timing of moult varied widely, both within and between species. In general, peak occurrence of moult occurred shortly after the peak time of breeding for many species (late rainy season). No broad differences in timing of moulting were identified across guilds

although insectivores moulted proportionally more in the wet season than granivores.

Overall this study has demonstrated the impact of reduced climate variability on the moult characteristics of birds in tropical areas. The results are discussed in the light of this difference from temperate species and the possible relationships between moult and other life history traits are examined.

Introduction

The replacement of feathers (moult) is a costly process with short-term thermoregulatory expense (Payne 1972), increased energy metabolism (King 1981; Lindström *et al.* 1993) and reduced flight performance (Swaddle & Witter 1997), balanced against future thermoregulation, signalling and flight performance gains. The timing of feather replacement and the length of time taken will also impact upon other essential processes (Langston & Rohwer 1996) unless it is efficiently incorporated within an annual schedule. This is especially important in temperate regions because of the strong seasonality of the climate (e.g. Cresswell & McCleery 2003; Crick 2004; Reed *et al.* 2006). In response, and because of the energetic costs associated with replacing feathers (Payne 1972; King 1981; Lindström *et al.* 1993), the replacement of feathers by individuals in temperate areas is generally scheduled to occur at the same time each year (Svensson & Hedenstrom 1999) such that there is minimal overlap with breeding (Payne 1969), migration (Holmgren & Hedenstrom 1995; Yuri & Rohwer 1997), autumnal territory defence and food storage (Jenni & Winkler 1994) or over-wintering (Barta *et al.* 2006). Although some annual variation will inevitably occur (due to differing weather conditions, timing of breeding and success), the time-constrained calendars of most temperate species will result in predictable and well-defined patterns of moult.

In contrast, moult strategies of tropical species are often considered more variable than those in temperate areas and less constrained by seasonal routine (Barta *et al.* 2006). As a result, tropical species have been found to have an array of supplemental moults not often found in temperate species (e.g. Miller 1961; Craig 1983; Brooke 1985; Herremans 2006). Further, and aside from the differences between species, there is also often assumed to be great variation and reduced synchrony in timing, duration and extent of moult the between individuals and populations in tropical areas (Jenni & Winkler 1994).

In this study I investigate the differences in moult characteristics between tropical and temperate species after first describing the characteristics of moult in a range of tropical African bird species. There have been comparatively few studies of moult in tropical birds in a life history context, despite it being an important component of avian life histories (Stiles & Wolf 1974 ; Tidemann & Woinarski 1994; Marini & Durães 2001; Pierce 2009), and even fewer for African resident birds (Payne 1969; Wilkinson 1983 ;Klaassen 1995; Oschadleus 2005; McGregor *et al.* 2007a). Therefore even basic descriptions of moult characteristics and phenology are needed to further our understanding of how seasonality and latitude constrains moult in birds. In this study I focussed on four specific hypotheses:

1. ***The sequence of moult in the wing and tail feathers will be similar in tropical and temperate species***. Since the sequence of moult has evolved in order to limit the impact of feather loss on aerial ability (Ginn & Melville 1983; Pennycuick 1975; Swaddle *et al.* 1996; Swaddle & Witter 1997), the requirement to maintain reasonable or good flight performance at all times of the year will result in the sequence of moult being the same for both temperate and tropical birds, i.e. for the remiges, Primaries → Secondaries → Tertials (= Inner Secondaries) and in the coverts, Primary Coverts → Greater Coverts → Carpal covert → Median Coverts → Alula.

2. ***Tropical species should take longer to complete moult than similar north temperate species***. The degree of seasonality in north temperate areas is more strongly defined than in most tropical areas (especially when considering the variation in daylight hours and temperature through the year). As a result, passerine species in north temperate areas are very strongly seasonal and predictable in their breeding and moulting periods. This seasonal constraint and the need to undertake a range of important behaviours (territory establishment and defence, breeding, moulting and preparation for harsh weather/migration) within an annual cycle is reflected in a comparatively short moult duration. Also, since birds induced to moult more rapidly produce feathers of reduced quality (Dawson 1998; Dawson *et al.* 2000) there must be an optimal duration of moult for each species in certain conditions to optimise the trade-off between feather quality, flight capability and clutch size/duration of breeding (e.g. Bensch *et al.* 1985; Jenni & Winkler 1994). If birds are adapted to the seasonal constraints operating in an environment then this should result in a reasonably stable moult strategy linked to that predictable seasonality. In comparison, tropical species generally have smaller clutch sizes and do not necessarily breed each year (Skutch 1949), which, because of the reduced definition in seasonality means that a greater period of time is available for the moult.

3. ***Pronounced seasonality should lead to a predictable pattern of timing and duration of moult for a species.*** Although seasonality is present in West Africa it is not as clearly defined as in temperate areas. I therefore predicted that timing of moult in tropical species would vary in a manner similar to that for moult duration.

4. ***Moult speed will be determined by size and taxonomy.*** The feather mass of larger and non-passerine species is, in most cases, much greater that of most passerines (Baker 1993; del Hoyo *et al.* 1994; Pyle 2006). Because the physiological processes necessary for feather production are energetically demanding (Walsberg 1983a; Walsberg

1983b) it follows that larger feathers take longer to produce than smaller feathers (Rohwer 1999). I therefore predicted that tropical species would show a similar relationship between size and moult duration as seen in temperate species (Ginn & Melville 1983; Jenni & Winkler 1994) and that moult duration in tropical non-passerines should be longer than passerines.

Methods

Field Methods

This study was conducted primarily in the Amurum Community Forest Reserve, near Jos (09° 52’N, 08° 58’E), and Yankari State Park (09°45’N, 10°30’E), near Bauchi, both in central Nigeria, between 2001 and 2008. Additional, much smaller, datasets are also available and included from mist-netting operations in Gwafan, Jos and Pankshin (both, Plateau State). The habitat at all sites consists primarily of savannah with smaller areas of riverine woodland and gallery forest. Continuous operation of nets (i.e. nets being opened in order to catch birds) over the course of several hours during one day, are referred to here as ringing ‘sessions’ and, where several of these occurred over consecutive days, these groups of sessions are referred to as ‘periods’. Nets were operated at Amurum in all months between November 2001 and May 2008 except for June and December 2003, June-August 2004, and July 2007. One final capture period was also made here in October 2008. Catches were made at Yankari in September and April 2006, February, April and October in 2007 and January, February and March in 2008.

Capture methods

Two capture approaches were used during the course of the study, one (the CES method) following an existing protocol operating at the Amurum Community Forest Reserve since 2001 and aimed at standardising capture effort, and the second (the ad hoc approach) aimed at generating larger datasets for more widespread analyses of data for more species.

The CES method

This approach was performed at Amurum study site only. This method required the use of a standard number and length of mist netting with nets placed in specific set locations in one area of the Reserve for 14 consecutive days usually during two periods each year - during the 'Spring' (February-April) and 'Autumn' (October-December). Between 2001-2004 a third session was often included operating between June and September each year. Locations of mist nets remained the same for all capture sessions and periods. Initially, 14 four-panel mist nets totalling 187m were used, however this was increased to 20 nets (270m) in 2006 in an effort to both improve species diversity and numbers of recaptures. The nets were opened daily between dawn (usually around 06:00) and 10:30am each day, occasionally being closed earlier if weather conditions posed a risk to the welfare of birds in the net. Nets were checked every 20 minutes in order to reduce the chances of heat stress to individual birds. On occasions where rain or very strong winds prevented catching, the CES period was increased to account for lost days.

During the period of this study, the majority of the CES periods and associated data collection, were performed by two researchers (McGregor 2001-2004 and Stevens 2006-2009). During the intervening 18-month period, a further three persons operated the CES sessions.

Ad hoc method

Aside from the standardised protocol operating for the CES, mist nets were erected and operated at numerous other locations (outside of the CES capture area and capture periods) around the Amurum Reserve during the course of this study. These ringing periods usually involved the use of 100-200m of mist net and lasted 5-10 days. *Ad hoc* ringing periods were also operated throughout the year across the other three study sites. Nets were opened mostly during the period between 06:00 – 10:30, however supplementary catches were also occasionally made between 16:00 –19:00 (dusk). Locations for these *ad hoc* sessions were rotated to improve coverage of the primary site. Data generated from these sessions is useful in terms of increasing the number of recaptures and resightings and provides for an improved diversity of species included within the study.

The majority of the data generated under the *ad hoc* approach and included within this study was generated by two people (myself and McGregor) however, data from a further six people were included in the analyses. These additional data were assessed before inclusion in order to identify obvious errors or discrepancies.

Data collection

Ageing

Where possible, all birds caught were aged and sexed (according to plumage characteristics and biometrics), fitted with uniquely numbered metal rings, and had the moult status of remiges and rectrices assessed. Because the lifecycles of tropical birds rarely follow a standard annual calendar (i.e. breeding does not necessarily fall during the middle of the calendar year), it was not possible to reliably apply the methods used in temperate systems for coding age of individuals (Redfern & Clark 2001). Age was therefore assessed according to plumage characteristics Five age categories were identified: 1 – pullus; 2 – unknown or indeterminate; 3 – full juvenile plumage; 4 – full adult plumage; 5 – immature plumage. Juveniles were determined as those individuals carrying their first plumage, i.e. that grown whilst in the nest. Certain species have juvenile plumage that is markedly different from that of the adult (e.g. *C.senegalensis, C.venustus* and *P.chrysoconus*) and determination of age category for these was straightforward. For others however, assessment was based on a variety of other characteristics including general feather structure (juvenile body feathers tend to be looser textured than adult feathers and have fewer and more widely-spaced barbs (Göhringer 1951)), feather shape (Jenni & Winkler 1994; Svensson 1992), colour of bare parts (e.g. iris (e.g. in many Sturnidae and Ploceidae species (Bannerman 1948)), orbital ring (e.g. in some Sylviidae (Gargallo 1992)), wattles (e.g. in Platysteiridae (Brooke & Manson 1979; Harris & Arnott 1988)), bill colour (e.g. in Prionopidae (Harris & Franklin 2000), the Estrildidae (Mackworth-Praed & Grant 1973) and Hirundinidae (Svensson 1992)) and tarsus and foot colour (e.g. in Sylviidae (Karlsson *et al.* 1988)), and presence of gape (Svensson 1992). Individuals were classified as immatures once any noticeable moult had occurred (even if just one feather), either in the body feathers or as a result of post-juvenile moult of remiges or rectrices. Conversely, adults were identified as those individuals having no trace of juvenile plumage.

Moult assessment

Moult scoring followed the system outlined by Ginn & Melville (1983) where an old feather was scored as a 0, growing and missing feathers scored between 1 and 4, depending upon length, and fully grown, new feathers, scored as 5. Moult score was therefore the sum of the scores for each tract. Occasionally some individuals lost remiges or rectrices as a result of handling. This was accounted for by recording all feathers found with the bird at the net (or in the bird bag) that could be attributed to the individual, and by identifying and noting all gaps in the plumage. Also, as each bird was fitted with a unique metal ring, it was possible to determine whether all unconventional or unusual moults were the result of feathers being lost during previous handling events. Moult of the major wing coverts (median, greater, carpal, alula and primary) was assessed using a simplified system in which feathers were scored either as old (0) or new (5). Missing or growing feathers were recorded as new. This method was used to provide a simple and rapid means of assessing the organisation and pattern of moult in the coverts.

Moult of the contour feathers was assessed by scoring the number of feathers growing in the various pterylae across the body. For body moult, a score of 0 indicated that no growing feathers could be seen on quick examination of the ventral, spinal, or crural tracts, up to 10 growing feathers was represented by a score of 1, 11 to 20 feathers as a 2 and more than 20 as a 3. On the head, scores of 0 – 3 were given when 0, 1-5, 6-20 and more than 20 growing feathers were recorded in any area of the capital tract. In reality a more subjective assessment of body and head moult was performed with the categories 0-3 referring to ‘zero’, ‘few’, ‘many’ and ‘lots/mostly’ of growing feathers, thus allowing for the differences in size between species.

Breeding assessment

Determination of breeding status was performed through examination of cloaca for seasonal enlargement (Svensson 1992) and checking for the presence of brood patches. Here tropical birds were assumed to show a progression of brood patch development similar to that in temperate species and, to prevent misidentification of breeding periods, only those individuals having brood patches defined by fully de-feathered breasts (i.e. stages 2-4 in Redfern (2008)) were considered to be actively engaged in breeding (Hinde 1962).

Other assessment

Other standard morphometrics were taken (wing length (maximum chord), mass, fat and muscle levels) according to British Trust for Ornithology protocols (Redfern & Clark 2001) to provide some measure of the variation in condition of the population at the sites and to further aid ageing and sexing.

Data analysis

Sequence of moult

Species were selected on the basis that they had a minimum of 15 individuals engaged in active moult. To ensure as many species as possible reached this criterion, data from multiple captures of the same individual were used. Although this introduces an element of pseudoreplication into the analyses it was felt that the information gained outweighed the negative statistical effects. 139 of these multiple captures were included, almost half (67) of which were for five species having some of the largest datasets (all >67 records). It is therefore unlikely that significant statistical biases were introduced for the species in the analyses. 44 Afrotropical bird species (40 of which were passerines) of 19 families were therefore assessed for moult sequence (mean = 49.9 individuals per species). The number of feathers moulting in each tract was assessed and the proportion of the tract in moult determined by dividing the observed moult score by the maximum possible moult score for the relevant tract. Sequential pairwise correlations (two-tailed, Pearson) of the proportion of feathers in moult in each of the tracts was used to generate a correlation matrix. This allowed the identification of the general progress of moult through the wing and tail for all species.

Timing and duration of moult

Tropical and larger birds may show an increased tendency to show suspended, arrested moult or *Staffelmauser* in their primaries making determination of the relative ages of feathers more difficult (e.g. Pyle 2006; Symes & Wilson 2008). As interruption and resumption of moult will also result in lengthened estimates of moult duration, individuals that appeared to have more than two generations of flight feathers were omitted from the main analyses. All species for which there were sufficient data for actively moulting birds (i.e. more than 15 cases of Type 3 data in Underhill & Zucchini 1988) to plot moult score against time were included in the analyses. This further reduced the number of species assessed to 29 (4 of which were non-passerines).

Ordinary linear regression of moult score regressed on date, using only actively moulting birds, generally produces incorrect results (Pimm 1976) due to heteroscedasticity (i.e. at the start and end of moult there is less variability in moult score than during the middle period of moult). The regression line produced using this method encompasses the start and end dates of the entire population under study and not the dates for the average individual (Pimm 1976; Summers *et al*. 1983). Changing the dependent variable to date and regressing this against moult score appears to resolve this (Pimm 1976) however, this places constraints on the residuals in the regression model such that they are not identically distributed and do not have a mean of zero (Underhill & Zucchini 1988). This failure to meet the model assumptions will often result in bias in parameter estimates in particular the start date (underestimated) and the duration (overestimated) (Underhill & Zucchini 1988. To counter this, species were selected for inclusion in the analysis on the basis of their having sufficient numbers of type 3 data (i.e. only birds actively moulting). The proportion of primaries in moult (i.e. observed moult score/50) was then plotted against date. In many cases the reference date (start date of the plot) was adjusted so that low moult scores (i.e. the start of moult) occurred at the start of the plot. Where possible this was identified from natural breaks in the data. This ensured that all plots showed a progressive increase in moult score through time and within the 12-month (or shorter) period shown by the plot. Extreme outliers that indicated likely mistakes in scoring were removed. The residuals of these new data were then assessed for normality using a Kolmogorov-Smirnov Goodness of fit test. Where the data breached the assumption of normality the plots were examined for normality within years or other logical capture periods (e.g. a period of catch of a few months when many moulting individuals were caught). If such periods could be identified, then these data were used in the moult regressions. If further, logical, data reduction did not lead to a normal distribution of residuals the species was excluded from analysis. These summary plots used in assessment of linearity are given in Appendix 1. Where sufficient data were available, and the grouped data met Levene's test for equality of error variances ($p > 0.05$), they were then tested for a year effect in timing and duration of moult using a general linear modelling approach. Where a significant year effect could be determined, data were analysed separately for each year. In certain cases, year effects could be attributed to scarcity of data in some years or a large difference in sample sizes between years. Removal of such data often resulted in a reduction or removal in the year effect (e.g. *Cyanomitra verticalis* and *Emberiza tahapisi*). Despite not showing a year effect it was necessary to partition data and calculate separate annual moult durations for certain species (e.g. *Chalcomitra senegalensis*) or to restrict analyses to certain years (e.g. *Estrilda melpoda*) because of significant differences in error variances. Where the regression failed to produce meaningful results (e.g. in *Colius striatus,* probably because of difficulties in scoring moult accurately in this species) or the partitioning of the data between years led to sample sizes too small for analysis (as with *Lagonosticta senegalensis* and *Lybius vieillotti*), the species was removed from the analysis with no moult duration estimate being made. Where no year effect was detected, data were pooled across years.

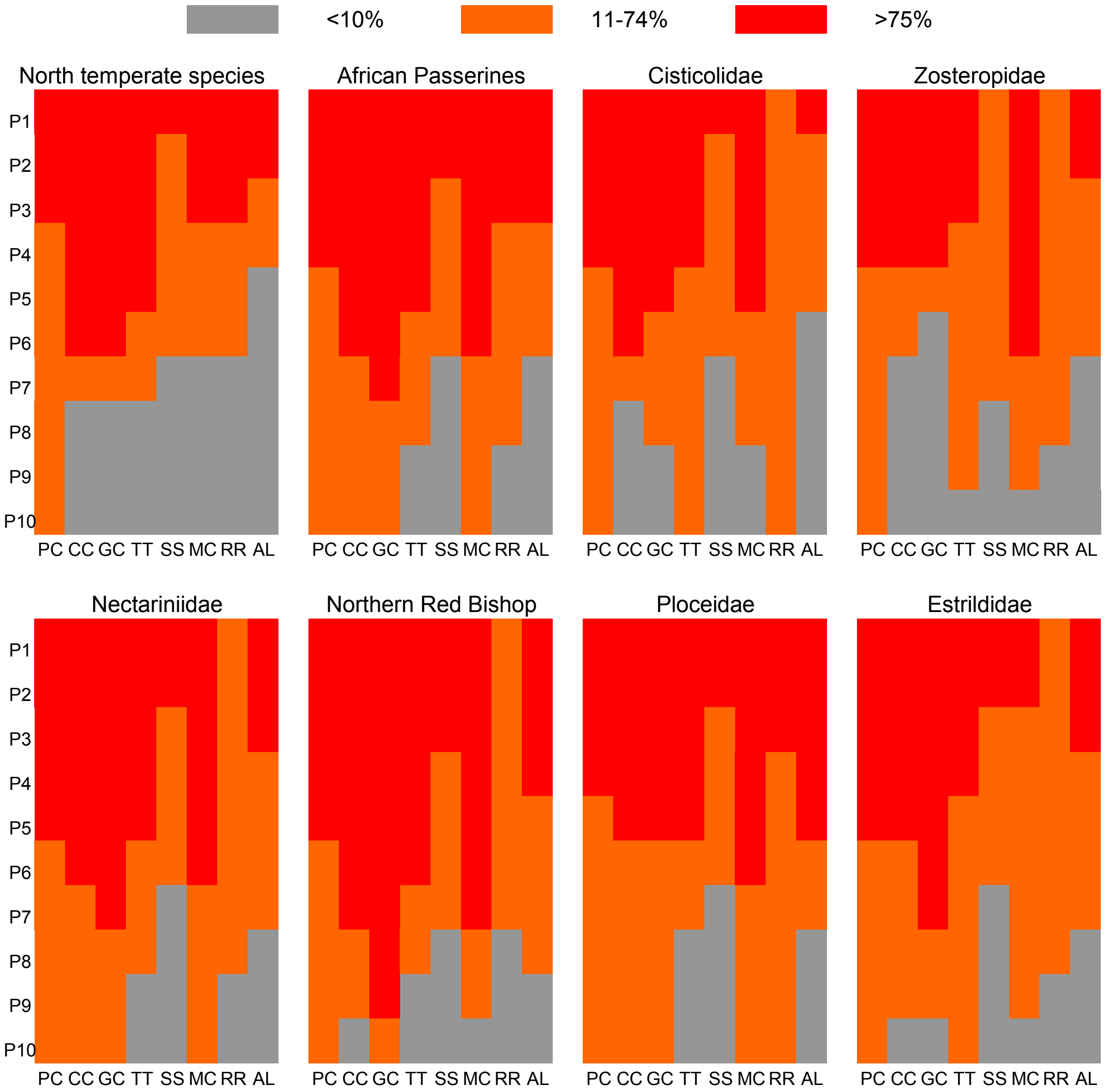
Mean start date of moult was then estimated from the intercept of the regression line with a proportion in primary moult value of 0. The mean date for moult completion was then calculated by adding the mean duration of moult (reported as the coefficient in the regression) to this date. Standard errors of the estimates were determined for all characteristics. Comparisons of moult duration were then made between species, guilds and other groups using t-tests. Relationships between size (mass and wing length) and moult duration were also explored using Pearson correlations and seasonality of moult was compared between species and guilds using Kruskal Wallis and Mann-Whitney tests. All statistical analyses were performed using SPSS 17.0 (*www.spss.com*).

Results

Sequence of moult

Moult of primaries was significantly correlated ($p<0.05$) with moult in all other remiges or rectrices in 93% (41 of 44) of the species assessed here. However, whereas moult in temperate species appears more limited in extent at any one particular time (i.e. few tracts are moulting at the same time) that of tropical African species is more extensive (Figure 1). For example, when P7 is moulting in (the representative) temperate species, moult is often recorded in only four other tracts. In contrast, significant moult is present in 5-8 other tracts in the tropical species during moult of P7. Similarly, the timing of relative moult of feather tracts in tropical species is more variable, e.g. significant moult among the greater and median coverts was recorded to occur any time from the moult of the first primary (P10). In comparison, moult of these tracts in temperate species is generally recorded after the third or fourth primary has already moulted. The apparent linkage between timings of replacement of primaries and the other tracts was apparent for all tracts in all species except for moult of the tail, where only 75% (33 of the 44) species showed a correlation (overlap) in moult.

Figure 1. Sequence of moult in tropical African resident passerine families compared to the typical sequence in a north temperate species (*Passer domesticus*, after Zeidler (1966)). Colours denote the proportion of feather tract actively moulting (or having completed moult) at the same time as the relevant primary. P10 is the innermost primary.



PC - *primary coverts;* CC - *carpal covert;* GC - *greater coverts;* TT - *tertials (3 innermost secondaries);* MC - *median coverts;* RR - *rectrices;* AL - *alula*

In general the basic sequence of adult moult in tropical African passerines is essentially the same as that in north temperate species (Figure 1). Moult generally progressed descendantly through the primaries, with the corresponding overlaying primary covert being moulted at the same time. Moult then started among the greater (*en bloc*), carpal and median coverts (ascendantly) during which time rectrix moult starts (and proceeds centrifugally) and replacement of the tertials occurs, here generally in the same order as in temperate species (shortest to longest - T8, T9, T7). The last tract to start moulting is usually the alula (+ alula covert) though replacement of these three feathers is often completed before the innermost secondaries are fully regrown.

Moult duration

Mean moult duration varied widely both within and between the 29 species assessed here, ranging from less than one month (Mean ± S.E. = 28 ± 16.46 days) in *Prinia subflava*, to almost nine months (270 ± 25.8 days) in *Spermestes cucullata* (Table 1). Overall mean moult duration (i.e. including all species and years) for the 29 species was between four and five months (131.33 ± 10.78 days). This was considerably less than the 170 days mean moult duration for similar species found at the same location by McGregor *et al.* (2007). Ten of the 14 species analysed in both studies differed in moult duration by at least 10%, and five by more than two months (Figure 2). Mean difference in duration estimates between the two studies (incorporating the directional differences) was <1 day (–0.61 ± 21.11 days) as indicated by the similarity of a number of results, in particular those for *Z. senegalensis* and *U. bengalus* (both <6 days difference). However, the mean absolute difference in overall duration was around seven weeks (Mean ± S.E. = 51.89 ± 15.44 days). As with the results of McGregor *et al*. (2007), we found that tropical species take longer (more than 2 months longer) to complete moult compared to similar passerine species in north-temperate areas (based on a mean duration of around 70-80 days for temperate species).

There was little evidence that completion of moult took longer in the larger and non-passerine species compared to passerines (t-test: small v large species, $F = 1.9$, $p = 0.18$ t = 0.6, 26 d.f. $p = 0.54$, two-tailed; passerines v non-passerines, $F = 3.3$, $p = 0.08$, t = 0.7, 26 d.f., $p = 0.52$, two-tailed), indeed, the 84 -138 day range for the three dove species found here was centred on the mean duration for all species combined. The standard error of the estimate for *Streptopelia senegalensis* was large (±108 days), though

Table 1. Mean moult periods for 29 West African bird species identifying start date, end date and duration.) Year indicates the period during which the dates and durations apply and show any significant annual variation. Results of tests for normality (Kolmogorov-Smirnov) and regression statistics are also provided. Bold type indicates significant R^2

Species	Year	Mean duration	SE	Mean Start date	Mean Finish date	SE	K-S Z	K-S. *p*	N	R^2
Streptopelia hypopyrrha	2008	84	33.89	4 Mar	27 May	22.34	1.047	0.223	19	0.221
Streptopelia senegalensis	2008	138	102.4	14 Feb	2 Jul	66.04	0.700	0.711	12	0.068
Turtur abyssinicus	2002/3/6-8	108	30.68	24 Jan	12 May	19.66	1.019	0.250	70	0.142
Pogoniulus chrysoconus	2007	150	68.06	3 Dec	2 May	40.53	0.431	0.992	13	**0.242**
	2008	86	57.44	10 Dec	6 Mar	31.89	0.637	0.811	22	0.056
Pycnonotus barbatus	2003	146	42.87	8 May	1 Oct	44.35	0.874	0.430	21	**0.807**
	2006	|	|	7 Jun	31 Oct	46.58	|	|	|	**0.807**
	2007	|	|	23 Mar	16 Aug	37.88	|	|	|	**0.807**
	2008	|	|	10Apr	3 Sep	32.96	|	|	|	**0.807**
Camaroptera brachyura	2007	164	16.89	25 Sep	8 Mar	11.92	1.174	0.127	58	**0.621**
	2008	37	40.97	13 Jan	19 Feb	34.18	0.933	0.349	27	-0.01
Cisticola cantans	2007	150	17.98	10Feb	10 Jul	16.40	0.688	0.730	18	**0.748**
	2008	|	|	6 Feb	6 Jul	20.21	|	|	6	**0.748**
Eremomela pusilla	2003/7/8	141	37.87	10 Aug	29 Dec	27.99	0.978	0.294	15	**0.497**
Prinia subflava	2008	28	16.46	6 Apr	4 May	6.44	0.452	0.987	7	0.249
Turdus pelios	2006	58	14.00	17 Sep	14 Nov	7.09	0.661	0.774	22	**0.277**
	2007	|	|	23 Aug	21 Oct	11.88	|	|	18	**0.317**
Zosterops senegalensis	2007	130	29.29	7 Sep	15 Jan	14.95	1.005	0.265	38	**0.370**
	2008	|	|	23 Sep	31 Jan	26.23	|	|	21	0.071
Cyanomitra verticalis	2003/7/8	188	28.87	4 Oct	10 Apr	14.12	0.989	0.282	34	**0.557**
Chalcomitra senegalensis	2007	185	14.13	6 Sep	10 Mar	12.35	1.288	0.073	53	**0.766**
	2008	201	22.93	28 Aug	17 Mar	19.23	0.852	0.463	28	**0.737**
Cinnyris pulchellus	2002/7/8	117	30.08	17 Nov	14 Mar	27.21	1.213	0.105	32	**0.311**
Cinnyris venustus	2003/6-8	263	45.98	24 Jan	14 Oct	21.81	0.589	0.879	23	**0.591**
Emberiza tahapisi	2007	51	13.93	5 Mar	28 Apr	6.09	0.383	0.999	40	**0.611**
Ploceus cucullatus	2007	143	13.32	26 Sep	15 Feb	5.91	1.045	0.224	67	**0.633**
	2008	167	16.98	9 Sep	23 Feb	14.17	1.297	0.069	38	**0.721**
Ploceus nigricollis	2007	39	15.34	16 Oct	24 Nov	6.98	0.689	0.729	17	0.251
Ploceus vitellinus	2007	140	8.63	7 Oct	24 Feb	4.08	1.269	0.080	56	**0.826**
	2008	107	54.46	16 Sep	1 Jan	42.59	0.586	0.883	17	0.153
Euplectes franciscanus	2008	73	4.32	23 Oct	11 Jan	2.35	0.779	0.579	96	**0.750**
Estrilda caerulescens	2007/8	149	16.14	10 Oct	8 Mar	13.45	0.817	0.518	63	**0.575**
Estrilda melpoda	2007	198	36.57	23 Aug	9 Mar	31.06	0.900	0.393	18	**0.624**
Estrilda troglodytes	2007	219	31.70	14 Nov	21 Jun	16.86	0.675	0.752	16	**0.757**
Uraeginthus bengalus	2007	135	23.54	13 Dec	27 Apr	13.68	0.909	0.381	33	**0.500**
	2008	187	17.09	31 Oct	2 May	9.88	0.483	0.974	20	**0.862**
Lagonosticta rara	2007	90	18	15 Jan	15 Apr	8.38	0.524	0.946	12	**0.659**
	2008	|	|	2 Feb	3 May	14.33	|	|	20	**0.298**
Lagonosticta rufopicta	2007/8	117	15.52	14 Dec	10 Apr	9.58	0.538	0.935	21	**0.737**
L. sanguinodorsalis	2007	32	10.44	27 Feb	31 Mar	6.68	1.293	0.071	46	**0.157**
	2008	127	24.56	10 Dec	16 Apr	14.09	0.873	0.432	30	**0.470**
Ortygospiza atricollis	2002/3/7	151	38.35	18 Feb	19 Jul	16.03	0.730	0.661	16	**0.494**
Spermestes cucullata	2007	210	8.62	16 Aug	14 Mar	5.79	0.846	0.471	48	**0.927**
	2008	270	25.80	19 Jul	15 Apr	20.28	1.066	0.206	24	**0.825**

even considering the maximum 95% confidence interval value for mean moult duration for the dove species would still have resulted in this species completing moult more rapidly than the small estrildine finch, *S. cucullata*. In fact, moult duration showed a negative correlation with species size, though not significantly so (duration vs. mean mass, Pearson two-tailed = -0.291, n=29, *p*=0.13; duration vs mean wing length, Pearson two-tailed = -0.254, n=29, *p*=0.18)).

Significant variation in the duration of moult with year was found in more than half (17 of 29, see Table 2.) of all species, e.g. *Camaroptera brachyura* varying between a duration of 164 days in 2007 and 37 days in 2008.

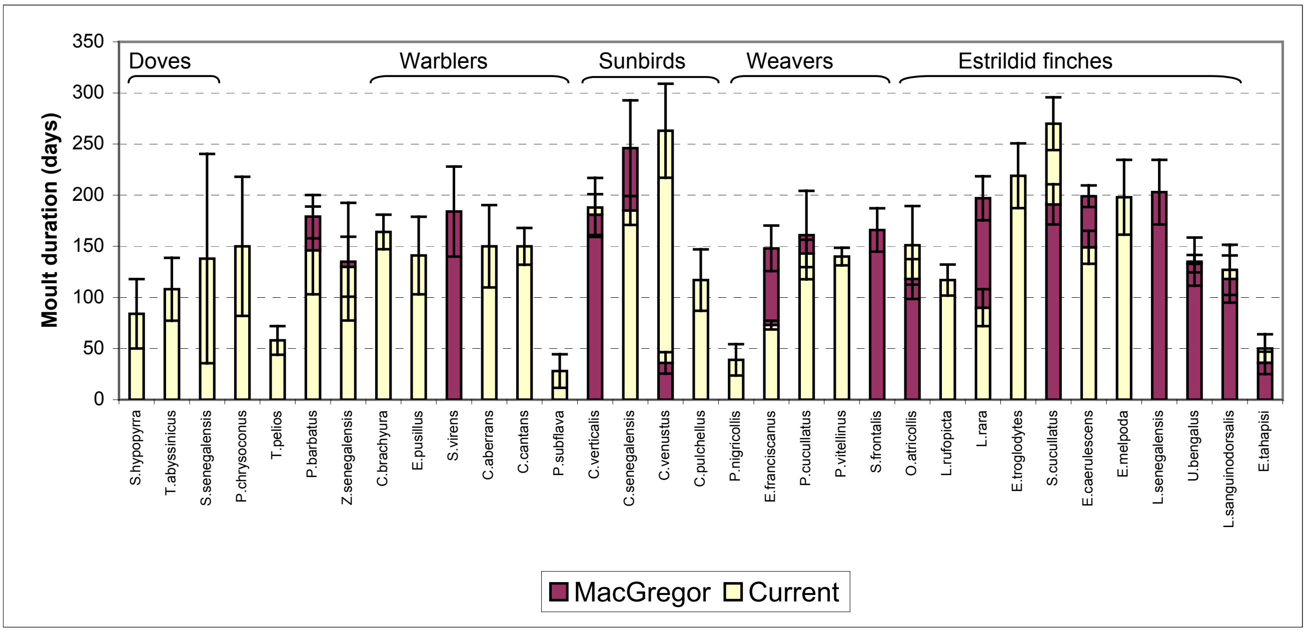
Table 2. Identification of year effect on moult duration. Data pooled across years and tested for equality of error variances (Levene's Test). Reduced datasets covering fewer years were used for species where the entire dataset resulted in significant Levene's Test. The extent of any year effect in timing of moult was then identified from the general linear model. Significant results are shown in bold.

Species	Year	Levene's Test			Interaction - Duration		
		F	*p*	df	F	p	R^2 Adj
Streptopelia hypopyrrha	2002, 2006-08	6.87	**0.004**	3,15	4.43	**0.036**	0.544
Streptopelia senegalensis	2006-08	0.73	0.510	2,9	0.16	0.704	0.930
Turtur abyssinicus	2002-03, 2006-08	1.18	0.327	4,65	0.35	0.707	0.210
Colius striatus	2004, 2006-09	16.54	**<0.001**	4,80	4.67	**0.005**	0.323
Pogoniulus chrysoconus	2003-04, 2007-09	6.74	**<0.001**	4,40	0.19	0.942	0.241
Lybius vieilloti	2006-08	1.43	0.295	2,8	18.92	**0.005**	0.942
Pycnonotus barbatus	2003, 2006-08	3.76	**0.031**	3,17	2.47	0.120	0.837
Camaroptera brachyura	2002-03, 2006-08	1.4	0.241	4,89	4.66	**0.005**	0.548
Cisticola cantans	2007-08	0.14	0.717	1,22	3.81	0.065	0.777
Eremomela pusilla	2003, 2007-08	3.16	0.079	2,12	3.35	0.097	0.517
Prinia subflava	2006-08	9.59	**0.003**	2,12	0.24	0.638	0.480
Turdus pelios	2002, 2006-08	3.09	**0.038**	3,39	0.47	0.628	0.417
	2006-07	2.3	0.138	1,38	0.52	0.477	0.414
Zosterops senegalensis	2002-04, 2007-09	8.54	**<0.001**	5,66	1.37	0.256	0.328
Cyanomitra verticalis	2003, 2006-09	0.86	0.496	4,35	0.89	0.484	0.615
	2003, 2007,2008	0.11	0.901	2,31	1.66	0.209	0.581
Chalcomitra senegalensis	2003, 2006-09	5.31	**0.001**	4,88	3.62	**0.016**	0.795
Cinnyris pulchellus	2002, 2007, 2008	1.69	0.202	2,29	0.8	0.379	0.331
Cinnyris venustus	2003, 2006-08	0.84	0.490	3,19	0.09	0.768	0.521
Emberiza tahapisi	2002-03, 2006-08	14.67	**<0.001**	4,24	1.21	0.333	0.622
	2003, 2007	1.24	0.282	1,16	5.46	**0.035**	0.497
Ploceus cucullatus	2003-04, 2006-09	5.41	**<0.001**	5,114	2.97	**0.035**	0.782
Ploceus nigricollis	2001-03, 2006-08	2.37	0.073	5,22	0.87	0.475	0.395
Ploceus vitellinus	2003, 2006-09	16.91	**<0.001**	4,72	0.49	**<0.001**	0.564
Euplectes franciscanus	2003-04, 2006-09	2.56	**0.028**	5,286	13.17	**<0.001**	0.787
Estrilda caerulescens	2003, 2006-09	2.87	**0.029**	4,67	0.10	0.957	0.621
	2007-08	2.32	0.133	1,61	0.25	0.619	0.563
Estrilda melpoda	2007-08	11.7	**0.002**	1,26	Na	na	0.577
Estrilda troglodytes	2002-04, 2007	1.01	0.414	3,15	Na	na	0.720
Lagonosticta rara	2007-08	0.09	0.765	1,30	0.45	0.507	0.491
Uraeginthus bengalus	2002-04, 2006-08	2.67	**0.026**	5,97	1.85	0.111	0.702
Lagonosticta rufopicta	2002-03, 2007-08	3.28	**0.046**	3,17	7.44	**0.004**	0.941
	2007-08	0.14	0.707	1,57	3.46	0.068	0.271
Lagonosticta senegala	2003, 2006-08	2.99	0.073	3,12	7.41	**0.013**	0.668
L. sanguinodorsalis	2002-03, 2006-09	5.76	**<0.001**	5,89	5.04	**0.001**	0.709
	2003,2008	4.86	0.052	1,10	0.26	0.624	-0.005
Ortygospiza atricollis	2002-03, 2007	1.45	0.271	2,13	0.46	0.511	0.416
Spermestes cucullata	2002-04, 2006-9	1.34	0.243	6,127	12.13	**<0.001**	0.865

Timing of moult

Timing of the start of moult varied widely between and within species (see Tables 1 & 3). Significant year effects were identified in all but one of the non-passerines and 19 of 27 passerines (e.g. the mean date for start of moult in *Pycnonotus barbatus* varied from March in 2007, April in 2008, May in 2003 and June in 2006. Analysis of timing of moult for these species was therefore performed separately for each year.

Figure 2.Moult duration (± SE) by species showing the comparison with data from McGregor *et al.* 2007. Single-coloured bars with only one set of error bars indicate species assessed in only one of the studies.

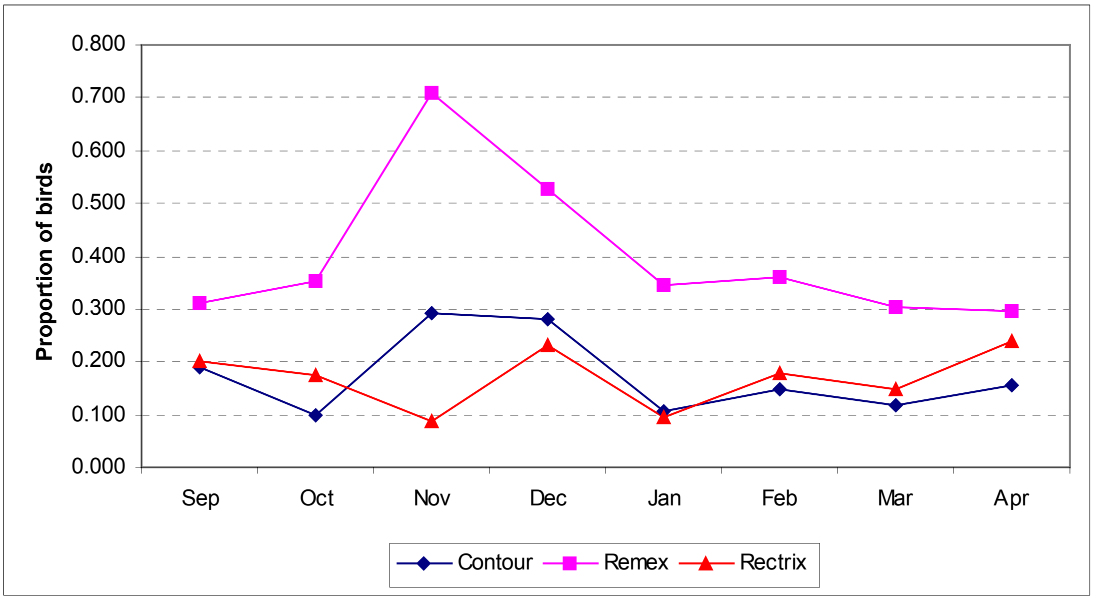


Certain groups of species (e.g. two of the sunbirds and the Ploceid weavers) showed both similar moult timing and moult durations (for the same years) however for the majority of species, taxonomic similarities were generally not strong predictors of moult timing or duration (see Figure 2.).

Active remex moult was recorded in at least one species in every month of the study. This was also the case for both rectrix moult and moult of the contour (head and body) feathers. Peak moult of the remiges (i.e. when the greatest proportion of individuals were moulting these feathers) occurred during

November and peak contour feather moult between November and December (see Figure 3.). Tail feather moult was bimodal, peaking in December (one month later than remex moult) and again in April.

Figure 3. Incidence of moult in different feather tracts through the year. Data are taken from all individuals across species. An individual was considered to be moulting if at least one feather was actively being replaced (and not thought to be a result of accidental loss).



No significant difference in seasonality was found between pooled species when grouped according to guild (Kruskal-Wallis, all combinations, $X^2 = 8.95$, d.f. = 4, $p = 0.06$) however, moult of insectivores was found to occur proportionally more (64.8% of total moult days) in the wet season than that of granivores (25.6% of moult days) (Mann-Whitney U = 33.5, Z = -2.76, $p = 0.004$). No significant differences were present between any other combinations of guilds (insectivores, granivores, frugivores, omnivores and nectarivores). *Turdus pelios*, *P.barbatus* and *P.subflava* were the only species recorded to moult entirely during the wet season (see Figure 4), although this varied between years for *P.barbatus* (in 2007 moult started earlier than in other years and 5% of moult duration occurred in the dry season). Similarly, few species moulted entirely during the dry season (*Cinnyris pulchellus*, *C.brachyura* and *Lagonosticta sanguinodorsalis* being the only ones, although only one day of the moult of *Uraeginthus bengalus* occurred in the wet season in 2008) and this was again subject to annual variation. Nectarivores (4 of 5), omnivores (7 of 7), insectivores (8 of 12) and granivores (10 of 15) predominantly started moult at the end of the wet season.

Table 3. Identification of year effect on timing of moult. Data for each species were pooled across years and tested first for equality of error variances (Levene's Test). Reduced datasets covering fewer years were used for species where the entire dataset resulted in significant Levene's Test. The extent of any year effect in timing of moult was then identified from the GLM. Significant results are shown in bold.

Species	Years	Number of years	Levene's Test			Year effect - Timing		
			F	*p*	df	***F***	p	R^2 Adj
Streptopelia hypopyrrha	2002, 2006-08	4	11.5	**<0.001**	3,15	1.83	0.188	0.321
Streptopelia senegalensis	2006-08	3	0.37	0.698	2,9	70.73	**<0.001**	0.938
Turtur abyssinicus	2002-03, 2006-08	5	1.14	0.347	4,65	2.83	**0.031**	0.226
Colius striatus	2004, 2006-09	5	12.87	**<0.001**	4,80	3.47	**0.011**	0.229
	2007-08	2	4.66	**0.034**	1,74	0.04	0.844	0.107
Pogoniulus chrysoconus	2003-04, 2007-09	5	5.078	**0.002**	4,40	3.37	**0.018**	0.304
	2007-08	2	6.64	**0.015**	1,33	1.52	**0.226**	0.139
Lybius vieilloti	2006-08	3	1.25	0.337	2,8	5.13	**0.042**	0.643
Pycnonotus barbatus	2003, 2006-08	4	1.07	0.390	3,17	1.6	0.228	0.807
Camaroptera brachyura	2002-03, 2006-08	5	0.7	0.596	4,89	3.35	**0.013**	0.491
Cisticola cantans	2007-08	2	0.21	0.649	1,22	6.4	**0.020**	0.748
Eremomela pusilla	2003, 2007-08	3	3.97	**0.048**	2,12	0.29	0.751	0.414
	2007-08	2	4.47	**0.037**	1,12	0.004	0.953	0.452
Prinia subflava	2006-08	3	7.76	**0.007**	2,12	6.89	**0.011**	0.516
	2007-08	2	13.77	**0.003**	1,12	13.76	**0.003**	0.529
Turdus pelios	2002, 2006-08	4	1.98	0.133	3,39	4.94	**0.005**	0.433
	2006-07	2	2.54	0.119	1,38	11.43	**0.002**	0.422
Zosterops senegalensis	2002-04, 2007-09	6	4.83	**0.001**	5,66	2.71	**0.028**	0.313
	2007-08	2	0.14	0.707	1,57	4.43	**0.04**	0.271
Cyanomitra verticalis	2003, 2006-09	5	0.66	0.625	4,35	3.71	**0.013**	0.620
	2003,2007,2008	3	0.11	0.894	2,31	1.2	0.315	0.563
Chalcomitra senegalensis	2003, 2006-09	5	2.6	**0.042**	4,88	3.17	**0.018**	0.777
	2007-08	2	6.67	**0.012**	1,79	0.32	0.574	0.753
Cinnyris pulchellus	2002, 2007, 2008	3	3.25	0.053	2,29	1.55	0.230	0.336
Cinnyris venustus	2003, 2006-08	4	0.87	0.474	3,19	0.3	0.829	0.545
Emberiza tahapisi	2002-03, 2006-08	5	8.03	**<0.001**	4,24	8.96	**<0.001**	0.612
	2003, 2007	2	0.48	0.498	1,16	0.02	0.901	0.347
Ploceus cucullatus	2003-04, 2006-09	6	2.8	**0.020**	5,114	9.06	**<0.001**	0.771
	2007-08	2	6.88	**0.010**	1,103	0.25	**0.617**	0.739
Ploceus nigricollis	2001-03, 2006-08	6	1.47	0.240	5,22	3.93	**0.011**	0.406
Ploceus vitellinus	2003, 2006-09	5	20.51	**<0.001**	4,72	4.82	**0.002**	0.570
	2007-08	2	76.46	**<0.001**	1,71	9.9	**0.002**	0.513
Euplectes franciscanus	2003-04, 2006-09	6	1.4	0.224	5,286	34.93	**<0.001**	0.750
Estrilda caerulescens	2003, 2006-09	5	2.87	**0.029**	4,67	2.65	**0.041**	0.636
	2007-08	2	2.62	0.111	1,61	0.13	0.725	0.569
Estrilda melpoda	2007-08	2	11.7	**0.002**	1,26	3.31	0.081	0.577
Estrilda troglodytes	2002-04, 2007	4	1.01	0.414	3,15	5.31	**0.012**	0.720
Uraeginthus bengalus	2002-04, 2006-08	6	0.66	0.656	5,97	1.39	0.236	0.688
Lagonosticta rara	2007-08	2	0.34	0.562	1,30	4.58	**0.041**	0.500
Lagonosticta rufopicta	2002-03, 2007-08	4	0.55	0.655	3,17	7.55	**0.002**	0.871
Lagonosticta senegala	2003, 2006-08	4	17.6	**<0.001**	3,12	2.14	0.153	0.281
	2003, 2008	2	3.79	0.080	1,10	1.31	0.282	0.078
L. sanguinodorsalis	2002-03, 2006-09	6	3.4	**0.007**	5,89	13.39	**<0.001**	0.656
	2007-2008	2	8.94	**0.004**	1,74	27.36	**<0.001**	0.458
Ortygospiza atricollis	2002-03, 2007	3	0.73	0.502	2,13	0.35	0.712	0.443
Spermestes cucullata	2002-04, 2006-9	7	5.73	**<0.001**	6,127	6.98	**<0.001**	0.793
	2007-08	2	12.76	**0.001**	1,70	3.18	0.079	0.877

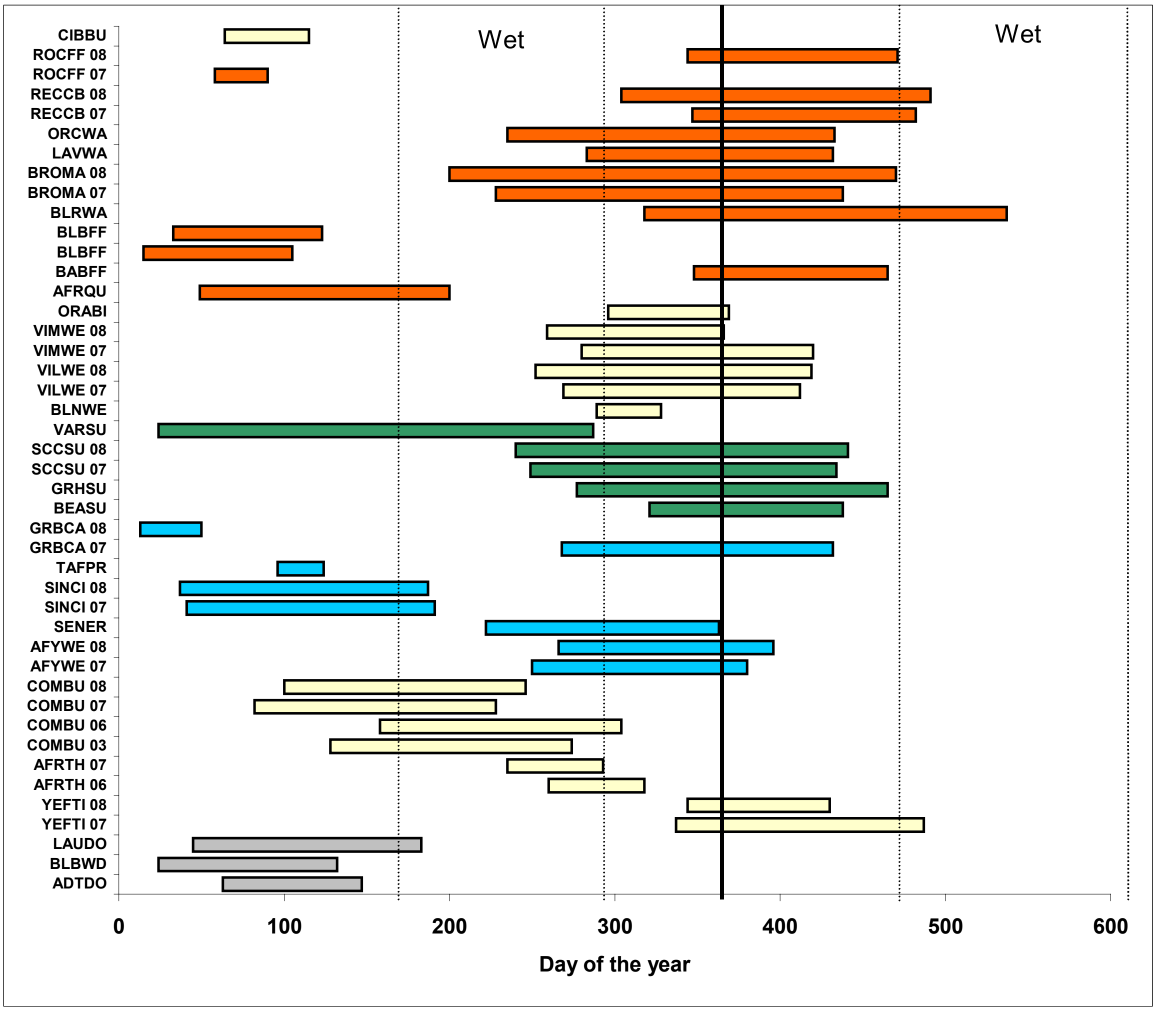
Discussion

Our data show that tropical passerine species essentially follow the same basic pattern of moult as in most north temperate species (Jenni & Winkler 1994) but show an increased variation in the sequence of moult in the wing coverts, and in the number of covert tracts moulting coincidentally. This overlap in moult between tracts may be a function of the protracted moult observed for many of the species in our study area, which itself may be a result of the reduced seasonality. Moult duration was much longer for the majority of species in our study compared to temperate species and did not appear to correlate with body size. We identify a number of possible reasons for these generally prolonged and unpredictable moult periods, including: (1) physiological constraints that prevent the fast growth of feathers or (2) select against it (Moreno 2004); and (3) reduced seasonality leading to less pronounced cues for breeding (Dawson *et al.* 2001; MacDougall-Shackleton *et al.* 2009), resulting in overlap of breeding with moult.

Potential sources of error

Moult in itself is a relatively straightforward process to quantify, since standardised approaches to assessing and recording feather growth have been used for at least the past 30 years (Ginn & Melville 1983). Capture of individuals allows for the detailed examination of all feathers and should result in minimal observer/recorder error. There are a number of important differences between tropical and temperate systems however which, in combination, can cause confusion when assessing age and moult of feathers of tropical species. Most tropical savannah species generally suffer more prolonged exposure to intense sunlight than temperate species. Exposure to such conditions may result in more rapid degradation of feather structure (Bergmann 1982; Montgomerie 2006) and quicker and more dramatic changes in feather colour and hue (e.g. Johnson & Jones 1993; Willoughby *et al.* 2002; Figuerola & Senar 2005; Surmacki 2008) than would occur in temperate zones. Alongside this, the habitat utilised by the species in this study is typified by dense, coarse vegetation and high aerial dust content. Mechanical interaction with each of these extrinsic factors will also lead to the

Figure 4. Moulting periods of all species. Species grouped by taxonomic similarity. Data for species showing a significant year effect in the model are treated separately and the relevant year is identified in the axis. Wet and dry seasons are indicated by hatched vertical lines, end of the calendar year indicated by bold vertical line.



* CIBBU – Cinnamon-breasted Bunting *Emberiza tahapisi*; ROCFF – Rock Firefinch, *Lagonosticta sanguinodorsalis*; RECCB – Red-cheeked Cordon-bleu, *Uraeginthus bengalus*; ORCWA – Orange-cheeked Waxbill, *Estrilda melpoda*; LAVWA – Lavender Waxbill, *E.caerulescens*; BROMA – Bronze Mannikin, *Spermestes cucullata*; BLRWA – Black-rumped Waxbill, *E.troglodytes*; BLBFF – Black-bellied Firefinch, *L.rara*; BABFF – Bar-breasted Firefinch, *L.rufopicta*; AFRQU – African Quailfinch, *Ortygospiza atricollis*; ORABI – Northern Red Bishop, *Euplectes franciscanus*; VIMWE – Vitelline Masked Weaver, *Ploceus vitellinus*; VILWE – Village Weaver, *P.cucullatus;* BLNWE – Black-necked Weaver, *P.nigricollis*; VARSU – Variable Sunbird, *Cinnyris venustus*; SCCSU – Scarlet-chested Sunbird, *Chalcomitra senegalensis*; GRHSU – Green-headed Sunbird, *Cyanomitra verticalis*; BEASU – Beautiful Sunbird, *Cinnyris pulchellus*; GRBCA – Grey-backed Camaroptera*, Camaroptera brachyura*; TAFPR – Tawny-flanked Prinia, *Prinia subflava*; SINCI – Singing Cisticola, *Cisticola cantans*; SENER – Senegal Eremomela*, Eremomela pusilla*; AFYWE – African Yellow White-eye, *Zosterops senegalensis*; COMBU – Common Bulbul, *Pycnonotus barbatus*; AFRTH – African Thrush, *Turdus pelios*; YEFTI – Yellow-fronted Tinkerbird, *Pogoniulus chrysoconus*; LAUDO – Laughing Dove, *Streptopelia senegalensis*; BLBWD – *Turtur abyssinicus*; ADTDO – *S.hypopyrrha*.

most exposed feathers more rapidly showing signs of abrasion and changes in colouration (Burtt 1986; Jenni & Winkler 1994) than for species occupying similar habitats in temperate areas. The rapidity of these effects in the study area may have led to errors in determining the generation to which a particular feather belonged – particularly in species having a prolonged moult. Very abraded and bleached feathers gave the impression that the individual had arrested moult when the feathers were in fact of the same generation (i.e. feathers moulted first appeared to be of a different generation to those moulted later in the moult sequence). The prevalence of feathers that looked most bleached and abraded was commonest in *Spermestes cucullatus* and *Ploceus vitellinus* both of which have moult durations in excess of 100 days. Early on in this study these feathers were recorded as being part of an arrested/suspended moult and such individuals were excluded from analyses. However, it later became apparent that, in many cases, these individuals had performed a standard complete moult and that the most abraded feather(s) were merely those that were most exposed (e.g. the tertials) or had been moulted earliest. The possibility that a number of individuals had suspended moult cannot be discounted however, and inclusion of these individuals will have resulted in a positive bias to the estimates of moult duration.

Aside from the difficulties in determining the ages of individual feathers occasional problems were also encountered in identifying the ages of individuals (i.e. whether juveniles, immatures or adults). In temperate systems individuals are generally aged according to a system of plumage examination and comparison and the relationship between this and a relatively stable breeding period, the timing of moult, and the calendar year (e.g. see Pyle *et al.* 1987; Jenni & Winkler 1994). The breeding season of tropical African species (see Chapter 3) is often variable between individuals, populations and years and because of spatial variation in climate does not conform as readily to a routine that can be easily defined according to an annual calendar. This, along with the relative paucity of detailed information relating to accurate ageing of individuals (as exists for temperate species – e.g. see Svensson 1992), may have resulted in errors in identification of ages of individuals during this study. This in turn will affect the identification of moult sequence and skew estimates of moult duration and timing if immature birds are included within adult datasets, since the characteristics of post-juvenile moult (in temperate species at least (Jenni & Winkler 1994) are often more variable than the complete moults in adults. There is likely to be significant heterogeneity in data-quality given that numerous individuals of varying skill and experience levels were involved in data collection over the course of the study. Despite this, all data items for which there was any doubt over age (or indeed any other variable) were removed from the analyses and the effect on estimates of the various characteristics of moult should therefore be minimal.

Lastly, sexual differences in timing and duration of moult are frequently observed in temperate species (Orell & Ojanen 1980; Francis *et al.* 1991; Jenni & Winkler 1994) with males often commencing moult earlier and females subsequently moulting at a faster rate. Such sexual differences have also been observed in tropical species, for example Oschadleus & Osborne 2005 found that moult duration was 17 days longer in males than females of *Ploceus rubiginosus* in northern Namibia. There were insufficient data to allow separate determination of moult characteristics for each sex here. This may have resulted in estimates of start of moult being skewed depending upon which sex was most dominant in captures and whether or not a sex effect operates in this study species. We might expect that, because fewer time constraints are thought to influence the moult process in tropical species, the estimates of moult duration here should not have been dramatically affected by failure to account for sex. But because insufficient data were available to test for the extent of any sex-related differences, estimates derived here must be treated as overall population estimates.

Does the basic moult sequence differ between temperate and tropical species?

There was no evidence that bird species in the tropical savannahs of West Africa departed from the basic sequence of moult typically found in temperate European landbird species (Ginn & Melville 1983). On the one hand this is perhaps surprising given the diversity of species under consideration and the difference in life histories between species in tropical and temperate areas (Moreau 1944; Skutch 1949; Martin 1996). Alternatively, because individuals in tropical areas must perform the same activities as those in temperate areas and must retain suitable flight performance, minimising the impact of moult on wing aspect ratios (Hedenström 1998), wing loading (Howland 1974) and overall aerodynamic performance (Katz & Plotkin 1991) will be an evolutionary priority for all species. Despite the overall similarity in the sequence of moult there is considerable difference in the coincidence of moulting feathers between the tropical passerine species assessed here and temperate species. Aside from the associated primary covert, moult of the innermost three primaries generally occurs in isolation of any other remiges or rectrices in European species (though moult of greater coverts may vary between species (Bährmann 1964; Dhondt 1973; Kasparek 1979; Mester & Prűnte 1982) and may be replaced during the moult of P9). In contrast, moult was present in three to five other tracts during the moult of P10 and P9 in species in this study (see Figure 1). Also, in certain species (e.g. *Euplectes franciscanus*) the greater coverts were almost entirely replaced by the time P8 begins moulting. The high level of coincidental moult between tracts is perhaps not surprising given that mean moult duration of the tropical species here was around 130 days. Averaging the rate of growth across the innermost nine primaries, this equates to a duration of at least 14 days for the complete replacement of each primary in tropical species. Replacement of the innermost six primaries might therefore feasibly take around three months to complete, providing ample time for the replacement of a significant proportion of the tracts of the much smaller coverts (Figure 1). In contrast, the rate of replacement of the primaries is much faster in temperate passerine species (around 90-100 days (Ginn & Melville 1983)). So although moult follows the same basic sequence in tropical species, it is perhaps not surprising that moult of the covert tracts occurs earlier, and is completed sooner, in comparison to the moult of primaries in temperate species.

How do our estimates compare with other published work?

Estimates of moult timing and duration identified here were similar to those found in earlier work at the same study site by McGregor *et al.* (2007) for most species (Figure 2). Only the timing of start of moult in *C.venustus* differed by more than two months (133 days earlier in our analysis). The reason for this difference is unclear, especially given the number of individuals available for analyses in both studies. This marked difference was also present in estimates of moult duration for this species, the estimate here being more than 220 days longer than found in the earlier study. Given that no year effect was detected in the analyses i.e. duration was not found to differ markedly between years, this difference does not appear to be solely due to annual variation. Of the remaining species, moult duration was similar between the two studies for all except *E.franciscanus* (75 days shorter in our study) and *Lagonosticta rufopicta* (107 days shorter here). Few individuals (7) were used in assessments of moult in both of these species in the earlier study and variation in the estimates is most likely attributable to this. Estimate for the moult duration of *E.franciscanus* (and those of the other weavers in this study) here lies comfortably within the range found in other studies of weavers and bishops (Oschadleus 2005; Oschadleus & Underhill 2006) whereas the estimate derived for this species by McGregor et al (2007) was much higher than for other studies. Overall our estimates are similar to those obtained in other studies of the same or taxonomically very similar tropical African species (e.g. Mann 1985; Craig *et al.* 2001; Bonnevie *et al.* 2003; Hulley *et al.* 2004; Oschadleus 2005; Symes & Wilson 2008)

Why does moult take longer to complete in tropical bird species?

Further evidence was produced here to support the general theory that the complete (primary) moult in adults is performed at a much slower rate in tropical species than for similar temperate species. The complete moult for the species under study here took between four and five months, around six to ten weeks longer than the average small north temperate passerine (Ginn & Melville 1983, Jenni & Winkler 1994; Mulvihill & Rimmer 1997). Similar moult durations have also been reported for other tropical species (e.g. Wyndham 1986; Tidemann & Woinarski 1994; McGregor *et al.* 2007a) suggesting that protracted moults may be the norm in tropical birds.

The process of moult involves significant physiological and ecological costs to the individual. A change in dietary needs (Dietz *et al.* 1992; Murphy 1996) and diversion of resources from other functions (Murphy & Taruscio 1995; Schieltz & Murphy 1997) is often necessary. Also, a disruption to the structure of the wing will also result in reduced flight capability (Swaddle & Witter 1997) and consequent increase in vulnerability to predation (Rivera *et al.* 1999; Lind 2001). Given these costs, why do tropical species prolong such an apparently disruptive process and potentially increase their risk? A number of hypotheses have been proposed based on ecological, climatological and physiological factors.

Firstly, it is widely accepted that there is a negative relationship between rate of moult and feather quality (Nilsson & Svensson 1996; Dawson *et al.* 2000; Hall & Fransson 2000). One hypothesis suggests that tropical species require longer moults to produce higher quality feathers than in temperate species (Moreno 2004). Temperate species require high quality feathers in order to improve thermal efficiency during harsh weather. However, moult is usually completed immediately prior to such cold-weather periods in these species and, because exposure to intense UV radiation does not generally occur, feathers should provide sufficient quality of insulation for the duration. In tropical species, as well as thermal efficiency, feathers are subject to the effect of bacterial and fungal processes (Burtt & Ichida 1999), high aerial dust content and abrasion against dense and coarse vegetaition (Burtt 1986; Jenni & Winkler 1994) and must also cope with the impact that prolonged exposure to intense sunlight has on feather structure (Montgomerie 2006). It may be the effect of this, rather than microbiological degradation or thermal efficiency, that influences feather quality and rate of growth in tropical species. This may be especially true if tropical species incorporate higher levels of melanin within their feathers than temperate species. Indeed, melanin manufacture is thought to be facilitated by higher levels of dietary mineral content at lower latitudes (Norris *et al.* 2009). High levels of melanin within feathers provides greater protection from macroparasites (Kose & Møller 1999), bacteria (Fogarty & Tobin 1996; Mackintosh 2001) and UV radiation (Krol & Liebler 1998) as well as conferring increased feather durability (Bonser 1995;

Fitzpatrick 1998). Such benefits are only gained with costs however and melanogenesis involves a lengthy and complex pathway, immunosuppression (Galván & Alonso-Alvarez 2008) as well as the production of a number of cytotoxic byproducts (Jawor & Breitwisch 2003). Moult may therefore be a protracted process in tropical species to facilitate the incorporation of higher levels of melanin within the plumage. Also, since melanin-based colouration in feathers is reliant on the availability of essential amino acids, it is likely to be significantly influenced by food availability (Jawor & Breitwisch 2003), condition (Norris *et al.* 2009) and levels of stress (Roulin *et al.* 2008). Annual variability in environmental conditions may therefore also lead to annual variation in duration of moult - as recorded here.

If this were the case then why were the moult durations of certain species in our study shorter than those of similar temperate species (e.g. *Turdus pelios*: 58 days cf. *T.merula*: 87 days (Snow 1969))? This too may be linked to differential melanin content between species. The plumage of the temperate thrush *T.merula* is entirely black in adult males and dark brown in adult females and its feathers are therefore likely to have higher melanin content than those of the olive-green *T.pelios* found in our study area. The difference in moult duration between these two species however is more likely due to *T.pelios* being a partial migrant and therefore needing to schedule moult around other time-restricted activities (see below). Although feather quality and melanin content provide an interesting hypothesis to explain the protracted moult in tropical species, further investigation into both the comparative levels of melanin-based pigmentation in feathers and the time necessary for its synthesis in both tropical and temperate species needs to be performed.

Following on from this, a second theory relating moult with condition suggests that rapid moult in tropical species is selected against because the process of moult decreases immune function (Møller 1998; Moreno 2004). Pathogens are reported to be more frequent (Janzen 1970) and have more severe effects on their hosts in tropical latitudes (Connell 1971). As a result, Møller (1998) suggested that tropical hosts need to invest more in parasite defence. Should this be the case then there may exist a resource trade-off in which investment in rapid moult results in a reduced immune response ultimately leaving an individual more prone to autoimmune disorders (Holt 1992; Ilmonen *et al.* 2000; Moreno 2004). A relationship between latitude, parasite loading and life history characteristics has been determined in other studies, most especially with regard to clutch size, number of clutches and age of first reproduction (Hochberg *et al.* 1992; Møller 1997; Oppliger *et al.* 1997) however, although some studies have investigated moult and parasite loading (e.g. Underhill *et al.* 1994; Langston & Hillgarth 1995) these have generally centred on non-passerines. High parasite loading in these two studies (of *Diomedea immutabilis* and *Calidris canutus*) resulted in reduced or delayed moult, effects that are likely to have significant life history consequences (reduced breeding potential and decreased survival). It is therefore possible that tropical land bird species exhibit slow rates of moult to decrease immunosuppression in response to higher local parasite risks. Further investigation and comparison of the effects of parasite loading on duration and extent of moult in bird species at different latitudes would provide valuable insight into whether a life history trade-off exists between rate of moult and parasite loading.

Alternatively, Moreno 2004 outlines a theory which proposes a functional response between rate of moult and food availability/diet and that nutritional constraints reduce the rate of the growth of feathers. Essentially this argument relates moult duration with the level of protein in the diet. Whilst this may perhaps hold for species with low-protein diets (e.g. frugivores), findings here were similar to those of Foster (1975) in that no meaningful relationship between duration (rate) of moult and diet could be identified in West African savannah species used here. This is perhaps not surprising given that none of the species in the study were obligate frugivores. Generally membership of a guild did not predict rate of moult, suggesting that some other factor had a greater influence on rate of moult than diet. Resources may affect moult duration in some other way however, for example, Murphy & King 1990; Murphy & King 1991a suggested that the cost of feather production is inversely proportional to day length and will therefore also relate to the latitude at which birds normally moult. Day length in our study remained relatively constant throughout the year and individuals therefore receive around 13 hours of daylight each day. Species moulting in temperate areas (usually commencing shortly after breeding and therefore between August and October each year) will receive between 13-17 hours of daylight each day when moulting. Therefore, if the assertion of Murphy and King is correct then the costs of moulting in tropical areas is higher than for species in temperate areas, potentially resulting in a longer moult duration for these species.

Perhaps the most straightforward explanation for the protracted moult in tropical species is that they generally do not face the same time-constraints as those species in temperate areas since there is often no period of long-distance migration or prolonged thermal stress to interfere with moult (Jenni & Winkler 1994; Ogden & Stutchbury 1996; Merilä 1997). A number of studies (Keast 1959; Immelmann 1971; Maclean 1971; Serventy 1971) have reported extended and opportunistic breeding of bird species in arid tropical areas. Without rigidly defined breeding periods, tropical species are able to spread the physiological and ecological costs of moult over a much longer period. Such a strategy might also explain the relatively high rate of moult-breeding overlap found within tropical species (Foster 1975; Dittami 1987; Tidemann & Woinarski 1994; see Chapter 6). When a suitable period for breeding is reached, either based on current and expected future environmental conditions or attainment of breeding condition, moult may continue to be performed slowly in the background whilst the majority of resources are diverted towards reproduction (Foster 1974). This may account for the long moult duration recorded here for *S.cucullata* (210-270 days; Table 1), a species raising several broods in the same nest and having a prolonged breeding season (Elgood *et al.* 1994). Alternatively, and given the high requirements for protein to sustain feather growth (Newton 1968; Payne 1972), develop and produce eggs (Romanoff & Romanoff 1949; O'Connor 1984) and to provision nestlings (Welty 1962; Krupa 2004; Mock *et al.* 2009), moult may be suspended when ideal breeding conditions are encountered and then resumed once nestlings have reached a certain stage. Depending upon the duration of suspension (and, based on estimates of mean incubation and brooding periods from a number of sources this is unlikely to be for more than 30 days), it is unlikely that the interruption to moult would be detected during field studies unless an individual is recaptured during the suspension period. Either of these approaches would enable tropical species to coincide breeding with what may be a temporally variable peak in suitability of environmental conditions. A similar response to environmental conditions has been observed among a limited number of temperate species. For example, the irruptive species *Loxia curvirostra* is an opportunistic breeder that shows a variable pattern, timing and duration of moult (Williamson 1957; Rymkevich 1990; Jenni & Winkler 1994). From an evolutionary perspective, such a strategy appears to make sense in order for a species to maintain plasticity in timing of breeding. This is especially useful for resident species faced with the difficulty of predicting the optimal time for breeding in a variable environment. Maintaining an almost continual low-level rate of moult ensures both the replacement of essential feathers and the exploitation of optimal breeding conditions as they are encountered.

In contrast, several species in this study were found to have very short moult durations (Figure 4), although moult of two of these (*C.brachyura* and *Lagonosticta sanguinodorsalis*) was found to show considerable annual variation. Of the remaining four species with rapid moults, both *T.pelios* and *E.franciscanus* show a more time-constrained life history cycle than the majority of species caught here. Many of the *T.pelios* individuals caught in the study area are thought to be partial migrants (Elgood *et al.* 1994) and a passage of birds was recorded through the study area both at the start and end of the wet seasons. Moult tends to start at the end of the rainy season, shortly after breeding and after arrival in the dry season areas, and is generally completed by the end of the dry season when birds move away from the study area. Timing of moult is therefore constrained to occur between migration periods and this may be the reason for it being more rapid than in other species here. The local population of *E.franciscanus* shows highly synchronous breeding (between July and September, late in the rainy season) and moulting (between October and December). Moult in this species may be constrained to occur at the period of peak seed abundance when large flocks are present at the study site. *E.franciscanus* are believed to behave in a similar manner to *E.orix* during the non-breeding season and become nomadic, dispersing from the breeding area shortly after completing moult, presumably to find alternative foraging areas (Craig 1980). Ensuring that feathers are replaced in this window of high food abundance before the need for dispersal may be the reason behind the rapid moult of this species compared to others here.

Does moult occur at regular and predictable periods in tropical passerine species?

The majority of species assessed here (23 of 31) showed significant annual variation in the timing of the main moult. At first this appears somewhat surprising given the relatively stable seasonality of climate in the study area. Although the timing and duration of the dry season was fairly constant during the course of the study, the timing and extent of peaks in rainfall did vary between years. Given that fluctuations in food availability are often associated with seasonal patterns of rainfall (Poulin *et al.* 1992; Crowley & Garnett 1999) one would also expect strongly seasonal patterns and predictable scheduling of life history processes for the species in here, as found in other studies (Britton 1978; Stiles 1980; Cruz & Andrews 1989). This generally proved to be the case although predictability is generally limited to identification of species as either wet or dry season breeders and significant variation in timing within these broad periods existed (see Chapter 3). Similarly, the timing of moult was generally similar between years (in terms of whether it was performed in the dry or rainy season) but again varied within these seasons. The majority of species here moulted mostly during the dry season, presumably because breeding attempts for most species occurred between the mid-points of the rainy season and the dry season (see Chapter 3 and Elgood *et al.* 1994). Two species were recorded moulting primarily during the wet season. *C.venustus* may do so because it is a dry season breeder. *P.barbatus* on the other hand is recorded as being a rainy season breeder by Elgood *et al.* (1994) which would conflict with the identification of moult period in this study for this species. In fact there was evidence that breeding occurred primarily between the middle and end of the dry season in this species (Chapter 3), which fits with the estimation of moulting period (from April to October). Timing of start of moult in *P.barbatus* varied annually between April and June (Figure 4) most probably in response to an annual variability in breeding period.

Whereas late-breeding individuals of temperate species tend to increase their rate of moult to ensure completion before periods of thermal stress or migration (e.g. Flegg & Cox 1969; Dolnik & Blyumental 1967; Meijer 1991), late-breeding tropical species do not face such time constraints and evidence here suggests that they continue to moult at the same ‘comfortable’ rate until moult is completed. Timing of the start of moult may therefore be more a function of when feathers need replacing rather than fitting to a rigid schedule. The removal of such time constraints has been found to affect timing and rate of moult in temperate species. For example, northern populations of *Emberiza schoeniclus* start moult earlier and moult more slowly than southern populations when they have one brood each year rather than two (Kasparek 1980). This suggests that these time constraints are of primary importance in determining timing and duration of moult in all birds and are therefore likely to be the most important reason behind differences in moult characteristics of temperate and tropical birds.

Do larger birds and non-passerine species take longer to moult than smaller birds and passerine species?

Larger feathers require more resources to produce (Rohwer 1999) and moult duration in larger species and non-passerines is expected to be longer than for passerines. This was not found to be the case in this study and moult duration in tropical species was generally not related to either size or passerine/non-passerine status. In fact, rather than smaller birds completing moult more quickly, in this study the species with the longest moult duration was a small passerine (mean mass = 6.3g), *C.venustus*. The moult duration of the largest species (*Streptopelia hypopyrrha* mean mass = 163.8g) was much less (84 days) than the median duration (130 days). Indeed the seven species with the longest moult durations were either sunbirds (*C.venustus, Chalcomitra senegalensis* and *Cyanomitra verticalis*) or estrildine finches (*S.cucullata*, *E.melpoda*, *E.troglodytes* and *Uraeginthus bengalus*), all with mean masses of less than 13g. The shorter and more stable moult durations in the larger species and non-passerines observed here may be a consequence of a more strongly defined pattern of seasonal breeding in these species. All breed during the dry season (Elgood *et al.* 1994) and are mostly frugivorous. The strongly seasonal pattern to the fruiting season in the study area may result in time and foraging constraints that require a more stable and predictable timing of essential life history processes in these species in a manner similar to that for temperate species. Overall however, the moult durations of the larger species observed here were in line with those of similar non-passerine temperate species. For example complete replacement of the primaries in *Streptopelia decaocto* takes between 75 and 130 days in England (Ginn & Melville 1983). Prolonged breeding seasons and number of nesting attempts made by the estrildine finches and sunbirds (Elgood *et al.* 1994) may explain the differences in moult duration between larger and smaller species, indeed long moult durations have been recorded in other studies of these families (e.g. Mann 1985). Where there may be only sufficient resources for a single nesting attempt before needing to breed in larger species, sufficient resources may be available for smaller birds to make repeated nesting attempts whilst either suspending moult activities or undergoing a moult of reduced rate and intensity. Many individuals in this study were found to be undergoing primary moult whilst also having active brood patches (see Chapter 6). Such a scenario would be facilitated in species that breed cooperatively (but see Jones *et al.* (1995)). More nesting attempts could be made at lower individual cost thereby allowing diversion of resources to simultaneous moult. Further investigation and comparison of the moult duration of cooperatively breeding individuals with individual breeders as well as the occurrence of overlap in moult and breeding will help determine whether such a process may occur in tropical species.

Conclusion

Duration and timing of moult in tropical birds shows much greater variation than in north temperate species and is not necessarily related to body size. Moult durations were considerably longer in most of the species studied here than for temperate species. A few exceptions were present however, usually amongst the more synchronously breeding species (e.g. *E.franciscanus*) and for these, moult durations were comparable with temperate areas. The reduced seasonality in tropical areas is considered to be the main driver behind longer moult durations possibly as a result of reduced regularity of scheduling of breeding activities. Should breeding periods not be constrained to occur during specific periods, as they are in temperate areas, then species may choose when to breed based on any number of factors such as body condition, availability of mates or perceived nest predation threat, rather than relying on the lower intensity seasonal cues. Capacity for breeding over a prolonged period may make the scheduling of moult problematical. Since it must occur for an individual to maintain condition, then undertaking moult as a slow, background process allows for the opportunistic exploitation of conditions as and when they arise. The phenology of moult may therefore provide a useful, though often infrequently considered, insight into a species' life history.

Chapter 3: Timing, duration and the influence of seasonality on breeding in tropical savannah birds

Summary

Breeding represents perhaps the most costly of all life history processes with parents investing heavily in time, energy and risk. A trade-off between current and future reproduction has long been established in life history theory and is thought to vary between tropical and temperate latitudes. In this study, the timing and duration of breeding periods was assessed in 42 tropical savannah bird species to determine whether reduced seasonality results in less constraint.

I first examined whether capture of juveniles could be used as a means of identifying breeding periods by comparing timing of capture with occurrence of active brood patches in adult birds. In general there was a lag of approximately one month between appearance of brood patches on adults and capture of juveniles. The prolonged interval between hatching and attaining full adult plumage (up to 5 months) meant that capture of immatures was not a reliable method of identifying breeding periods. Adults with brood patches, juveniles and immatures were caught in all months of the year suggesting that breeding was generally less constrained by seasonal climate variation than in temperate areas. Very little synchrony was identified in timing of breeding either within or between species. This resulted in long durations of breeding periods (mean 122 days) and breeding throughout the year. A peak in breeding was identified during the late rains and early dry season but comparatively few species had breeding seasons that extended into the late dry and early rainy season. There was also some evidence of a relationship between timing of breeding and guild with frugivorous species generally nesting earlier in the year than granivores or insectivores. This suggests

that timing of breeding may be loosely linked to food availability but that other factors (possibly nest predation) may play a more significant role.

Introduction

Strong seasonality in a climate will generally result in animals partitioning essential life history processes into specific periods of the calendar (e.g. Payne 1972; van Noordwijk *et al.* 1995; Cresswell & McCleery 2003). In temperate regions the level of seasonality generally results in periods of high food abundance coupled with favourable temperatures alternating with periods of food shortages and thermal stress. Periods where conditions for breeding are optimal tend to be relatively short and this is reflected by the apparently hectic scheduling of reproduction by bird species in temperate areas (Murton & Westwood 1977; Stutchbury & Morton 2001). Although many tropical environments were traditionally considered almost aseasonal, and tropical bird species thought to be able to breed at almost any time of the year (Skutch 1950), it is now accepted that in many areas, species have similarly well-defined breeding seasons to their temperate counterparts (Wikelski *et al.* 2000; Marini & Durães 2001).

Birds living at higher latitudes occupy regions characterised by strong seasonal predictability in environmental conditions. This has enabled the evolution of a behavioural linkage between optimal conditions for breeding and the regular and wide annual variation in photoperiod (Murton & Westwood 1977; Wingfield & Kenagy 1991). The extent and predictability of this seasonal variation in conditions declines with decreasing latitude, as does the variation in photoperiod potentially reducing its suitability as a cue for breeding in tropical species. Hau *et al.* (2000) determined that tropical birds are capable of discerning the slight seasonal variations in photoperiod and may use this as a cue to initiate the development of their gonads just prior to the expected breeding season. The rate of development is then fine-tuned according to other seasonal and annually variable conditions such as food availability (Moreau 1950; Skutch 1950; Miller 1963; Snow & Snow 1964; Karr 1971; Britton 1978; Bell 1982). As a result, the seasonal variation in rainfall (Leigh *et al.* 1996) and its concomitant effects on plant phenology and primary productivity (Bourliere & Hadley 1970; van Schaik *et al.* 1993) are thought to be the ultimate factors affecting timing of reproduction in tropical species. This approach therefore allows individuals to be in a state of preparedness in order to take advantage of suitable local conditions for breeding in a manner similar to the opportunistic breeding hypothesis proposed by Immelmann (1971) and Serventy (1971).

In this study, I attempted to further qualify whether a suite of common bird species in tropical West Africa had specific and identifiable breeding seasons by assessing the occurrence of juveniles, immatures and the presence of adult birds in breeding condition (i.e. with brood patches), in mist-net catches. Although these data would later be used in assessing the life history trade-offs between moult, breeding and survival, the intentions in this chapter were to use the data on timing of breeding to identify the following:

1. To determine whether occurrence of juveniles and immatures in mist net samples provided a suitable means of identifying breeding periods through comparison with occurrence of brood patches
2. Produce baseline data on breeding seasonality of species at the study site.
3. Identify guild- and family-specific variations in timing of breeding.
4. Compare breeding seasonality of birds at Amurum with previously published data for tropical savannah bird species.

Methods

I attempted to identify the peak periods of breeding activity for an array of bird species caught in mist nets at four locations in central Nigeria between October 2001 and October 2008. Three of the sites were centred in mixed Guinea savannah woodland and farmland in Plateau state (Amurum Community Forest Reserve and neighbouring Gwafan, Jos (N 09° 52', E 08° 58'), and Pankshin (N 09° 20', E 09° 26'). The fourth site (Yankari Game Park - N 09° 45', E 10° 30') was located in Sudan savannah and riparian woodland in the neighbouring state of Bauchi.

Data collection

Birds were caught in mist nets across the study sites according to the methods outlined in Chapter 2. All birds were aged and sexed and their breeding condition assessed.

Assessment of breeding condition

The presence of brood patches and enlarged cloacal protuberances was used to identify timing and duration of breeding periods. Assessment of brood patches was made using a five-stage scoring system as outlined by Redfern (2008). It was assumed that tropical species show a similar progression of brood patch development to temperate species. Only birds with brood patch scores of 2 (breast and belly fully de-feathered, some wrinkling of skin evident and signs of oedema), 3 (skin of belly opaque and engorged, broad swollen wrinkles) and 4 (skin shows thin wrinkles, no longer engorged) were considered to have active brood patches since all of these stages generally occur during the period of incubation and brooding (Hinde 1962; Jones 1971). Individuals at stages 1 and 5 of brood patch development were omitted from the analyses to reduce observer error (these stages were found to be frequently confused with juvenile birds replacing/growing breast feathers by inexperienced fieldworkers). All birds with brood patches were included in analyses irrespective of sex since males of a number of species covered here were also known to incubate (e.g. Fry *et al.* 2004; Brandt 2007). Because the aim here was to identify the general breeding periods of these species, multiple captures of individuals were included in the analyses since these data will also help in identifying the range of such periods. Few of these data existed however and, across the 22 species assessed, only 19 multiple captures were included. These were mostly for the species with the largest datasets (i.e. *E.franciscanus* (5), *U, bengalus* (3) and *L.sanguinodorsalis* (3) accounting for <8% of data for each) and will therefore have had little impact on assessed dates. Timing of start and ends and duration of breeding periods for each species was therefore given by the first and latest dates (and the interval between these) of occurrence of brood patches on individuals.

Comparison of use of brood patches and occurrence of juveniles to indicate breeding period

I attempted to use the mean dates of capture of juveniles and immatures to determine breeding period for species with limited brood patch data. Most species of temperate (European) passerines start to moult body feathers from juvenile to adult type within around one month of leaving the nest (Gwinner 1969; Glutz von Blotzheim & Bauer 1991; Bensch & Lindström 1992; Rymkevich 1990) although a maximum of two months has been recorded for certain Fringillidae (Iovchenko & Smirnov 1987) and Emberizidae (Ginn & Melville 1983; Jenni & Winkler 1994). Temperate passerine species unconstrained by the need to migrate also take longer before commencing post-juvenile moult (see Jenni & Winkler 1994) and, given the resident nature of many of the species assessed in this study, I assumed a similar process and timeframe for tropical species. Capture dates of juveniles and immatures were plotted together with mean dates for presence of brood patches to determine the extent of overlap. This was then used to determine the viability of using mean capture dates of juveniles and immatures to assess timing of breeding period using correlation analysis.

Four guilds were identified for analysis (Table 1) with membership determined according to information on diet given in Elgood *et al.* (1994) and Urban *et al.* (1997).

Table 1. Number of species and families used in assessment of breeding period by guild

Guild	Family	No. Species (Brood patch)	No. Species (Juveniles)
Nectarivore	Nectariniidae	0	3
		0	**3**
Frugivore	Columbidae	-	1
	Coliidae	-	1
	Lybiidae	2	-
	Pycnonotidae	1	1
	Zosteropidae	1	1
		4	**4**
Insectivores	Meropidae	-	1
	Indicatoridae	-	1
	Cisticolidae	2	3
	Sylviidae	2	1
	Muscicapidae	-	6
	Turdidae	-	1
	Platysteiridae	-	1
	Malaconotidae	-	2
		4	**16**
Granivores	Emberizidae	1	1
	Passeridae	-	1
	Ploceidae	5	7
	Estrildidae	8	6
	Viduidae	-	1
		14	**16**

Duration of time between fledging and post-juvenile moult

Successive recaptures of individuals were used to identify the latest dates that each species was recorded as a juvenile or immature and the earliest dates that they were recorded to have started moulting or attained full adult plumage. The means of these dates were then subtracted from the mean dates of breeding to identify durations of both the juvenile and immature plumage phases. Such an approach worked well where several recaptures were available for each individual, periods between successive recaptures were short, and the individual had not changed age category (i.e. 3-3, 5-5). Where successive captures occurred after a period of more than 4 months and the individual had changed from a juvenile to immature plumage, the midpoint between these dates was used to indicate the start of post-juvenile moult. In cases where successive captures were made after more than 4 months and the individual had moulted from an immature to adult plumage only the last known capture as an immature was used for determining period of immature plumage phase. Individuals recaptured as adults within 4 months of being recorded with an immature plumage were included within the dataset, however the point of change to adult plumage was considered to be the mid-point between the two captures in these cases.

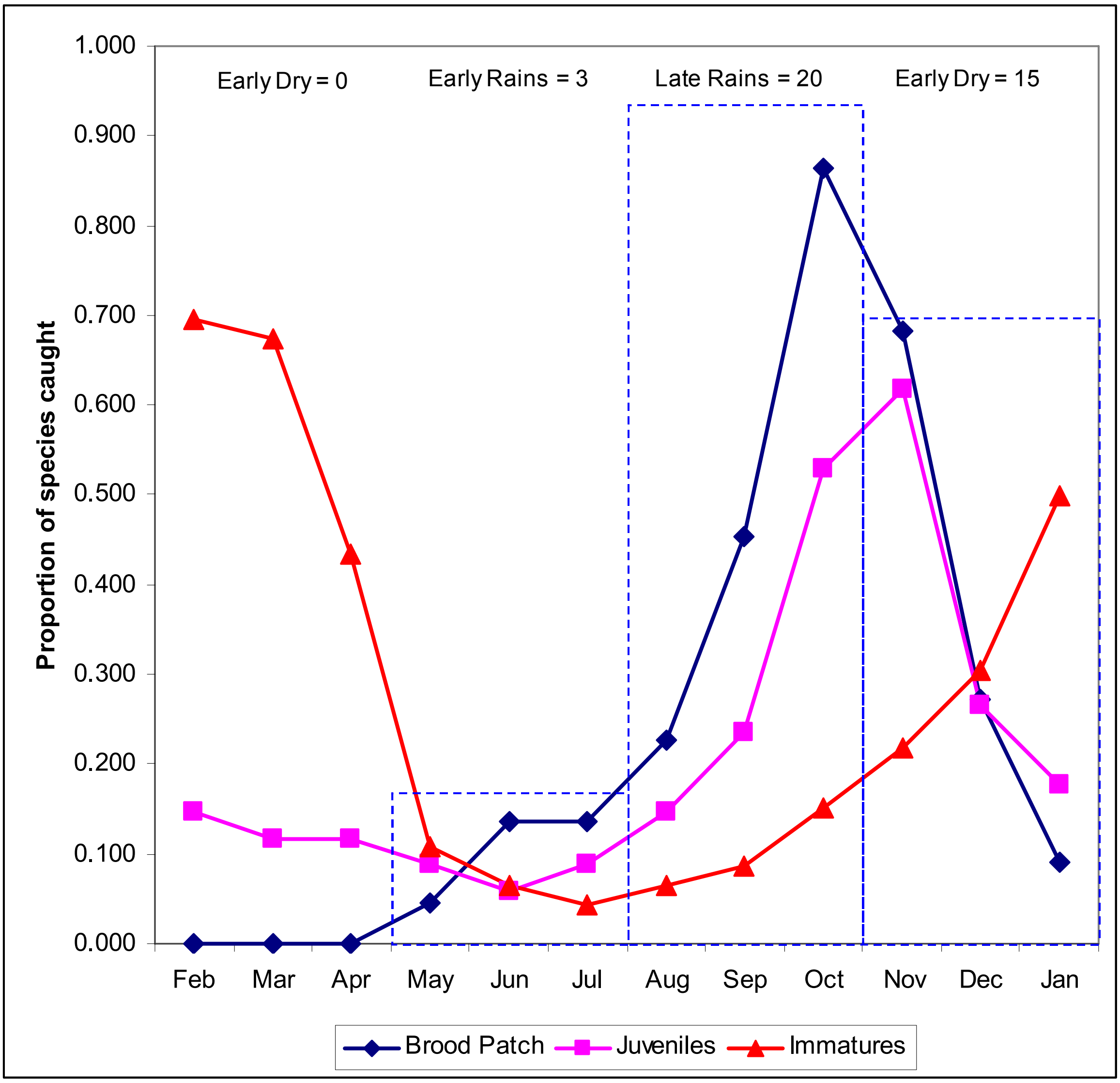
Data analysis

Comparison of data generated from dates introduces both logical and statistical problems when individuals have data at both the start and end of the year. To counter this, all data were plotted on a scale spanning two years with brood patch dates always considered to occur earlier than dates for juvenile/immature presence. The breeding period was therefore identified from reasonably continuous sequences of data with mean dates (of both brood patch and juvenile occurrence) calculated from these. Timing and duration of breeding periods was compared for and between members of families and guilds (using one-way analysis of variance). General linear models were used to assess relationships between timing and duration of breeding in relation to seasonality. For this, seasons were determined as Late dry – February to April, Early rains – May to July, Late rains – August to October or Early dry – November to January.

Results

The capture of 1939 juveniles, 2918 immatures and 633 adults with active brood patches enabled assessment of likely breeding periods for 6 non-passerine and 36 passerine species of Nigerian birds.

Figure 1. Proportion of species caught having juveniles, immatures and adults with brood patches in the population. Columns represent number of species recorded breeding (i.e. species with active brood patches) during each of the seasons.



Juveniles, immatures and adults with brood patches were caught in all months of the year (Figure 1). The peak period for breeding across all species occurred from the late rainy season into the early dry season. More than 90%) of the 22 species assessed here had brood patches in October (Table 2). Juvenile occurrence peaked one month later (21 of 34 species) and the peak presence of immatures (32 of 46 species) occurred four months later, in February. Mean capture date for juveniles was 8

October ± 16.38 (se), nine months earlier than that for immatures (4 July ± 22.15) when using the same group of 40 species.

Table 2. Timing of occurrence of brood patches on birds caught in mist-nets in Nigeria. No. days identifies the duration in days between the confidence intervals.

Species	Mean date ± se	Breeding Range	Duration (days)	n
Pogoniulus chrysoconus	31 Jul ± 26.83	22 Jan – 10 Dec	323	18
Lybius vielloti	28 Oct ± 13.6	25 Sep – 15 Jan	112	6
Pycnonotus barbatus	1 Aug ± 33.73	1 Feb – 10 Dec	314	12
Cisticola cantans	18 Nov ± 17.44	16 Oct – 1 Apr	167	8
Camaroptera brachyura	11 Oct ± 6.04	17 Sep – 10 Nov	54	11
Heliolais erythropterus	21 Sep ± 10.67	4 Sep – 19 Oct	45	5
Sylvietta brachyura	11 Oct ± 8.58	17 Sep – 31 Oct	44	5
Zosterops senegalensis	12 Dec ± 19.97	24 Sep – 21 Apr	209	14
Emberiza tahapisi	5 Nov ± 8.34	9 Oct – 11 Dec	62	8
Ploceus vitellinus	17 Oct ± 2.99	25 Sep – 6 Nov	42	15
Ploceus cucullatus	19 Oct ± 2.36	19 Sep – 7 Nov	49	21
Euplectes hordeaceus	28 Oct ± 3.96	17 Oct – 8 Nov	22	5
Euplectes franciscanus	30 Oct ± 0.92	24 Sep – 9 Dec	76	221
Euplectes macrourus	14 Oct ± 2.52	*25 Sep – 20 Oct*	25	10
Estrilda caerulescens	19 Oct ± 9.99	29 Aug – 15 Jan	139	12
Estrilda troglodytes	29 Oct ± 4.49	19 Oct – 11 Nov	23	6
Uraeginthus bengalus	19 Oct ± 3.36	29 Aug – 17 Mar	200	45
Ortygospiza atricollis	12 Nov ± 25.11	17 Sep – 16 Feb	152	7
Lagonosticta rufopicta	28 Oct ± 16.40	18 Sep – 31 Jan	135	7
Lagonosticta senegala	25 Nov ± 7.63	7 Sep – 18 Apr	223	56
Lagonosticta sanguinodorsalis	15 Nov ± 2.41	10 Sep – 23 Apr	225	38
Spermestes cucullata	26 Oct ± 4.16	1 Oct – 10 Nov	40	12

Mean difference in capture dates between juveniles and immatures (Table 3) was just over 5 months (158 days). The capture periods of immatures of certain species of both non-passerines and non-passerines (Figure 2) (e.g. *S.hypopyrrha, E.franciscanus* and *U.bengalus*) occurred during discrete time periods and within a short time of those for juveniles, however, for many others (e.g. *Z.senegalensis* and *L.sanguinodorsalis*) the capture periods for immatures were more variable and occurred at least three months later than for juveniles. Protracted breeding seasons and the unknown variability in timing of post-juvenile moult (e.g. see Glutz von Blotzheim & Bauer (1991), Iovchenko & Smirnov (1987)) therefore meant that the use of capture dates of immature birds was unreliable in identifying breeding period and I therefore concentrated solely on capture dates of juveniles and the occurrence of brood patches in adults.

Table 3. Mean dates (± standard error) of occurrence of juvenile and immature birds in mist-net catches. Capture range indicates the dates between which juveniles or immatures were caught.

Species	Age	Mean date ± se	Capture range	No. days	n
Columbidae					
Streptopelia hypopyrrha	Juv	25 Mar ± 11.47	19 Jan – 15 Apr	86	7
	Imm	31 Mar ± 4.22	25 Sep – 8 May	215	86
Streptopelia vinacea	Imm	1 Mar ± 16.32	31 Jan – 22 Apr	81	5
Streptopelia senegalensis	Imm	19 Apr ± 3.56	26 Mar – 13 May	48	15
Turtur abyssinicus	Imm	5 Mar ± 7.85	12 Aug – 30 Apr	261	44
Coliidae					
Colius striatus	Juv	23 Sep ± 15.77	18 Jun – 20 Nov	155	10
	Imm	18 Nov ± 22.97	19 Sep – 19 Apr	212	11
Meropidae					
Merops bulocki	Juv	18 Apr ± 6.57	8 Mar – 13 Jun	97	15
	Imm	28 Mar ± 9.02	22 Oct – 3 May	193	27
Indicatoridae					
Indicator indicator	Juv	6 Oct ± 17.49	18 Jun – 5 Apr	291	20
	Imm	22 Feb ± 11.47	16 Aug – 13 May	270	36
Pycnonotidae					
Pycnonotus barbatus	Juv	9 Nov ± 6.01	4 Oct – 28 Nov	55	10
	Imm	23 May ± 24.03	3 Mar – 10 Dec	282	13
Cisticolidae					
Camaroptera brachyura	Juv	9 Nov ± 8.56	9 Oct – 20 Mar	162	21
	Imm	25 Jan ± 11.82	17 Sep – 10 Apr	126	33
Cisticola aberrans	Juv	30 Oct ± 7.23	4 Oct – 15 Nov	42	5
	Imm	9 Oct ± 29	20 Jun – 7 Dec	256	5
Cisticola cantans	Juv	24 Oct ± 10.54	30 Sep – 11 Dec	72	6
	Imm	31 Dec ± 30.63	3 Oct – 11 Apr	190	7
Heliolais erythropterus	Imm	13 Feb ± 2.06	7 Feb – 18 Feb	11	7
Prinia subflava	Imm	1 Dec ± 37.29	15 Aug – 31 Mar	228	7
Sylviidae					
Eremomela pusilla	Imm	16 Jan ± 24.66	10 Oct – 21 Apr	193	9
Sylvietta brachyura	Imm	6 Feb ± 21.62	6 Oct – 17 Apr	193	9
Muscicapidae					
Melaenornis pallidus	Imm	4 Apr ± 19.22	8 Dec – 10 Jun	184	8
Cossypha niveicapilla	Juv	10 Oct ± 15.05	1 Sep – 20 Nov	80	5
	Imm	24 Feb ± 12.68	10 Sep – 11 Jul	304	64
Cercomela familiaris	Juv	3 Sep ± 20.19	7 May – 5 Dec	212	14
	Imm	8 Feb ± 9.99	13 Aug – 17 May	277	42
Turdidae					
Turdus pelios	Juv	1 Oct ± 7.48	17 Jun – 21 Nov	157	28
	Imm	12 Feb ± 7.95	17 Sep – 16 Jun	272	120
Platysteiridae					
Platysteira cyanea	Juv	23 Dec ± 9.67	18 Nov – 27 Jan	70	11
	Imm	20 Mar ± 8.53	30 Oct – 9 May	191	25
Zosteropidae					
Zosterops senegalensis	Juv	25 Oct ± 5.43	24 Sep – 27 Nov	64	14
Nectariniidae					
Cyanomitra verticalis	Juv	24 Oct ± 7.62	11 Aug – 3 Dec	114	21
	Imm	5 Feb ± 16.35	15 Sep – 1 May	228	25
Chalcomitra senegalensis	Juv	27 Nov ± 11.89	18 Aug – 19 Apr	255	44
	Imm	5 Feb ± 6.37	12 Aug – 14 Jun	305	159
Cinnyris venustus	Juv	10 Jul ± 16.73	15 Jan – 8 Dec	342	40
	Imm	27 Apr ± 7.67	8 Feb – 21 Oct	255	67
Cinnyris pulchellus	Imm	25 Feb ± 2.17	31 Jan – 11 Aug	192	119
Malaconotidae					
Malaconotus sulfureopectus	Juv	20 Aug ± 44.90	21 Mar – 13 Dec	267	7
	Imm	14 Mar ± 17.61	1 Nov – 13 May	193	14
Laniarius barbarus	Juv	20 Nov ± 1.99	14 Nov – 25 Nov	12	5
	Imm	28 Feb ± 17.80	3 Oct – 12 May	221	19
Sturnidae					
Lamprotornis purpureus	Imm	17 May ± 24.60	21 Apr – 17 Sep	149	6

Emberizidae					
Emberiza tahapisi	Juv	3 Feb ± 15.02	12 Oct – 16 Apr	186	17
	Imm	27 Mar ± 3.85	30 Oct – 24 Apr	176	75
Fringillidae					
Serinus mozambicus	Imm	16 Feb ± 5.25	10 Dec – 24 Feb	76	14
Passeridae					
Petronia dentata	Juv	12 Mar ± 28.23	26 Oct – 19 Apr	175	6
	Imm	15 Mar ± 16.01	10 Dec – 20 Apr	131	11
Ploceidae					
Ploceus luteolus	Juv	8 Nov ± 12.62	25 Sep – 5 Dec	71	5
	Imm	13 Nov ± 16.94	13 Aug – 5 Apr	235	23
Ploceus vitellinus	Juv	7 Nov ± 7.57	15 Sep – 19 Jun	277	45
	Imm	13 Jan ± 12.32	12 Aug – 21 Jun	312	73
Ploceus heuglini	Juv	23 Jan ± 31.31	21 Oct – 12 May	203	8
	Imm	29 Apr ± 11.78	11 Feb – 19 Aug	189	28
Ploceus cucullatus	Juv	14 Oct ± 8.23	22 Apr – 7 Dec	229	29
	Imm	14 Jul ± 7.21	28 Jan – 9 Dec	315	168
Ploceus nigricollis	Juv	3 Nov ± 6.93	22 Aug – 10 Mar	200	38
	Imm	11 Feb ± 11.81	12 Aug – 11 May	272	36
Euplectes hordeaceus	Juv	29 Oct ± 2.03	21 Oct – 6 Nov	16	9
	Imm	30 Jan ± 36.94	24 Sep – 14 May	232	7
Euplectes franciscanus	Juv	6 Nov ± 1.46	7 Oct – 24 Apr	189	268
	Imm	4 Dec ± 5.81	12 Aug – 17 Mar	217	86
Estrildidae					
Pytilia phoenicoptera	Juv	16 Jan ± 13.25	10 Dec – 24 Feb	76	7
Estrilda caerulescens	Juv	25 Nov ± 4.40	9 Oct – 9 Mar	151	38
	Imm	3 Mar ± 7.34	16 Aug – 21 Jun	309	85
Uraeginthus bengalus	Juv	28 Nov ± 5.13	10 Oct – 27 Jan	109	30
	Imm	27 Jan ± 10.16	20 Aug – 20 Apr	243	35
Ortygospiza atricollis	Imm	26 May ± 24.41	21 Mar – 21 Aug	153	8
Lagonosticta rufopicta	Imm	21 Jan ± 30.60	17 Aug – 11 May	267	11
Lagonosticta senegala	Juv	9 Jan ± 7.40	20 Oct – 5 May	197	53
	Imm	2 Mar ± 4.93	23 Aug – 11 Jul	322	154
Lagonosticta sanguinodorsalis	Juv	11 Dec ± 6.90	16 Oct – 16 Mar	156	44
	Imm	8 Mar ± 6.08	9 Aug – 22 May	286	88
Lagonosticta rara	Imm	3 Jun ± 28.72	31 Jan – 30 Oct	272	10
Spermestes cucullata	Juv	6 Nov ± 2.68	24 Sep – 1 Mar	158	108
	Imm	20 Feb ± 2.76	27 Sep – 29 Apr	214	312
Viduidae					
Vidua chalybeata	Juv	15 Nov ± 2.21	29 Oct – 20 Nov	22	9
	Imm	13 Dec ± 48.19	19 Aug – 9 Dec	212	5

Too few non-passerine species (three) were caught as both juveniles and adults with brood patches to allow meaningful comparison of the timing of these two events. In contrast, 39 species of passerines had both pieces of data and of these, 11 species had more than 10 samples for each variable. *Pycnonotus barbatus* and *Zosterops senegalensis* were excluded from analyses because of known issues with determination of juvenile/immature status (inexperienced fieldworkers frequently misidentified ages in these species). For the nine remaining species, mean juvenile capture date (21 Nov ± 18 days) was significantly later than mean date of brood patch presence in adults (28 Oct ± 12 days; paired *t*-test, $t(8) = -5.3$, $p = 0.001$) and the two were significantly related, ($t(8) =$

3.5, p = 0.011, R^2 = 0.692) (Figure 3). The presence of juveniles in catches was therefore considered a suitable and reasonably reliable method of identifying breeding periods for species with limited brood patch data. Based on the results for the nine species assessed above, I assumed that breeding periods occurred around 24 days earlier than the mean date of juvenile capture. Aside from the nine species having data for both juvenile capture and brood patch occurrence, data for eight other species were used to predict timing of breeding based on brood patch occurrence alone and 17 using just timing of juvenile capture. Because brood patch presence is a more reliable indicator of timing of breeding period, this was always used in preference and analyses using timing of juvenile occurrence used only when insufficient data on brood patches were available.

Timing of breeding

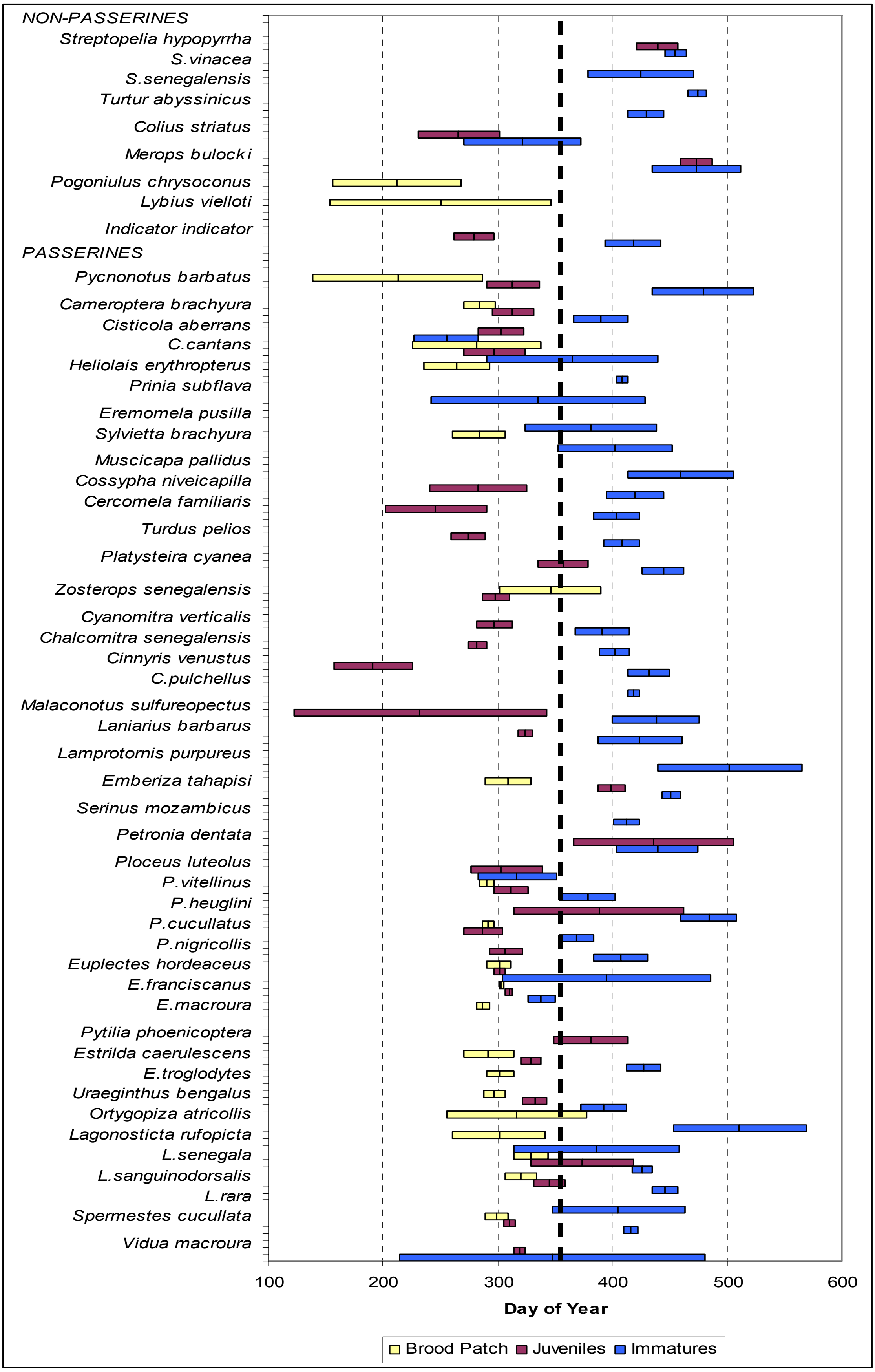
Non-passerines

Few data were available for assessing timing of brood patch presence or juvenile occurrence in the non-passerines and all mean dates reported here are subject to considerable variability. Assessment of timing of brood patch presence was possible in the Lybiidae (comprising *Lybius vieillotti* and *Pogoniulus chrysoconus*) only. Data were available to assess timing of breeding periods on the basis of capture of juveniles for four non-passerine species, (*Streptopelia hypopyrrha*, *Colius striatus*, *Merops bulocki* and *Indicator indicator* - Figure 2).

Passerines

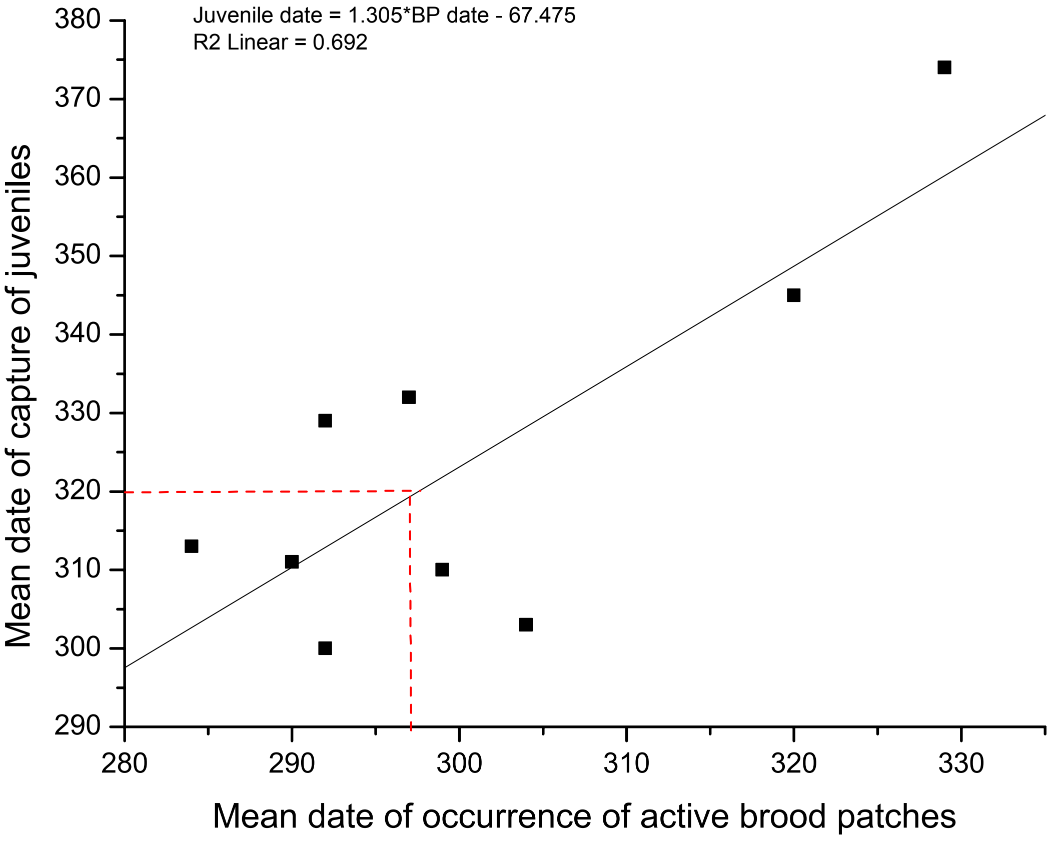
Sufficient data were available for 16 species from 6 families to assess timing of breeding season based on brood patch presence. As expected, mean date for brood patch presence varied widely across the 16 species from 1 June in *S.cucullatus* to 1 November in *Estrilda troglodytes* i.e. from the middle of the rainy season to the early dry season (Figure 2). Mean date of brood patch presence across these species was 6 September ± 43 days. Data on the timing of occurrence of juveniles in captures were

Figure 2. Mean timing of occurrence of brood patches, capture of juveniles and immatures (± 95% confidence intervals) for a range of non-passerine and passerine bird species. Species are grouped by family. Bold vertical dashed line indicates start/end of year.



available for identification of breeding periods in a further 18 species from 10 families. In these species, the range of mean dates of capture of juveniles was as wide as for the brood patch data (from 12 May in *Petronia dentata* to 16 January in *Pytilia phoenicoptera*). Breeding in these species was similarly concentrated in the period between the mid-late rains and early-mid dry season (Figure 2) with the mean date of juvenile occurrence 27 September ± 82 days.

Figure 3. Scatter plot of mean date of juvenile occurrence on mean date of brood patch presence in adults. Dotted line identifies 23-day mean difference between date of brood patch occurrence and capture of juveniles.



Family summaries

A summary of the timing of breeding for each of the families caught during the study based on either brood patch or juvenile capture data is given below. The power of the statistical comparisons between species within families was low in most cases because of small sample sizes. I proceeded with assessment despite this in order to identify whether or not determination of general breeding periods for each family was possible. In the following summaries, *n* denotes the number of individuals.

Columbidae

No data were available on brood patch presence for this family and determination of main breeding was possible using dates of capture of juveniles for only one species, *Streptopelia hypopyrrha* (*n* = 7). Juveniles of this species were caught between January and April with the mean date occurring in March. Based on these data breeding is likely to occur between December and March each year.

Lybiidae

27 individuals from two barbet species (*L.vielloti* and *P.chrysoconus*) were available for assessment of timing of brood patch presence. No significant variation in the timing of breeding was detected between the two species (Kruskal-Wallis, *K* = 0.15, df = 1, *p* = 0.7) and the mean date of breeding for the family was identified as 19 August (se ± 19.08, n = 27).

Coliidae

No data were available to assess timing of breeding on the basis of brood patch presence however 10 juvenile *Colius striatus* were caught during the study and these were used instead. Since juveniles were caught between June and November (Table 3), the main breeding season is likely to occur between April and September for this species.

Meropidae

Data for assessing breeding periods was only available in the form of catches of juveniles and this for one species only (*Merops bullocki, n* = 15 – Table 3). Juveniles were caught mostly between February and April each year suggesting a breeding season of January – April.

Indicatoridae

21 juveniles were caught during the course of the study, of which 20 were *Indicator indicator* (Table 3). Juveniles of this species were caught throughout the year suggesting a prolonged and variable breeding season dependent on the timing of breeding of their hosts.

Pycnonotidae

13 individuals of two species were caught with active brood patches although only *Pycnonotus barbatus* had sufficient data (*n* = 12) to allow determination of timing of breeding from this. Active brood patches were identified on individuals throughout the year making determination of a specific breeding period difficult. To try and narrow these dates the timing of occurrence of juveniles in catches was also assessed. Ten were caught in total, all between October and November suggesting a main breeding period here covering September and October.

Cisticolidae

33 individuals of three species were caught which had active brood patches, however only *Camaroptera brachyura* (*n* = 11), *Heliolais erythropterus* (*n* = 5) and *Cisticola cantans* (*n* = 9) had sufficient data for individual assessment of timing of breeding. Mean date of brood patch presence did not vary significantly between these species (*K* = 5.6, df 2, *p* = 0.06, *n* = 25) and the overall mean across the family was 4 October ± 28 days (se ± 6.36). *H.erythropterus* was the earliest breeder and *C.brachyura* the latest (Table 2). Additionally, the mean date of capture of juvenile *Cisticola aberrans* occurred at a similar time of year (Table 3).

Sylviidae

13 individuals of three species in this family were caught that had active brood patches but, of these, only *Sylvietta brachyura* had sufficient data (*n* = 5) to assess timing of breeding (Table 2). Brood patches were observed on individuals between September and October identifying this as the peak breeding period.

Muscicapidae

Only four individuals were caught with active brood patches and assessment of timing of breeding period was not possible using this method. Two other species were caught in sufficient numbers to assess breeding based on timing of capture of juveniles (*Cossypha niveicapilla* (n = 5) and *Cercomela familiaris* (n = 14) – Table 3). Juvenile *C.familiaris* were caught throughout a large portion of the year whereas the period of occurrence of *C.niveicapilla* in mist net catches was much shorter (81 days between September and November). Despite this, timing of capture of juveniles did not vary significantly between the two species ($K = 0.42$, df = 1, $p = 0.52$, $n = 19$), allowing the calculation of a mean date (± se) of juvenile occurrence for the family of 22 September ± 18.5 and main breeding periods for *C.familiaris* during the rainy season (March to November), and for *C.niveicapilla* of August to October.

Turdidae

During the course of the study 28 juvenile *Turdus pelios* were caught between June and November each year. Despite this apparently broad range of dates, the majority of captures occurred between September and October (Table 3) suggesting a peak breeding period between July and September.

Platysteiridae

Insufficient data were available to assess mean date of brood patch presence for any species from this family. All 11 *Platysteira cyanea* juveniles were caught between November and January with a mean date of capture towards the end of December (Table 3). This suggests a concentration of breeding in this species between October and January.

Zosteropidae

Only one species regularly occurs in the study area and 14 individuals were caught that were actively engaged in breeding activities. Brood patches were evident throughout a large portion of the year (September – April – Table 2) with mean breeding activity centred in December.

Nectariniidae

Few (n = 5) sunbirds were caught which carried active brood patches and assessment of timing of breeding was therefore based solely on timing of capture of juveniles. Five species were caught as juveniles, however only three of these (*Cyanomitra verticalis* (n = 21), *Chalcomitra senegalensis* (n = 44) and *Cinnyris venustus* (n = 41)) were caught in sufficient numbers to assess breeding period (Table 3). Timing of capture of juveniles varied significantly between these three species (K = 14.4, df = 2, p = 0.001, n = 105)). Although juvenile *C.venustus* were recorded throughout the year, the mean date was earliest in this species (July), with means of both *C.senegalensis* and *C.verticalis* occurring in October.

Malaconotidae

Nine individuals of species in this family were caught that had active brood patches however this was not sufficient to assess timing of breeding based on this characteristic. Four species were caught as juveniles however only two (*Malaconotus sulfureopectus* (n = 7) and *Laniarius barbarus* (n = 5)) were caught in sufficient numbers to use this data to make some assessment of timing of breeding (Table 3). Although mean date of capture was in August for *M.sulfureopectus* and November for *L.barbarus,* the range of dates meant that dates of capture overall did not vary significantly between the two species (K = 0.8, 1 df, p = 0.37, n = 12). The overall family mean for date of capture of juveniles here was 5 October ± 46.

Emberizidae

The only bunting to occur regularly in catches during the course of the study was *Emberiza tahapisi* and only 8 of the adults assessed had active brood patches. This species appeared to have a protracted breeding season with individuals recorded as having active brood patches between October and April, however the mean date for breeding occurred in November (Table 2). This breeding period is also suggested when assessing timing of capture of juveniles (Table 3), the mean date for which occurs during early February.

Passeridae

Six juvenile *Petronia dentata* were caught during the study, all between October and April. The mean date of capture occurred in March and, from the range of dates the main breeding period in the study area was determined to lie between September and April.

Ploceidae

286 individuals of seven species were caught that had active brood patches however only five species had sufficient data for analysis of timing of breeding (Table 2). Timing of brood patch presence varied significantly between these five species (K = 41.8, df 4, p < 0.001, n = 280) although the mean date for all five species varied by no more than 16 days, *Euplectes macrourus* (n = 10) being the earliest (14 October) and *E.franciscanus* (n = 229) the latest (30 October). In addition, three other species (*Ploceus luteolus* (n = 5)*, P.heuglini* (n = 8) and *P.nigricollis* (n = 38)) were caught in sufficient numbers to allow assessment of breeding periods based on juvenile presence (Table 3). Timing of juvenile occurrence varied significantly between the seven species having sufficient data (K = 24.8, df = 6, p < 0.001, n = 402) however there was no significant variation between the three species for which this was the only means of assessing timing of breeding (K = 5.4, df = 2, p = 0.07, n = 51). The mean date of juvenile occurrence across these species was 2 December ± 114 days (se = 26.21). The range of dates of juvenile capture suggested a breeding period lying between August and March.

Estrildidae

204 individuals of 11 species were caught that had active brood patches although only eight of these had sufficient numbers to use this to assess timing of breeding. Timing of brood patch occurrence varied significantly across these eight species (K = 19.1, df 7, p = 0.008, n = 196) although mean date for all species occurred between mid-October and mid-November. Additionally, juvenile *Pytilia phoenicoptera* were caught in sufficient numbers to identify the main breeding period (Table 3), which,

given the range of dates of capture of juveniles (December to February), is most likely to be between October and February.

Viduidae

Members of this family are brood parasites and assessment of breeding seasons is therefore based entirely on the timing of occurrence of juveniles in mist-net captures. Sufficient data (n = 9) were available to identify breeding periods for *Vidua chalybeata* (Table 3) only which, given the range of dates of capture of juveniles (October to November), suggests a likely breeding period for these birds between September and November.

Seasonality of breeding

Timing of breeding across the 42 species was not evenly spread between the seasons and occurred predominantly during the late rains and early dry season ($X^2_3 = 36.5$, $p < 0.001$) (Table 4; Figure 1). The majority of species (29 of 42) started breeding during the 92-day late-rains period and at least part of the breeding period occurred during this season in 38 of the 42 species. The entire breeding period was located within this season for six species, and at least half of the breeding period occurred here for a further eight. In most cases (for 16 species), where breeding was not contained entirely within the late-rainy season, it extended into the early dry season (rather than starting in the early rains and extending into the late rains). 32 species bred at some point within the early dry season with just two completing their breeding entirely within this season. Few species started to breed during the late dry or early rainy seasons and only one species (*M.bullocki*) was recorded to breed entirely during these seasons. There was little taxonomic difference in seasonality of breeding mostly because of the widespread occurrence of breeding during the late rainy season. The breeding season was protracted for many species with 16 breeding throughout more than nine months of the year.

Table 4. Identification of breeding seasonality in 42 West African savannah bird species. Breeding durations determined from dates of capture of juveniles (J) or of occurrence of active brood patches (BP). Number of days denotes the length of breeding period for the species occurring during that season. Percentages and cell colours identify the proportion of the total breeding period for that species occurring during that season (Blank 0%, ░ <10%, ▒ 10 – 49%, ▓ 50 – 89%, 🟥 ≥ 90%).

Species	**Method**	**Late Dry (Feb – Apr)**	**Early Rains (May – Jul)**	**Late Rains (Aug – Oct)**	**Early Dry (Nov – Jan)**
Streptopelia hypopyrrha	J	44 days (51%)			42 days (49%)
Colius striatus	J		73 days (47%)	82 days (53%)	
Merops bullocki	J	84 days (87%)	13 days (13%)		
Indicator indicator	J	33 days (11%)	74 days (25%)	92 days (32%)	92 days (32%)
Pogoniulus chrysoconus	BP	89 days (28%)	92 days (28%)	92 days (28%)	50 days (15%)
Lybius vielloti	BP			37 days (33%)	75 days (67%)
Pycnonotus barbatus	BP	89 days (28%)	92 days (29%)	92 days (29%)	41 days (13%)
Cisticola aberrans	J			42 days (100%)	
Cisticola cantans	BP	59 days (35%)		16 days (10%)	92 days (55%)
Camaroptera brachyura	BP			45 days (82%)	10 days (18%)
Heliolais erythropterus	BP			45 days (100%)	
Sylvietta brachyura	BP			44 days (100%)	
Cossypha niveicapilla	J			80 days (100%)	
Cercomela familiaris	J	24 days (11%)	92 days (43%)	92 days (43%)	4 days (2%)
Turdus pelios	J		75 days (48%)	82 days (52%)	
Platysteira cyanea	J			12 days (17%)	58 days (83%)
Zosterops senegalensis	BP	79 days (38%)		38 days (18%)	92 days (44%)
Cyanomitra verticalis	J		19 days (17%)	92 days (81%)	3 days (3%)
Chalcomitra senegalensis	J	59 days (23%)	12 days (5%)	92 days (36%)	92 days (36%)
Cinnyris venustus	J	89 days (26%)	92 days (27%)	92 days (27%)	69 days (20%)
Malaconotus sulfureopectus	J	69 days (26%)	92 days (34%)	92 days (34%)	14 days (5%)
Laniarius barbatus	J			12 days (100%)	
Emberiza tahapisi	BP			21 days (34%)	41 days (66%)
Ploceus luteolus	J			67 days (94%)	4 days (6%)
Ploceus heuglini	J	71 days (35%)		40 days (20%)	92 days (45%)
Ploceus nigricollis	J	8 days (4%)	8 days (4%)	92 days (46%)	92 days (46%)
Ploceus vitellinus	BP			36 days (86%)	6 days (14%)
Ploceus cucullatus	BP			42 days (86%)	7 days (14%)
Euplectes hordeaceus	BP			14 days (64%)	8 days (36%)
Euplectes franciscanus	BP			37 days (49%)	39 days (51%)
Euplectes macrourus	BP			25 days (100%)	
Pytilia phoenicoptera	J				76 days (100%)
Estrilda caerulescens	BP			63 days (45%)	76 days (55%)
Estrilda troglodytes	BP			12 days (52%)	11 days (48%)
Uraeginthus bengalus	BP	45 days (23%)		63 days (32%)	92 days (46%)
Ortygospiza atricollis	BP	16 days (11%)		44 days (29%)	92 days (61%)
Lagonosticta rufopicta	BP			43 days (32%)	92 days (68%)
Lagonosticta senegala	BP	77 days (35%)		54 days (24%)	92 days (41%)
Lagonosticta sanguinodorsalis	BP	82 days (36%)		51 days (23%)	92 days (41%)
Spermestes cucullata	BP			30 days (75%)	10 days (25%)
Vidua chalybeata	J			2 days (9%)	20 days (91%)

Duration of breeding period

Mean duration of the breeding period, based on dates of capture of individuals with brood patches, was around 18 weeks (121.9 days ± 20.02 (se), n = 22) although the periods for individual species ranged from 22 days (in *E.hordeaceus*) to 323 days (in *P.chrysoconus*) (Table 2). Duration of breeding periods based on juvenile captures were slightly longer, (152.08 days ± 20.13, *n* = 39) but not significantly so (*t*(13) = -0.7, *p* = 0.5). The range of durations based on capture of juveniles was less than that for brood patches (12 – 342 days - in *Laniarius barabarus* and *Cinnyris venustus* respectively). The wide ranges of breeding periods, even within families, meant that duration of breeding period did not vary between the four families for which there were sufficient data (Table 5). Similarly there were no significant differences in the length of breeding durations between guilds (Table 6).

Table 5. One-way ANOVA comparing duration of breeding periods between families using both brood patch and timing of juvenile capture data. Levene's Test : $F_{3,21} = 1.72$, $p = 0.193$

	Sum of squares	df	F	Sig.
Between Groups	41255.7	3	2.03	0.14
Within Groups	141828.3	21		
Total	183084	24		

Post Hoc Tukey Tests

Family A	Family B	Mean Difference	S.E	Sig.
Cisticolidae	Estrildidae	-57.78	49.39	0.652
	Nectariniidae	-118.25	58.11	0.207
	Ploceidae	-9	50.33	0.998
Estrildidae	Cisticolidae	57.78	49.39	0.652
	Nectariniidae	-60.47	49.39	0.619
	Ploceidae	48.78	39.93	0.621
Nectariniidae	Cisticolidae	118.25	58.11	0.207
	Estrildidae	60.47	49.39	0.619
	Ploceidae	109.25	50.33	0.164
Ploceidae	Cisticolidae	9	50.33	0.998
	Estrildidae	-48.78	39.93	0.621
	Nectariniidae	-109.25	50.33	0.164

Table 6. One-way ANOVA comparing duration of breeding periods between guilds using both brood patch and timing of juvenile capture data. Levene's Test : $F_{3,38} = 1.84$, $p = 0.157$

	Sum of squares	df	F	Sig.
Between Groups	49321.7	3	2.01	0.13
Within Groups	311540.8	38		
Total	360862.5	41		

Post Hoc Tukey Tests

Guild A	Guild B	Mean Difference	S.E	Sig.
Frugivore	Granivore	90	45.27	0.21
	Insectivore	69	47.65	0.478
	Nectarivore	2.75	60.74	1
Granivore	Frugivore	-90	45.27	0.21
	Insectivore	-21	32.26	0.915
	Nectarivore	-87.25	49.59	0.308
Insectivore	Frugivore	-69	47.65	0.478
	Granivore	21	32.26	0.915
	Nectarivore	-66.25	51.77	0.581
Nectarivore	Frugivore	-2.75	60.74	1
	Granivore	87.25	49.59	0.308
	Insectivore	66.25	51.77	0.581

Breeding period by guild

The distribution of overall mean date of breeding periods shows a concentration of breeding during the late rains in all guilds (Figure 4). Despite this there was a significant difference in timing of breeding between the four guilds used here, both when using the brood patch data alone and when supplementing this with the additional species whose breeding periods were determined from the timing of capture of juveniles (Table 7 & 8). In contrast to the other three guilds, the overall mean date of breeding for frugivores occurred in the early rains. This was apparent when pairwise comparisons of guilds were made when the only significant differences in timing were observed between the frugivores and both the granivores and insectivores. But this was only the case when the dataset was restricted to just the 22 species with brood patch data. When the juvenile data were included, the only significant difference in timing of breeding between guilds occurred between frugivores and granivores.

Figure 4. Box plot showing variation in timing of breeding by guild based on both date of brood patch occurrence and (for species with insufficient brood patch data) timing of capture of juveniles. Boxes identify 25-75th percentiles and median. Range bars identify 1-99th percentiles. Means are given as filled squares, outliers are identified by asterisks and dotted lines indicate seasons.

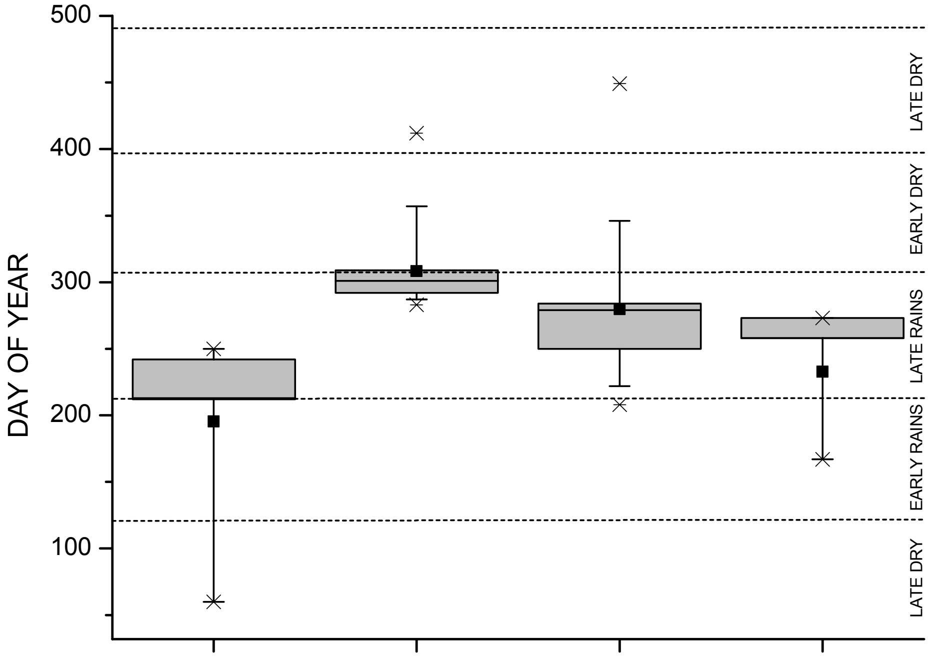


Table 7. One-way ANOVA comparing timing of breeding between guilds using brood patch data only. Levene's Test : $F_{2,19} = 2.44$, $p = 0.114$

	Sum of squares	**df**	**F**	**Sig.**
Between Groups	14955.9	2	21.01	<0.001
Within Groups	6762.9	19		
Total	21718.8	21		

Post Hoc Tukey Tests

Guild A	**Guild B**	**Mean Difference**	**S.E**	**Sig.**
Frugivore	**Granivore**	**-77.714**	**12.003**	**< 0.001**
	Insectivore	**-67.0**	**13.78**	**< 0.001**
Granivore	**Frugivore**	**-77.714**	**12.003**	**< 0.001**
	Insectivore	10.714	9.83	0.532
Insectivore	**Frugivore**	**67.0**	**13.78**	**< 0.001**
	Granivore	-10.714	9.839	0.532

Table 8. One-way ANOVA comparing timing of breeding between guilds using both brood patch and timing of juvenile capture data. Levene's Test : $F_{3,38} = 0.57$, $p = 0.638$

	Sum of squares	**df**	**F**	**Sig.**
Between Groups	41313.3	3	3.61	0.022
Within Groups	144837.1	38		
Total	186150.4	41		

Post Hoc Tukey Tests

Guild A	**Guild B**	**Mean Difference**	**S.E**	**Sig.**
Frugivore	**Granivore**	**-94.5**	**30.87**	**0.020**
	Insectivore	-58.17	32.16	0.285
	Nectarivore	-37.27	45.09	0.842
Granivore	**Frugivore**	**94.5**	**30.87**	**0.020**
	Insectivore	36.33	21.51	0.344
	Nectarivore	57.23	38.22	0.449
Insectivore	Frugivore	58.17	32.16	0.285
	Granivore	-36.33	21.51	0.344
	Nectarivore	20.9	39.28	0.951
Nectarivore	Frugivore	37.27	45.09	0.842
	Granivore	-57.23	38.22	0.449
	Insectivore	-20.9	39.28	0.951

Discussion

Potential sources of error

Determination that an individual is engaged in breeding can be achieved by many means (e.g. discovery of nests and eggs/chicks) but in a field situation it is perhaps easiest through direct observation of behavioural cues such as a parent carrying food, or making repeated visits to a piece of vegetation, distraction behaviour, or copulation and reinforcement of pair bonds between adults. In this study, identification of timing and duration of breeding periods was made through assessment of the timing of presence of physiological signs in adults (i.e. the presence of active brood patches) and in young birds (plumage characteristics). Approaches such as these, which are based on assessment rather than measurement, are inevitably open to a degree of subjectivity. During the course of the study attempts were made to minimise observer effect by including data on brood patches from one field worker only. Although reducing the effect of variation between recorders, this did not remove the temporal variability in assessment by an individual (i.e. an individual may have scored a brood patch as three on one day and as a two on the following day). This was known to occur on a number of occasions, but in most instances will not have affected the analyses since brood patch scores of two, three or four were all treated as ‘active’. There may have been occasions where individuals with a brood patch score of one or five (i.e. just starting or nearly finished – inactive) were scored as two or four, and therefore misidentified as ‘active’, however this was likely to have been infrequent and its infrequency should not have significantly affected the results. In a similar manner, ageing of individuals is open to considerable subjectivity and the use of data generated by inexperienced field staff will have included individuals that had been aged incorrectly. Inclusion of such data (i.e adults or immatures aged as juveniles) may have resulted in a positive bias to the duration of the breeding period and an alteration to the mean date of breeding. Where possible, only those data obtained from experienced fieldworkers were included, however this does not guarantee that all individuals were aged, or indeed recorded, correctly.

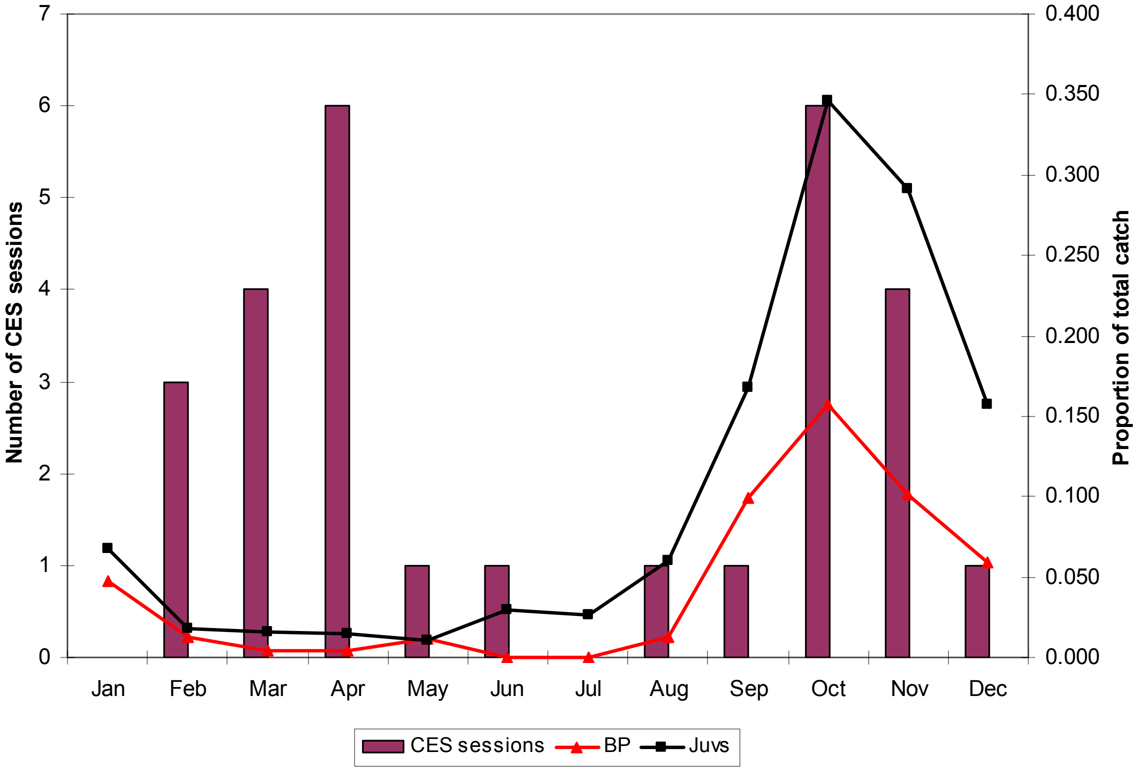
Aside from potential errors occurring during the collection of data the method of identifying timing of breeding may have resulted in significant errors, especially where this was based on the occurrence of juveniles in captures. These analyses assume that individuals and species do not show significant variation in the age at which they commence the post-juvenile moult. Few studies have detailed the age at which post-juvenile moult occurs in tropical passerine species. Those that have (e.g. Franklin *et al.* (1999); Jones *et al.* (2002)) suggest that the post-juvenile moult occurs between seven and 12 weeks after hatching, similar to that observed for temperate passerine species (Jenni & Winkler 1994). Other studies however have found that individuals of certain tropical species rarely undertake a post-juvenile moult (e.g. Speckled Warblers (*Chthonicola sagittata*) (Gardner *et al.* 2008) however I found no evidence that any of the species in this study adopted such a strategy. Using a mean fledging period for tropical passerine species of 16.83 days (se ± 0.373, n = 204 - derived from data in Byers *et al.* (1995); Restall (1996); Feare *et al.* (1998); Harris & Franklin (2000) and Cheke *et al.* (2001)) suggests that juveniles for most species therefore maintain complete juvenile plumage for between 32 and 67 days after fledging before commencing post-juvenile moult. The estimate that juveniles were caught on average 24 days after fledging is therefore perhaps an underestimate of the true fledging date. This is likely since the brood patches on many species may remain (brood patch stage 4) even after the chicks have fledged (pers. obs.). The difference in time between mean brood patch and juvenile occurrence dates will therefore be shorter than the true length. As a result and when generalising across all species, the mean date of breeding period should perhaps be considered as occurring up to one month earlier than the dates given here.

Both methods will also be affected by the tendency of individuals of certain species to have either protracted breeding periods, to make repeated breeding attempts or to vary timing of breeding between years and show little seasonality (e.g. *P.barbatus*, *C.senegalensis*). All of these scenarios may result in juveniles and individuals with active brood patches being present throughout the year. At the very least this will lengthen breeding periods and affect identification of mean breeding date and may even prevent determination of particular breeding periods e.g. Elgood *et al.* (1994) reports that a pair of *C.senegalensis* raised three successive broods in an 8 month period in south west Nigeria and a second pair raised three broods at 6 month intervals in central Nigeria. This would not be an issue if the analysis were based on data from just one location since it would still reflect the overall breeding period, however, because data from four geographical locations with wide variation in altitude (Amurum – 1300m, Yankari – 150-300m) were used it is possible that differing environmental conditions may have led to specific differences in timing of breeding between sites especially if species use locally variable environmental cues for timing of breeding (Moore *et al.* 2005). However, the effect of this should be minimal however since 90% of the data used in the analyses were from Amurum and the majority of the remainder were for species poorly represented at this site.

The sampling protocol may also have affected the identification of breeding periods and biased these towards certain periods of the year. Much of the data was generated during twice–yearly constant effort catching periods (14-day periods in which 20 mist nets were operated in fixed positions at Amurum, one between February-June and the second at some point between August-December). Because these CES catches were performed during the same periods each year the chances of encountering breeding individuals is likely to be higher at these times (because of the large numbers of individuals caught during these periods) leading to a bias in the reporting of breeding periods. Catches were made at other times of the year (i.e. outside of the CES periods) and so some coverage was provided throughout the majority of the year reducing this bias. In fact, assessing the proportion of captured individuals that were juveniles or which had active brood patches (Figure 5) suggests that these assessments of breeding activity were not biased by the number of CES periods and that breeding was focussed mostly during the period between August and January. Ultimately though, incorporation of a more systematic and quantitative method of determining level of breeding activity (e.g. through assessment of testis size and gonadal development) would considerably improve the accuracy of identification of breeding periods than the approaches used here.

Lastly, because of data shortages it was not possible to test for annual variation in timing or duration of breeding and all data for all species were pooled across years. This, along with annual variation in environmental conditions (e.g. timing and extent of rainfall, invertebrate abundance, phenology of fruiting or flowering trees or occurrence of grassfires), may have resulted in large variations in timing of nesting between individuals within species each year. This effect however, should only have been noticeable or significant in species with few individuals and may provide an alternative reason for some of the larger ranges of mean breeding period.

Figure 5. Proportion of all adults caught that have active brood patches and proportion of total catches that were juveniles compared to number of CES catches made per month throughout the eight years of the study.



Timing and duration of breeding

The aim here was to provide summaries of the timing of breeding for a variety of species for later investigation of how different life history processes are scheduled. This was achieved for a diverse range of species whilst also identifying a concentration of breeding linked to the seasonality in the savannah study area. For the vast majority of species the data on timing closely followed those from other sources covering this region and latitude (e.g. Moreau 1937; Elgood *et al.* (1994); Urban *et al.* (1997); Brandt 2007) many of which relied on more direct observation of nesting. Five exceptions were noted however (*C.striatus*, *I.indicator*, *P.chrysoconus*, *S.brachyura* and *L.senegala*), all of which were recorded breeding around one month later in the study. Brandt (2007) noted that *L.senegala* had a prolonged breeding season within the study area and the presence of birds with brood patches in the early rains (and the mean date of breeding determined across this broad range of dates) is the most likely reason for the assessment of timing being later here than for other studies. Overall however, the estimates can be considered reasonably representative of the breeding periods for all species assessed here.

Various authors (e.g. Baker 1939; Miller 1960; MacArthur 1964; Wyndham 1986) have proposed that the reduced seasonal extremes of habitats at lower latitudes permits tropical bird species to spend proportionally more of the year engaged in breeding. This would allow for the production of multiple broods and provide a mechanism to compensate for the reduced clutch sizes of tropical species. The mean duration of breeding season across all species in this study however, lasted for around four months (range <1 – 12 months). This is considerably less than that proposed by Wyndham (1986) (around 7 months) for species at the same latitude as the study area used here (9^{o}N). This suggests that although the potential exists for species to have prolonged breeding seasons in tropical areas, and for them to have the capability to have multiple broods (Elgood *et al.* 1994), many species may not do this (Fogden 1972; König & Gwinner 1995; Martin 1996). In fact, there appears to be considerably greater synchrony in timing of breeding in the tropical species than expected (Stutchbury & Morton 2001). This suggests that environmental factors such as food or water availability may serve to constrain the period of time in which optimal conditions for breeding exist.

The fact that timing of reproduction was found to be quite strongly seasonal is perhaps unsurprising given that the peak period coincides with the latter stages of the rainy season. During this period food abundance starts to increase for both insectivores (Poulin *et al.* 1992) and granivorous species (Ward 1965; Crowley & Garnett 1999) and drinking water is still widely available to facilitate digestion of seeds (Immelmann & Immelmann 1967). Optimal timing of breeding then will ensure maximum potential reproductive success whilst also minimising the energetic expense to parents. Breeding during this period will also ensure that newly fledged individuals have an abundance of food to enable rapid growth whilst also allowing parents to maintain condition during the energetically costly period of nesting, incubation and rearing of young. In contrast, because more humid areas tend to have reduced definition between seasons, periods of food and water shortages are likely to be less severe.

Similar levels of seasonality to those found here have been found in other studies (e.g. Diamond 1974; Britton 1978; Prys-Jones 1982) although many of these have found timing of reproduction to be coincident with the end of the dry season. The difference in timing of peak reproductive behaviour between this study and those identified above may reflect an overall difference in water availability within the habitat throughout the year (Bourliere & Hadley 1970; van Schaik *et al.* 1993). This is particularly apparent when considering the timing of breeding between guilds. In many other studies undertaken in humid tropical habitats, frugivores and nectarivores have been found to concentrate breeding in the dry season (Skutch 1950; Stiles 1980; Bell 1982; but see Greig-Smith 1980), granivores either during the dry (Bell 1982) or wet seasons (Thiollay 1970; Karr 1971), and insectivorous species during the late-dry and early rainy seasons (Moreau 1950; Britton 1978; Sinclair 1978). In contrast, the study area used here is generally quite arid for much of the year with a mean annual rainfall of around 1400mm (see data in Elgood *et al.* (1994)) concentrated between May and August. As a result, timing of breeding was found to be concentrated within the late rains-early dry season for almost all guilds (except for the frugivores) and most species, and more closely followed the results of studies undertaken in similarly arid tropical habitats (e.g. Wunderle 1982; Cruz & Andrews 1989).

Increased seasonality results in more dramatic peaks and troughs in food availability in arid tropical areas (Janzen & Schoener 1968) than in the more humid forests (Fogden 1972). This is particularly evident in arthropods whose abundance declines rapidly during the harsher dry seasons of savannahs (Janzen 1973; Wolda 1977) but remains reasonably constant in forests (Buskirk & Buskirk 1976). Large, soft-bodied arthropods form an important part of the diet fed to growing nestlings of tropical bird species regardless of guild (Greenberg 1981), because of their high protein content (Ward 1969; Berthold 1976; Boag & Grant 1984). Greenberg (1995) also suggested that the reproductive success of tropical landbirds was linked to arthropod abundance and that the variation in abundance served to constrain the timing and success of breeding attempts. Other workers have since provided support for this theory (e.g. Poulin *et al.* 1992; Johnson *et al.* 2006) with findings that suggest very few bird species engage in breeding activities during dry seasons in arid environments when arthropod abundance is low. Such a constraint would restrict the available periods during which successful breeding could be expected thereby concentrating breeding during other, more favourable periods (which in this study occurred from the late rains into the early dry season). The lack (or reduced duration) of these severe drought periods in more humid areas results in relative constancy of arthropod availability (e.g. Fogden 1972; Smythe 1982) thereby allowing for a greater range in timing of breeding across both individuals and species.

The study area used here lies at the interface between those habitats characterised as humid (annual rainfall >1500mm) or dry (<1500mm) and this, alongside the altitude of the site (1300m), may mitigate some of the factors causing a decline in arthropod abundance allowing for a slightly increased diversity in breeding periods compared to other, more extremely arid, habitats. This was apparent both when comparing timing and duration of breeding between frugivorous and granivorous species, the former breeding at various locations throughout the year and having a longer apparent duration than the (generally smaller) seed-eating species. Further information relating to invertebrate abundance and diets of individuals during the different stages of reproduction would help improve understanding of the influence of diet and seasonality on the timing of breeding in tropical species. Also, because the variety of habitats in tropical areas is at least as diverse as those in temperate areas, consideration of this environmental variability is essential if comparisons of life history parameters between species in differing tropical regions or habitats are to be valid.

Conclusion

This study has shown that seasonality exerts some control over the timing of breeding for the majority of species in tropical savannahs. However, these constraints are generally less restrictive than for species in temperate areas, allowing for much longer breeding seasons in many of the species here. Much reduced synchrony of breeding was observed for many species (as suggested by Baker 1939) although the results provide only broad estimates of the timing and duration of breeding. A number of species were able to make breeding attempts throughout the year apparently regardless of seasonal fluctuations in rainfall or food availability. Whether this is an adaptation to combat the higher levels of nest predation presumed to occur in tropical areas is open to question and demands further investigation. It was not possible to determine whether or not individuals repeatedly renested or had multiple broods in this study and so identification of whether or not the prolonged breeding seasons were a result of nest predation is still unclear. Further work following the reproductive activity of marked individuals would be especially useful in identifying the frequency of renesting in tropical species. Similarly the use of nest cameras and nest observation would help in identifying whether or not nest predation is a significant factor in determining breeding season duration in tropical species and provide insights in to the primary nest predators of the region.

Chapter 4: Analysis of survival of tropical savannah birds

Summary

Despite the long-established paradigm identifying latitudinal variation in life history traits there have still been relatively few studies generating empirical data on survival in tropical areas. Many of those that have been produced have focussed on comparatively few sites and species in Neotropical areas with even fewer in the Afrotropics. I used capture-mark-recapture models to estimate adult survival in 40 species of tropical land bird and first-year survival in 13 species, in Nigeria, West Africa, using data collected between 2001 and 2008. For adults, models assuming constant survival provided best fit for 36 of the species with the remainder being best described by models that accounted for transience. Models incorporating constancy in survival were also the best supported for juveniles although I derived estimates of first year survival from models incorporating two age-classes (first year and subsequent years). Average annual adult survival (all species: 0.63 ± 0.02) was higher than previous estimates obtained from this site and was comparable with estimates from other Afrotropical and Neotropical areas, although rates varied greatly between species. Apparent survival was relatively constant between most families and guilds but significantly lower for the granivores and Estrildine finches. First year survival was lower than that for subsequent years but did not vary between families or guilds. The results here suggest that both first years and adult tropical bird species suffer lower mortality than similar temperate species. These results are discussed throughout this chapter in the context of life history theory. I also examine how other life history traits of tropical species may vary from northern temperate counterparts to allow such a difference.

Introduction

Life history theory identifies linkages between the relative importance of survival, reproduction and growth, such that increased investment in one component necessitates reduced investment in another (Williams 1966a; Martin 1992; Roff 1992; Stearns 1992; Charlesworth 1994). Reduced effort expended in reproduction (either through small clutch sizes, few successful breeding attempts per year, reduced level of nest defence etc) should therefore lead to increased annual survival (e.g. Ekman & Askenmo 1986; Martin 1996). Such population characteristics are now viewed as the norm in tropical passerine birds whose populations are generally characterised as having smaller clutch sizes (Moreau 1944; Lack 1968; Yom-Tov *et al.* 1994; Geffen & Yom-Tov 1999) and higher adult survival (Snow 1962; Faaborg & Arendt 1995; de Swardt & Peach 2001; Peach *et al.* 2001; Ghalambor & Martin 2001; McGregor *et al.* 2007b) than their north temperate counterparts.

Work by McGregor (2005) suggested that the widely-accepted high survival / low clutch size paradigm generally holds true when using data from numerous tropical locations to compare with temperate estimates. For his primary study location however, he found considerable variability in the rates of annual adult survival and rates for some species were much lower than in north temperate species (e.g. for *Colius striatus*, 0.194). Here, new data building upon the initial work of McGregor is analysed with a view to more accurately identifying adult annual survival for later use in assessing how the scheduling of moult and breeding relates to survival and seasonality in tropical species (Chapter 6). As an extension of this, I also present preliminary estimates of annual juvenile/immature survival in an attempt to identify whether significant age-dependence exists in survival of tropical species. The annual parameter estimates derived and reported here are also compared with those from studies performed in other tropical areas both to examine their likely validity and assess the extent of geographical variability in rates.

Methods

Study site and field methods

Birds were captured at the Amurum Community Forest Reserve using mist nets following the capture protocols outlined in Chapter 2. All birds were aged, sexed and ringed with unique metal rings. Where possible (depending on species and tarsus length) all individuals were also fitted with a unique combination of three plastic colour rings. Resightings of colour-ringed individuals were made regularly across the reserve and throughout the year. Resightings made during the CES periods were included as part of the CES captures.

Because resightings of certain species proved difficult to achieve, additional mist netting operations were performed at several other locations around the reserve (outside of the CES capture area and capture periods) for 5-10 day periods in rotation in an attempt to further improve recapture and resighting rates.

These extra mist-netting sessions were also used in conjunction with the primary CES periods in assessing survival using standard CJS model approaches. For this only recaptures were analysed (i.e. resightings were excluded from the MARK input files). Capture periods were determined by dividing all mist-net sessions undertaken within the reserve between 2002-2008 into 20-day periods. 20-day periods were chosen firstly to ensure coverage during those occasions when additional capture days were necessary (i.e. because of abandonment of sessions during the CES periods on days with unsuitable weather). Secondly, shorter ringing periods were frequently held around the reserve. To help ease the incorporation of these short capture periods into a survival analysis more straightforward, they were grouped into specific ringing periods of 20 days. Those periods in which no target species were caught (either new or retraps) were excluded from identification of ringing periods in a further attempt to reduce parameterisation (through the reduction of capture occasions).

Survival analyses

Estimation of apparent survival rates for the species in this study was initially to follow the protocol used by McGregor (2007) and to use the Barker Model. This approach allows recapture data to be supplemented with resighting data. Parameter estimates using this approach would then have been directly comparable with those obtained form previous studies undertaken at this site between 2001-2004 (McGregor *et al.* 2007b). Unfortunately, difficulties in obtaining suitable $\hat{c}$ values (i.e. <3), for even the least parameterised model for the majority of species, meant that this approach was abandoned. Chapter 5 details the procedures and models tested using the Barker approach and examines why this approach proved unsuitable for this dataset.

The method for assessing survival in this study was therefore modified and a standard CMR (Capture, mark, recapture – i.e. excluding resightings) modelling approach was used to estimate both juvenile and adult survival for a range of tropical bird species. Methods were selected to account for trap shyness and transience (Lebreton *et al.* 1992) by inclusion of a time-since-marking (TSM) factor to the model set (Pradel *et al.* 1997, Sandercock 2006). Data were analysed using program MARK (White & Burnham 1999) using standard, time-dependent and TSM, Cormack-Jolly-Seber (CJS) models (i.e. Φ_{t} p_{t} or $\Phi a2\text{-}_{t/t}$ $pa2\text{-}_{t/t}$, where Φ is the probability that an animal alive at i is alive at $i + 1$, and p is the probability that an animal at risk of capture at i is captured at $i + 1$, t indicates time-dependence, and a2 indicates a different estimation of the parameter between the first and subsequent occasions).

Time intervals

Variation in the intervals between each of the capture periods will affect the estimates of survival and the way in which the probability of recapture is determined. MARK accounts for this by allowing input of the relative length of each interval in relation to any chosen standard (e.g. day, week, month). Here, in order to produce annual estimates of survival, all intervals entered were calculated as proportionate to one year (i.e. total number of days between each capture period, divided by 365.25), MARK then treats this time interval as an exponent of the estimated parameter (survival). The interval was calculated as the time between mid-points of the capture periods (since some periods ran consecutively and would otherwise have resulted in intervals of less than 1 day). Because of the scarcity of data for certain species in some years (and the negative impact on modelling that this has – see Chapter 5), the number and timing of capture periods was not uniform for all species - save for the fixed CES periods. For example, no Vitelline Masked Weavers were caught in 2001 and so capture periods started in 2002 for this species. All outputs of survival estimates presented here are annual estimates rather than between-period estimates.

Goodness of fit testing

The effective application of mark-recapture models is reliant on data meeting a number of assumptions. There are four standard assumptions relating to the fate of individuals (Lebreton *et al.* 1992), these are:

1. that marks are not lost or missed;
2. that the capture of individuals is an instantaneous event relative to the interval between each capture occasion;
3. that all marked individuals in the population at time (i) have the same probability of surviving to time (i+1); and,
4. that all marked individuals in the population at time (i) have the same probability of recapture (p_i).

To ensure that all assumptions of the model were met by the data, goodness of fit tests were performed on the general starting model (here, the fully time-dependent models, $\Phi_t\ p_t$). A reasonable fit of this model to the data is essential if reduced parameter models are to be compared and assessed against it later. Where fit of the general model was inadequate, progressively less parameterised models were tested (e.g. a time-since-marking (TSM) model, $\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$,) in order to find a suitable starting model for all species.

A measure of the extent of the lack of fit of the model to the data (i.e. the degree of over-dispersion) is estimated using the Variance Inflation Factor ($\hat{c}$).

Here, ĉ was determined using the median c-hat technique from within MARK, in which a specified number of simulated deviances are generated for a specified range of ĉ values. Logistic regression is then used to identify the point (and the ĉ value) for which half of the simulated deviances are below and half above (i.e. the median) the observed value. This technique is now considered statistically superior in application to the bootstrapping approach previously used (E.Cooch pers.comm.). In this study 10 replicates were used for each of 10 design points between bounds for the ĉ of 1 – 3. Perfect model fit is given when the resulting ĉ = 1. Providing 1 < ĉ < 3 the model is not considered to be significantly over-dispersed. Where ĉ ≠ 1, the likelihood of the general and nested reduced parameter models was corrected using the 'c-hat adjustment' function within MARK. Where the ĉ < 1, the model is considered under-dispersed and I followed the generally accepted convention of adjusting ĉ = 1, providing ĉ > 0.5. Where ĉ > 3, a less parameterised general model was used. Usually this was the TSM model if the time-dependent model showed unacceptable fit. All models corrected using the variance inflation factor automatically have their AICc (Akaike's Information Criteria (Akaike 1985)) statistics adjusted to incorporate the ĉ within the likelihood term. This gives the quasi-likelihood adjusted QAIC_c's which are then used instead of the original AIC_c's for model selection (after Lebreton *et al.* (1992) and Burnham & Anderson (1998)).

$$\mathrm{QAIC}_c = -2\ln(L)/\hat{c} + 2K + 2K(K+1)/n_{ess} - K - 1$$

Where, L is the model likelihood, K is the number of estimable parameters, n_{ess} is the effective population size, and ĉ is quasi-likelihood adjustment for overdispersion.

Further examination of the potential causes of heterogeneity in the data was performed using of the series of goodness of fit tests (Pradel 1993; Pradel *et al.* 1997) within program U-CARE (Choquet *et al.* 2005) designed to highlight potential issues with transients and trap dependence. These tests assess whether the assumptions of equality of fates across individuals or whether previous trapping history affects future probability of capture or survival are met. Significant results for test 3.SR indicates age-dependence in the data and significance of test 2.Ct, trap dependence.

Lack of data can result in MARK having difficulty in estimating some parameters. This can result in MARK missing parameters that are estimable but at the boundary (i.e. φ or p are 0 or 1) and reporting 'false' results for the Model weights, AIC and Model Likelihoods which can then lead to incorrect model selection. This was overcome in all cases by checking for these boundary estimates within output and then fixing the value for one of the parameters (usually p) to be 1. The parameter set to unity will not be calculated and the other parameter will be the estimate of the product of the two parameters (since, if p=1, $\varphi \times p = \varphi$). Where such procedures result in the parameter then becoming identifiable the model output (number of parameters) can then be corrected using the 'Number of Parameters' function within MARK. This automatically adjusts the relevant results in the browser. Where this process does not identify the parameter estimate, the number of parameters estimated by MARK is taken as the true value.

Model Selection

Models were selected using the information theoretic methods (AICc – a corrected AIC which performs better for small sample sizes). The AICc/QAICc scores allow comparison of models on the principal of parsimony, lower values ascribed to those models which best fit the data with fewest parameters. This method is known to prove unreliable when the difference between models is <2 AIC, and so, where this occurred, nested models were compared using Likelihood Ratio tests. The Model Likelihood and the AICc Weight facilities within MARK produce evidence ratios which provide a supplementary means of assessing the relative likelihoods of each model in the model set. The normalised AICc weights and Model Likelihood functions essentially provide a measure of the Kullback-Leibler distances (i.e. an assessment of the information lost from the model in comparison to a perfect 'true' model).

Parameter Estimation

The use of the logit-link function in the model constrains all parameters to be within the range 0-1 which, if the data are sparse or show high variance, may lead to parameter estimates of 0 or 1. Where parameter estimates approached these two limits their confidence intervals were recalculated using Profile Likelihood. This enabled the selective exclusion of those species for which the data were insufficient or unsuitable for determining survival rates. MARK assesses support for each of the models in the model set and ranks them accordingly. For many species, several models had a degree of support/likelihood (given by its model weighting). Where support for a model was greater than 5% it was used alongside the higher ranked models to provide a composite estimate of survival. This model averaging procedure incorporates all of the supported models and weights their input to the survival estimate according to the normalised AIC_c weights *sensu* Buckland *et al.* (1997). Survival estimates from both the most supported model and the averaged model are reported.

Results

Data selection

Between 2001 and 2008, 16779 captures of 12760 individuals of 183 species of bird were recorded at Amurum Community Forest Reserve, Jos, Nigeria. 21 of these species were Palearctic migrants and were therefore excluded from survival analyses. Of the remainder, the median number of captures per species was 12 (range 1 - 1582) and recaptures per species, 7 (range 0 – 400). Between-period recaptures were generally scarce (median = 1, range 0 – 200), however 40 species had ≥10 individuals with between-period recaptures as adults. These 40 species were used to assess the apparent survival probabilities of adult Afro-tropical guinea savannah bird species. Modelling of the juvenile/immature survival probabilities of thirteen of these species was also attempted, using those species having ≥7 individuals with between-period recaptures. 35 of the study species were passerines and all species weighed less than 60g.

Table 1. Numbers of captures and recaptures for 38 bird species in Amurum Community Forest Reserve, Jos, Nigeria, return rates (individuals recaptured/total number of individuals captured), the general starting model used in MARK to determine goodness of fit of the model set, and the variance inflation factor ($\hat{c}$) used to adjust parameter estimates.

Species	No individuals captured during first 7 yrs	Number of recaptures	Number of individuals recaptured	Return rate	General Model^a	$\hat{c}$
Columbidae						
Turtur abyssinicus	68	44	20	0.294	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.922
Coliidae						
Colius striatus	223	95	51	0.229	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.97
Lybiidae						
Pogoniulus chrysoconus	186	134	45	0.242	Φ_{c} $p_{a2-c/c}$	0.97
Lybius vieilloti	36	33	16	0.444	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.024
Pycnonotidae						
Pycnonotus barbatus	311	111	68	0.219	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.013
Chlorocichla flavicollis	34	24	14	0.424	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.922
Cisticolidae						
Camaroptera brachyura	137	168	53	0.387	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.462
Cisticola guinea	30	29	12	0.400	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.649
Cisticola aberrans	57	28	16	0.281	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.002
Cisticola cantans	39	26	12	0.308	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.886
Sylviidae						
Melocichla mentalis	24	17	11	0.458	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.375
Eremomela pusilla	33	21	13	0.394	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.154
Sylvietta brachyura	32	31	18	0.563	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.154
Muscicapidae						
Cossypha niveicapilla	80	75	27	0.338	Φ_{c} $p_{a2-c/c}$	1.172
Cercomela familiaris	45	37	15	0.333	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.433
Myrmecocichla cinnamomeiventris	41	11	7	0.171	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	2.65
Turdidae						
Turdus pelios						
Adults	190	87	55	0.289	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.059
Juveniles	110	42	25	0.227	$\Phi_{pa2-c/c}$ p_{c}	0.914
Platysteiridae						
Platysteira cyanea	51	53	24	0.471	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.078
Zosteropidae						
Zosterops senegalensis	152	55	31	0.204	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.285
Nectariniidae						
Cyanomitra verticalis						
Adults	87	80	34	0.391	Φ_{c} $p_{a2-c/c}$	1.325
Juveniles	36	19	11	0.306	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.842
Chalcomitra senegalensis						
Adults	202	62	39	0.193	Φ_{c} p_{t}	1.024
Juveniles	162	21	10	0.062	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.189
Cinnyris venustus						
Adults	206	42	25	0.122	Φ_{c} $p_{a2-c/c}$	0.694
Juveniles	81	20	7	0.086	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	2.33
Malaconotidae						
Malaconotus sulfureopectus	25	14	12	0.480	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.614
Tchagra senegalus	41	24	15	0.366	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.972
Emberizidae						
Emberiza tahapisi	226	31	16	0.071	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.014
Passeridae						
Sporopipes frontalis	62	41	19	0.307	$\Phi_{a2-c/c}$ p_{t}	1.843
Ploceidae						
Ploceus luteolus	45	26	17	0.378	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	1.839
Ploceus cucullatus						
Adults	301	34	27	0.090	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.97
Juveniles	191	18	11	0.058	$\Phi_{a2-c/c}$ $p_{a2-c/c}$	0.79

Species	No individuals captured during first 7 yrs	Number of recaptures	Number of individuals recaptured	Return rate	General Model[a]	Ĉ
Ploceidae						
Ploceus nigricollis						
Adults	116	63	41	0.353	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.006
Juveniles	66	17	13	0.197	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.459
Ploceus vitellinus						
Adults	205	76	45	0.220	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.107
Juveniles	104	47	22	0.212	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.798
Euplectes hordeaceus	165	47	27	0.164	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.845
Euplectes franciscanus						
Adults	1252	360	200	0.160	$\Phi_t\ p_t$	0.922
Juveniles	309	100	44	0.142	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.221
Estrildidae						
Estrilda caerulescens						
Adults	378	326	144	0.381	$\Phi_t\ p_t$	1.171
Juveniles	100	79	39	0.390	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.842
Estrilda troglodytes	136	24	14	0.103	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.953
Uraeginthus bengalus						
Adults	498	226	104	0.209	$\Phi_{a2-c/c}\ p_{a2-t/c}$	0.899
Juveniles	51	26	9	0.176	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.94
Lagonosticta rufopicta	62	38	21	0.339	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.015
Lagonosticta senegala						
Adults	400	137	88	0.220	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.141
Juveniles	151	74	38	0.252	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.19
Lagonosticta sanguinodorsalis						
Adults	305	300	109	0.357	$\Phi_t\ p_t$	1.072
Juveniles	88	101	36	0.409	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.23
Lagonosticta rara	34	26	14	0.412	$\Phi_{a2-c/c}\ p_{a2-c/c}$	1.259
Spermestes cucullata						
Adults	424	43	27	0.064	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.807
Juveniles	348	53	32	0.092	$\Phi_{a2-c/c}\ p_{a2-c/c}$	0.613

[a] General starting model, φ – apparent survival probability, *p* – apparent recapture probability, *t* – time dependence, *c* – constancy, *a2-c/c* – time since marking model with constancy in 1st and 2nd+ capture intervals.

Model Selection

Minor over- or under-dispersion was indicated in most of the study species, however ĉ was <1.9 (mean 1.06) for 39 of 40 (Table 1) tested as adults. Only *M.cinnamomeiventris* exceeded this but, with a ĉ of 2.65, this was still within the boundaries of acceptable limits and this species was retained within the analyses. Similar patterns of dispersion were present in tests of the juveniles (ĉ < 1.85 for 12 of 13 species (overall mean 1.18)) and all had ĉ < 3. All model outputs and parameter estimates were adjusted to account for their departure from perfect model fit. Limitations of the datasets required that the general starting model for most species (36 of 40 adults, all juveniles) was a time-since-marking (TSM) model, i.e. less parameterised than the fully time-dependent CJS model. Larger datasets for the adults allowed the testing of more heavily parameterised starting models for certain species (e.g. for *E.caerulescens*, *L.sanguinodorsalis*).

Table 2. Mark-recapture models of probability of apparent annual survival (φ) and recapture (p) for bird species at Amurum Community Forest Reserve, Nigeria. Models ranked according to quasi-Akaike Information Criterion ($QAIC_c$) and show the model set, departure from the 'best' model ($\Delta QAIC_c$), Akaike weight (w_i), number of parameters (K) and P values for Likelihood Ratio chi-squared tests between nested models. LRT test values relate to tests between 1st listed model for that species and model for that row.

Species	Model^a	$QAIC_c$	$\Delta QAIC_c$	w_i	K	Deviance	LR Test, P
Columbidae							
T.abyssinicus	$\Phi_c\ p_c$	241.49	0	0.44	2	142.87	-
	$\Phi_c\ p_{a2\text{-}c/c}$	242.4	0.91	0.28	3	141.64	0.269
	$\Phi_{a2\text{-}c/c}\ p_c$	243.26	1.76	0.18	3	142.5	0.321
	$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	244.45	3	0.1	4	141.51	0.718
Coliidae							
C.striatus	$\Phi_c\ p_c$	734.42	0	0.49	2	426.89	-
	$\Phi_c\ p_{a2\text{-}c/c}$	735.79	1.37	0.25	3	426.22	0.421
	$\Phi_{a2\text{-}c/c}\ p_c$	736.46	2.03	0.18	3	426.89	0.930
	$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	737.8	3.37	0.09	4	426.17	0.707
Lybiidae							
P.chrysoconus	$\Phi_c\ p_c$	644.39	0	0.65	2	394.32	-
	$\Phi_c\ p_{a2\text{-}c/c}$	645.62	1.23	0.35	3	393.5	0.366
L.vieilloti	$\Phi_c\ p_c$	158.55	0	0.74	2	99.68	-
	$\Phi_c\ p_{a2\text{-}c/c}$	160.68	2.14	0.26	3	99.59	0.769
Pycnonotidae							
P.barbatus	$\Phi_c\ p_{a2\text{-}c/c}$	916.23	0	0.4	3	459.62	-
	$\Phi_c\ p_c$	916.69	0.46	0.32	2	462.11	0.115
	$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	918.06	1.83	0.16	4	459.41	0.647
	$\Phi_{a2\text{-}c/c}\ p_c$	918.66	2.42	0.12	3	462.05	N/a
C.flavicollis	$\Phi_c\ p_c$	166.4	0	0.51	2	116.07	-
	$\Phi_{a2\text{-}c/c}\ p_c$	168.14	1.74	0.22	3	115.56	0.477
	$\Phi_c\ p_{a2\text{-}c/c}$	168.32	1.93	0.2	3	115.74	0.570
	$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	170.28	3.88	0.07	4	115.35	0.700
Cisticolidae							
C.brachyura	$\Phi_c\ p_c$	491.19	0	0.51	2	301.91	-
	$\Phi_c\ p_{a2\text{-}c/c}$	492.9	1.71	0.22	3	301.56	0.556
	$\Phi_{a2\text{-}c/c}\ p_c$	493.12	1.93	0.19	3	301.78	0.719
	$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	494.74	3.55	0.09	4	301.33	0.749
C.guinea	$\Phi_c\ p_c$	173.37	0	0.6	2	117.86	-
	$\Phi_c\ p_{a2\text{-}c/c}$	174.2	0.83	0.4	3	116.41	0.228
C.aberrans	$\Phi_c\ p_{a2\text{-}c/c}$	159.24	0	0.6	3	96.58	-
	$\Phi_c\ p_c$	160.06	0.82	0.4	2	99.57	0.083
C.cantans	$\Phi_c\ p_c$	170.87	0	0.71	2	122.87	-
	$\Phi_c\ p_{a2\text{-}c/c}$	172.7	1.83	0.29	3	122.47	0.530
Sylviidae							
M.mentalis	$\Phi_c\ p_c$	231.89	0	1	2	162.79	N/a
E.pusilla	$\Phi_c\ p_{a2\text{-}c/c}$	125.63	0	0.63	3	93.86	-
	$\Phi_c\ p_c$	126.68	1.04	0.37	2	97.16	0.069
S.brachyura	$\Phi_c\ p_{a2\text{-}c/c}$	130.44	0	0.78	3	92.7	-
	$\Phi_c\ p_c$	133.01	2.58	0.22	2	97.53	**0.028**
Muscicapidae							
C.niveicapilla	$\Phi_c\ p_c$	329.79	0	0.74	2	202.7	-
	$\Phi_c\ p_{a2\text{-}c/c}$	331.88	2.09	0.26	3	202.69	0.912
M.cinnamomeiventris	$\Phi_c\ p_c$	33.52	0	0.56	2	21.23	-
	$\Phi_c\ p_{a2\text{-}c/c}$	35.65	2.13	0.19	3	21.09	0.710
	$\Phi_{a2\text{-}c/c}\ p_c$	35.67	2.15	0.19	3	21.11	0.730
	$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	37.83	4.31	0.06	4	20.89	0.844

Species		Model[a]	$QAIC_c$	$\Delta QAIC_c$	w_i	*K*	Deviance	LR Test, *P*
C.familiaris		$\Phi_c\ p_c$	340.36	0	0.45	2	225.74	-
		$\Phi_c\ p_{a2\text{-}c/c}$	341.64	1.28	0.24	3	224.81	0.336
		$\Phi_{a2\text{-}c/c}\ p_c$	342.13	1.77	0.19	3	225.31	0.512
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	343.05	2.69	0.12	4	223.95	0.409
Turdidae								
T.pelios								
	Adults	$\Phi_c\ p_c$	584.15	0	0.52	2	253.93	-
		$\Phi_c\ p_{a2\text{-}c/c}$	585.92	1.77	0.21	3	253.65	0.599
		$\Phi_{a2\text{-}c/c}\ p_c$	586.2	2.05	0.19	3	253.92	0.952
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	587.99	3.86	0.08	4	253.65	0.871
	Juveniles	$\Phi_c\ p_c$	295.84	0	0.49	2	180.33	-
		$\Phi_{a2\text{-}c/c}\ p_c$	297.1	1.27	0.26	3	179.5	0.827
Platysteiridae								
P.cyanea		$\Phi_c\ p_c$	253.44	0	0.54	2	166.74	-
		$\Phi_c\ p_{a2\text{-}c/c}$	253.79	0.35	0.46	3	164.93	0.180
Zosteropidae								
Z.senegalensis		$\Phi_c\ p_c$	298.61	0	0.56	2	160.35	-
		$\Phi_c\ p_{a2\text{-}c/c}$	299.06	0.45	0.44	3	158.74	0.204
Nectariniidae								
C.verticalis								
	Adults	$\Phi_c\ p_{a2\text{-}c/c}$	355.52	0	0.65	3	242.37	-
		$\Phi_c\ p_c$	356.8	1.28	0.35	2	245.74	0.067
	Juveniles	$\Phi_c\ p_c$	82.49	0	0.47	2	62.26	-
		$\Phi_{a2\text{-}c/c}\ p_c$	85.54	1.05	0.28	3	61.05	0.272
		$\Phi_c\ p_{a2\text{-}c/c}$	84.54	2.04	0.17	3	62.05	0.646
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	85.81	3.32	0.09	4	60.97	0.525
C.senegalensis								
	Adults	$\Phi_c\ p_c$	523.42	0	0.63	2	283.04	-
		$\Phi_c\ p_{a2\text{-}c/c}$	514.48	1.06	0.37	3	282.05	0.319
		$\Phi_c\ p_t$	523.98	10.55	0.003	31	226.42	**0.002**
	Juveniles	$\Phi_c\ p_c$	119.51	0	0.54	2	71.56	-
		$\Phi_{a2\text{-}c/c}\ p_c$	121.54	2.03	0.2	3	71.52	0.842
		$\Phi_c\ p_{a2\text{-}c/c}$	121.58	2.07	0.19	3	71.56	0.982
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	123.64	4.13	0.07	4	71.51	0.979
C.venustus								
	Adults	$\Phi_c\ p_c$	523.99	0	0.69	2	290.81	-
		$\Phi_c\ p_{a2\text{-}c/c}$	525.64	1.65	0.31	3	290.4	0.524
	Juveniles	$\Phi_{a2\text{-}c/c}\ p_c$	62.76	0	0.51	3	45.33	
		$\Phi_c\ p_c$	64.05	1.29	0.27	2	48.76	0.064
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	65.55	2.79	0.13	4	45.92	<0.001
		$\Phi_c\ p_{a2\text{-}c/c}$	65.98	3.22	0.1	3	48.54	-
Malaconotidae								
M.blanchoti		$\Phi_c\ p_c$	176.85	0	0.72	2	111.56	-
		$\Phi_c\ p_{a2\text{-}c/c}$	178.72	1.87	0.28	3	111.09	0.494
T.senegalus		$\Phi_c\ p_c$	167.36	0	0.64	2	118.62	-
		$\Phi_c\ p_{a2\text{-}c/c}$	168.54	1.18	0.36	3	117.57	0.307
Emberizidae								
E.tahapisi		$\Phi_c\ p_c$	210.83	0	0.35	2	99.67	-
		$\Phi_{a2\text{-}c/c}\ p_c$	211.47	0.65	0.25	3	98.26	0.236
		$\Phi_c\ p_{a2\text{-}c/c}$	211.55	0.72	0.24	3	98.34	0.249
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	212.53	1.7	0.15	4	97.25	0.299
Passeridae								
S.frontalis		$\Phi_c\ p_c$	111.28	0	0.6	2	64.26	-
		$\Phi_c\ p_{a2\text{-}c/c}$	112.13	0.85	0.4	3	62.96	0.255
Ploceidae								
P.luteolus		$\Phi_c\ p_c$	106.38	0	0.53	2	72.25	-
		$\Phi_{a2\text{-}c/c}\ p_c$	108.06	1.75	0.22	3	71.83	0.516
		$\Phi_c\ p_{a2\text{-}c/c}$	108.48	2.17	0.18	3	72.25	0.958
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	110.28	3.97	0.07	4	71.81	0.803

Species		Model^a	QAIC$_c$	ΔQAIC$_c$	w_i	K	Deviance	LR Test, *P*
P.cucullatus								
	Adults	$\Phi_c\ p_c$	356.85	0	0.51	2	178.39	-
		$\Phi_{a2\text{-}c/c}\ p_c$	358.6	1.75	0.21	3	178.1	0.593
		$\Phi_c\ p_{a2\text{-}c/c}$	358.72	1.87	0.2	3	178.23	0.686
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	360.46	3.61	0.16	4	177.91	0.787
	Juveniles	$\Phi_c\ p_c$	221.19	0	0.45	2	128.26	-
		$\Phi_{a2\text{-}c/c}\ p_c$	222.13	0.94	0.28	3	127.13	0.290
		$\Phi_c\ p_{a2\text{-}c/c}$	223.25	2.06	0.16	3	128.26	N/a
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	224.1	2.92	0.11	4	127.03	0.542
P.nigricollis								
	Adults	$\Phi_c\ p_{a2\text{-}c/c}$	421.41	0	0.66	3	204.4	-
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	422.97	1.56	0.3	4	203.86	0.460
		$\Phi_c\ p_c$	428.28	6.87	0.02	2	213.34	**0.003**
		$\Phi_{a2\text{-}c/c}\ p_c$	429.	7.59	0.01	3	211.99	N/a
	Juveniles	$\Phi_c\ p_c$	95.48	0	0.42	2	55.15	-
		$\Phi_{a2\text{-}c/c}\ p_c$	96.17	0.69	0.3	3	53.68	0.225
		$\Phi_c\ p_{a2\text{-}c/c}$	97.29	1.81	0.17	3	54.8	0.553
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	98.35	2.87	0.1	4	53.64	0.471
P.vitellinus								
	Adults	$\Phi_c\ p_c$	480.81	0	0.44	2	221.57	-
		$\Phi_{a2\text{-}c/c}\ p_c$	481.93	1.11	0.25	3	220.64	0.334
		$\Phi_c\ p_{a2\text{-}c/c}$	482.38	1.56	0.2	3	221.09	0.488
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	483.71	2.89	0.1	4	220.36	0.545
	Juveniles	$\Phi_c\ p_c$	357.72	0	0.37	2	200.06	-
		$\Phi_{a2\text{-}c/c}\ p_c$	358.41	0.69	0.26	3	198.66	0.236
		$\Phi_c\ p_{a2\text{-}c/c}$	358.82	1.1	0.21	3	199.06	0.318
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	359.39	1.67	0.16	4	197.52	0.280
E.hordeaceus		$\Phi_c\ p_{a2\text{-}c/c}$	354.15	0	0.35	3	131.95	-
		$\Phi_c\ p_c$	354.53	0.38	0.29	2	134.39	0.1181
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	355.07	0.92	0.22	4	130.79	0.281
		$\Phi_{a2\text{-}c/c}\ p_c$	355.82	1.67	0.15	3	133.62	N/a
E.franciscanus								
	Adults	$\Phi_{a2\text{-}t/c}\ p_t$	2316.67	0	0.86	53	347.15	-
		$\Phi_c\ p_t$	2321.18	4.51	0.09	27	406.68	0.076
		$\Phi_{a2\text{-}c/c}\ p_t$	2322.31	5.64	0.05	28	405.73	0.073
	Juveniles	$\Phi_c\ p_c$	366.50	0	0.49	2	87.17	-
		$\Phi_c\ p_{a2\text{-}c/c}$	368.06	1.56	0.23	3	86.7	0.490
		$\Phi_{a2\text{-}c/c}\ p_c$	368.45	1.95	0.19	3	87.09	0.770
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	369.84	3.34	0.09	4	86.43	0.691
Estrildidae								
E.caerulescens								
	Adults	$\Phi_{a2\text{-}c/c}\ p_t$	1394.85	0	0.56	36	579.45	-
		$\Phi_c\ p_t$	1395.31	0.45	0.44	35	582.18	0.099
	Juveniles	$\Phi_c\ p_{a2\text{-}c/c}$	525.53	0	0.55	3	299.16	-
		$\Phi_c\ p_c$	527.60	2.08	0.19	2	303.31	**0.042**
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	527.63	2.11	0.19	4	299.15	0.955
		$\Phi_{a2\text{-}c/c}\ p_c$	529.66	4.13	0.07	3	303.29	N/a
E.melpoda		$\Phi_c\ p_c$	168.19	0	0.5	2	78.27	-
		$\Phi_{a2\text{-}c/c}\ p_c$	169.79	1.6	0.22	3	77.79	0.489
		$\Phi_c\ p_{a2\text{-}c/c}$	170.03	1.84	0.2	3	78.02	0.619
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	171.75	3.56	0.08	4	77.63	0.726
U.bengalus								
	Adults	$\Phi_c\ p_{a2\text{-}c/c}$	1517.77	0	0.39	3	725.24	-
		$\Phi_c\ p_c$	1518.1	0.33	0.33	2	727.59	0.125
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	1519.74	1.97	0.15	4	725.19	0.819
		$\Phi_{a2\text{-}c/c}\ p_c$	1519.91	2.14	0.13	3	727.38	N/a
	Juveniles	$\Phi_c\ p_c$	124.66	0	0.55	2	82.61	-
		$\Phi_c\ p_{a2\text{-}c/c}$	126.73	2.08	0.2	3	82.47	0.712
		$\Phi_{a2\text{-}c/c}\ p_c$	126.85	2.19	0.19	3	82.59	0.891
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	128.97	4.31	0.06	4	82.42	0.911

Species		Model^a	QAIC$_c$	ΔQAIC$_c$	w_i	K	Deviance	LR Test, P
L.rara		$\Phi_c\ p_c$	184.66	0	0.54	2	97.25	-
		$\Phi_c\ p_{a2\text{-}c/c}$	186.61	1.95	0.2	3	97.05	0.652
		$\Phi_{a2\text{-}c/c}\ p_c$	186.78	2.12	0.19	3	97.22	0.859
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	188.82	4.16	0.07	4	97.04	0.900
L.senegalensis								
	Adults	$\Phi_c\ p_c$	779.89	0	0.42	2	314.92	-
		$\Phi_c\ p_{a2\text{-}c/c}$	780.78	0.88	0.27	3	313.78	0.286
		$\Phi_{a2\text{-}c/c}\ p_c$	781.33	1.44	0.2	3	314.33	0.444
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	782.5	2.6	0.11	4	313.47	0.483
	Juveniles	$\Phi_{a2\text{-}c/c}\ p_c$	337.91	0	0.53	3	188.07	-
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	339.9	1.98	0.2	4	187.96	0.742
		$\Phi_c\ p_c$	339.97	2.06	0.19	2	192.2	**0.042**
		$\Phi_c\ p_{a2\text{-}c/c}$	341.55	3.63	0.09	3	191.71	N/a
L.sanguinodorsalis								
	Adults	$\Phi_c\ p_t$	1492.58	0	1	40	765.81	N/a
	Juveniles	$\Phi_c\ p_c$	367.94	0	0.45	2	239.77	-
		$\Phi_c\ p_{a2\text{-}c/c}$	368.84	0.9	0.28	3	238.58	0.276
		$\Phi_{a2\text{-}c/c}\ p_c$	369.87	1.93	0.17	3	239.61	0.690
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	370.91	2.97	0.1	4	238.53	0.539
L.rufopicta		$\Phi_c\ p_c$	71.49	0	0.41	2	35.71	-
		$\Phi_c\ p_{a2\text{-}c/c}$	72.31	0.81	0.27	3	34.2	0.219
		$\Phi_{a2\text{-}c/c}\ p_c$	72.65	1.16	0.23	3	34.55	0.281
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	74.44	2.94	0.09	4	33.88	0.400
S.cucullata								
	Adults	$\Phi_c\ p_c$	422.3	0	0.5	2	187.05	-
		$\Phi_c\ p_{a2\text{-}c/c}$	423.9	1.59	0.23	3	186.61	0.510
		$\Phi_{a2\text{-}c/c}\ p_c$	424.31	2.	0.18	3	187.02	0.878
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	425.86	3.56	0.09	4	186.54	0.777
	Juveniles	$\Phi_c\ p_{a2\text{-}c/c}$	535.95	0	0.35	3	240.18	-
		$\Phi_c\ p_c$	536.1	0.15	0.33	2	242.36	0.140
		$\Phi_{a2\text{-}c/c}\ p_c$	537.46	1.51	0.17	3	241.69	N/a
		$\Phi_{a2\text{-}c/c}\ p_{a2\text{-}c/c}$	537.68	1.73	0.15	4	239.87	0.576

[a] *c* – constant; *t* – time dependent; *a2-c/c* – tsm model with constancy in 1st and 2nd+ capture occasion; *a2-t/c* – tsm model with time dependence in 1st capture interval and constancy in subsequent intervals. Bold type indicates significant *P* values.

The observed encounter histories were generally best described by a model with constant survival and recapture probabilities. This proved the case in 27 of the 40 species tested as adults, and 10 of 13 juveniles (Table 2). The remaining species (except *T.pelios*, *E.franciscanus*, *E.caerulescens* and *L.sanguinodorsalis*) were best modelled using a TSM approach in either recapture or resighting probability. Most species showed similar support under the QAIC*c* for both the constant model and the recapture TSM model and in most cases QAIC*c*'s for these models differed by <2. Likelihood Ratio tests of all nested models within each model set were non-significant for all adult tests unless some element of time-dependence was present in the model (e.g. see *C.senegalensis*). Adult *C.niveicapilla*, *S.brachyura*, *S.frontalis* and *P.nigricollis* each had between 2-4 times more support (when comparing Akaike weights) for the TSM recapture model than for the constant model. Significant LRT tests were found only within these species when comparing the time-dependent and constant models. Amongst the juveniles, LRT tests were significant for *L.senegalensis* and *E.caerulescens* only when comparing TSM models in resighting and survival with the constant model. Few species were best modelled using time-dependence in either survival or recapture and those that were tended to be species with the largest datasets (Table 1. i.e. *C.senegalensis*, *E.franciscanus*, *E.caerulescens* and *L.sanguinodorsalis*).

Parameter Estimates

Adults

Estimates of apparent survival, φ (i.e. the product of true survival (S), site fidelity (F)) and probability of encounter, p (the product of site propensity (δ) and true detection (p^*)), varied widely between the 40 study species (φ range: 0.269 – 0.948, mean = 0.634; p range: 0.002 – 0.28. Table 3). Most families showed considerable variability between species, however the Ploceidae (0.694 – 0.786) and Estrildidae (0.456 – 0.571) had similar survival estimates for all members except one (*P.luteolus* and *S.cucullata* respectively). Mean survival varied significantly across all families (ANOVA, $F_{8,25}$ = 2.9, p =0.018; Levene's test $F_{8,25}$ = 0.5, p = 0.83) most likely due to the generally lower survival in the estrildine finches (Tukey, Estrildidae v Sylviidae, mean difference = -0.3, p = 0.035; all other tests between families p > 0.05). Substantially lower annual survival in the Passeridae, Emberizidae and Zosteropidae than in other passerine families was also reported (since the estimates were lower than that of the Estrildidae) but was not tested as only one representative species was available for each of these families. No significant differences in survival were found for any other combinations of familes. Survival varied significantly between the four guilds (ANOVA, $F_{3,36}$ = 3.9, p = 0.016; Levene's test $F_{3,36}$ = 0.4, p = 0.74) as a result of the significantly lower survival of the granivores compared to the insectivores (Tukey, mean difference = -0.165, p = 0.012). Estimates of p were low across all species. For most species, standard errors of the parameter estimates were acceptable (<0.10) although the confidence intervals reflected relatively low precision. This was especially noticeable for species with the smallest datasets (i.e. *M.mentalis* and *M.cinnamomeiventris*).

Although mist-netting studies have generally been found to report lower parameter rates in the first year after catching than for subsequent years (the reason for application of the TSM model (Pradel *et al.* 1995, 1997, Sandercock 2006), the nine species for which the TSM model was applied here showed significantly higher parameter estimates for p_1 (mean = 0.1) than for p_{2+} (mean = 0.073) ($t(16) = 0.4$, two-tailed $p < 0.01$).

Table 3. Estimates of apparent survival (φ) and recapture (p) probabilities for 40 Afro-tropical bird species at Amurum Community Forest Reserve, Nigeria. Standard type-face indicates estimates from the model with lowest QAIC$_c$. Greyed rows indicate weighted average estimates from the model set. Where time-since-marking models are used for generating the estimates, the relevant interval is indicated as either 1st or 2+. For models incorporating time-dependence in either parameter, only the minimum and maximum parameter estimates are listed.

				φ				**P**	
Species	**Model**	**Catch**	**Estimate**	**SE**	**95% CI range**	**Catch**	**Estimate**	**SE**	**95% CI range**
Columbidae									
T.abyssinicus	$\Phi_c p_c$	All	0.606	0.08	0.449 – 0.745	All	0.105	0.03	0.065 – 0.165
	$\Phi_c p_c$		*0.547*	*0.19*	*0.216 – 0.841*		*0.095*	*0.04*	*0.045 – 0.188*
Coliidae									
C.striatus	$\Phi_c p_c$	All	0.619	0.05	0.509 – 0.718	All	0.045	0.01	0.033 – 0.061
	$\Phi_c p_c$		*0.631*	*0.26*	*0.162 – 0.938*		*0.041*	*0.01*	*0.025 – 0.069*
Lybiidae									
P.chrysoconus	$\Phi_c p_c$	All	0.416	0.05	0.322 – 0.516	All	0.096	0.01	0.072 – 0.127
	$\Phi_c p_c$		*0.412*	*0.05*	*0.317 – 0.513*		*0.090*	*0.02*	*0.059 – 0.135*
L.vieilloti	$\Phi_c p_c$	All	0.599	0.09	0.410 – 0.763	All	0.182	0.05	0.106 – 0.294
	$\Phi_c p_c$		*0.602*	*0.1*	*0.409 – 0.768*		*0.186*	*0.06*	*0.099 – 0.321*
Pycnonotidae									
P.barbatus	$\Phi_c p_{a2\text{-}c/c}$	All	0.668	0.05	0.560 – 0.760	1st	0.045	0.01	0.027 – 0.075
	$\Phi_c p_{a2\text{-}c/c}$		*0.614*	*0.21*	*0.215 – 0.902*		*0.039*	*0.01*	*0.021 – 0.072*
						2+	0.027	0.01	0.019 – 0.038
							0.029	*0.01*	*0.020 – 0.041*
C.flavicollis	$\Phi_c p_c$	All	0.844	0.08	0.639 – 0.943	All	0.125	0.03	0.073 – 0.206
	$\Phi_c p_c$		0.776	0.2	0.289 – 0.970		0.121	0.04	0.059 – 0.232
Cisticolidae									
C.brachyura	$\Phi_c p_c$	All	0.636	0.06	0.523 – 0.735	All	0.098	0.02	0.072 – 0.132
	$\Phi_c p_c$		*0.603*	*0.17*	*0.280 – 0.856*		*0.104*	*0.03*	*0.063 – 0.166*
C.guinea	$\Phi_c p_c$	All	0.510	0.09	0.343 – 0.674	All	0.233	0.05	0.145 – 0.353
	$\Phi_c p_c$		*0.498*	*0.09*	*0.331 – 0.665*		*0.209*	*0.07*	*0.109 – 0.364*
C.aberrans	$\Phi_c p_{a2\text{-}c/c}$	All	0.650	0.15	0.348 – 0.866	1st	0.141	0.05	0.068 – 0.273
	$\Phi_c p_{a2\text{-}c/c}$		*0.611*	*0.14*	*0.330 – 0.834*		*0.121*	*0.05*	*0.051 – 0.258*
						2+	0.055	0.03	0.021 – 0.133
							0.068	*0.03*	*0.027 – 0.163*
C.cantans	$\Phi_c p_c$	All	0.806	0.11	0.520 – 0.941	All	0.077	0.02	0.043 – 0.135
	$\Phi_c p_c$		*0.800*	*0.11*	*0.515 – 0.938*		*0.071*	*0.03*	*0.031 – 0.152*
Sylviidae									
M.mentalis	$\Phi_c p_c$	All	0.948	0.13	0.092 – 0.999	All	0.082	0.02	0.046 – 0.142
E.pusilla	$\Phi_c p_{a2\text{-}c/c}$	All	0.586	0.13	0.332 – 0.801	1st	0.033	0.04	0.004 – 0.228
	$\Phi_c p_{a2\text{-}c/c}$		*0.612*	*0.14*	*0.335 – 0.832*		*0.065*	*0.06*	*0.012 – 0.289*
						2+	0.161	0.05	0.082 – 0.292
							0.145	*0.05*	*0.070 – 0.278*
S.brachyura	$\Phi_c p_{a2\text{-}c/c}$	All	0.875	0.12	0.452 – 0.984	1st	0.259	0.09	0.127 – 0.455
	$\Phi_c p_{a2\text{-}c/c}$		*0.854*	*0.12*	*0.467 – 0.975*		*0.232*	*0.09*	*0.098 – 0.456*
						2+	0.080	0.04	0.034 – 0.180
							0.092	*0.04*	*0.036 – 0.216*

				Φ				P	
Species	**Model**	**Catch**	**Estimate**	**SE**	**95% CI range**	**Catch**	**Estimate**	**SE**	**95% CI range**
Muscicapidae									
C.niveicapilla	$\Phi_c\ p_c$	All	0.779	0.06	0.631 – 0.880	All	0.080	0.02	0.052 – 0.119
	$\Phi_c\ p_c$		*0.780*	*0.06*	*0.629 – 0.881*		*0.080*	*0.02*	*0.045 – 0.139*
M.cinnamomeiventris	$\Phi_c\ p_c$	All	0.657	0.25	0.177 – 0.945	All	0.069	0.05	0.014 – 0.279
	$\Phi_c\ p_c$		*0.597*	*0.4*	*0.052 – 0.975*		*0.077*	*0.07*	*0.012 – 0.363*
C.familiaris	$\Phi_c\ p_c$	All	0.539	0.06	0.414 – 0.659	All	0.144	0.03	0.099 – 0.206
	$\Phi_c\ p_c$		*0.585*	*0.18*	*0.252 – 0.855*		*0.131*	*0.04*	*0.077 – 0.215*
Turdidae									
T.pelios									
Adults	$\Phi_c\ p_c$	All	0.799	0.06	0.659 – 0.891	All	0.052	0.01	0.037 – 0.073
	$\Phi_c\ p_c$		*0.793*	*0.17*	*0.342 – 0.966*		*0.050*	*0.01*	*0.031 – 0.080*
Juveniles	$\Phi_c\ p_c$	All	0.600	0.08	0.433 – 0.746	All	0.044	0.01	0.027 – 0.071
	$\Phi_c\ p_c$		*0.589*	*0.09*	*0.418 – 0.740*		*0.042*	*0.01*	*0.025 – 0.071*
	$\Phi_{a2\text{-}c/c}\ p_c$	1st	0.261	0.25	0.027 – 0.819	All	0.049	0.01	0.029 – 0.081
		2+	0.643	0.1	0.441 – 0.805				
Platysteiridae									
P.cyanea	$\Phi_c\ p_c$	All	0.700	0.07	0.560 – 0.810	All	0.153	0.03	0.103 – 0.221
	$\Phi_c\ p_c$		*0.709*	*0.07*	*0.563 – 0.822*		*0.183*	*0.06*	*0.094 – 0.326*
Zosteropidae									
Z.senegalensis	$\Phi_c\ p_c$	All	0.527	0.08	0.375 – 0.675	All	0.076	0.02	0.047 – 0.119
	$\Phi_c\ p_c$		*0.547*	*0.09*	*0.376 – 0.707*		*0.087*	*0.03*	*0.046 – 0.159*
Nectariniidae									
C.verticalis									
Adults	$\Phi_c\ p_{a2\text{-}c/c}$	1st	0.654	0.06	0.530 – 0.760	1st	0.069	0.03	0.025 – 0.174
	$\Phi_c\ p_{a2\text{-}c/c}$		*0.661*	*0.06*	*0.534 – 0.768*		*0.093*	*0.05*	*0.034 – 0.228*
						2+	0.160	0.03	0.111 – 0.225
							0.153	*0.03*	*0.104 – 0.219*
Juveniles	$\Phi_c\ p_c$	All	0.677	0.15	0.356 – 0.888	All	0.085	0.04	0.036 – 0.188
	$\Phi_c\ p_c$		*0.545*	*0.25*	*0.146-0.894*		*0.088*	*0.04*	*0.033 – 0.218*
	$\Phi_{a2\text{-}c/c}\ p_c$	1st	0.327	0.23	0.059 – 0.790	All	0.104	0.04	0.043 – 0.227
		2+	0.844	0.22	0.179 – 0.993				
C.senegalensis									
Adults	$\Phi_c\ p_c$	All	0.769	0.07	0.611 – 0.876	All	0.026	0.01	0.017 – 0.039
	$\Phi_c\ p_c$		*0.779*	*0.07*	*0.608 – 0.889*		*0.031*	*0.03*	*0.006 – 0.155*
Juveniles	$\Phi_c\ p_c$	All	0.832	0.2	0.233 – 0.988	All	0.007	<0.01	0.003 – 0.021
	$\Phi_c\ p_c$		*0.871*	*0.47*	*0.002 – 0.999*		*0.007*	*<0.01*	*0.001 – 0.015*
	$\Phi_{a2\text{-}c/c}\ p_c$	1st	0.789	0.29	0.114 – 0.991	All	0.007	0.01	0.001 – 0.030
		2+	0.971	0.8	-				
C.venustus									
Adults	$\Phi_c\ p_c$	All	0.534	0.06	0.410 – 0.655	All	0.035	0.01	0.023 – 0.052
	$\Phi_c\ p_c$		*0.529*	*0.07*	*0.402 – 0.653*		*0.033*	*0.01*	*0.020 – 0.055*
Juveniles	$\Phi_c\ p_c$	All	0.700	0.2	0.270 – 0.937	All	0.023	0.01	0.007 – 0.075
	$\Phi_c\ p_c$		*0.558*	*0.29*	*0.115 – 0.925*		*0.026*	*0.02*	*0.006 – 0.112*
	$\Phi_{a2\text{-}c/c}\ p_c$	1st	0.002	0.01	0.001 – 0.640	All	0.056	0.04	0.014 – 0.193
		2+	0.827	0.2	0.241 – 0.986				
Malaconotidae									
M.sulfureopectus	$\Phi_c\ p_c$	All	0.923	0.09	0.523 – 0.992	All	0.112	0.03	0.065 – 0.187
	$\Phi_c\ p_c$		*0.917*	*0.09*	*0.536 – 0.991*		*0.104*	*0.04*	*0.050 – 0.203*
T.senegalus	$\Phi_c\ p_c$	All	0.660	0.1	0.455 – 0.819	All	0.093	0.03	0.051 – 0.161
	$\Phi_c\ p_c$		*0.674*	*0.1*	*0.452 – 0.838*		*0.107*	*0.04*	*0.046 – 0.228*
Emberizidae									
E.tahapisi	$\Phi_c\ p_c$	All	0.491	0.13	0.266 – 0.721	All	0.017	0.01	0.008 – 0.035
	$\Phi_c\ p_c$		*0.522*	*0.14*	*0.262 – 0.771*		*0.021*	*0.01*	*0.008 – 0.051*
Passeridae									
S.frontalis	$\Phi_c\ p_c$	All	0.592	0.18	0.257 – 0.859	All	0.095	0.04	0.045 – 0.189
	$\Phi_c\ p_c$		*0.623*	*0.2*	*0.240 – 0.900*		*0.114*	*0.05*	*0.043 – 0.270*
Ploceidae									
P.luteolus	$\Phi_c\ p_c$	All	0.487	0.11	0.280 – 0.700	All	0.201	0.06	0.107 – 0.345
	$\Phi_c\ p_c$		*0.421*	*0.2*	*0.127 – 0.784*		*0.207*	*0.08*	*0.096 – 0.391*
P.cucullatus									
Adults	$\Phi_c\ p_c$	All	0.694	0.09	0.496 – 0.840	All	0.013	<0.01	0.008 – 0.022
	$\Phi_c\ p_c$		*0.691*	*0.09*	*0.489 – 0.839*		*0.012*	*0.01*	*0.006 – 0.25*

					Φ				P	
Species		**Model**	**Catch**	**Estimate**	**SE**	**95% CI range**	**Catch**	**Estimate**	**SE**	**95% CI range**
P.cucullatus										
	Juveniles	$\Phi_c\ p_c$	All	0.737	0.12	0.458 – 0.902	All	0.010	<0.01	0.005 – 0.020
		$\Phi_c\ p_c$		*0.582*	*0.27*	*0.140 – 0.923*		*0.012*	*0.01*	*0.004 – 0.031*
		$\Phi_{a2-c/c}\ p_c$	1st	0.844	0.16	0.320 – 0.984	All	0.015	0.01	0.006 – 0.039
			2+	0.346	0.24	0.060 – 0.815				
P.nigricollis										
	Adults	$\Phi_c\ p_{a2-c/c}$	All	0.786	0.08	0.606 – 0.900	1st	0.129	0.03	0.077 – 0.206
		$\Phi_c\ p_{a2-c/c}$		*0.784*	*0.08*	*0.602 – 0.900*		*0.127*	*0.03*	*0.074 – 0.209*
							2+	0.043	0.01	0.026 – 0.071
								0.044	*0.01*	*0.026 – 0.073*
	Juveniles	$\Phi_c\ p_c$	All	0.328	0.14	0.127 – 0.621	All	0.094	0.04	0.040 – 0.203
		$\Phi_c\ p_c$		*0.534*	*0.47*	*0.027 – 0.980*		*0.083*	*0.04*	*0.032 – 0.199*
		$\Phi_{a2-c/c}\ p_c$	1st	0.186	0.15	0.033 – 0.603	All	0.067	0.04	0.024 – 0.176
			2+	0.799	0.62	0.002 – 0.999				
P.vitellinus										
	Adults	$\Phi_c\ p_c$	All	0.726	0.09	0.534 – 0.860	All	0.052	0.01	0.036 – 0.074
		$\Phi_c\ p_c$		*0.599*	*0.24*	*0.174 – 0.914*		*0.050*	*0.01*	*0.030 – 0.084*
	Juveniles	$\Phi_c\ p_c$	All	0.805	0.08	0.609 – 0.916	All	0.052	0.01	0.035 – 0.078
		$\Phi_c\ p_c$		*0.714*	*0.19*	*0.282 – 0.941*		*0.058*	*0.02*	*0.034 – 0.097*
		$\Phi_{a2-c/c}\ p_c$	1st	0.876	0.1	0.552 – 0.976	All	0.063	0.02	0.038 – 0.102
			2+	0.550	0.18	0.226 – 0.837				
E.hordeaceus		$\Phi_c\ p_{a2-c/c}$	All	0.786	0.08	0.581 – 0.907	1st	0.013	0.01	0.004 – 0.046
		$\Phi_c\ p_{a2-c/c}$		*0.808*	*0.09*	*0.585 – 0.926*		*0.020*	*0.01*	*0.007 – 0.056*
							2+	0.013	0.01	0.020 – 0.059
								0.031	*0.01*	*0.017 – 0.056*
E.franciscanus										
	Adults	$\Phi_c\ p_t$	All	0.720	0.03	0.649 – 0.782	Min	0.002	<0.01	0.001 – 0.011
		$\Phi_c\ p_t$		*0.646*	*0.15*	*0.337 – 0.868*		*0.002*	*<0.01*	*0.001 – 0.008*
							Max	0.183	0.03	0.135 – 0.244
								0.187	*0.03*	*0.135 – 0.253*
	Juveniles	$\Phi_c\ p_c$	All	0.741	0.1	0.511 – 0.887	All	0.036	0.01	0.022 – 0.057
		$\Phi_c\ p_c$		*0.738*	*0.16*	*0.352 – 0.936*		*0.037*	*0.01*	*0.022 – 0.060*
		$\Phi_{a2-c/c}\ p_c$	1st	0.763	0.12	0.478 – 0.924	All	0.038	0.01	0.022 – 0.064
			2+	0.676	0.23	0.212 – 0.942				
Estrildidae										
E.caerulescens										
	Adults	$\Phi_c\ p_t$	All	0.566	0.04	0.486 – 0.643	Min	0.012	0.01	0.001 – 0.094
							Max	0.283	0.08	0.151 – 0.468
	Juveniles	$\Phi_c\ p_{a2-c/c}$	All	0.571	0.07	0.434 – 0.697	1st	0.099	0.02	0.069 –0.140
		$\Phi_c\ p_{a2-c/c}$		*0.559*	*0.12*	*0.337 – 0.759*		*0.095*	*0.02*	*0.063 – 0.400*
							2+	0.054	0.02	0.031 – 0.093
								0.051	*0.02*	*0.023 – 0.139*
		$\Phi_{a2-c/c}\ p_c$	1st	0.581	0.2	0.223 – 0.870	1st	0.099	0.02	0.065 – 0.148
			2+	0.567	0.09	0.391 – 0.728	2+	0.054	0.02	0.030 – 0.096
E.melpoda		$\Phi_c\ p_c$	All	0.571	0.13	0.312 – 0.796	All	0.029	0.01	0.014 – 0.060
		$\Phi_c\ p_c$		*0.581*	*0.14*	*0.305 – 0.814*		*0.031*	*0.01*	*0.013 – 0.070*
U.bengalus										
	Adults	$\Phi_c\ p_{a2-c/c}$	All	0.456	0.04	0.379 – 0.535	1st	0.067	0.01	0.047 – 0.093
		$\Phi_c\ p_{a2-c/c}$		*0.470*	*0.15*	*0.216 – 0.741*		*0.060*	*0.01*	*0.040 – 0.088*
							2+	0.048	0.01	0.037 – 0.061
								0.050	*0.01*	*0.038 – 0.066*
	Juveniles	$\Phi_c\ p_c$	All	0.614	0.15	0.309 – 0.850	All	0.043	0.02	0.019 – 0.092
		$\Phi_c\ p_c$		*0.609*	*0.25*	*0.164 – 0.925*		*0.044*	*0.02*	*0.019 – 0.100*
		$\Phi_{a2-c/c}\ p_c$	1st	0.628	0.19	0.263 – 0.889	All	0.044	0.02	0.017 – 0.109
			2+	0.559	0.41	0.048 – 0.970				
L.rufopicta		$\Phi_c\ p_c$	All	0.564	0.09	0.392 – 0.722	All	0.164	0.04	0.100 – 0.256
		$\Phi_c\ p_c$		*0.580*	*0.19*	*0.240 – 0.858*		*0.168*	*0.05*	*0.095 – 0.280*
L.senegalensis										
	Adults	$\Phi_c\ p_c$	All	0.515	0.06	0.407 – 0.622	All	0.047	0.01	0.034 – 0.064
		$\Phi_c\ p_c$		*0.525*	*0.06*	*0.409 – 0.638*		*0.051*	*0.01*	*0.033 – 0.080*
	Juveniles	$\Phi_{a2-c/c}\ p_c$	1st	0.141	0.08	0.053 – 0.325	All	0.055	0.02	0.032 – 0.094
				0.300	*0.12*	*0.140 – 0.632*		*0.060*	*0.02*	*0.034 – 0.104*
			2+	0.614	0.3	0.120 – 0.949				
				0.525	*0.24*	*0.094 – 0.922*				

			Φ				P		
Species	**Model**	**Catch**	**Estimate**	**SE**	**95% CI range**	**Catch**	**Estimate**	**SE**	**95% CI range**
L.sanguinodorsalis									
Adults	$\Phi_c\ p_t$	All	0.559	0.04	0.482 – 0.632	Min	0.011	0.01	0.001 – 0.078
						Max	0.270	0.07	0.153 – 0.432
Juveniles	$\Phi_c\ p_c$	All	0.494	0.07	0.364 – 0.626	All	0.111	0.02	0.077 – 0.158
	$\Phi_c\ p_c$		*0.517*	*0.11*	*0.320 – 0.709*		*0.116*	*0.03*	*0.076 – 0.174*
	$\Phi_{a2\text{-}c/c}\ p_c$	1st	0.547	0.16	0.260 – 0.806	All	0.108	0.02	0.072 – 0.159
		2+	0.466	0.1	0.288 – 0.653				
L.rara	$\Phi_c\ p_c$	All	0.528	0.15	0.263 – 0.779	All	0.249	0.1	0.110 – 0.472
	$\Phi_c\ p_c$		*0.570*	*0.18*	*0.244 – 0.845*		*0.270*	*0.11*	*0.115 – 0.513*
S.cucullata									
Adults	$\Phi_c\ p_c$	All	0.269	0.07	0.162 – 0.413	All	0.022	0.01	0.014 – 0.036
	$\Phi_c\ p_c$		*0.280*	*0.21*	*0.047 – 0.756*		*0.021*	*0.01*	*0.011 – 0.038*
Juveniles	$\Phi_c\ p_{a2\text{-}c/c}$	All	0.218	0.09	0.095 – 0.427	1st	0.018	0.01	0.006 – 0.055
	$\Phi_c\ p_{a2\text{-}c/c}$		*0.199*	*0.1*	*0.068 – 0.456*		*0.038*	*0.01*	*0.026 – 0.056*
						2+	0.038	0.01	0.026 – 0.054
							0.028	*0.01*	*0.011 – 0.071*
	$\Phi_{a2\text{-}c/c}\ p_c$	1st	0.093	0.06	0.024 – 0.301	All	0.036	0.01	0.024 – 0.055
		2+	0.203	0.1	0.068 – 0.468				

Support for time-dependence was found within the model sets of various species, however MARK had difficulty generating believable parameter estimates for some of these (e.g. the majority producing $\varphi > 0.999$ with SE of zero). Where this was the case, these time-dependent models were removed from the candidate model set and model averaging was performed with the remaining less-parameterised models. This removed the influence of these high outliers and typically resulted in a lower averaged value of φ. Model averaging generally produced parameter estimates within 10% of those obtained from the best-supported model. In 17 of 37 species this was greater than the estimate derived from the single model. Overall, the mean weighted average model was 0.011 (2%) less than the mean obtained from the single models (0.627 v 0.638).

Return rates across all species varied between 0.064 in *S.cucullata* to 0.563 in *S.brachyura* (Table 1), and species with low return rates had low survival estimates (Pearson $r_{37} = 0.42$, $p < 0.01$).

Juveniles and immatures

For all species other than *Lagonosticta senegalensis*, survival in individuals caught as juveniles or immatures was best described by a model incorporating constant survival and recapture probabilities. Estimates of φ

and *p* for the 13 species tested as juveniles and immatures, varied widely as for the adults (for the best models: φ range: 0.141 – 0.832, mean = 0.577; *p* range: 0.007 – 0.111 (Table 3.)). Mean survival did not vary significantly between families (ANOVA, $F_{3,8} = 1.3$, $p = 0.34$). Poor precision was reflected in high standard errors for most estimates (SE range 0.069 – 0.297) and was most likely a consequence of the small sample sizes. Estimates derived from these models (i.e. having constant survival across the duration of the study) are inadequate if the aim is to determine how survival in the first year of life differs from that of adults. To allow for this, output from more biologically useful models that differentiate between survival in first and subsequent years is also given in Table 3. These showed that first year survival was higher than that of subsequent years in 6 of the 13 species, although overall mean survival across all species was significantly higher after the first year (mean ± se; first year: 0.454 ± 0.09 (range - 0.002 – 0.876); subsequent years: 0.620 ± 0.06 (range - 0.203 – 0.971): matched pairs $t(25) = -9.7$, $p < 0.001$). As for adults mean estimates of juvenile survival did not vary significantly between families (ANOVA, $F_{2,9} = 1.1$, $p = 0.39$).

Return rates for juveniles varied similarly to those for adults (range 0.058 - 0.409 (Table 1)). Return rates for adults were higher than for juveniles for all species except three *Estrildidae*. Paired comparisons of return rates showed that, despite the mean overall return rate for juveniles (0.201) being lower than for adults (0.235), there was no significant difference between age-groups ($t(12) = 1.9$, two-tailed $p = 0.07$).

Comparisons between adult and juvenile estimates

Matched pair comparisons of mean apparent survival revealed no significant difference between adult and juvenile passerines when comparing all species (mean ± SE: adult 0.62 ± 0.043; juvs 0.464 ± 0.086; matched pairs $t(11) = 2$, $p = 0.08$) although the small sample sizes and lack of power may be masking any effect. There was no significant interaction between family and age class on mean survival ($F_{2,24} = 0.7$, $p = 0.66$).

Comparisons with other studies

Estimates of apparent adult survival rates showed greater agreement when species and families were compared between the current study and those from Malawi (Peach *et al.* 2001) than for comparisons with estimates from the previous work in Nigeria 2004 (Table 4.), e.g. for *Cinnyris venustus,* estimates for this study differed from the Malawi estimates by 0.02 but from the earlier Nigeria study by 0.43. Mean absolute differences between the five species common to the three studies was 0.122 between this study and Malawi, and 0.334 between this study and Nigeria 2004.

Estimates of adult mean apparent survival rates (Table 4) were higher in this study (0.624 ± 0.02) than those of McGregor *et al.* (2007) (0.596 ± 0.05) when comparing 21 species used in both studies, but lower than those obtained by Peach *et al.* (2001) (0.626 ± 0.05 v 0.632 ± 0.12) for five species common to both studies. Overall comparisons, which included all species used in the studies, again revealed similar estimates between this and the Malawi study (0.64 ± 0.02 v 0.637 ± 0.03) and a 5% difference between this study and the previous Nigerian work (0.64 ± 0.02 v 0.59 ± 0.05). In all cases, apparent precision of estimates was greater in the current study.

Table 4. Comparison of reported adult survival rates (± standard error) of Afro-tropical bird species between the current study, previous work by McGregor *et al.* 2007b in Nigeria (2001-2004), and from Malawi (1974-1989 - Peach et al. 2001).

Species	Nigeria 2009	Nigeria 2004	Malawi 1989	*Mean*
Columbidae				
Turtur abyssinicus	0.61 ± 0.08	0.90 ± 0.05	-	***0.76 ± 0.15***
Coliidae				
Colius striatus	0.62 ± 0.05	0.19 ± 0.19	-	***0.41 ± 0.22***
Lybiidae				
Pogoniulus chrysoconus	0.42 ± 0.05	-	-	
Lybius vieilloti	0.60 ± 0.09	0.90 ± 0.08	-	*0.75 ± 0.15*
Mean for family by study	*0.51 ± 0.09*			
Overall mean for family				***0.64 ± 0.14***
Non-passerine families overall mean (study) ± SE	***0.58 ± 0.04***	***0.66 ± 0.24***	-	
Non-passerine families overall mean ± SE				***0.62 ± 0.49***
Pycnonotidae				
Pycnonotus barbatus	0.67 ± 0.05	0.36 ± 0.08	0.74 ± 0.04	*0.59 ± 0.12*
Phyllastrephus terrestris	-	-	0.74 ± 0.05	
Andropadus importunus	-	-	0.68 ± 0.03	
Chlorocichla flavicollis	0.84 ± 0.08	0.45 ± 0.26	-	
Mean for family by study	*0.76 ± 0.09*	*0.41 ± 0.05*	*0.72 ± 0.02*	
Overall mean for family				***0.61 ± 0.07***
Cisticolidae				
Camaroptera brachyura	0.64 ± 0.06	0.46 ± 0.11	0.74 ± 0.06	*0.61 ± 0.08*
Prinia subflava	-	-	0.60 ± 0.08	
Apalis flavida	-	-	0.68 ± 0.07	

Species	Nigeria 2009	Nigeria 2004	Malawi 1989	*Mean*
Cisticola erythrops	-	-	0.53 ± 0.08	
Cisticola guinea	0.51 ± 0.09	-	-	
Cisticola cantans	0.81 ± 0.11	-	-	
Cisticola aberrans	0.65 ± 0.15	-	-	
Mean for family by study	*0.65 ± 0.06*		*0.64 ± 0.05*	
Overall mean for family				***0.62 ± 0.04***
Sylviidae				
Acrocephalus baeticatus	-	-	0.77 ± 0.07	
Acrocephalus gracilirostris	-	-	0.56 ± 0.09	
Eremomela pusilla	0.59 ± 0.13	-	-	
Sylvietta brachyura	0.88 ± 0.12	-	-	
Sylvietta rufescens	-	-	0.80 ± 0.07	
Mean for family by study	*0.74 ± 0.15*		*0.71 ± 0.08*	
Overall mean for family				***0.72 ± 0.06***
Muscicapidae				
Cossypha niveicapilla	0.78 ± 0.06	-	-	
Cossypha heuglini	-	-	0.83 ± 0.07	
Cercomela familiaris	0.54 ± 0.06	-	-	
Myrmecocichla cinnamomeiventris	0.66 ± 0.25	-	-	
Mean for family by study	*0.66 ± 0.07*			
Overall mean for family				***0.70 ± 0.07***
Turdidae				
Turdus pelios	0.80 ± 0.06	-	-	***0.80 ± 0.06***
Platysteiridae				
Platysteira cyanea	0.70 ± 0.07	0.73 ± 0.15	-	***0.72 ± 0.02***
Zosteropidae				
Zosterops senegalensis	0.53 ± 0.08	0.34 ± 0.17	-	***0.44 ± 0.1***
Nectariniidae				
Hedydipna collaris	-	-	0.76 ± 0.08	
Cyanomitra verticalis	0.65 ± 0.06	0.60 ± 0.24	-	*0.63 ± 0.03*
Chalcomitra senegalensis	0.77 ± 0.07	0.39 ± 0.19	0.90 ± 0.08	*0.69 ± 0.15*
Cinnyris venustus	0.53 ± 0.06	0.96 ± 0.03	0.55 ± 0.08	*0.68 ± 0.14*
Cinnyris bifasciatus	-	-	0.76 ± 0.09	
Cinnyris cupreus	-	-	0.60 ± 0.07	
Mean for family by study	*0.65 ± 0.07*	*0.65 ± 0.17*	*0.71 ± 0.06*	
Overall mean for family				***0.68 ± 0.05***
Malaconotidae				
Malaconotus sulfureopectus	0.92 ± 0.09	-	-	
Tchagra senegalus	0.66 ± 0.1	0.45 ± 0.24	-	*0.56 ± 0.11*
Mean for family by study	*0.79 ± 0.13*			
Overall mean for family				***0.68 ± 0.14***
Emberizidae				
Emberiza tahapisi	0.49 ± 0.13	-	-	***0.49 ± 0.13***
Fringillidae				
Serinus mozambicus	-	-	0.65 ± 0.08	
Serinus sulphuratus	-	-	0.52 ± 0.07	
Mean for family by study			*0.59 ± 0.07*	
Overall mean for family				***0.59 ± 0.06***
Passeridae				
Sporopipes frontalis	0.59 ± 0.18	0.42 ± 0.25	-	***0.51 ± 0.09***
Ploceidae				
Ploceus xanthopterus	-	-	0.70 ± 0.03	
Ploceus luteolus	0.49 ± 0.19	0.53 ± 0.5	-	*0.51 ± 0.02*
Ploceus vitellinus	0.73 ± 0.09	0.87 ± 0.09	-	*0.80 ± 0.07*
Ploceus cucullatus	0.69 ± 0.09	-	-	
Ploceus nigricollis	0.79 ± 0.08	0.48 ± 0.16	-	*0.64 ± 0.16*
Euplectes hordaceus	0.79 ± 0.08	-	-	
Euplectes franciscanus	0.72 ± 0.03	-	-	
Euplectes orix	-	-	0.72 ± 0.04	
Euplectes capensis	-	-	0.54 ± 0.09	
Mean for family by study	*0.70 ± 0.05*	*0.63 ± 0.12*	*0.65 ± 0.06*	
Overall mean for family				***0.67 ± 0.04***

Species	Nigeria 2009	Nigeria 2004	Malawi 1989	*Mean*
Estrildidae				
Pytilia melba	-	-	0.52 ± 0.04	
Estrilda caerulsecens	0.57 ± 0.04	0.68 ± 0.13	-	*0.63 ± 0.06*
Estrilda troglodytes	0.57 ± 0.13	-	-	
Estrilda astrild	-	-	0.61 ± 0.05	
Uraeginthus angolensis	-	-	0.46 ± 0.09	
Uraeginthus bengalus	0.46 ± 0.04	0.53 ± 0.2	-	*0.50 ± 0.04*
Lagonosticta rufopicta	0.56 ± 0.09	0.75 ± 0.11	-	*0.66 ± 0.1*
Lagonosticta senegala	0.52 ± 0.06	0.89 ± 0.39	0.23 ± 0.1	*0.55 ± 0.19*
Lagonosticta rhodopareia	-	-	0.50 ± 0.06	
Lagonosticta sanguinodorsalis	0.56 ± 0.04	0.66 ± 0.18	-	*0.61 ± 0.05*
Lagonosticta rara	0.53 ± 0.15	-	-	
Spermestes cucullata	0.27 ± 0.07	-	-	
Vidua chalybeata	-	-	0.54 ± 0.12	
Mean for family by study	*0.51 ± 0.04*	*0.70 ± 0.06*	*0.48 ± 0.05*	
Overall mean for family				***0.55 ± 0.03***
Fringillidae				
Serinus mozambicus	-	-	0.65 ± 0.08	
Serinus sulphuratus	-	-	0.52 ± 0.07	
Mean for family by study			*0.59 ± 0.06*	
Overall mean for family				***0.59 ± 0.06***
Passerine Families Overall Mean (study) ± SE	***0.66 ± 0.03***	***0.52 ± 0.05***	***0.64 ± 0.03***	
Passerine Families Overall mean ± SE				***0.61 ± 0.02***
Overall Family Mean (study) ± SE	***0.63 ± 0.02***	***0.60 ± 0.05***	***0.64 ± 0.03***	
Overall Family Mean ± SE				***0.63 ± 0.02***

Discussion

Age-related survival of a range of tropical African bird species was examined using capture-mark-recapture methods. Using data from mist-net catches made between 2001 and 2008 it was possible to estimate apparent adult survival for 40 species with reasonable precision, and juvenile/immature survival for 13 species (though with lower precision). Although no meteorological data were included for analysis within this study there was not thought to be any significant variation in overall rainfall or temperature at the site between years (see data in Brandt (2007)). Despite this assumption I attempted to test for temporal variation in survival in those species for which there were sufficient data.

The primary aim of this study was to develop acceptably precise estimates of survival for later inclusion in assessments of how moult, survival and timing of breeding are related in tropical bird species and to further compare these estimates with those of north temperate species to identify whether and how they fitted into the high survival – low clutch size tropical-temperate paradigm (Moreau 1944; Martin 1996) (Chapter 6). As well as this, the intention was to produce estimates of survival that could be compared against other studies undertaken both in the Afrotropical and Neotropical regions to provide some means of assessing the diversity of rates in tropical areas.

Potential sources of error

The use of standard capture-mark-recapture protocols for assessing apparent annual survival is predicated on a number of assumptions about the behaviour of individuals i.e. that they are independent, have equal probability of detection/capture (i.e. are not prone to trap dependence) or that they remain within the study area and do not emigrate (i.e. show significant transience) (Lebreton *et al.* 1992). Failure to account for such behaviours can introduce significant heterogeneity to analyses reducing the value and accuracy of any estimates derived.

During the 8 years of this study, the majority of birds were caught within the confines of the Constant Effort Site at Amurum. The opening of nets at this location every morning for 14 successive days, twice each year, would be expected to lead to birds becoming accustomed to net locations and avoiding certain areas. In fact, although capture rates declined throughout each CES period (see Chapter 5), the results of the test for trap dependence (test 2.Ct in U-CARE) closely followed those of Peach *et al.* (2001) and revealed no evidence of this either for the 40 adult species or the 13 species assessed as juveniles/immatures. If modelling had focused solely on the CES catches then it is possible that the analyses for many of the species will have shown some element of trap shyness. The inclusion of catches at other locations around the reserve and between CES periods is likely to have removed these effects.

Generally, survival models based on mark-recapture methods will underestimate true survival if the population of marked individuals contains a significant proportion of juvenile birds or transient individuals (Lebreton *et al.* 1992; Pradel *et al.* 1997; Parker *et al.* 2006). Survival in the first year of life is typically lower than that for subsequent years (Ricklefs 2000b) and pooling first year individuals with adults will often result in a reduced survival estimate compared to that for adults alone (Jullien & Clobert 2000; Ricklefs 2000b; Blake & Loiselle 2002). Similarly, the indirect effects, and often age-specific variability in levels, of site fidelity, natal and breeding dispersal will also have an impact on estimates of survival (Sæther & Bakke 2000; Peach *et al.* 2001) unless explicitly incorporated within any model (Arnason 1973; Schwarz *et al.* 1983; Nichols & Kendall 1995; Grosbois & Tavecchia 2003; Devillard & Bray 2009). Although attempts were made to model juvenile and adult survival separately, the paucity of detailed information relating to the ageing and sexing of many west African bird species is likely to mean that a number of individuals were incorrectly aged or sexed. Since post-juvenile dispersal is common in many passerine species (Greenwood & Harvey 1982) incorrect ageing will either increase estimated juvenile survival (where adults are mistaken for juveniles/immatures) or decrease adult survival rates (where juveniles/ immatures are misidentified as adults). Despite this it is assumed that the majority of birds were aged correctly during this study and, given that there was no evidence that transience was a problem, any effects on survival estimates are likely to have been negligible.

Not all individuals caught within an area will stay in the locality and these individuals are unlikely to appear in subsequent catches. This transience may be a result of factors such as partial migration, catches being made at the edge of the normal home range of the individual, natal or breeding dispersal. Whatever the causes, transience is a common problem in mist-netting mark-recapture studies of passerines (Peach 1993) and can result in CJS-type models underestimating apparent survival (Johnston *et al.* 1997; Brawn *et al.* 1999). Assessment of transience using the goodness of fit tests within U-CARE revealed only limited impact on this study. Transience affected modelling (i.e. significance in test 3.SR, $p<0.05$) in only three of 40 species tested as adults (*Pycnonotus barbatus*, *Uraeginthus bengalus*, *Cinnyris venustus*) and none of the tests for the 13 species tested as juveniles/immatures were significant. Transience was accommodated and accounted for in the analyses with the use of TSM models and this two age-class model is likely to have prevented significant negative biases to estimates caused by transient individuals (Pradel *et al.* 1997). Many of the species caught in this study are representatives of families also present in the study in Malawi (Peach *et al.* 2001). As in Malawi, transience, whether a result of breeding dispersal, natal dispersal, or some other cause, was not found to be a major biasing factor in assessment of annual survival for most families here. This is somewhat surprising given the level of anthropogenic pressures and influences to which the study site is subjected. Annual variation in both negative pressures such as the collection of wood, removal of trees, grazing, conversion of savannah to agriculture, hunting and burning, and positive conservation efforts including reforestation, fire management and habitat protection, will all have contributed to changes in the habitat composition and structure (Robinson *et al.* 1979; Force 1981; Rowe-Rowe & Lowry 1982). These changes may have led to decreased suitability of the habitat for certain species (e.g. through the loss of scrub, woodland, invertebrate diversity and abundance (e.g. Sileshi & Mafongoya 2006), or burning of grassland) leading to emigration of species caught earlier in the study, and a consequent negative impact on estimated apparent survival rates. Such effects have not manifested themselves in low survival rates or high levels of transience here. This may be due to complex ecological mechanisms (e.g. environmental plasticity, (Uys *et al.* 2006)) or high levels of tolerance and adaptability of certain species (e.g. as has been proposed for certain Sahelian species - Stevens et al. 2010). Alternatively, the reasons may be altogether more prosaic. For example, those species that are most susceptible to habitat change may have been caught in such low numbers that they were excluded from the analyses. Similarly, Blake & Loiselle (2008) identified plot size as a significant factor in determining apparent transience in mark-recapture studies. Since smaller plots hold fewer individuals of tropical species (Terborgh *et al.* 1990), and only relatively short movements are necessary to take individuals away from the catching area, the chances of recapture of an individual are reduced, thereby resulting in a higher level of apparent transience and lower estimate of survival (e.g. see Cilimburg *et al.* 2002). In contrast, such effects are likely to be much reduced where the catching area is centred in larger plots. These effects have been reported in study plots with areas <10ha (e.g. Johnston *et al.* 1997; Peach *et al.* 2001).

The low level of transience identified here may therefore simply be a consequence of the large study plot at Amurum (120ha).

Finally, although the datasets for many of the species used in this study are relatively large, several had limited numbers of recaptures. In almost all species, recapture probabilities were very low (generally $p<0.2$). As a result ability to identify differences between survival models here may have been compromised (Lebreton *et al*. 1992). Also, as identified by Sandercock *et al.* (2000), although survival in tropical species is expected to remain reasonably constant between years given the stable climatic conditions, many tropical regions still show annual and seasonal variation in rainfall (Karr *et al.* 1990), which often influences annual survival (Gibbs & Grant 1987; Stiles 1992; but see Covas *et al.* 2004). In spite of this, most studies fail to incorporate time-dependence in mark-recapture studies either through an assumption that it is not present or because of limitations of datasets. Those studies that have accommodated time-dependent survival have tended to do so only for species with largest datasets (e.g. Faaborg & Arendt 1995) and have removed time-dependence from models of the remaining species. The limitations of the data here resulted in adoption of a similar strategy. Successful incorporation and assessment of time dependence in survival was possible in only three of 36 starting models and this may have resulted in a lack of power to the analyses for several species. Interestingly though, later model selection led to replacement of time-dependence with TSM or time-constant models in all occasions for which time-dependent models were the general models, again suggesting that species assessed here were not subject to time-dependent survival over the period of the study.

Adult survival

Too few species were caught in this study to make many generalisations about survival rates in tropical non-passerine landbirds. Of those caught in sufficient numbers to allow estimation of survival, all four species were frugivorous and, as they share some similarities in basic ecology, limited comparisons were made. Estimates here were very different to those produced by McGregor *et al.* (2007) for all non-passerine species (mean difference = 0.34) but not in a consistent direction. This may be a result of the very small sample sizes used in the earlier study and the associated difficulties here in applying the Barker method (used in their study) to such data (see Chapter 5).

Survival was fairly consistent across three of the four non-passerines species at around 0.61, but was markedly lower in *Pogoniulus chrysoconus*. Traditionally this difference would have been accounted for on the basis of the difference in size between the species involved (Sæther 1989; Dobson 1990; Brawn *et al.* 1995; Ricklefs 2000a) - *P.chrysoconus* having a mean mass (10.8 ± 0.04, *n* = 331) less than 25% of that of the other species in the analysis. This size effect is generally reported to result in survival of non-passerine land bird species being significantly higher than that for passerines in temperate areas (e.g. Dobson 1987; Schulz *et al.* 1996; Small *et al.* 2008) however, the relatively high mean rate of survival across the passerine species assessed here meant that no evidence was found for this. Mean annual survival here was similar between non-passerines and passerines (mean ± se: 0.61 ± 0.01 v 0.64 ± 0.03; $t(37) = -1.1$, $p = 0.26$) agreeing with the findings of McGregor (2005).

Among the passerine species, apparent adult survival varied widely when comparing across all species and between species within families and no consistent trend was evident. The potential reasons behind this are unclear but may relate to factors such as differential vulnerability to predation (e.g. van den Hout *et al.* 2008), variable levels of competition between certain species groups or guilds (e.g. among the nectarivores (Gill & Wolf 1979; Chaskda & Mwansat 2006)), differential mortality of the sexes and sex-biases in mist-net captures (e.g. Oatley 1982; Dowsett 1985) or simply a result of estimates for certain species being based on much smaller datasets. Estimates for certain species (and closely-related species) were comparable with those achieved in other studies and this geographical replication suggests that these estimates may be relatively robust. On a broader scale, mean survival was reasonably stable and high (0.65-0.79) for all, except three predominantly granivorous, families (Estrildidae, Emberizidae and Passeridae) and the Zosteropidae (range 0.49 - 0.53)(Table 4).

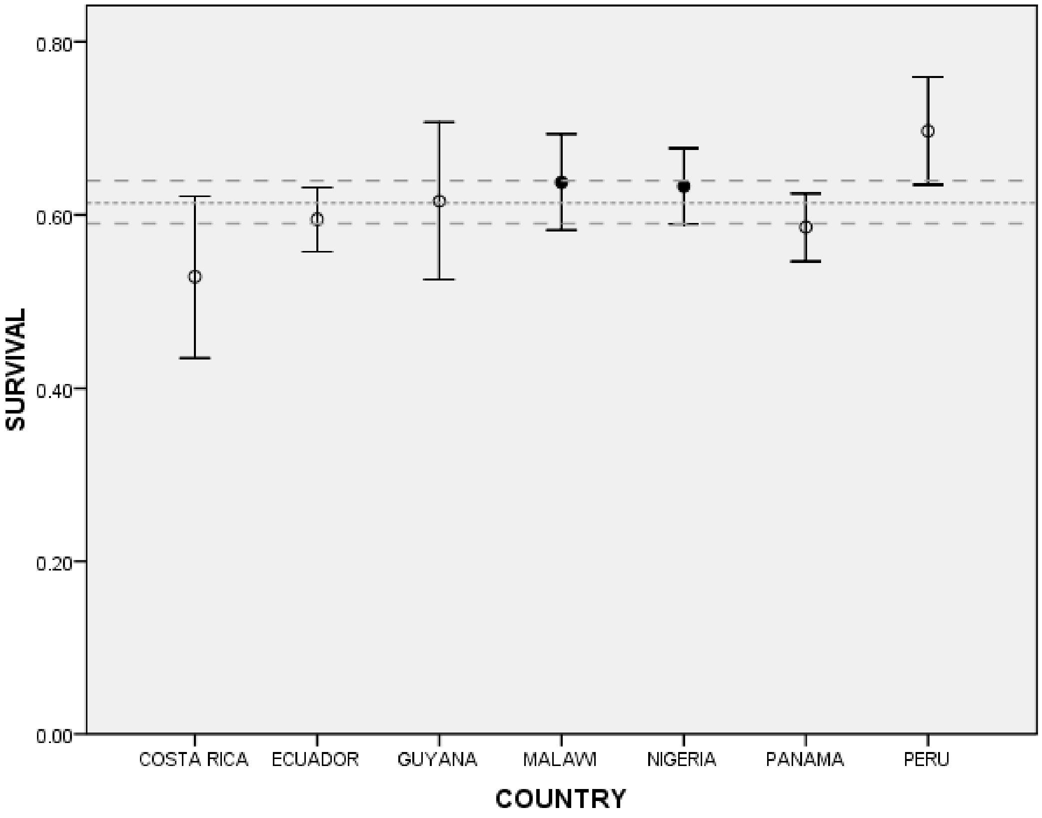
Across all species and guilds the lowest estimate of apparent annual survival in passerines was found in the granivores (0.27 in *Lonchura cucullatus*) and highest for insectivorous species (0.92 in *Malaconotus sulfureopectus*). The significantly lower survival of estrildine species in this study mirrors the low survival in small, granivorous tropical passerines reported from a number of other studies, and has been linked to seasonality (e.g. Morel 1966; Yom-Tov *et al.* 1992; Peach *et al.* 2001). Given that Brandt (2007) found seed availability in the study area to decline from a high and stable concentration during the early dry season to almost negligible levels by the wet season, it seems reasonable to assume that food availability regulated by seasonality (Maclean 1971; Harrison *et al.* 1997) might play an important role in the survival of granivores. In fact Brandt (2007) found no evidence for a seasonal variation in starvation risk among granivores. This suggests that individuals may attempt to reduce potential mortality either by adopting one of several possible strategies. They may forego breeding opportunities during periods where gaining suitable body condition is not possible (Ashmole 1963; Skutch 1985; Brandt 2007), temporarily disperse to find more suitable feeding areas (Herremans *et al.* 1995; Lloyd 1999) or adjust foraging habits and switch to an alternative and more abundant food source (e.g. Maclean 1971; Smith *et al.* 1978). Alternatively, seasonality may influence survival of granivorous species through the availability of water (Peach *et al.* 2001) rather than food limitation. Many species rely on a source of drinking water to facilitate digestion of seeds during the dry season (Immelmann & Immelmann 1967; Skaed 1975), indeed certain estrildine species (*L.sanguinodorsalis* and *L.rara*) were regularly observed to congregate at the limited water sources throughout the study area during early morning and late evening (pers. obs.). The failure of (inexperienced) individuals to take advantage of, or successfully compete for access to, dwindling water supplies may explain the lower survival observed among the estrildines. Of the other granivorous species included within this study, survival in *Sporopipes frontalis* and *Emberiza tahapisi* was also low, most likely as a result of their similar general ecology. In contrast, survival across the Ploceidae was >0.69 for all species (except *P.luteolus*). Higher survival for these species may be a result their more catholic diet (of insects, fruit, flowers and nectar as well as seeds (Fry *et al.* 2004)). Invertebrates in tropical Africa remain sufficiently numerous throughout the year that insectivorous birds are rarely thought to suffer serious food shortages (Lack 1986; Chambers & Samways 1998). Species dependent upon insects or able to switch between foods should therefore rarely face increased mortality as a result of food limitation. Also, several of the Ploceids (e.g. *Euplectes franciscanus* and *E.hordeaceus*) show an increased tendency to undertake short-scale, local movements to find alternative foraging. This strategy would again provide increased opportunity for overcoming the problems associated with temporal and spatial unpredictability in food and water availability. The potential causes for the markedly lower survival in *P.luteolus* are uncertain since they have similarly varied diets, but may reflect more on the sample sizes and precision of the estimates than on species ecology. Both recent survival estimates for this species have had relatively high standard errors (0.194 here; 0.503 for McGregor (2005)).

Comparisons of adult rates with other tropical studies

A wide range of techniques have been employed for estimating survival in tropical species, however the most frequently used include the assessment of return rates (e.g. Snow & Lill 1974; Greenberg & Gradwohl 1986), systematic mist-netting and mark-recapture modelling (e.g. Karr *et al*. 1990; Faaborg & Arendt 1995) or mist-netting and mark-resighting (e.g. McGregor *et al*. 2007b). Although each of these techniques provides a degree of utility, comparisons of estimates will undoubtedly be affected by the biases inherent in each. Return rates and mark-recapture studies will both tend to underestimate true survival because they fail to account for heterogeneity of detection probabilities (Lebreton *et al*. 1992) and the extent of transience (Johnston *et al*. 1997) (unless specifically incorporated within the model set (Pradel *et al*. 1997)) respectively. In contrast, mark-resighting studies typically focus only on specific portions of the population that can be easily surveyed and may be open to greater influence of differential effort – previous resighting attempts and experiences often influencing future effort. This may lead to a positive bias in survival estimates compared to those derived from systematic mist net studies (see review of published data on Neotropical passerines in Blake & Loiselle 2008 Appendix S1). Such effects may be the reason behind some of the differences between the current study and that of McGregor et al. (2007). For example, the estimate of apparent annual survival in Cinnyris venustus in 2004 was almost twice that observed for the current data (0.96 cf. 0.53 – see Table 4). This species is especially apparent around the study site and, its behaviour is such (it frequently visits favoured feeding areas and is unconcerned by human presence) that resightings are generally easily made. For the majority of species however, estimates of survival were higher in the current study than for 2004. Again this is likely to be a result of problems in applying the methodology of the mark-resighting approach (see Chapter 5). There may also be a number of smaller negative biases in the mark-resighting approach not typical of mark-recapture methods, such as loss or removal of colour-rings by the birds, errors in resightings or duplication in application of colour-rings. An assumption of most mark-recapture (or resighting) studies is that loss of individual marks (or misidentification) is minimal, however the rate of reported error during the assessment of mark-resighting techniques in this study (i.e. reporting errors, ring losses or ring removals by species divided by the number of individuals carrying colour-rings) was high (e.g. 24% in Ploceus cucullatus, 7% in P.nigricollis). As this study was an extension of that of McGregor et al. (2007), the level of error identified here, although not in itself enough to be entirely responsible for the differences in estimates, may have been sufficiently high to result in a slight negative bias in estimates of survival for certain species (e.g. P.nigricollis 0.79 in 2008 cf. 0.48 in 2004).

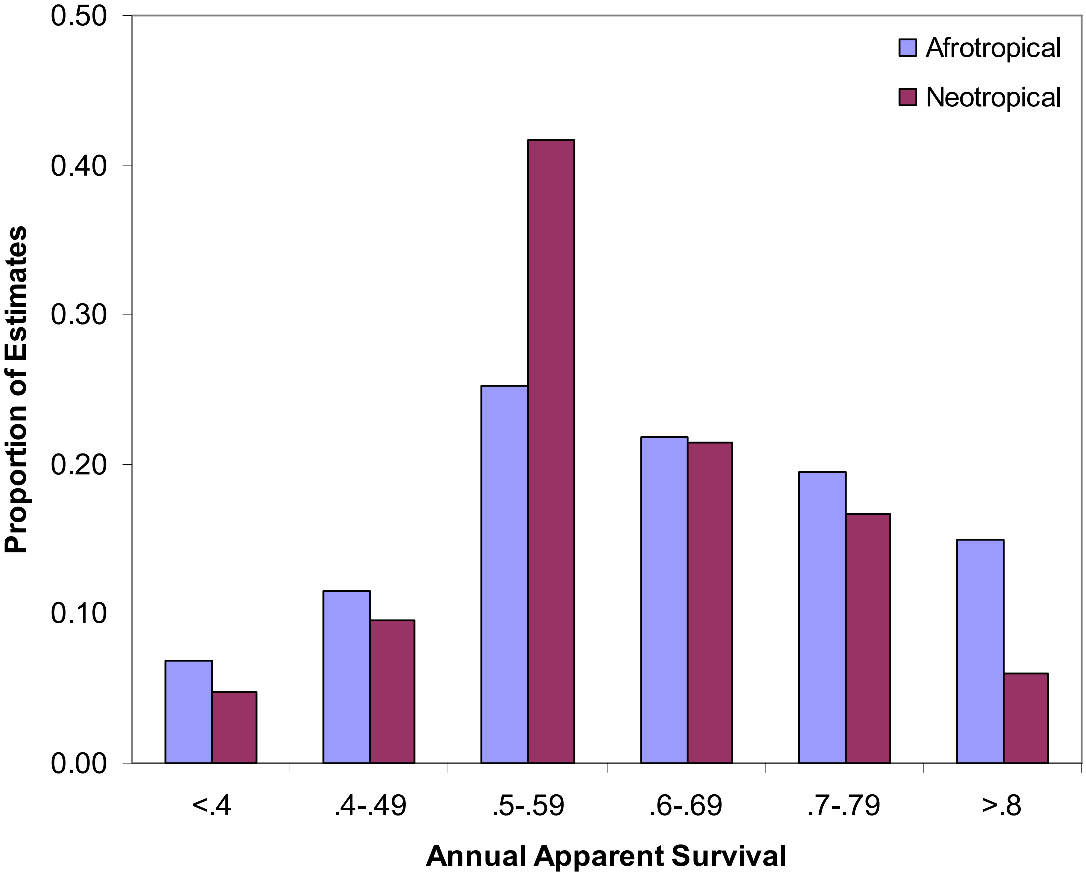
Generalisations made about the latitudinal variation in survival of tropical species compared to those of temperate areas (Ashmole 1963; Skutch 1949; Ricklefs 1997) should, if correct, apply equally across broad geographical areas and regions. Survival across Afrotropical areas should be comparable to those of Neotropical, tropical Australasian and tropical Indo-Malayan areas. Most studies assessing survival across tropical regions (usually within a specific ecozone) have found considerable variability in survival rates for species (e.g. Karr *et al.* 1990; Faaborg & Arendt 1995; Blake & Loiselle 2008) presumably as a result of variation in both environmental factors such as altitudinal gradients (Ricklefs 1997, Bears *et al.* 2009; Tieleman 2009) and ecological conditions (e.g. varying populations of predators (Francis *et al.* 1999)). There has however, been little in the way of formal testing of rates between countries or regions. Comparing Afrotropical data, there was no significant variation between survival estimates from this study and those from Malawi (Peach *et al.* 2001) (mean ± se, Malawi: 0.638 ± 0.272, N=27; Nigeria: 0.633 ± 0.218, n = 39; $t(64) = 0.13$, $p = 0.9$). This is perhaps not surprising given the similar species composition of the studies. In contrast however, there was significant variation in the survival estimates obtained from five Neotropical countries (data from Blake & Loiselle (1998)) ($F_{4,79} = 2.9$, $p = 0.029$) although this difference appears to be driven by the data from a single site (Peru) (Figure 1). In fact species composition may account for much of

Figure 1. Mean estimated survival from Neotropical and Afrotropical mark-recapture studies. Data from current study, Blake & Loiselle 2008 and Peach et al. 2001). Hatched lines represent overall mean and 95% confidence intervals.



the difference between estimates since families with higher mean survival estimates (Dendrocolaptidae, 0.67 and Thamnophilidae, 0.63) composed more of the data from Peru (64%) (the site with highest mean survival estimate), than for the other countries (range 26-62%). To reduce taxonomic bias, comparisons of survival between geographical regions should (as far as is possible) only be made where there is equal representation of families, although this is not always possible when comparing between ecozones since most species will have only distant phylogeny.

Figure 2. Distribution of estimates of apparent annual survival from combined data for Neotropical and Afrotropical sites (after Blake & Loiselle 2008) $X^2_5 = 3.04$, $p = 0.69$.



Aside from within regions, no significant difference in mean survival was found between Afrotropical and Neotropical estimates, ($t(148) = -1.5$, $p = 0.14$; Levene's test, $F = 2.0$, $p = 0.16$) or when all data were combined (ANOVA, $F_{6,143} = 1.9$, $p = 0.08$). This suggests that although there may be some geographical variation between estimates for individual species, (in both tropical (e.g. Karr *et al.* 1990; Faaborg & Arendt 1995) and temperate areas (e.g. Reid *et al.* 2006; Bond *et al.* 2009)) longitudinal variation is not a significant issue when comparing overall estimates of tropical and temperate survival and the distribution of survival rates is equally variable in both Afrotropical and Neotropical studies (Figure 2). Indeed, across all seven countries in both Neotropical and Afrotropical regions the mean (± se) estimate of survival was 0.62 ± 0.01, very close to this study (overall survival 0.63) and that in Malawi (0.64). These estimates are lower than those predicted from earlier studies (e.g. Snow 1962; Fogden 1972) but are nevertheless higher than mean rates for similar-sized temperate species (Peach *et al.* 2001) and may provide a useful ‘general estimate’ of survival in tropical species.

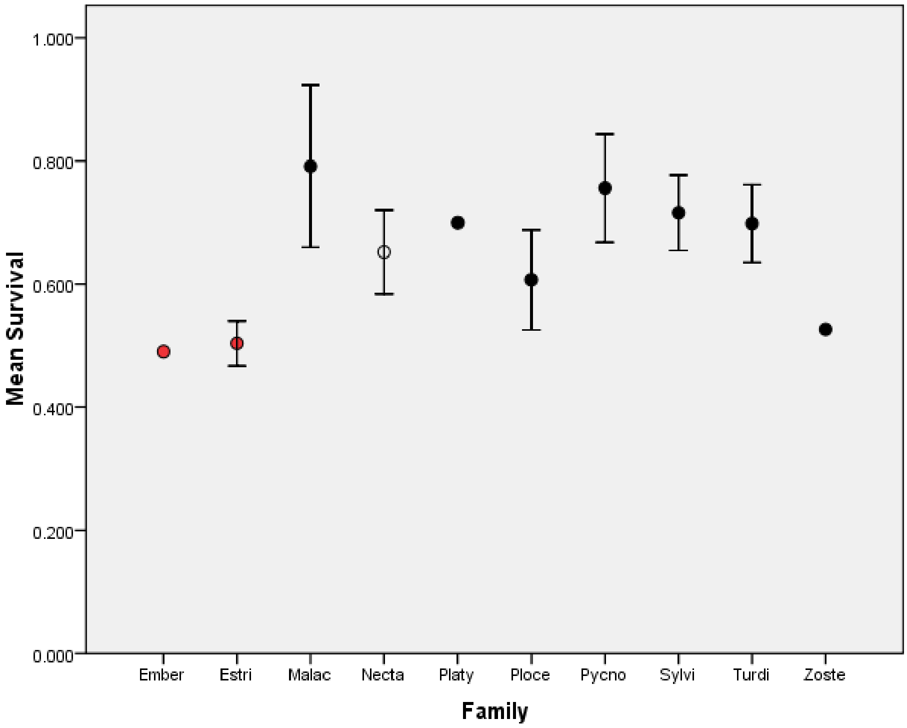
Juvenile survival

Very few studies have attempted to estimate juvenile/first-year survival of tropical passerine bird species using current mark-recapture methodologies (e.g. Covas et al. 2004; Schaefer et al. 2004). Indeed, there are as yet still comparatively few studies of survival of adult Afrotropical species using such techniques (e.g. Peach *et al*. 2001; Schaefer *et a*l. 2004; McGregor *et al*. 2007b). Despite the lack of detailed examination, it has been suggested that increased juvenile survival may be one of the mechanisms by which tropical species maintain stable populations in the face of reduced clutch sizes (Cody 1966; Pianka 1970; MacArthur 1972; Skutch 1976; Martin 1996; Geffen & Yom-Tov 1999).

The results of the current examination of 13 species (using TSM models to separate first year and subsequent survival) showed that in spite of this expectation, first year survival was significantly lower than subsequent years. This is in spite of the assertion that factors such as increased parental investment through prolonged parental care (Ghalambor & Martin 2000) or accommodation and tolerance of offspring within the natal territory (Fogden 1972; Dittami & Gwinner 1985; Rowley et al. 1991) should result in improved survival (e.g. see Covas *et al*. 2004). Although mean first year survival here

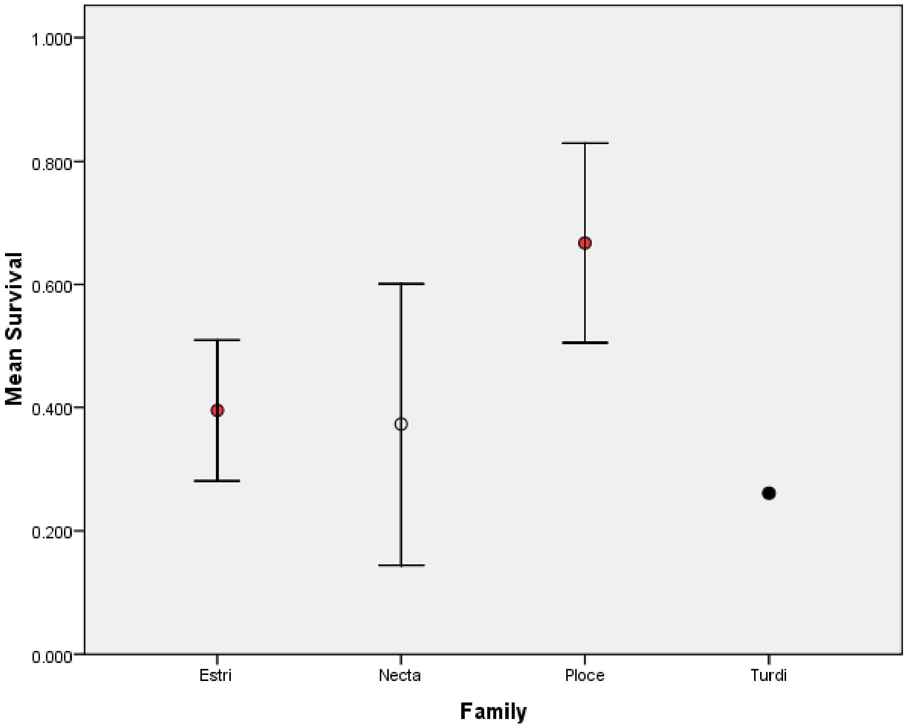
(0.45 ± 0.09) was less than that for adults (0.62 ± 0.06) across 13 species, this was considerably higher than that reported in most temperate species (e.g. 0.34 in Savannah Sparrows (Martin et al. 2009); 0.11 across nine passerine grassland species in USA (Lehnen & Rodewald 2009)).

Figure 3. Mean adult survival by family for species in the current study. Error bars relate to ± 1 se and are missing for families with only one representative. Red points represent granivorous species, open points nectarivores and filled black points insectivores.



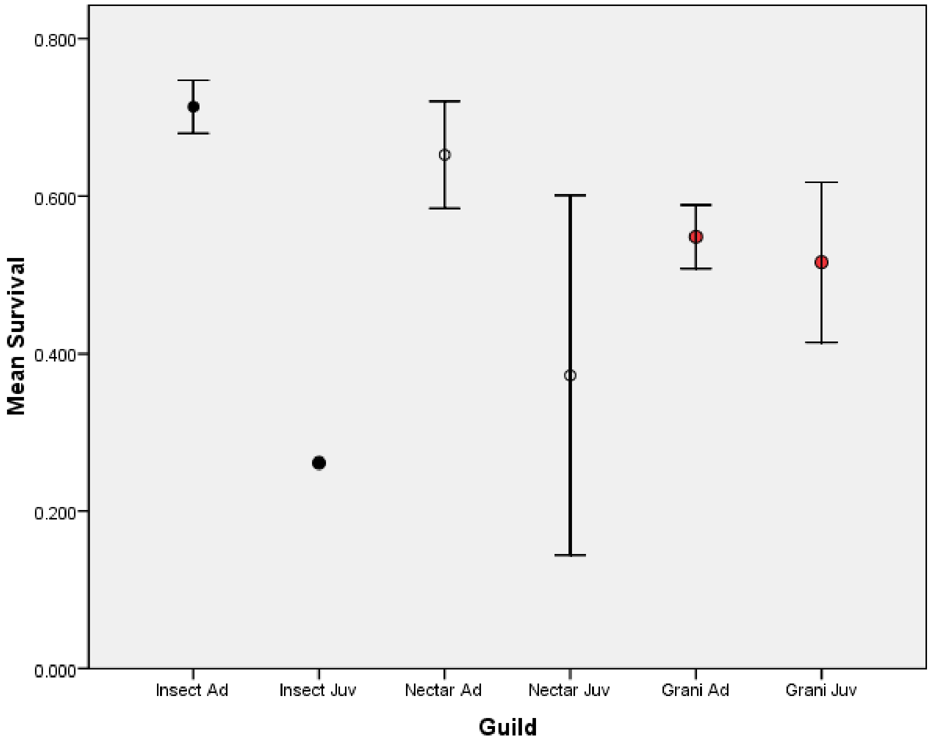
Since juveniles of tropical tropical species suffer similar stresses (predation, inexperience and physical condition (Conway et al. 1995; Anders *et al*. 1997; King *et al*. 2006; Whittaker & Marzluff 2009)) as their temperate counterparts, some other factor must serve to reduce these effects. It is possible therefore that the assistance provided to juveniles by parents and other family members (through extended parental care) may be a significant factor in ensuring improved post-fledging and juvenile survival and subsequent population stability or growth. Indeed this ‘assisted start’ may be the reason for the finding here that in almost half of the species (6 of 13), juvenile survival was higher than, or very similar to, adult survival. Parental care may provide a means by which population stability can be maintained in spite of the small clutch sizes observed in tropical species (Skutch 1949; Fogden 1972; Murray 1985; Martin 1996; Murray 1985).

Figure 4. Mean juvenile survival of four families from the current study. Error bars relate to ± 1 se and are missing for families with only one representative. Red points represent granivorous species, open points nectarivores and filled black points insectivores



However, not all tropical passerine species have small clutch sizes. Many tropical granivorous species in this study (particularly the Estrildines) lay clutches of 4-6 eggs (e.g. Byers et al. 1995; Restall 1996; Peach et al. 2001). First-year survival in these was not significantly different to that of insectivores and nectarivores (which lay smaller clutches) (*t*(11) = -0.9, p = 0.38). In fact, the mean across species was higher (0.52 ± 0.10) than for insectivores and nectarivores (combined mean ± se: 0.35 ± 0.16). High survival in both first years and adults can only occur if some other mechanism serves to regulate the population. Carrying capacity would otherwise be exceeded if reproductive effort in tropical species mirrored that of temperate species. It is therefore interesting to note that adult survival of the estrildine finches (the group with largest clutch size) was lower than that for the Ploceidae (having mid-range clutch sizes (Ambedkar 1968; Da Camara-Smeets 1980; Metz *et* *al.* 2009)), which in turn was lower than the remaining insectivorous species (See Figure 3). This follows similar results obtained by Peach *et al*. (2001) (see their Figure 2) (see also Covas et al. (2004)). Juvenile survival (Figures 4 and 5) shows a reversal of this trend with insectivorous species having lowest survival (though this is on the basis of the results from one species). The nectarivorous species included here are also known to feed on insects (Cheke *et al*. 2001). Overall then, adult and juvenile survival rates appear to covary in tropical environments, potentially as a result of extended parental care. Although the greater variability in climate in temperate areas may prevent adults in such areas from increasing their level or duration of care, it is nevertheless unlikely that this would result in higher juvenile survival. Harsh over-winter conditions provide a challenge for the most experienced adults in temperate areas, therefore maximising output of young during a season will almost certainly provide better odds of recruitment than investing more in fewer young. The ability of some tropical species to increase juvenile survival will result in higher average survival across all species compared to temperate species which are unable to achieve these increases to juvenile survival.

Figure 5. Mean adult and first year survival by guild from the current study. Error bars relate to ± 1 se and are missing for families with only one representative.



Of course, many of the estimates for first-year survival derived here must also be considered alongside their (general) lack of precision. This issue of precision must be addressed and more focused attempts at improving estimates of age- and sex-related demographic rates in tropical species must be made before greater advances in understanding life history evolution in birds can be made.

Chapter 5: Comparison of use of mark-recapture vs mark-recapture-resighting models in this study

Summary

I compare and assess both the field and analytical methods used to derive survival estimates based on models incorporating resightings with those using traditional mark-recapture techniques. Overall, the benefits gained on using the larger dataset (i.e. including resightings) were lost by the increased parameterisation of the Barker model. This had the effect of reducing the number of estimable parameters and producing unrealistic estimates of survival and resighting rates. Estimates generated from the reduced parameter CJS model (i.e. mark-recapture data only) were more robust, had smaller standard errors and proved more biologically realistic. In light of this further ways of improving both the capture protocol and analyses approaches for this long-running dataset are discussed.

Introduction

Chapter 4 outlined the use of capture-mark-recapture models for the estimation of apparent survival rates of tropical African bird species in Nigeria. These methods, and the use of the program MARK (White & Burnham 1999), are now employed as standard throughout ornithology and generally vary only in the choice of model to generate the estimates (e.g. Cormack-Jolly-Seber (Lebreton *et al.* 1992): combined data types (Burnham 1993, Barker 1999), Robust design (Pollock *et al.* 1990, Kendall 2001) Multi-strata models (Brownie *et al.* 1993, Lebreton & Pradel 2002)). Working at the same study site, McGregor *et al.* (2007) utilised the Barker (1999) model, which allows for the inclusion of resightings and recoveries alongside retraps, to determine apparent survival rates of Nigerian birds. Inclusion of resighting data should allow for the acquisition of large datasets with minimal need for handling. Their survival estimates were constrained by the limited dataset (three years worth of mark-recapture data) restricting model-testing to those models containing minimal time-dependent effects across the parameters (i.e. in apparent survival (φ) and recapture (p) probability only).

I attempted to use the same approach to determine annual and period (i.e. mean annual) survival to compare with previous studies and to identify whether there is significant annual variation in survival, but using more years' data accumulated from continuing the CES. The current study forms an extension of that earlier work, supplementing it with data from an additional five years of field seasons. Long-running mark-recapture studies are considered to produce better estimates of mean annual survival than those operating over short time periods (Lebreton *et al.* 1992; Sandercock 2006) allowing an element of compensation which smoothes the effects of both good and poor years. Examination of individual annual survival also permits identification of these good and bad years and a potential for identification of the level of environmental stochasticity.

The intention therefore was to produce survival estimates using the larger dataset (eight years of mark-resighting) using the same techniques (the Barker model) and to compare the parameter estimates with the earlier study. However, a number of factors prevented the efficient application of the Barker model to the longer dataset and this ultimately resulted in the adoption of an alternative approach: the CJS method. Use of this method to determine survival rates has a number of analytical and methodological consequences for determining survival rates from CES data. This chapter is a quantitative appraisal of the best techniques for determining survival rates using long term CES data generated from the APLORI study. Specifically, the Barker approach is compared critically against the CJS method in an attempt to assess the benefits of each. The reasons behind the difficulties encountered in applying the Barker model to a larger dataset and an assessment of how the field methodology could be improved are also explored along with an examination of the methodology used in obtaining the data for the Barker model. Although this chapter is a specific case study to examine the best CES ringing and analysis methodology to apply to APLORI, the conclusions should inform future best practice for assessing survival rates from constant effort ringing programs in other tropical savannah situations.

The Barker Model

The Barker model, as used in MARK, consists of seven parameters:

Φ_i = probability that an animal alive at *i* is alive at *i*+1

p_i = probability that an animal at risk of capture at *i* is captured at *i*

r_i = probability that an animal that dies in *i*, *i* +1 is found dead and the ring reported

R_i = probability that an animal that survives from *i* to *i* + 1 is resighted (alive) some time between *i* and *i* + 1

R'_i = probability that an animal that dies in *i*, *i* + 1 without being found dead is resighted alive in *i*, *i* + 1 before it died

F_i = probability that an animal at risk of capture at *i* is at risk of capture at *i* +1

F'_i = probability that an animal not at risk of capture at *i* is at risk of capture at *i* + 1

MARK enforces a number of logical constraints to the Barker model to ensure that certain joint probabilities are never greater than the unconditional probabilities (e.g. the compound probability of an animal first being resighted alive in one capture period and then surviving to the next capture period is less than the single probability of it merely being seen alive in the first capture period). The way MARK interprets the Barker model also allows for temporary emigration from the study area and is governed by the *F* (fidelity) & *F'* (return) parameters. This differs from the original parameterisation of the Barker model, where *F'* was the probability of an animal remaining outside the study area and therefore unavailable for capture.

The reason for the failure of MARK to produce reasonable and believable apparent survival estimates using the Barker model is likely to be a result of there being too few data items (recaptures and resightings) to provide meaningful estimates within the numerous resighting occasions. A large number of capture occasions, and therefore resighting periods, leads to a large number of parameters when the model is viewed from a time-dependent perspective (107 parameters in the fully time-dependent Barker model in this study, see below).

This factor, along with the low number of resightings and recaptures, means that MARK often fails to predict differential probabilities for each resighting history.

The CJS approach

In contrast, focusing solely in those individuals that are recaptured (rather than including resightings) reduces the parameterisation of each model through the omission of a number of now ‘immeasurable’ parameters (recoveries, *r*, resightings *R* & *R’*, and fidelity *F* and *F’*). This also results in a removal of the potential errors and biases associated with differential observer ability/effort when reading ring combinations and the effects of ring loss or removal by birds. This reduction of the model to its most basic components results in a suite of open-population survival models built on only two parameter types:

Φ_i = (apparent survival probability) = probability that an animal alive at i is alive at i+1 and will not permanently emigrate between these two periods.

p_i = (apparent encounter probability or capture probability) = probability that an animal at risk of capture at i is captured at i.

In its most parameterised version, i.e. with full time-dependence, this model is referred to as the Cormack-Jolly-Seber (CJS) model. Hereafter, all reference to the CJS approach in this chapter relates to the use of models with only apparent survival and capture probabilities.

The approach in this chapter is therefore to identify the key factors, and their optimum characteristics in determining the successful implementation of survival rate analysis to CES data. These include methodological concerns:

1. Variation in catch rates
2. Trap shyness
3. Resighting rates

And also analysis concerns:

1. Goodness of fit of models
2. Reduction in the number of parameters
3. Model selection
4. Identification of realistic models
5. Overall recapture rates

Methodological Concerns

Analysis of survival rates from CES data depends crucially on the amount and type of data collected. Therefore it is important to define exactly what information is available for the APLORI CES. CES methods were detailed in Chapter 4, but the main details are summarised below.

Table 1. Time intervals between capture occasions in days and years.

Period No.	Capture Period Date	Interval Length (days)	Proportion vs year
1	7 -23 Jun 2002	-	-
2	1 -14 Dec 2002	161	0.441
3	1 -15 Apr 2003	108	0.296
4	11 -24 Aug 2003	88	0.241
5	18 Oct -1 Nov 2003	55	0.151
6	5 -18 Feb 2004	86	0.235
7	1 -14 Apr 2004	42	0.115
8	19 Oct -1 Nov 2004	219	0.600
9	19 Feb – 4 Mar 2005	110	0.301
10	24 Sep – 7 Oct 2005	173	0.474
11	21 Mar – 3 Apr 2006	165	0.452
12	29 Oct – 11 Nov 2006	240	0.657
13	29 Mar – 12 Apr 2007	138	0.378
14	12 – 25 Oct 2007	183	0.501
15	14 – 29 Apr 2008	140	0.383
16	15 – 28 Oct 2008	169	0.463

Birds were caught during 14-day, capture periods (hereafter referred to as the Constant Effort (Scheme) period or CES) in the spring (generally March or April) and autumn (usually October or November) each year. Between 2002 and 2004 the timing of the capture periods was less rigidly determined (some occurring in February or September) and some additional capture periods were also included. During the CES, 14, four-panel mist-nets (totalling 187m) were operated in set locations within the Amurum reserve between 2002 and 2008 (Table 1). The number of nets was increased to 20 (270m) in 2006 to improve both the variety of species caught and recapture rates. These locations remained the same for all capture periods. The nets were opened daily between dawn and 10:30am each day, occasionally being closed earlier if weather conditions posed a risk to the welfare of birds in the net. On occasions where rain or very strong winds prevented catching, the CES period was increased to account for lost days.

The Constant Effort approach can generally be defined as the standardised capture of birds using a fixed number of nets at set locations and for specific periods of time. Mist nets are usually operated for a specified number (usually 10-12) of single days through the breeding season, and various demographic parameters (population size, breeding success and survival) are determined on the basis of the numbers of recaptures and the proportions of birds caught of different age groups. The strict CES method is therefore only used in those areas showing sufficient seasonality to result in bird species having reasonably stable and defined breeding seasons. In contrast, the method employed here was intended solely as a means of standardising catching effort in order to efficiently assess survival.

All birds caught were aged, sexed and ringed with uniquely numbered metal rings. Where possible (depending on species and tarsus length) all individuals were also fitted with a unique combination of three plastic colour rings. Birds were handled quickly to reduce stress, and any birds injured or suffering stress were released without being colour-ringed.

Attempts to obtain resightings of colour-ringed individuals were made regularly across the reserve and throughout the year using a Zeiss Diascope 65 with 20-60x eyepiece. Various routes around the reserve were walked for 2-4 hours on at least two afternoons/evenings and one morning each week between September and May. Resightings made during the CES periods were treated as part of the CES captures.

Variation in catch rates

Over the course of the 16 CES periods, lasting a total of 224 days and approximately 896 hours, a total of 6954 captures were made of 5445 individuals of 158 species (Table 2). Within the total catches, sufficient data were available to attempt the modelling of adult survival for 17 species (Table 3), species being selected on the basis that they had a combined total of at least 10 recaptures and resightings.

Table 2. Daily and session catch statistics for CES periods by season (adult individuals only).

	Spring			Autumn			Combined		
	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE
Daily (by year)									
Yr 1									
New	12 – 75	29.6	4.9	11 – 51	25.8	3.3	11 – 75	27.7	2.9
Retrap	1 – 9	4	0.6	1 – 14	7.4	1.2	1 – 14	5.7	0.7
Total	17 – 78	33.6	4.9	13 – 88	36.4	5.9	13 – 88	35	3.8
Yr 2									
New	21 - 47	33.8	2.2	5 – 31	17.3	1.2	5 – 47	22.7	1.6
Retrap	2 – 15	6.1	0.8	1 – 10	4.6	0.4	1 – 15	5.1	0.4
Total	24 – 56	39.9	2.4	7 – 35	21.6	1.2	7 – 56	27.6	1.7
Yr 3									
New	3 - 67	26.7	3.0	16 – 81	41.2	6.8	3 – 81	31.5	3.2
Retrap	0 – 23	4.1	1.2	0 – 29	9.9	2.0	0 – 29	6.1	1.1
Total	3 – 90	30.8	3.6	22 – 97	51.1	7.9	3 – 97	37.6	3.8
Yr 4									
New	5 – 20	12.6	1.4	4 - 36	19.6	2.6	4 - 36	16.1	1.6
Retrap	1 – 8	5	0.6	2 – 8	4.3	0.5	1 – 8	4.6	0.4
Total	9 – 25	17.3	1.6	6 – 44	23.9	2.9	6 – 44	20.6	1.7
Yr 5									
New	7 – 45	23.3	2.8	3 – 57	26.2	3.5	3 - 57	24.8	2.2
Retrap	2 – 13	8.2	0.9	7 – 24	14.4	1.5	2 – 24	11.3	1.0
Total	10 – 55	31.5	3.3	12 – 81	40.6	4. 5	10 – 81	36.1	2.9
Yr 6									
New	0 – 24	5.3	2.2	14 – 50	29.9	2.7	0 – 50	17.6	2.9
Retrap	0 – 17	4.7	1.5	4 – 18	8.9	1.1	0 – 18	6.8	1.0
Total	0 – 41	10	2.9	23 – 58	38.8	2.9	0 – 58	24.4	3.4
Yr 7									
New	9 – 54	27.5	3.6	14 – 38	20.4	1.7	5 – 54	23.4	2.1
Retrap	2 – 21	9.5	1.3	2 – 12	6.5	0.8	2 – 21	7.9	0.8
Total	13 – 73	37	4.6	19 – 48	26.9	2.1	7 – 73	31.3	2.7
Daily (Total)									
New	0 – 75	22.9	1.4	3 – 75	25.1	1.4	0 – 75	24	1.0
Retraps	0 – 23	5.7	0.5	0 – 29	7	0.5	0 – 29	6.3	0.3
Total	0 – 90	28.8	1.6	6 – 97	32.5	1.7	0 – 97	30.6	1.2
Period									
New	74 – 473	326.3	51.3	252 – 577	354.4	39.8	74 – 577	340.3	31.6
Retrap	8 – 145	80.9	14.9	31 – 202	99.1	19.5	8 – 202	90	12.1
Total	140 – 562	409.8	52.4	313 - 716	459.5	52.2	140 – 716	434.6	36.3

Overall catch rates of adults varied widely between days, periods and years (Tables 2 & 3; Figure 1). Heteroscedasticity meant that the results of comparisons of catch rates across all time scales were unreliable and so only the seasonal variation with year (GLM total catches, year*season, Total catches, $F_{7,211}$ = 8.9, p = <0.001, Levene's test, $F_{15,211}$ = 3.8, p = <0.001; Retraps, $F_{7,211}$ = 9.4, p = <0.001, Levene's test, $F_{15,211}$ = 6.02, p = <0.001; New birds, $F_{7,211}$ =

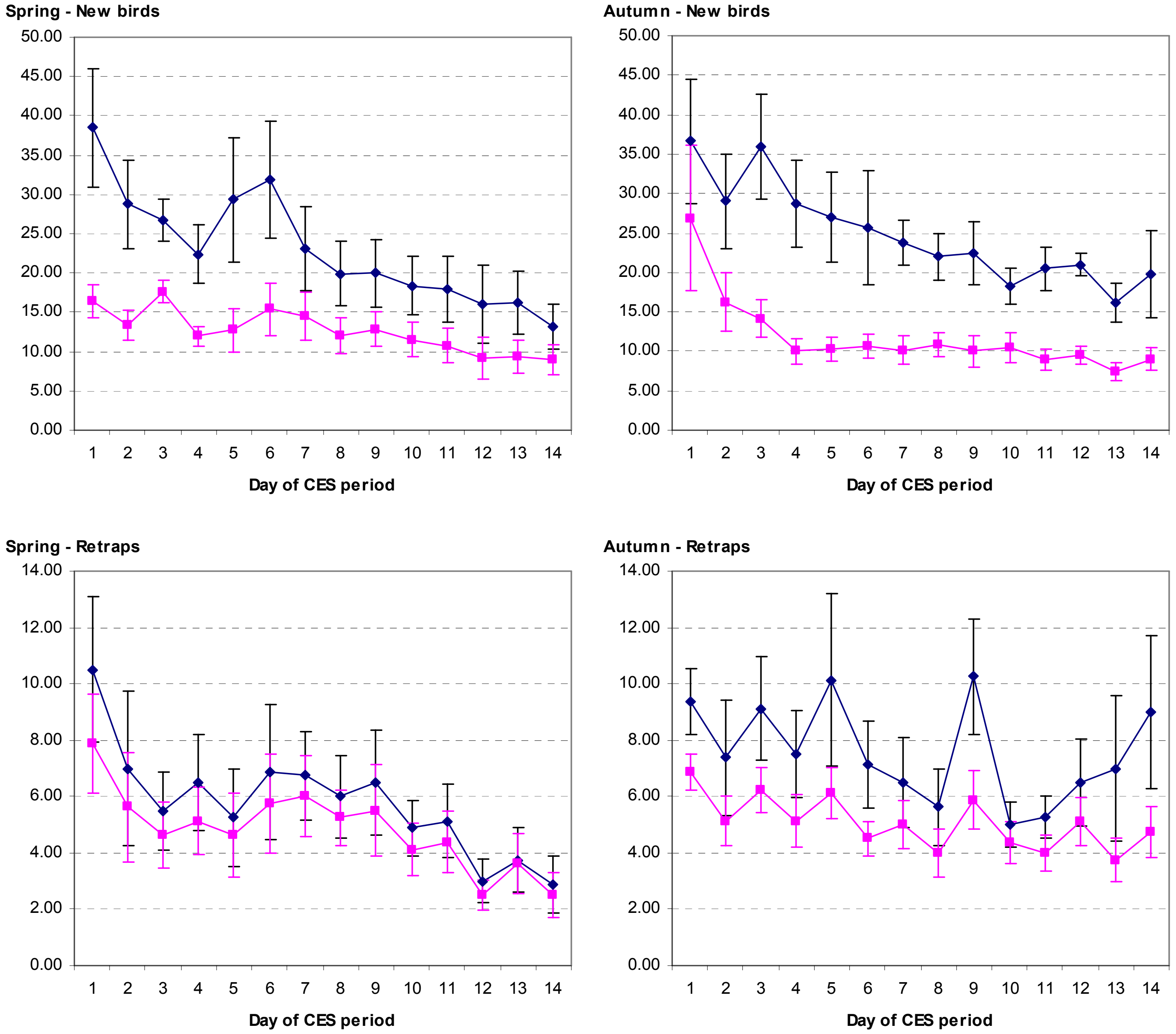
11.1, p = <0.001, Levene's test, $F_{15,211}$ = 3.8, p = <0.001;) was assessed. Significant differences in variance of capture rates between seasons within years also prevented their meaningful comparison. Significant annual variation in catch rates for all categories will have an effect on both the modelling approach used (i.e. whether sufficient data are available to incorporate time-dependence) and the estimates produced, since time-independent models produce 'averages' of survival over the course of the study. Such annual or period-related differences in capture may arise for reasons that are entirely disjunct from the factors directly responsible for annual survival (e.g. poor catching conditions related to timing of the CES period) yet have an important effect on the estimates produced.

Table 3. Summary of captures, recaptures and resightings of adults for species used in the Barker model and number of individuals captured on more than one occasion under the CJS approach. Percentages indicate the increase in recapture data available when using the alternative CJS approach

Species	Individuals recaptured	Proportion recaptured	Individuals resighted	Proportion resighted	Individuals ringed	Individuals recaptured (CJS)
Colius striatus	20	0.213	21	0.223	94	51 (+255%)
Pycnonotus barbatus	35	0.161	24	0.110	218	68 (+194%)
Turdus pelios	25	0.132	23	0.122	189	55 (+220%)
Camaroptera brachyura	14	0.333	13	0.310	42	53 (+300%)
Cisticola aberrans	5	0.263	6	0.316	19	16 (+320%)
Cyanomitra verticalis	7	0.140	13	0.260	50	34 (+486%)
Chalcomitra senegalensis	14	0.135	16	0.154	104	38 (+271%)
Zosterops senegalus	18	0.202	14	0.157	89	31 (+172%)
Ploceus cucullatus	5	0.037	9	0.067	135	27 (+540%)
Ploceus nigricollis	7	0.146	14	0.292	48	41 (+586%)
Ploceus vitellinus	9	0.191	4	0.085	47	45 (+500%)
Euplectes franciscanus	79	0.087	58	0.064	911	200 (+253%)
Estrilda caerulescens	23	0.189	34	0.279	122	144 (+626%)
Uraeginthus bengalus	29	0.119	33	0.136	243	104 (+359%)
Lagonosticta sanguinodorsalis	15	0.181	22	0.265	83	109 (+727%)
Lagonosticta rara	5	0.143	7	0.200	35	14 (+280%)
Emberiza tahapisi	6	0.060	13	0.130	100	16 (+267%)
Mean	**18.59**	**0.161**	**13.23**	**0.187**	**206.75**	**61.53 (+374%)**
S.E.	**± 4.38**	**± 0.017**	**± 3.21**	**± 0.021**	**± 50.14**	**± 12.25**

Lack of normality in the catch data (Kolmogorov-Smirnov tests $p < 0.05$ for all groups) meant that comparison of catches between autumn and spring seasons was performed using non-parametric tests. There were no significant differences in either total catches (U = 5597, n = 112, p = 0.16), p = 0.16) or catches of new birds (U = 5884, n = 112, p = 0.42) p = 0.38 – 0.96) when autumn and spring periods were compared. Catches of retraps however, were significantly lower in spring than in autumn (U = 4934.5, n = 112, p = 0.01). When pooled according to CES periods the data were approximately normally distributed (Kolmogorov-Smirnov test with Lilliefors correction, p > 0.14 for all groups). Assessment of mean captures of new birds, retraps and combined totals using t-tests revealed no significant differences between autumn and spring catches (New birds, *t*(14) = 0.39, *p* = 0.7 (Levene's test *p* = 0.57); Retrap catch, *t*(14) = 01.13, *p* = 0.28 (Levene's test, *p* = 0.62); Total catch, *t*(14) = 0.76, *p* = 0.46 (Levene's test *p* = 0.57); all tests two-tailed).

Figure 1. Daily total catches and species richness of new birds and retraps in spring and autumn CES periods (—■— Individuals, —■— species, adult individuals only).

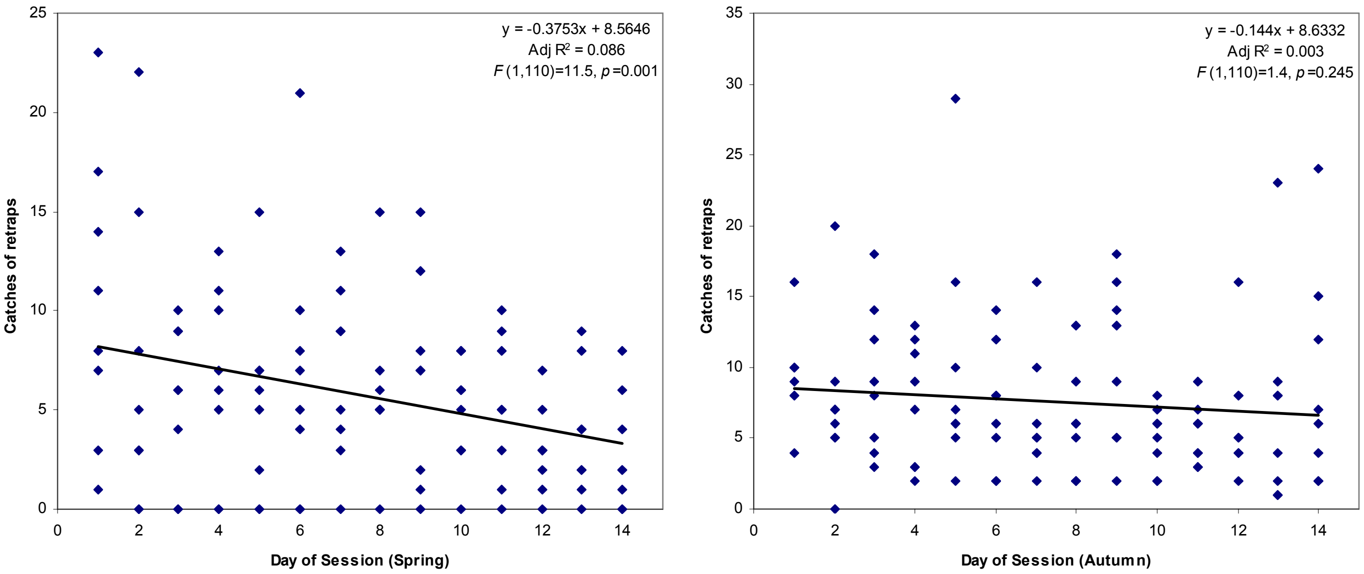


Intensive mist-net capture at one site over prolonged periods will inevitably result in some trap shyness in local bird populations and an expectation of reduction in catch rates over time (Elder 1985). Since the CES method used here centres on catches made in mist nets open for 14 successive days, trap shyness was expected to be an important factor in assessments. To test this, General Linear Modelling was used to assess catches of Afrotropical species during CES periods with respect to season (spring or autumn) and session (i.e. day1-14). For African species there was no significant interaction between day and season (GLM: $F_{1,220} = 0.2$, $p = 0.7$) on catches of new birds, or any effect of season when this interaction was removed ($F_{1,221} = 0.9$, $p = 0.34$). There was however, a significant effect of day (i.e. a decline) on catches (Levene's Test: $F_{1,222} = 2.1$, $p = 0.15$; GLM: $F_{1,221} = 39.2$, $p < 0.001$; $R^2 = 0.15$). Catches declined to around 50% of those of the first day by day 10 suggesting. Although this may be indicative of trap shyness it is more likely that it reflects more significantly the effectively closed nature of many of the bird populations within the study (CES) area. Because individuals are restricted by habitat availability (i.e. the habitat quality appears markedly reduced outside of the confines of the reserve, the majority of ringed individuals may remain within the study area, steadily increasing the proportion of individuals that carry rings.

Of the 1065 adult individuals that were retrapped during CES sessions, the majority (1022) were retrapped fewer than four times over the course of the study (mean = 1.44, range = 1-9). Eight individuals of four species (*Camaroptera brachyura, Pogoniulus chrysoconus, Cisticola guinea* and *Cisticola cantans*) were retrapped more than five times during the course of the study. Captures of these individuals occurred over the course of between three and six years and between three and seven CES periods.

No significant interaction was identified between season and day (GLM: $F_{1,220} = 2$, $p = 0.16$) when assessing total numbers of retraps of adults of African species. However, significant season and day effects were found in the model after removing the interaction term (Levene's Test: $F_{1,222} = 0.4$, $p = 0.53$; GLM season: $F_{1,221} = 7.3$, $p = 0.008$; day: $F_{1,221} = 9.8$, $p = 0.002$). Catches of retraps in spring show a significant decline over the course of the period (Adjusted $R^2 = 0.086$, $F_{1,110}=11.5$, $p < 0.001$; Figure 2a). No significant decline in absolute numbers of retraps caught was noted during autumn periods (Adjusted $R^2 = 0.003$, $F_{1,110}=1.4$, $p = 0.245$; Figure 2b).

Figure 2. Variation in recapture rate of adults of African species with session during spring (a) and autumn (b) CES periods. Please note that the interaction season*day was not significant, so the decline in capture rate was the same for both seasons (i.e. the slopes of both lines are the same). Separate graphs are plotted however, for clarity.



The reasons behind the seasonal differences in catches may be numerous, however of key importance is likely to be the difference in numbers of bishops (*Euplectes* sp.) within catches. During autumn catches, large numbers of *Euplectes franciscanus* and *E.hordeaceus* are present throughout the reserve. Many of these are recaptured several times during the course of autumn CES periods inflating the total numbers of retraps. In contrast, large flocks of bishops are not present at the site during the spring (mean catch ± SE: Autumn: 31 ± 14.72; Spring: 2.13 ± 1.03). Further examination of retrap rate of African species in terms of day of period, season and proportion of catch which was E.*franciscanus* using a GLM incorporating all interactions (Table 5) revealed significant effects with day of period and proportion of bishops in the catch (as well as interactions between the two and with season). All other terms were not significant. Seasonal differences between retrap rates were therefore probably influenced by the variation in presence of *E.franciscanus* in the area between spring and autumn CES periods.

Table 5. GLM model of retrap rate with regard to day, season and captures of *E. franciscanus.* (Day=day of period; Season=spring or autumn; ORABI=proportion of retrap ORABIS in total retrap catch). (Adjusted R^2 = 0.165).

Source	Sum of Squares	df	F	Sig.
Corrected Model	1140.78	7	7.29	<0.001
Intercept	2411.57	1	107.86	<0.001
Day	261.36	1	11.7	**0.001**
Season	2.83	1	0.13	0.722
ORABI	138.53	1	6.2	**0.014**
Day*Season*ORABI	132.7	1	5.93	**0.016**
Day*Season	0.004	1	<0.001	0.989
Season*ORABI	112.82	1	5.05	**0.026**
Day*ORABI	84.03	1	3.76	0.054
Error	4830.06	216		
Total	15882	224		
Corrected Total	5970.84	223		

Levene's Test = $F_{1,222}$ = 0.25, p=0.621

Resightings

Resighting rates (proportion of individuals ringed that were resighted) for the 17 species analysed (that had sufficiently large sample sizes for analysis – see above) varied widely during each of the seven years (Table 3). Total numbers of individuals resighted of the species used in the Barker model ranged from a minimum of 4 in 2004 to a peak of 132 in 2006 and exceeded 100 in only two years (2003 and 2006). Large numbers of resightings were made for certain species, however many of these were of the same individual (e.g. one *P. barbatus* was resighted on 17 occasions). Annual resighting rates were low for all 17 species for which survival estimation was attempted (range 0.06 – 0.32, mean ± SE = 0.187 ± 0.021). An average of less than four individuals of each of the 17 species included here were resighted each year during the seven years of the study. Almost half of these (47%) were made for just four species (*E. franciscanus* and *E. caerulescens, U, bengalus* and *P.barbatus*) leaving an average of two individuals resighted each year for the remainder of the species. Datasets for several other species included individuals with multiple resightings (e.g. *Cercomela familiaris* and *Myrmecocichla cinnamomeiventris* each had several individuals with more than 10 resightings) but had an insufficient total of resighted/retrapped individuals for inclusion.

Of the 397 resightings included in the adult survival analyses, the number ringed in each season (i.e. CES periods in Feb-Jun (spring) or Aug-Dec (autumn)) was approximately even. 114 (29%) of the total resightings were made in the resighting interval immediately following ringing. The distribution of resightings varied significantly between seasons, either when including (Williams corrected G-test G_{adj} = 13.61, p <0.001) or excluding (Williams corrected G-test G_{adj} = 5.74, p=0.018) those individuals resighted immediately after ringing, with significantly more resightings made during the autumn resighting period (i.e that period between the autumn CES period and the following spring CES period). This is likely due to the increased resighting effort made in this period, and increased detectability due to the dry season – the spring resighting period being partly curtailed by the wet season. The increased apparency of certain species, either through their increased abundance or their feeding or displaying in more obvious locations, may also have influenced this.

When assessing species individually, only *E.franciscanus* showed any significant differences in the distribution of resightings between seasons (Williams corrected G-test G_{adj} = 7.07, p=0.004) however this is almost certainly due to greater abundance of this species across the reserve during the period between October and February. The results for *E.caerulescens* bordered significance (Williams corrected G-test G_{adj} = 3.57, p=0.053) when all data were included but was again non-significant when the 'immediate' resightings were removed (Williams corrected G-test G_{adj} = 1.64, p=0.22).

One particular disadvantage of the CES/Barker approach of using resightings is that it can increase the level of potential error in estimates. The potential for human error is greater when using colour rings (than for methods using metal rings alone), either through duplication of colour combinations, failure to record correctly the order of rings applied or difficulties in guaranteeing the correct recording of field observations. A number of species included within this study also proved especially adept at removing colour rings leading to an inability to correctly identify an individual. This was also made easier by the weakening of the ring through the prolonged effect of UV exposure. UV exposure can also lead to fading of the colours used further increasing the potential for observer error.

Where possible any rings affected by fading (or any other factor which could increase the chances for error) were replaced on recapture, however not all individuals were retrapped and some effect on the analyses is likely. Colour-rings were initially applied only to those individuals caught within the CES until January 2007 after which date all individuals caught were fitted with these supplementary rings. As a result of this earlier colour-ringing policy there are many more individuals in the study population that carry only metal rings. These individuals are not available for inclusion in the CES/Barker approach but were incorporated in the CJS method.

Analysis considerations

Goodness of fit of Models

To ensure that all assumptions of the model were met by the data, goodness of fit tests were performed on the general starting model for all species (Table 6). Acceptable fit of this model to the data is essential if reduced-parameter models are to be compared and assessed against it later. Because of data shortages, McGregor et al (2007) used general starting models in which time variability was restricted to the survival and recapture parameters only. Here, because of the addition of data from a further ten capture occasions, I attempted to use a fully time-dependent model as the starting model and, where relevant, allowed for most permutations of time-dependence and constancy in each of the seven parameters. Where this model proved unsuitable, progressively less-parameterised models were tested until one was found that showed an acceptable level of fit.

A measure of the extent of the lack of fit of the data to the model (i.e. the degree of over-dispersion) is estimated using the Variance Inflation Factor ($\hat{c}$). Perfect model fit is given when the resulting $\hat{c} = 1$. Providing $1 < \hat{c} < 3$ the model is not considered to be significantly under- or over-dispersed. Where the $1.25 < \hat{c} < 3$, the likelihood of the general and nested reduced parameter models can be corrected using the ‘c-hat adjustment’ function within MARK.

Table 6. Evaluation of goodness of fit of general starting models for survival estimation for all species assessed using the Barker approach. The aim is to show both the poor fit of the model to the data using the Barker approach (for most species) but also to demonstrate the inability of MARK to identify and estimate many of the expected parameters. [†]Number of parameters calculated manually; [‡]number of parameters for which there are enough data for MARK to determine estimates (percentages represent the number of identifiable parameters/total number of parameters for the models tested for each species); *N/a indicates that ĉ could not be computed, either because the deviance df was ≤ 0 or because the observed ĉ value was greater than or less than all of the simulated values; - nested model assumed to have acceptable fit. Bold type indicates the 'best' model and ĉ values for those models with an acceptable level of fit.

Species	Model	Expected parameters[†]	MARK parameters[‡]	Deviance df	Observed ĉ	Median ĉ
Coliidae						
Colius striatus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	25	3	68.697	N/a*
	$\Phi_t p_t r_t R.R'.F.F'.$	50	20	8	36.144	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	22	6	48.112	3.19
	$\Phi_t p_{.} r_{.} R.R'.F.F'.$	22	12	16	20.667	**1.725**
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$	9	6	22	17.571	-0.051
			80/224 (36%)			
Pycnonotidae						
Pycnonotus barbatus	**$\Phi_t p_t r_t R_t R'_t F_t F'_t$**	107	29	14	27.099	**2.29**
	$\Phi_t p_t r_t R.R'.F.F'.$	50	20	23	21.388	-
	$\Phi_t p_{.} r.R.R'.F.F'.$	22	10	33	16.677	-
	$\Phi_t p_t r_{.} R.R'.F.F'.$	36	18	25	23.154	-
	$\Phi_{.} p_t r_t R.R'.F.F'.$	35	17	26	37.899	-
	$\Phi.p.r.R.R'.F.F'.$	7	4	39	26.805	-
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	5	38	27.508	-
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$	9	7	36	29.055	-
	$\Phi.p_{a2-./.} r.R.R'.F.F'.$	8	6	37	30.141	-
			116/282 (41%)			
Turdidae						
Turdus pelios	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	20	8	17.928	5.137
	$\Phi_t p_t r_t R.R'.F.F'.$	50	20	8	32.221	5.538
	$\Phi_t p_t r.R.R'.F.F'.$	36	21	7	36.824	9.649
	$\Phi_t p.r_t R.R'.F.F'.$	36	10	18	15.433	**2.115**
	$\Phi_t p.r.R.R'.F.F'.$	20	9	19	13.559	-
	$\Phi.p.r.R.R'.F.F'.$	7	4	24	16.354	-
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	6	22	16.650	-3.905
			90/264 (34%)			
Sylviidae						
Camaroptera brachyura	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	27	-10	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	21	-4	0	N/a
	$\Phi_{.} p_t r_t R.R'.F.F'.$	35	12	5	47.165	**2.772**
	$\Phi_{.} p_t r.R.R'.F.F'.$	21	13	4	58.945	-
	$\Phi_t p_{.} r_t R.R'.F.F'.$	36	13	4	59.283	5.422
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	5	12	22.404	-
	$\Phi.p.r.R.R'.F.F'.$	7	4	13	20.972	-
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$	9	6	11	24.441	**1.884**
	$\Phi_{.} p_{a2-./}.r.R.R'.F.F'.$	8	5	12	22.710	-
			106/281 (38%)			
Cisticola aberrans	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	11	-4	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	10	-3	0	N/a
	$\Phi_{.} p_t r_t R.R'.F.F'.$	21	7	0	0	N/a
	$\Phi.p.r_t R.R'.F.F'.$	21	4	3	25.528	N/a
	$\Phi.p_{a2-./.} r.R.R'.F.F'.$	8	6	1	73.075	N/a
	$\Phi_t p.r_t R.R'.F.F'.$	36	9	-2	0	N/a
	$\Phi.p.r.R.R'.F.F'.$	7	7	3	25.528	12.700
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$	9	7	0	0	N/a
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	6	1	76.571	N/a
			67/257 (26%)			
Nectariniidae						
Cyanomitra verticalis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	23	-5	0	N/a
	$\Phi_t p.r.R.R'.F.F'.$	22	10	8	32.144	3.199
	$\Phi_t p_{.} r_t R.R'.F.F'.$	36	11	7	36.668	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	16	2	120.910	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	19	-1	0	N/a
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	5	13	22.361	**2.692**
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$	9	6	12	24.213	N/a
	$\Phi.p.r.R.R'.F.F'.$	7	4	14	22.072	-
	$\Phi_{.} p_{a2-./}.r.R.R'.F.F'.$	8	5	13	23.768	N/a
			99/285 (35%)			

Species	Model	Expected parameters†	MARK parameters‡	Deviance df	Observed ĉ	Median ĉ
Chalcomitra senegalensis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	0	0	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	16	6	41.261	4.873
	$\Phi_t p_t r.R.R'.F.F'.$	36	17	5	49.481	N/a
	$\Phi_t p.r_t R.R'.F.F'.$	36	8	14	20.271	**2.504**
	$\Phi_t p_{.} r_{.} R.R'.F.F'.$	22	11	11	25.178	**-**
	$\Phi_{.} p_t r.R.R'.F.F'.$	21	11	11	58.891	**1.319**
	$\Phi.p.r.R.R'.F.F'.$	7	5	17	40.186	**-**
	$\Phi.p_{a2-./.}r.R.R'.F.F'.$	8	6	16	42.641	**-**
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	8	6	16	84.039	**-**
	$\Phi_{a2-./.}p_{a2-./.}r.R.R'.F.F'.$	9	7	15	89.607	-1.384
			87/304 (29%)			
Zosteropidae						
Zosterops senegalus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	28	-5	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	21	2	139.275	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	21	2	139.275	N/a
	$\Phi_t p.r.R.R'.F.F'.$	22	12	11	29.076	**2.375**
	$\Phi.p_t r_t R.R'.F.F'.$	35	13	10	31.589	**1.109**
	$\Phi.p_t r.R.R'.F.F'.$	21	13	10	31.589	**-**
	$\Phi.p.r.R.R'.F.F'.$	7	4	19	18.697	**-**
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	8	5	18	19.148	**-**
			117/286 (41%)			
Ploceidae						
Ploceus cucullatus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	16	-3	0	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	13	0	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	14	-1	0	N/a
	$\Phi_t p.r_t R.R'.F.F'.$	36	11	2	38.768	N/a
	$\Phi_t p_{.} r_{.} R.R'.F.F'.$	22	13	0	0	N/a
	$\Phi.p_t r.R.R'.F.F'.$	21	8	5	21.307	8.620
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	8	5	8	14.549	N/a
	$\Phi_{a2-./.}p_{a2-./.}r.R.R'.F.F'.$	9	7	6	18.670	N/a
	$\Phi.p_{a2-./.}r.R.R'.F.F'.$	8	6	7	16.701	N/a
			93/297 (31%)			
Ploceus nigricollis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	14	1	51.495	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	13	2	51.705	N/a
	$\Phi_t p_{.} r_{.} R.R'.F.F'.$	22	12	3	35.883	N/a
	$\Phi.p_t r.R.R'.F.F'.$	21	6	9	14.491	N/a
	$\Phi_t p.r_t R.R'.F.F'.$	36	14	1	115.404	N/a
	$\Phi.p_{a2-./.}r.R.R'.F.F'.$	8	5	10	14.883	-
	$\Phi_{a2-./.}p_{a2-./.}r.R.R'.F.F'.$	9	6	9	16.372	**1.125**
	$\Phi.p.r.R.R'.F.F'.$	7	5	10	14.990	-
			75/260 (29%)			
Ploceus vitellinus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	12	-4	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	9	-1	0	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	13	-5	0	N/a
	$\Phi_t p_{.} r_{.} R.R'.F.F'.$	22	9	-1	0	N/a
	$\Phi.p_t r.R.R'.F.F'.$	21	6	2	51.226	N/a
	$\Phi.p_t r_t R.R'.F.F'.$	35	7	1	102.440	N/a
	$\Phi_t p.r_t R.R'.F.F'.$	36	11	-3	0	N/a
	$\Phi.p.r.R.R'.F.F'.$	7	5	3	44.142	5.223
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	8	6	2	65.459	N/a
	$\Phi.p_{a2-./.}r.R.R'.F.F'.$	8	6	2	66.196	N/a
			84/330 (25%)			
Euplectes franciscanus	**$\Phi_t p_t r_t R_t R'_t F_t F'_t$**	107	27	27	10.127	**1.553**
	$\Phi_t p_t r_{.} R.R'.F.F'.$	36	19	35	11.697	-
Euplectes franciscanus	$\Phi_t p_t r_t R.R'.F.F'.$	50	18	36	14.359	-
	$\Phi_t p_{.} r.R.R'.F.F'.$	22	12	42	14.623	-
	$\Phi_t p_{.} r_t R.R'.F.F'.$	36	9	45	15.747	-
	$\Phi_{.} p_t r.R.R'.F.F'.$	21	13	41	18.306	-
	$\Phi_{a2-./.}p_{a2-./.}r.R.R'.F.F'.$	9	6	48	18.643	-
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	8	7	47	19.505	-
	$\Phi.p_{a2-./.}r.R.R'.F.F'.$	8	5	49	19.208	-
	$\Phi.p.r.R.R'.F.F'.$	7	5	49	19.830	-
			121/304 (40%)			
Estrildidae						
Estrilda caerulescens	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	33	6	32.355	N/a
	$\Phi_t p_{.} r.R.R'.F.F'.$	22	12	27	13.235	-
	$\Phi_t p_t r_t R.R'.F.F'.$	50	22	17	19.739	**2.827**

Species	Model	Expected parameters†	MARK parameters‡	Deviance df	Observed ĉ	Median ĉ
Estrilda caerulescens	$\Phi_t p_{.} r_t R.R'.F.F'.$	36	14	25	14.282	-
	$\Phi_t p_t r_{.} R.R'.F.F'.$	36	23	16	20.971	-
	$\Phi_{a2-./.} p_{a2-./.} r_{.} R.R'.F.F'.$	9	6	33	12.326	-
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	5	34	12.036	-
	$\Phi.p.r.R.R'.F.F'.$	7	4	35	11.866	-
	$\Phi.p_{a2-./.} r.R.R'.F.F'.$	8	5	34	12.182	-
			124/283 (44%)			
Uraeginthus bengalus	$\boldsymbol{\Phi_t p_t r_t R_t R'_t F_t F'_t}$	107	28	15	12.966	**1.174**
	$\Phi_t p_t r.R.R'.F.F'.$	36	22	21	15.062	-
	$\Phi_t p.r_t R.R'.F.F'.$	36	12	31	11.283	-
	$\Phi_t p_{.} r.R.R'.F.F'.$	22	15	28	12.432	-
	$\Phi.p_t r_{.} R_{.} R'_{.} F_{.} F'.$	21	15	28	14.173	-
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	5	38	11.245	-
	$\Phi.p.r.R.R'.F.F'.$	7	4	39	11.052	-
			101/237 (43%)			
L. sanguinodorsalis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	31	-1	0	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	22	8	32.851	N/a
	$\Phi_t p.r_t R.R'.F.F'.$	36	14	16	18.477	**2.985**
	$\Phi.p_t r_{.} R_{.} R'_{.} F_{.} F'.$	21	15	15	19.570	**1.826**
	$\Phi_t p_{.} r.R.R'.F.F'.$	22	15	15	19.639	-
	$\boldsymbol{\Phi_{a2-./.} p.r.R.R'.F.F'.}$	8	5	25	12.981	-
	$\Phi.p.r.R.R'.F.F'.$	7	5	25	13.132	-
	$\Phi_{a2-./.} p_{a2-./.} r_{.} R.R'.F.F'.$	9	6	24	13.489	**1.140**
			113/246 (46%)			
Lagonosticta rara	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	11	-1	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	10	0	0	N/a
	$\Phi_t p_t r.R.R'.F.F'.$	36	11	-1	0	N/a
	$\Phi.p_t r.R.R'.F.F'.$	21	8	2	41.501	N/a
	$\varphi_t p.r.R.R'.F.F'.$	22	10	0	0	N/a
	$\Phi.p.r.R.R'.F.F'.$	7	5	5	21.301	17.570
			55/244 (23%)			
Emberizidae						
Emberiza tahapisi	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	107	14	0	0	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$	50	15	-1	0	N/a
	$\Phi_t p_{.} r.R.R'.F.F'.$	22	11	3	43.522	N/a
	$\Phi_t p_{.} r_t R.R'.F.F'.$	36	12	2	65.240	N/a
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$	8	6	8	19.532	-
	$\Phi_{.} p_t r_t R.R'.F.F'.$	35	8	6	25.637	**2.144**
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$	9	7	7	22.314	**1.696**
	$\Phi.p.r.R.R'.F.F'.$	7	5	9	18.659	-
	$\Phi_{.} p_{a2-./}.r.R.R'.F.F'.$	8	6	8	20.953	-
			84/282 (30%)			

Where the 1.25 < ĉ < 3, the likelihood of the general and nested reduced parameter models can be corrected using the 'c-hat adjustment' function within MARK. All models corrected using the variance inflation factor also have their AICc statistics adjusted to incorporate the ĉ within the likelihood term. This then gives the quasi-likelihood adjusted QAICc. Where the ĉ < 1, the model is considered marginally under-dispersed and the generally accepted convention is to adjust ĉ = 1.

Goodness of fit can be determined using one of three methods from within MARK: use of program RELEASE (Burnham *et al.* 1987), parametric bootstrapping, or a new method, the median ĉ. RELEASE can only assess goodness of fit for live encounter data and is not appropriate for our data, which includes recoveries. Both parametric bootstrapping and the median $\hat{c}$ methods use simulation and resampling to generate an estimate of $\hat{c}$. McGregor et al (2007) used the parametric bootstrapping approach for assessing goodness of fit however White (2002) has shown that this approach becomes less effective with increasing numbers of encounter occasions and is out-performed by the median $\hat{c}$ approach under such conditions. Here, model fit was assessed using the median $\hat{c}$ technique. This technique determines the best estimate of the variance inflation factor as being that for which the observed deviance $\hat{c}$ (the deviance of the model divided by the degrees of freedom for the model) lies at the midpoint of the distribution of all possible deviance $\hat{c}$'s produced from a simulation which assumes that a given value of $\hat{c}$ is the true value. The use of a range of inputted $\hat{c}$ values allows the tester to restrict the simulation to those values that are of use (i.e. $1 < \hat{c} < 3$). Failure of the model to produce a $\hat{c}$ in this range indicates poor fit. Similarly, if none of the simulated values overlap with the observed $\hat{c}$ then the logistic regression procedure used to estimate the median $\hat{c}$ cannot be performed and the model is considered a poor fit (Table 6). The median $\hat{c}$ is only of use if the estimates of the observed deviance $\hat{c}$ (or any of the factors used in its computation) are reliable. For many of the models assessed here this was not the case since the deviance degrees of freedom ≤ 0.

Table 7. GLM of variance inflation factor ($\hat{c}$) with number of resightings showing lack of effect of number of parameters. GLM model incorporates number of parameters in the survival model, number of resightings, quadratic function of resightings, and the interaction between resightings and number of parameters. The model uses the 7-year datasets for the 13 species whose survival was assessed using the Barker model.

Source	Sum of Squares	df	F	Sig.
Corrected Model	270.9[a]	5	8.3	<0.001
Intercept	196.9	1	30.17	<0.001
Number of Parameters	4.9	1	0.76	0.387
Number of Resightings	154.8	1	23.72	**<0.001**
(Number of Resightings)^2	143.8	1	22.04	**<0.001**
Parameters*Retraps	11.8	1	1.8	0.182
Parameters*Retraps^2	15.1	1	2.31	0.132
Error	724.4	111		
Total	1445.9	117		
Corrected Total	995.3	116		

[a] Adjusted $R^2 = 0.239$

The supplementing of the original dataset (i.e. that of McGregor *et al* (2007)) with a further five years' worth of data failed to improve the overall mean proportion of individuals retrapped/resighted (0.39 v 0.35), and increases in proportions of retraps and resightings were observed for only four of the 11 species common to both studies. In fact, it appears that the absolute numbers of individuals retrapped or resighted is more important in determining goodness of fit than is the proportion of the marked population retrapped or resighted. The number of recaptures was strongly correlated with both the number of resightings (Pearson $r(117) = 0.927$, $p < 0.001$) and the number of individuals in the marked population ($r(117) = 0.969$, $p < 0.001$) and so recaptures and resightings were dealt with separately when modelling the relationship between goodness of fit and numbers of retraps/resightings. The numbers of both recaptures and resightings were a significant factor in identifying goodness of fit when incorporated as a quadratic function in the model (Tables 7 and 8). This was the case irrespective of the number of parameters (in the Barker model) (Tables 7 & 8). For the data here it therefore appears that a threshold of at least 8 retrapped individuals (Figure 3) or 15 resighted individuals (Figure 4) for each species was important in identifying whether the Barker model would achieve acceptable model fit.

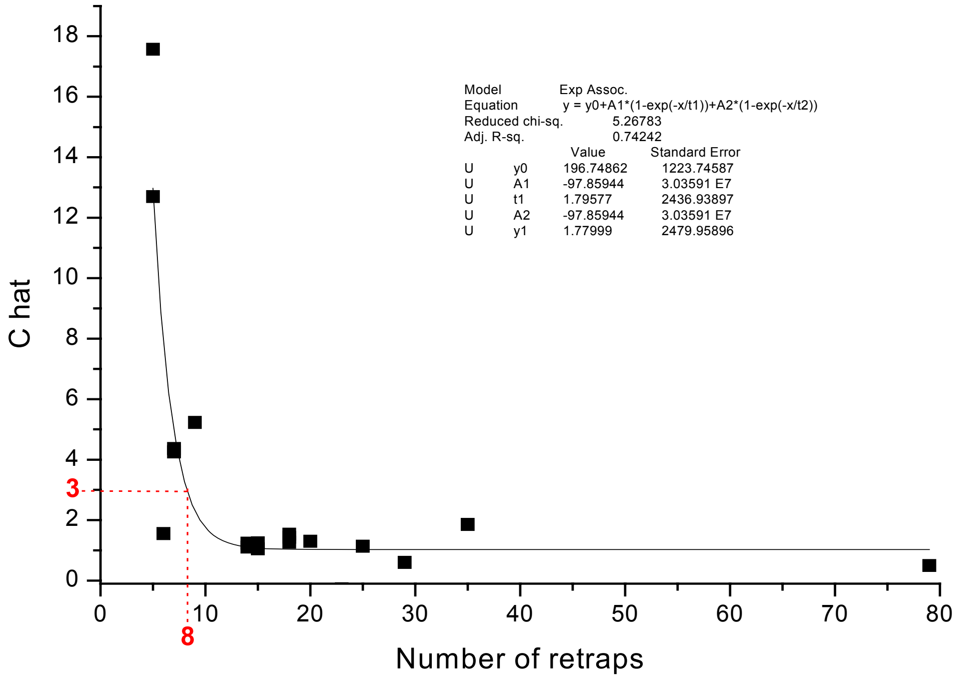
Table 8. GLM of variance inflation factor (ĉ) with number of retraps showing lack of effect of number of parameters. GLM model incorporates number of parameters in the survival model, number of retraps, quadratic function of retraps, and the interaction between retraps and number of parameters. The model uses the 7-year datasets for the 13 species whose survival was assessed using the Barker model.

Source	Sum of Squares	df	F	Sig.
Corrected Model	186.1[a]	5	5.11	<0.001
Intercept	149.7	1	20.53	<0.001
Number of Parameters	0.04	1	0.01	0.942
Number of Retraps	109.0	1	14.95	**<0.001**
(Number of Retraps)^2	106.7	1	14.64	**<0.001**
Parameters*Retraps	4.3	1	0.58	0.446
Parameters*Retraps^2	7.1	1	0.98	0.324
Error	809.2	111		
Total	1445.9	117		
Corrected Total	995.3	116		

[a] Adjusted $R^2 = 0.150$

It is likely that improvement in the goodness of fit of the data and the ability to apply more complex models could therefore have been achieved with the recapture or resighting of a larger number of individuals of each species. Had such data increases been achieved then the Barker model may have proved the most suitable approach for the modelling of survival with this data, as it had previously for McGregor *et al* (2007). Unfortunately, acceptable goodness of fit in itself does not result in a model producing sensible parameter estimates (Table 9). The species with largest numbers of resightings and recaptures (*E.franciscanus*) still failed to produce reliable (time-specific) parameter estimates despite having a ĉ of 1.55 for the fully parameterised starting model. Time-specific variation in survival was identified however estimates of φ for all time periods was >0.5 (indeed 13 of the 16 estimates are given as 1.00) suggesting a mean φ of >0.8. However, φ in other models (i.e. time-independent and TSM models) was never above 0.43. The extent of unreliability in these estimates (95% of all estimates for the time-specific models for these species) suggests that despite the addition of five years' worth of data to those of McGregor (2007), there were still insufficient recaptures or resightings to assess time-variable survival using this approach. This suggests that other factors (perhaps number of capture occasions or total number of parameters) may play a significant role in determining accuracy and precision of estimates.

Figure 3. Plot of variance inflation factor (ĉ) against number of individuals recaptured for models with 7 parameters. Plotted data are from the full 7-year dataset for all species and the fitted line is a negative exponential function. Acceptable ĉ values lie in the range of 1-3 and correspond to a minimum of 8 recaptures.



```
Model           Exp Assoc.
Equation        y = y0+A1*(1-exp(-x/t1))+A2*(1-exp(-x/t2))
Reduced chi-sq.         5.26783
Adj. R-sq.              0.74242
                 Value           Standard Error
U      y0        196.74862        1223.74587
U      A1        -97.85944        3.03591 E7
U      t1        1.79577          2436.93897
U      A2        -97.85944        3.03591 E7
U      y1        1.77999          2479.95896
```

Figure 4. Plot of variance inflation factor (ĉ) against number of individuals resighted for models with 7 parameters. Plotted data are from the full 7-year dataset for all species and the fitted line is a negative exponential function. Acceptable ĉ values lie in the range of 1-3 and correspond to a minimum of 15 resightings.

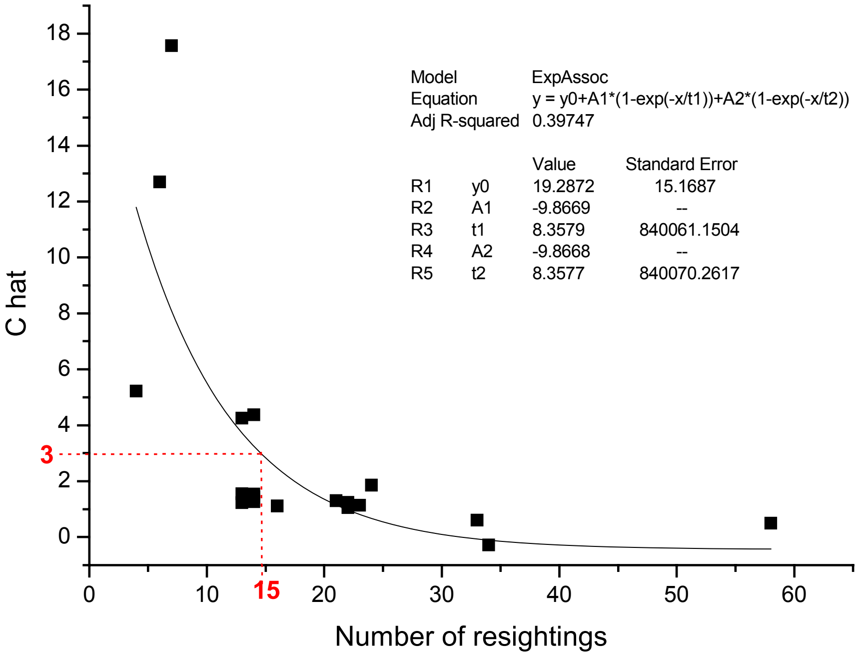


Table 9. Apparent adult survival estimates (φ) ± standard errors for the 'best' models for 13 African bird species generated using the Barker approach. Best models were identified using AICc and likelihood ratio tests. Where the best model produces unrealistic or unlikely estimates for φ (denoted by N/a), this is reported along with the next best model. *Interval* denotes the period under the time-dependent model for which the estimate is provided. (R) (in Model) denotes estimates made using the reduced encounter histories. The annual estimates derived using models under the CJS approach (i.e. excluding resightings and including *ad hoc* captures) are given for comparison.

	Barker (resighting) approach			**CJS approach**	
Species	Model	Interval	Φ ± SE	Model	Φ ± SE
Colius striatus	$\Phi_{t}p.r.R.R'.F.F'.$	10	0.828 ± 0.25		
		11	0.386 ± 0.2		
		12	0.568 ± 0.33		
		13	0.779 ± 0.27		
	$\Phi.p.r.R.R'.F.F'.$	1	0.419 ± 0.06	$\Phi.p.$	0.619 ± 0.05
	$\Phi.p_{t}r_{t}R.R'.F.F'.$ (R)	1	0.320 ± 0.06		
Pycnonotus barbatus	$\Phi_{t}p_{t}r_{t}R_{t}R'_{t}F_{t}F'_{t}$	1	0.213 ± 0.21		
	$\Phi.p.r.R.R'.F.F'.$	1	0.993 ± 0.001	$\Phi_{.}p_{a2-./.}$	0.668 ± 0.05
Turdus pelios	$\Phi_{t}p.r_{t}R.R'.F.F'.$	11	0.406 ± 0.15		
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.070 ± 0.03		
		2	0.509 ± 0.06		
	$\Phi._{.}p.r.R.R'.F.F'.$	1	0.311 ± 0.04	$\Phi_{.}p_{.}$	0.799 ± 0.06
	$\Phi.p_{t}r_{t}R.R'.F.F'.$ (R)	1	0.307 ± 0.05		
Camaroptera brachyura	$\Phi._{.}p_{.}r_{.}R.R'.F.F'.$	1	0.395 ± 0.1	$\Phi_{.}p_{.}$	0.636 ± 0.06
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.201 ± 0.15		

	Barker (resighting) approach			**CJS approach**	
Species	Model	Interval	Φ ± SE	Model	Φ ± SE
Camaroptera brachyura		2	0.494 ± 0.14		
	$\Phi_{.}.p.r_tR.R'.F.F'.$ (R)	1	0.459 ± 0.09		
Cyanomitra verticalis	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.056 ± 0.07		
		2	0.653 ± 0.13		
	$\Phi.p.r.R.R'.F.F'.$ (R)	1	0.499 ± 0.1	$\Phi_{.}p_{a2-./.}$	0.654 ± 0.06
Chalcomitra senegalensis	$\Phi_{a2-./.}p.r_{.}R.R'.F.F'.$	1	0.104 ± 0.09	$\Phi_{.}p_{.}$	0.769 ± 0.07
		2	0.555 ± 0.09		
	$\Phi_tp_tr_tR_tR'_tF_tF'_t$ (R)	8	0.875 ± 0.08		
Zosterops senegalensis	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.100 ± 0.09	$\Phi_{.}p_{.}$	0.527 ±0.08
		2	0.587 ± 0.1		
Ploceus cucullatus	$\Phi_tp_tr_tR_tR'_tF_tF'_t$ (R)	N/a	N/a		
	$\Phi.p_tr_tR.R'.F.F'.$ (R)	1	0.206 ± 0.06	$\Phi_{.}p_{.}$	0.694 ± 0.09
Ploceus nigricollis	$\Phi.p_{a2./.}r.R.R'.F.F'.$	1	0.326 ± 0.07	$\Phi_{.}p_{a2-./.}$	0.786 ± 0.08
	$\Phi_{a2-./.}p_{a2-./.}r.R.R'.F.F'.$	1	0.160 ± 0.11		
		2	0.406 ± 0.11		
	$\Phi.p_tr_tR.R'.F.F'.$ (R)	1	0.206 ± 0.09		
Ploceus vitellinus	$\Phi_tp_tr_tR_tR'_tF_tF'_t$ (R)	N/a	N/a		
	$\Phi.p_tr_tR.R'.F.F'.$ (R)	1	0.434 ± 0.05	$\Phi_{.}p_{.}$	0.726 ± 0.09
Euplectes franciscanus	$\Phi_tp_tr_tR_tR'_tF_tF'_t$	3	0.876 ± 0.09		
		14	0.893 ±0.04		
	$\Phi_{.}p_tr.R.R'.F.F'.$	1	0.282 ± 0.02	$\Phi_{.}p_t$	0.72 ± 0.03
	$\Phi_{a2-./.}p_{a2-./.}r.R.R'.F.F'.$	1	0.043 ± 0.02		
		2	0.426 ± 0.04		
Estrilda caerulescens	$\Phi_tp_tr_tR.R'.F.F'.$	9	0.254 ± 0.21		
		11	0.234 ± 0.14		
		13	0.448 ± 0.28		
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.124 ± 0.08		
		2	0.371 ± 0.1		
	$\Phi.p.r.R.R'.F.F'.$	1	0.274 ± 0.07	$\Phi_{.}\ p_t$	0.566 ± 0.04
Uraeginthus bengalus	$\Phi_tp_tr_tR_tR'_tF_tF'_t$	N/a	N/a		
	$\Phi.p_tr.R.R'.F.F'.$	1	0.224 ± 0.04	$\Phi_{.}\ p_{a2-./.}$	0.456 ± 0.04
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.094 ± 0.05		
		2	0.271 ± 0.06		
Lagonosticta sanguinodorsalis	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.158 ± 0.13		
		2	0.435 ± 0.12		
	$\Phi.p.r.R.R'.F.F'.$	1	0.354 ± 0.08		
	$\Phi_tp_tr_tR_tR'_tF_tF'_t$ (R)	2	0.307 ± 0.13		
		3	0.912 ± 0.05		
		4	0.638 ± 0.14		
		6	0.121 ± 0.06		
		7	0.904 ± 0.1		
		9	0.031 ± 0.01		
	$\Phi.p_tr_tR.R'.F.F'.$ (R)	1	0.377 ± 0.03	$\Phi_{.}\ p_t$	0.559 ± 0.04
Emberiza tahapisi	$\Phi_tp_tr_tR_tR'_tF_tF'_t$	11	0.875 ± 0.08		
	$\Phi_{a2-./.}p.r.R.R'.F.F'.$	1	0.022 ± 0.02		

	Barker (resighting) approach			**CJS approach**	
Species	Model	Interval	Φ ± SE	Model	Φ ± SE
Emberiza tahapisi		2	0.394 ± 0.14		
	$\Phi.p_t r_t R.R'.F.F'.$	1	0.158 ± 0.06		
	$\Phi_t p_t r_t R_t R'_t F_t F'_t$ (R)	N/a	N/a		
	$\Phi.p.r.R.R'.F.F'.$ (R)	1	0.745 ± 0.14	$\Phi_.\ p_.$	0.491 ± 0.13

Reduction in the number of parameters

MARK uses an information matrix (derived from the maximum likelihood estimators for the survival, recapture and resighting parameters) to assess the number of parameters. The effective rank of the variance-covariance matrix is an estimate of the maximum number of estimable parameters. A threshold value is produced in MARK against which the other values are tested, values greater than this threshold are considered to be parameters that can be estimated. MARK then employs a second test (based on identification of the sudden large gaps between consecutive values of the conditioned singular vector) to identify those *ß* (compound) parameters that are not assessed. In general, the fewer the number of estimable parameters, the less relevant is the structure of the model to the data. This is an important consideration when assessing suitability and 'fit' of the models.

To determine whether the increased number of recapture occasions (and therefore parameters) was a significant factor affecting the performance of the CES/Barker method, I also tested the response of the model to a reduced number of recapture occasions i.e. manually selecting three-five year's worth of data. Recapture occasions were selected to minimise the loss of retraps and resightings and, where possible, consecutive runs of periods were used. Where capture occasions are omitted from the centre of a run of data (e.g. year 3 of a study running from year 1 to 5) the resightings are retained since they are recorded between capture occasions. Loss of resightings therefore only occurs when initial or terminal encounter occasions are removed (e.g. year 1 or 5 in a study running from year 1 to 5).

Table 10. Goodness of fit testing of general starting models using reduced time periods. CES periods identifies the number of the original 16 periods used here for modelling; Estimated Parameters denotes the number of parameters for which MARK can generate estimates. Dev d.f. = Deviance.d.f.

Species	Model	CES periods	Expected Parameters	Estimated Parameters	Dev d.f.	Observed $\hat{c}$	Median $\hat{c}$
C.striatus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	8	51	17	2	53.301	1.254
P.barbatus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	11	72	20	11	16.549	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		35	14	17	16.477	N/a
	$\Phi_t p.r_t R.R'.F.F'.$		26	9	22	14.845	N/a
	$\Phi.p_t r_t R.R'.F.F'.$		25	11	20	15.872	N/a
	$\Phi_{a2-./.} p_{a2-./.} r.R.R'.F.F'.$		9	6	25	13.453	N/a
	$\Phi_{a2-./.} p.r.R.R'.F.F'.$		8	4	27	17.784	9.030
	$\Phi.p.r.R.R'.F.F'.$		7	4	27	13.071	N/a
T.pelios	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	21	N/a	N/a	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		31	13	33	0.1516	N/a
	$\Phi_t p.r_t R.R'.F.F'.$		24	10	33	40.782	1.007
C.brachyura	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	11	72	22	N/a	N/a	N/a
	$\Phi_t p.r_t R.R'.F.F'.$		26	8	8	24.493	1.337
C.verticalis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	20	N/a	N/a	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		31	13	4	42.413	N/a
	$\Phi_t p.r_t R.R'.F.F'.$		24	9	8	22.832	3.157
	$\Phi_t p.r.R.R'.F.F'.$		16	9	8	23.105	2.692
C.senegalensis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	62	15	4	45.838	0.882
Z.senegalensis	$\Phi.p_t r_t R.R'.F.F'.$	11	25	9	3	46.817	N/A
	$\Phi_t p.r_t R.R'.F.F'.$		26	8	4	35.781	4.063
	$\Phi.p.r.R.R'.F.F'.$		7	5	7	22.995	1.961
P.cucullatus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	13	N/a	N/a	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		31	11	2	85.289	1.638
P.nigricollis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	11	72	10	2	10.200	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		35	9	3	18.739	0.715
P.vitellinus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	9	N/a	N/a	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		32	8	1	105.563	N/a
	$\Phi.p_t r_t R.R'.F.F'.$		23	6	3	43.234	0.482
E.franciscanus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	15	14	59.325	N/a
	$\Phi_t p_t r.R.R'.F.F'.$		24	12	17	57.378	N/a
	$\Phi_t p.r_t R.R'.F.F'.$		24	9	20	54.795	N/a
	$\Phi.p_t r_t R.R'.F.F'.$		23	7	22	49.726	N/a
	$\Phi_t p.r.R.R'.F.F'.$		16	9	20	55.138	N/a
	$\Phi.p_{a2-./.} r.R.R'.F.F'.$		8	5	24	51.308	N/a
	$\Phi.p.r.R.R'.F.F'.$		7	4	25	49.832	N/a
E.caerulescens	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	26	11	14.400	N/a
	$\Phi_t p.r_t R.R'.F.F'.$		24	10	27	10.132	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		32	17	20	13.038	N/a
	$\Phi.p.r.R.R'.F.F'.$		7	6	31	10.045	N/a
U.bengalus	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	11	72	26	14	21.487	N/a
	$\Phi_t p_t r_t R.R'.F.F'.$		35	17	23	18.667	N/a
	$\Phi_t p.r.R.R'.F.F'.$		17	12	28	16.344	N/a
	$\Phi.p.r.R.R'.F.F'.$		7	6	34	14.903	N/a
L.sanguinodorsalis	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	10	65	23	5	28.475	0.308
E.tahapisi	$\Phi_t p_t r_t R_t R'_t F_t F'_t$	7	44	9	1	27.625	4.873
	$\Phi_t p_t r_t R.R'.F.F'.$		23	9	1	51.005	3.219
	$\Phi_t p.r_t R.R'.F.F'.$		18	6	4	13.329	1.217

The encounter histories of L.rara and C.aberrans could not be reduced further without losing too much information and so these species were excluded from this assessment. Of the remaining 15 species, MARK was less able to identify acceptable general models when using the reduced encounter histories and goodness of fit was an issue in four of the reduced datasets (Table 10). These species had the largest number of recaptures and resightings and had previously achieved acceptable goodness of fit using the original datasets. In contrast, the same process resulted in an improvement during model testing for P.cucullatus, P.vitellinus and C.verticalis. Nevertheless, as for the tests performed using the original dataset, parameter estimates for the best models for each species still appeared unreliable in most cases.

The reduction in the number of parameters (i.e. through the reduction in the number of encounter occasions) failed to provide a general improvement in the goodness of fit of models (under the CES/Barker approach). The resulting loss of data from recaptures of birds in these periods can also lead to unacceptable and improbable parameter estimates. No improvement in survival estimation was gained from using the reduced encounter occasion datasets.

Model Selection

The fully parameterised, time-dependent model proved suitable as a starting model for only three of the 17 species assessed (Table 6). These species (*P.barbatus, E.franciscanus* and *U.bengalus*) were also those with the greatest number of captures and resightings from the CES periods (Table 3). Some degree of time-dependence in the survival parameter was acceptable in all models for which a general model was determined (i.e. 13 of the 17 species) although three of these allowed time-dependence only in the form of a two-stage, time-since-marking model. Where the fully time-dependent general model was unsuitable as a starting model, all subsequent models for that species were tested with constant resighting (*R* and *R'*) and fidelity (*F* and *F'*) parameters. MARK failed to identify starting models for 4 of the 17 species, and these were the species with the fewest number of retraps and resightings (combined total 11-14). Insufficient data prevented further modelling of survival for these species using the CES/Barker method. As with the CJS method, the variance inflation factor was used to correct all model statistics allowing more suitable model selection.

Models were selected using information theoretic methods employing a corrected Akaike's Information Criterion (AICc) (Akaike 1985) which performs better for small sample sizes. All models for which $\hat{c} \neq 1$ were adjusted using $\hat{c}$ to give a quasi-likelihood adjusted QAICc. The AICc/QAICc scores allow comparison of models on the principal of parsimony, lower values ascribed to those models which best fit the data with fewest parameters. Since this method is known to underperform when the difference between models is <2 AIC, Likelihood Ratio tests were used on nested models in cases where this situation occurred.

Identification of realistic models

Despite the goodness of fit of starting models for 13 of the 17 species identified for assessment, most of the models themselves produced highly variable and questionable parameter estimates (Table 6). For example, the MARK output for the Common Bulbul data suggests that a fully time-dependent Barker model ($\varphi_t p_{t.} r_t R_t R'_t F_t F'_t$) is acceptable ($\hat{c} = 2.29$) and indeed the best and most parsimonious model (Table 6) despite only around one quarter of the parameters being estimable (29 of 107). Examination of the annual estimates that this model produces for apparent survival of the species reveals that most are unusable (15 of 16 are dubious with $0.05<\varphi>0.95$). Reducing the model to its least parameterised version ($\varphi.p.r.R.R'.F.F'.$) still results in MARK failing to estimate around 50% of the parameters and the estimate of survival again appears questionable. Under the fully time-dependent model, survival for interval one was 0.213 ± 0.210 (and $\varphi < 0.100$ for three other intervals) yet when using the constant model the 'average' survival is estimated as 0.993 ± 0.001. This estimate also differs considerably from that found by McGregor et al. (2007) during the first 3 years of the study (0.36 ± 0.84), that obtained by Peach et al. (2001) in Malawi (0.74 ± 0.038) and the estimate obtained here using the less parameterised CJS approach ($\varphi_c p_c$: 0.670 ± 0.052). This suggests either a serious problem with model structure or an insufficient dataset size to use this modelling approach.

The importance of recapture data

The CJS approach finally adopted for the estimation of survival (see Chapter 4) allowed for the incorporation of data from a greater number of capture occasions – i.e. those from the rigidly identified CES periods as well as the more ad hoc 5-15 day catches performed at other times. This resulted in an increase in the total number of individuals ringed, retrapped, and available for inclusion in estimation of survival per species of 328% (Barker retraps mean 18.6, CJS retraps mean 61.5 – Table 3) and the consequent increase in the number of species for which survival could be estimated. Comparing total catches of all species under both methods, an additional 3330 individual captures from an extra 497 days of mist-netting were made available when using the CJS method. Overall, a mean of 14.20 (10284/724) birds per day were caught under the CJS method compared with 30.63 (6954/227) using the CES method. Daily catch rate of retraps was similar between the two methods, 4.42 (1757/495) being caught each day using the CJS method and 6.34 (1440/227) during the CES periods. This suggests a greater efficiency in using the CJS method given that this approach used a reduced length of mist-net (usually around 30% of that operated under the CES) and operated at each location for fewer consecutive days. When considering only those species used for survival analysis under the CES/Barker method, the CJS method increased the number of recaptures and the daily recapture rates from 316 = 1.39 catches per day (observed from the CES periods), to 2179 = 3.75 catches per day. This increase in the number of recaptures and likely greater diversity in encounter histories is likely to have aided the performance of the less-parameterised CJS-style models against the Barker model.

Table 11. Comparison of survival estimates for species using both the CES/Barker model approach and those generated using the CJS approach using models with similar φ and p parameterisation. (M) denotes apparent survival estimate obtained from McGregor *et al* (2007); (R) after the Barker Model description denotes reduced encounter model (used where acceptable goodness of fit was not achieved for the model containing the full 7-year dataset). (M) after the Barker model description denotes models that are comparable with the Barker models since the listed parameter estimate, φ is always the same as for the fully time-independent model (Φ.p.r.R.R'.F.F'.).

Species	Barker Model	Φ ± SE	95% CI	CJS Model	Φ ± SE	95% CI
Colius striatus	Φ.p.r.R.R'.F.F'. Φ.p.r.R.R'.F.F'. (M)	0.419 ± 0.06 0.194 ± 0.19	0.308 – 0.540	Φ.p.	0.619 ± 0.05	0.509 – 0.718
Pycnonotus barbatus	$\Phi.p_{a2-./.}r.R.R'.F.F'.$ Φ.p.r.R.R'.F.F'.(M)	0.993 ± 0.001 0.359 ± 0.08	0.992 – 0.995	$\Phi.p_{a2-./.}$	0.668 ± 0.05	0.560 – 0.760
Turdus pelios	Φ.p.r.R.R'.F.F'.	0.311 ± 0.04	0.242 – 0.390	Φ.p.	0.799 ± 0.06	0.659 – 0.891
Camaroptera brachyura	Φ.p.r.R.R'.F.F'. Φ.p.r.R.R'.F.F'.(M)	0.395 ± 0.1 0.461 ± 0.11	0.219 – 0.603	Φ.p.	0.636 ± 0.06	0.523 – 0.735
Cyanomitra verticalis	$\Phi.p_{a2-./.}r.R.R'.F.F'.$ Φ.p.r.R.R'.F.F'.(M)	0.452 ± 0.11 0.599 ± 0.24	0.264 – 0.655	$\Phi.p_{a2-./.}$	0.654 ± 0.06	0.530 – 0.760
Chalcomitra senegalensis	Φ.p.r.R.R'.F.F'. Φ.p.r.R.R'.F.F'.(M)	0.990 ± 0.003 0.386 ± 0.19	0.983 – 0.994	Φ.p.	0.769 ± 0.07	0.611 – 0.876
Zosterops senegalus	Φ.p.r.R.R'.F.F'. Φ.p.r.R.R'.F.F'.(M)	0.464 ± 0.07 0.339 ± 0.17	0.325 – 0.609	Φ.p.	0.527 ± 0.08	0.375 – 0.675
Ploceus cucullatus	Φ.p.r.R.R'.F.F'. (R)	0.136 ± 0.04	0.073 – 0.241	Φ.p.	0.694 ± 0.09	0.496 – 0.840
Ploceus nigricollis	$\Phi.p_{a2./.}r.R.R'.F.F'.$ Φ.p.r.R.R'.F.F'.(M)	0.326 ± 0.07 0.478 ± 0.16	0.205 – 0.476	$\Phi.p_{a2-./.}$	0.786 ± 0.08	0.606 – 0.900
Ploceus vitellinus	$\Phi.p_t r_t R.R'.F.F'.$ (R) Φ.p.r.R.R'.F.F'.(M)	0.391 ± 0.05 0.865 ± 0.09	0.293 – 0.499	Φ.p.	0.726 ± 0.09	0.534 – 0.860
Euplectes franciscanus	$\Phi.p_t r.R.R'.F.F'.$	0.282 ± 0.02	0.244 – 0.324	$\Phi.p_t$	0.720 ± 0.03	0.649 – 0.782
Estrilda caerulescens	$\Phi.p_t r.R.R'.F.F'.$ Φ.p.r.R.R'.F.F'.(M)	0.279 ± 0.07 0.678 ± 0.13	0.168 - 0.427	$\Phi.p_t$	0.566 ± 0.04	0.486 – 0.643
Uraeginthus bengalus	$\Phi.p_{a2./.}r.R.R'.F.F'.$ Φ.p.r.R.R'.F.F'.(M)	0.205 ± 0.04 0.533 ± 0.2	0.143 – 0.285	$\Phi.p_{a2-./.}$	0.456 ± 0.04	0.379 – 0.535
L.sanguinodorsalis	$\Phi.p_t r.R.R'.F.F'.$ Φ.p.r.R.R'.F.F'.(M)	0.352 ± 0.08 0.658 ± 0.18	0.208 – 0.528	$\Phi.p_t$	0.559 ± 0.04	0.482 – 0.632
Emberiza tahapisi	Φ.p.r.R.R'.F.F'.	0.159 ± 0.06	0.077 – 0.300	Φ.p.	0.491 ± 0.13	0.266 – 0.721

Using a number of mist-netting locations around the reserve also resulted in the capture of a greater range of species than that caught at the CES alone, due to nets being placed in, or near to, a greater variety of habitats. The repeated use of one site (i.e. the CES site) meant that the potential for catching was restricted only to those individuals regularly using or transiting this area. The inclusion of mist-netting sites away from the standard CES inevitably resulted in the inclusion of more individuals in the study thereby improving the number of individuals with encounter histories that included at least one recapture. The combined 'CJS' approach therefore proved more effective than the CES/Barker approach because of the improved range of encounter histories and the larger counts of individuals for each recapture history. Since MARK attempts to derive estimates of the model parameters based on the likelihood of observing frequencies of individuals having the observed encounter histories, larger frequencies for each encounter history allows finer-scale estimation than is possible if frequencies are low. Low frequencies are often ‘flagged’ as a warning during the running of MARK. More acceptable (and potentially more precise) parameter estimates are therefore more likely as mean frequency of encounter histories increases.

A combination of the small encounter history frequencies and large numbers of parameters also leads to problems for parameter estimation. This is especially apparent for many of the attempts to model survival using the CES/Barker approach (even when time-dependence is constrained to those parameters of most immediate interest – φ, p and r). As discussed above, the fully parameterised Barker model for this dataset, incorporating all 16 capture/recapture events, comprises 107 parameters, yet for all species across all models incorporating any time-dependence, the maximum number of parameters that MARK was able to determine was 71% (for *L.sanguinodorsalis*, model: $\Phi_{.}p_{t}r_{.}R_{.}R'_{.}F_{.}F'_{.}$, 15 or 21 parameters). Data shortages meant that, as expected, the proportion of estimable parameters was generally lowest in the models with more parameters (e.g. those incorporating time dependence). Assessing groups of models with similar characteristics (i.e. the number of time-dependent parameters) revealed that the number of estimable parameters (*K)* was significantly correlated with number of individuals recaptured for all models containing time-dependent parameters (Pearson $r > 0.47$, $p<0.023$, N>15) but not for time-independent or tsm models ($r(39) = -0.30$, $p=0.07$; Figure 4a). The number of resightings was also important in determining *K*, and was highly significant in all models containing time-dependent terms ($r > 0.63$, $p \leq 0.001$, N>15; Figure 4b) except for those containing 2 time-dependent parameters ($r(21)=0.42$, $p=0.06$) and in the time-independent and tsm models ($r(39) = -0.31$, $p = 0.06$). Generally, the number of individuals in the dataset (i.e. initially captured) was also significantly positively correlated with *K*, especially for the more heavily parameterised, time-dependent models. Here, correlations with models having one ($r(23)=0.44$, $p=0.035$), three ($r(14)=0.56$, $p=0.039$) and seven

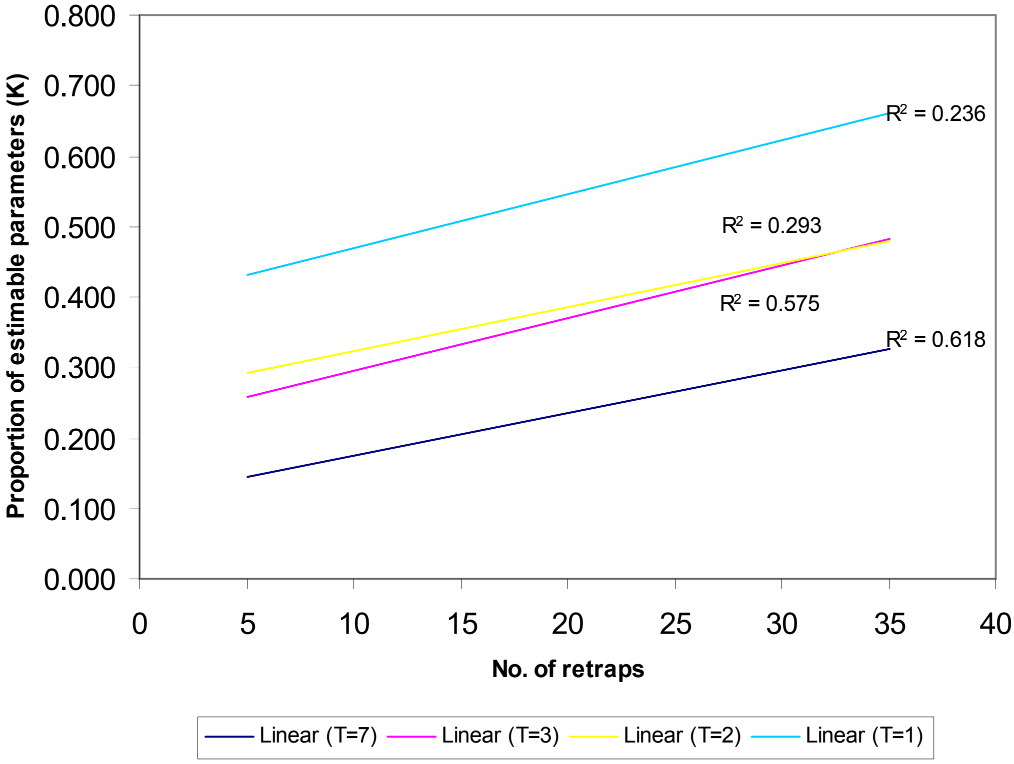
($r(15)=0.53$, $p=0.041$) time-dependent parameters were significant. Neither the proportion of individuals retrapped or resighted were significantly correlated with the number of estimable parameters regardless of the number of time-dependent parameters (e.g. for fully time dependent model, K v proportion retrapped: $r(15)=0.22$, $p=0.42$; K v proportion resighted: $r(15)=0.10$, $p=0.72$; and for time independent models, K v proportion retrapped: $r(39)=-0.07$, $p=0.69$; K v proportion resighted: $r(39)=-0.02$, $p=0.92$). In contrast, all estimable parameters were identified and determined by MARK when using the CJS approach - including the highly parameterised models incorporating time dependence (e.g. for *E. franciscanus:* $\Phi_{a2\text{-}t/c}\ p_t$ = 53 parameters) (see Table 2, Chapter 4).

Greater inclusion of time-dependence (or at the least, time-since marking factor) within starting models under the CJS method meant that this approach allowed for a more thorough and systematic testing of a more varied group of models. Often these were excluded under the CES/Barker approach because of a failure to identify acceptable general models that included time-dependence.

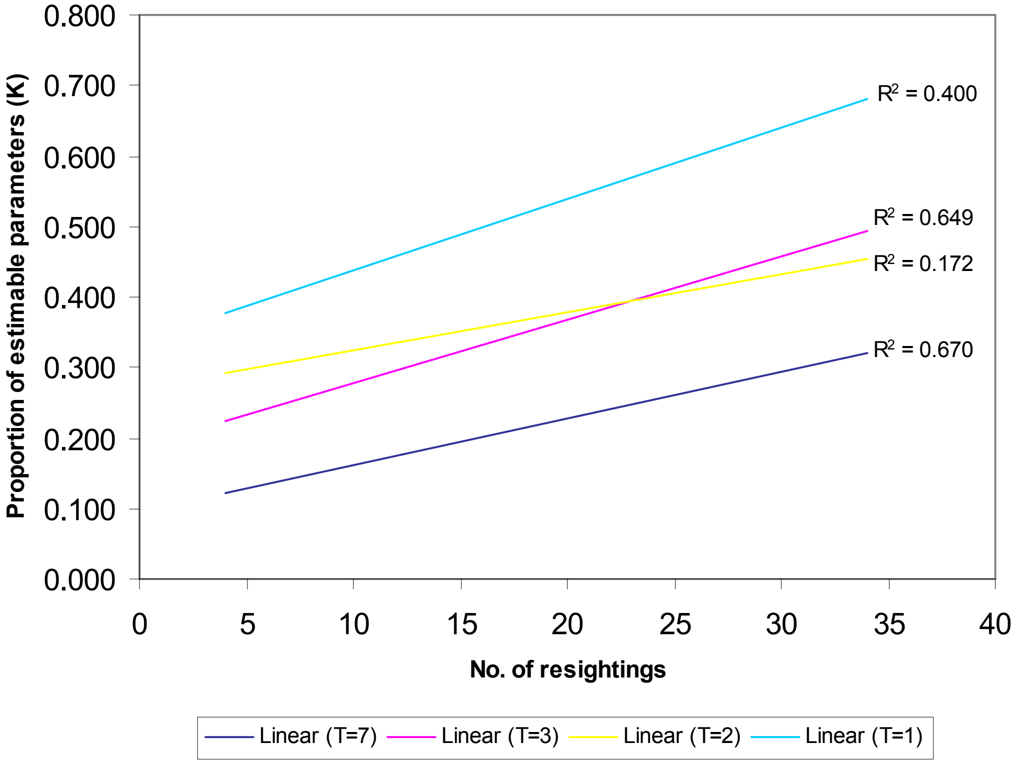
Regression of the estimates of apparent survival on an index of encounter frequency (given by total number of individuals ringed / total number of resightings + number of recaptures) produces a near significant, positive relationship for the data of McGregor (2005) ($F_{1,9} = 3.7$, $p=0.09$) but no real relationship either when using the CJS or current CES/Barker approach data from this study (CJS, $F_{1,15} = 0.001$, $p=0.98$; CES/Barker, $F_{1,12} = 2.0$, $p=0.18$). In contrast, the level of precision of the estimates shows a near significant positive relationship under the CJS method ($F_{1,15} = 3.4$, $p=0.09$) yet is non-significant for either McGregor's data ($F_{1,9} = 0.2$, $p=0.65$) or that produced using the Barker data from the current study ($F_{1,12} = 3.0$, $p=0.11$). Improving resighting and recapture rates will therefore much improve both the estimate of survival (under the CES method) and the precision of the estimate under the CJS approach (see Table 11).

Precision of the apparent survival estimates is markedly improved when the data are analysed using the CJS method compared to those obtained under the original CES approach (Wilcoxon signed rank, $W = -2.93$, $p=0.003$). This improvement in precision occurs alongside a near-significant increase in the estimate of survival (*W* = -1.69, *p*=0.09). Although not necessarily an indication that the estimates obtained under the newly adopted method are correct, their improvement, both in terms of precision and absolute value (see Table 11), more closely mirror those estimates produced in other studies (i.e Peach *et al* 2001 – see Chapter 4).

Figure 5. Relationship between proportion of estimable parameters and (a) number of retraps; and (b) number of resightings. Proportion of estimable parameters = number identified by MARK/the theoretical number of parameters in the model. T represents groupings based on the number of time-dependent parameters. So, T=7 represents time-dependence in all seven parameters of the Barker model (i.e. $\Phi_t p_t r_t R_t R'_t F_t F'_t$) and T=0 represents a fully time-independent model (i.e. $\Phi_. p_. r_. R_. R'_. F_. F'_.$).



Assessment of the two methods is perhaps best made by comparing the derived estimates of survival and their precision (Figure 5 and Table 11). For the majority of species (13 of 15), the estimates derived under the CJS approach were considerably higher than those obtained using the CES/Barker method. The absolute difference in derived estimates between the two methods for all species (except *Z.senegalensis*) was >0.2, with a mean difference of 0.31 (± 0.03) (paired samples *t*(14)=2.3, *p* = 0.036). A similar result was found when comparing the paired means of species assessed under the CJS method with those made by McGregor et al. (2007) using the Barker approach. Here 8 of 12 estimates were higher under the CJS method, with a mean difference of 0.23 (± 0.04) (paired *t*(10)=1.8, *p* = 0.1). Paired comparisons of estimates made under the Barker approach for the data up to 2004 with those of this study were non-significant (*t*(10)=0.1, *p*=0.89; Figure 6) suggesting a degree of consistency. In truth however, despite the mean survival for the 11 species common to both studies being similar (Mean ± se: Barker 2004: 0.50 ± 0.06; Barker 2009: 0.48 ± 0.08), the difference in estimates between the studies was less than 0.10 for only one species (*C.brachyura*, difference 0.066). In the remaining cases the absolute difference between paired estimates varied widely (0.154 – 0.634).



The lack of consistency between estimates suggests a failing in the CES/Barker method for this dataset (Figure 7). Indeed on assessing the range of estimates between methods, only those determined under the CJS approach (range = 0.456-0.786 (0.33), se ± 0.031; Figure 8) were in any way comparable to previously published estimates for similar African species (e.g. de Swardt & Peach 2001; Peach *et al.* 2001; Covas *et al.* 2004). In contrast, the values obtained under both Barker datasets showed considerable variation (current Barker range=0.205-0.993 (0.785), se ± 0.080; Barker data up to 2004, range= 0.194-0.865 (0.671), se ± 0.057) and were very different to published estimates of survival for tropical African passerine species.

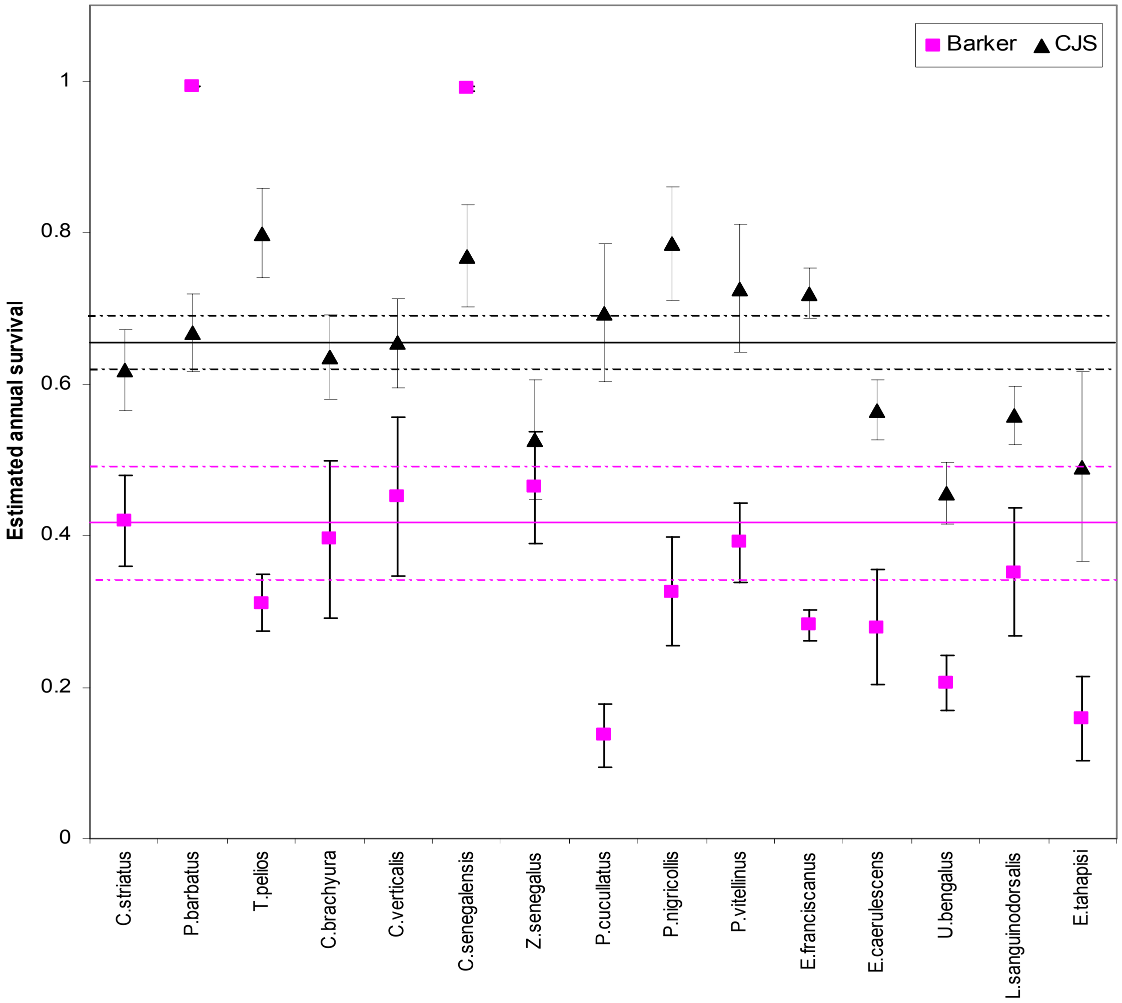
Conclusion

Overall assessment of the CES/Barker method as used here

It is clear from much of the discussion above that a number of problems exist with the current CES methodology and that these may have affected both the quality and quantity of data obtained during the eight years of this study. Identification of these factors may go some way to explaining the difficulties in applying the data to the Barker model. Alternative methods (the CJS/continual approach) did produce reasonably precise parameter estimates, however this necessitated the inclusion of supplementary data from capture occasions outside the CES periods. There are therefore a number of points to address in suggesting methods by which the capture protocol and survival assessment could be improved: firstly, to determine whether the current capture methodology is a suitable and efficient approach for generating sufficient resightings and recaptures for the Barker model, and secondly, to identify whether or not the Barker model (in concert with the current CES protocol) is the most efficient method of modelling such data.

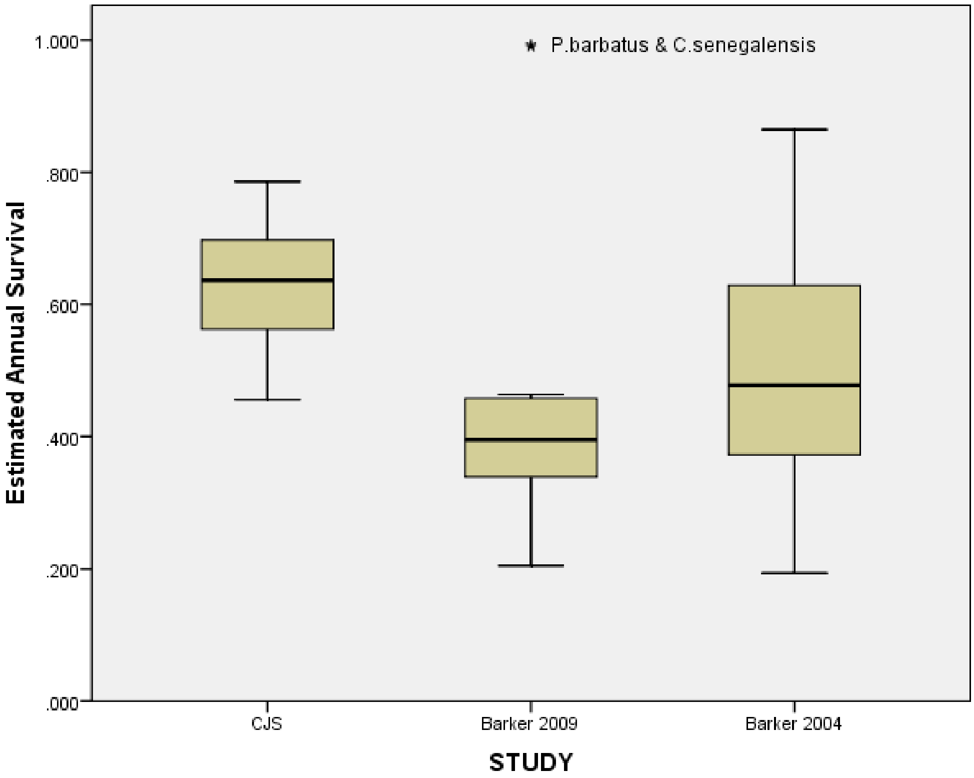
The CES method was adopted as a means of standardising the capture of individuals within the study area. The method allowed the identification of 14-day capture periods to minimise the impact of transients (through the avoidance of periods of peak migration) and limit the disruption caused by periods of unsuitable weather (heavy rain or strong winds). The guaranteeing of a run of 14 successive days without strong winds, harmattan or rainfall is difficult in most months and some degree of disruption was observed in many periods with a number of sessions (particularly those in April, May or September) being abandoned. This standardised catching effort was not repeated in the attempts to obtain resightings, which were made across the entire reserve. The regular operation of mist-nets at only one site, for specific periods of time and at particular times of the year, also enabled a standardisation and control of capture/recapture effort.

Figure 6. Comparison of annual survival estimates and precision for the 15 species assessed under both the CES/Barker and CJS methods. Solid lines indicate the overall means for the two methods and the dotted lines ±1 standard errors of these means.



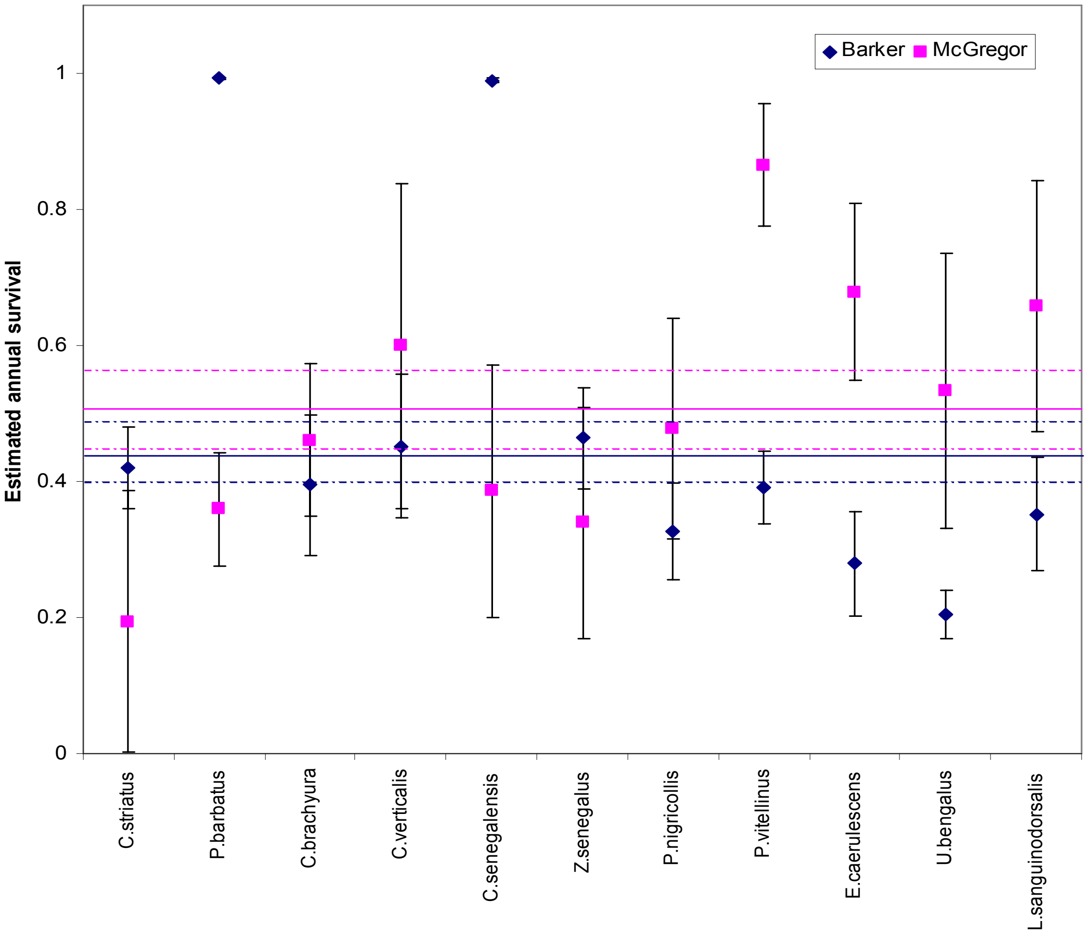
The CES method proved inefficient in dealing with transients, particularly of certain species (e.g. *E. franciscanus*), and the focussing on one particular location inevitably resulted in a reduced pool of individuals available for inclusion within the study than would be the case if more sites were operated. Similarly the restriction of the capture method to one area also resulted in it being more vulnerable to human-induced habitat change than would be the case if several mist-net sites had been used. Over the course of the study, grazing, cutting of firewood and the deliberate burning of the site resulted in sudden changes in the nature of the site (i.e. through the loss of standing vegetation) and change in species composition (e.g. the increase in *E. tahapisi* after periods of burning and the decline in catches of *Sporopipes frontalis*).

Figure 7. Ranges, means and standard errors for 11 species used in the three analyses of estimated annual survival. CJS and Barker 2009 use all data between 2001-2008 and Barker 2004 data from 2001-2004. Two outliers (*P.barbatus* and *C.senegalensis*) in the Barker 2009 data are noted separately.



This method was expected to produce good numbers of between-period recaptures due to the presence of individuals resident within, bordering or otherwise frequently using, the CES area. In reality, the lengthy duration of each CES period resulted in notable declines in catches across all CES periods. Numbers of recaptures were lower than expected suggesting that the use of two 14-day morning periods each year produces an insufficient likelihood of already marked individuals being present and available for capture. Although more recaptures are added with each period, there is a trade-off between this extra information gained and the increase in parameterisation.

Figure 8. Comparison of annual survival estimates and precision for the 11 species assessed under the CES/Barker method in this study and in 2004 (McGregor et al 2007). Solid lines indicate the overall means for the two methods and the dotted lines ±1 standard errors of these means.



Particular problems of colour-ringing and resightings

The incorporation of a colour-ringing protocol into the mark-recapture scheme was intended to increase the number of encounters of individuals that would otherwise only be recorded during the CES periods each year. This would also provide a means to counter trap shyness by increasing the potential for individuals to be encountered away from standardised netting locations. Although providing a potential for improving encounter rates there are a number of issues with colour-ringing. Firstly, the application of extra rings inevitably results in an increase in handling times and is likely to result in increased stress levels of the bird. All attempts were made to minimise this, however it is difficult to determine the potential impact of this extra handling on apparent survival. Secondly, there is an increased layer of potential errors when using colour-rings (see above).

Although not determined here, these errors may significantly affect parameter estimates. Thirdly, certain individuals will be more obvious in the environment either because of their method of foraging, display flights or their choice of territory (e.g. near to human habitation, along a regularly used path) thereby rendering them more likely to be resighted. Although the modelling approach will attempt to iron-out the impact of such individuals through the inclusion of differential resighting or recapture probabilities (which may be further diluted with the incorporation of time-dependence in the model), the small sample sizes obtained in this study will reduce the effectiveness of such ‘smoothing’ and lead to imprecise and inflated parameter estimates. Finally, the use of strictly determined capture periods (and the inclusion and analysis of only these data) resulted in the loss of much data from the thousands of other individuals from an increased range of species caught outside of these periods and at other locations around the reserve. Also, because many of these extraneous individuals were colour-ringed, significant time was wasted attempting to determine their colour combinations thereby reducing the available time and effort available for resighting CES individuals.

Resighting effort varied widely over the course of the study, being greatest during the early and later years. Standardisation of resighting effort and methodology was possible in the earliest years of the study because resightings were made by just one individual. The number of field visits, the areas sampled and the duration of each field visit could each be controlled and effort therefore spread evenly across the reserve. In contrast, resighting effort between 2004 and 2006 was more variable and performed on a more *ad hoc* basis by a variety of personnel. Although effort was expended attempting to obtain resightings it was frequently focussed in areas away from the CES. Many of the individuals observed had been ringed during periods outside of the CES and were therefore not available for inclusion within the original survival assessments. Inexperienced field staff often recorded incorrect colour combinations or colours that had not been used in the study. Control of effort and quality in resightings was therefore difficult during this period and may have had important effects on the effectiveness of the mark-resighting approach. The low overall resighting rate (despite increased effort in later years) appears to be the most significant factor in the failure of the data under the Barker model. Although large numbers of resightings or recaptures are of considerable use in the modelling process (Figure 5), it is apparent that greater success in modelling (apparent survival) rates can only be achieved with a concomitant increase in the number of individuals resighted or retrapped. Since data from these individuals forms the basis of the analyses, insufficient individual resightings (or recaptures) prevents the model from attaining either a suitable goodness of fit or from being able to generate parameter estimates (Figure 4). Many of the species under study here had very few individuals that were resighted (Table 3) preventing realistic analyses of the data. Similarly, although attempts were made to improve numbers of resightings through the addition of data from additional years, it is clear that the resultant increased parameterisation requires a proportional increase in numbers of individuals resighted (or retrapped).

Recommendations for future data collection methods and analysis to assess apparent survival

Despite the successful application of the CES approach (along with the Barker model) by McGregor (2005) numerous difficulties were encountered here both in terms of data generation, goodness of fit testing of models and parameter estimation. Although it would be possible to reorganise the CES protocol to ensure the inclusion of more resightings and recaptures, there is still little guarantee that the produced data would prove suitable for assessment using the Barker model. Instead a number of modifications to the protocol can be made which would allow incorporation of the previous long-running dataset with new data, as was performed here using the CJS/continual approach:

1. Adopt a programme that includes a standard number of ringing periods to be performed each year whilst accounting for the difficulties of catching during the wet season (five would allow catches in January, March, May, September and November). Each of these ‘mandatory’ periods should last 5-7 days and involve the use of a minimum number of nets (10). The use of two or three defined locations around the reserve (and three/two catches at each, each year) would reduce the effect of trap shyness and

should result in more individuals being incorporated into the study each year.

2. The entire reserve should be considered the ‘CES’ site rather than operating in only a small section. The impact of habitat change on catches will be lessened and a greater number and variety of species would be caught and available for inclusion in analyses. Also, given that many of the species from the original CES protocol were caught or resighted in areas away from the main CES area (especially *Ploceus* species), recapture probabilities should not be detrimentally affected for most species.
3. Supplementary periods can also be included but should conform to this protocol (in terms of period duration and number of nets) to allow ease of inclusion in survival analyses. All data generated from such periods (both new and retrapped individuals) would be available for inclusion in the models.
4. Where possible, supplementary periods should rotate through different sites around the reserve to make catch effort across the site as uniform as possible.
5. The adoption of more periods through the year would also provide greater scope for assessment of the breeding periods and productivity (as under the British CES scheme).
6. The benefits of continuing with a colour-ringing programme are debatable. By operating at more sites throughout the reserve the probability of resighting of individuals should increase (since colour-ringed birds will be distributed over a wider area) which may improve the ability of the Barker model to estimate survival. It is more likely however that this approach is best suited to single-species studies rather than the blanket-catching of a range of species as performed here.
7. Colour-ringing increases the parameterisation of the models making the survival estimation process progressively more data-hungry with each period. Unless a more rigid field protocol for obtaining resightings is introduced, this is unlikely to result in any noticeable benefits (and may even result in poor model fit, as found here).

8. Because of the difficulties in ensuring effort and quality in obtaining resightings it may be more efficient to abandon the use of a mark-resighting approach. By doing so, and removing or adapting the current standardised catching protocol, data from the large number of *ad hoc* ringing sessions or periods performed around the reserve could also be included for analysis of survival rates. At present there is a steady stream of visiting ringers through the reserve all of whom wish to ring. Similarly there is an ongoing programme of ringing training and a number of other projects in which birds are ringed. Ordinarily these data are excluded from the study as they will not have been obtained from the CES periods. This represents a considerable loss of information which, if included in the analysis, could result in dramatically increased sample sizes and potentially, much improved survival estimates.
9. The use of models based solely on recaptures is likely to prove the most efficient method of dealing with the data generated using both the current standardised capture protocol and that incorporating ringing sessions or periods performed outside of the CES. Acceptable goodness of fit of starting models and believable and reasonably precise parameter estimates were obtained under the CJS approach even with return rates (number of retrapped individuals/number of individuals ringed) as low as 0.06 (e.g. for *C. senegalensis*) and total number of retraps of less than 15 (e.g. *M.sulfureopectus*). Data requirements under this method are therefore much less demanding than similar Barker models. These models are also likely to be less parameterised than the Barker model yet sophisticated enough to allow for the inclusion of time-dependence and group/age effects.
10. The large number of capture occasions will lead to increasing parameterisation (depending upon model selection), however this need not prove a significant problem under the CJS approach (e.g. 53 parameters for *E.franciscanus* and acceptable goodness of fit in this study). Also, should sufficient numbers of supplementary periods be operated i.e. such that it forms a (near) continuous capture period with a mandatory period, then these can be considered as one for purposes of analysis.

Chapter 6: The relationships between moult, breeding and survival and their role in determining avian life histories

Summary

I investigated the relationships between empirically derived estimates of a variety of life history characteristics in order to assess their role in influencing avian life histories. Modelling of duration and timing of breeding period revealed that both factors were independent of all other measured characteristics except the time taken to attain full adult plumage. Timing and duration of moult were similarly unrelated to other life history traits except body mass. The lengthy moult and breeding periods for many species meant that overlap of these two activities was more frequent and extensive than in temperate species. Species breeding earlier in the year (the late dry season) had young that took longer to moult into full adult plumage. Juvenile survival was found to be similar to that of adults.

No significant relationships were identified between between any of the derived estimates for a variety of life history traits and adult survival other than clutch size. Both adult survival and clutch size covaried with body size. These findings are discussed with in the context of current life history theory regarding nest predation, extended parental care and seasonality.

Introduction

The basic concept of life history theory centres on the notion that demographic parameters show strong patterns of covariation across species (Skutch 1949; Lack 1954; Sæther 1987). Essentially, animals that maximise one aspect of their fitness reduce their ability to maximise other aspects, or put another way, allocation of resources to one activity results in fewer resources to allocate to another. This trade-off is especially apparent in the consideration of cost of reproduction, in which increased fecundity results in reduced adult survival (Stearns 1992). Nowhere is this more apparent than in the comparison of life history traits of tropical and temperate species. Tropical birds have generally been found to have smaller clutch sizes (Moreau 1944; Lack 1947; Murray 1985), lay more clutches per year (Ricklefs 1969a) and have higher adult survival (Skutch 1949; Woinarski 1985; Martin 1996; Blake & Loiselle 2008) than similar temperate species. Although these differences have been further elaborated upon in empirical studies and comparisons of various demographic parameters of species in these areas (Martin 1995; Sandercock *et al.* 2000; Peach *et al.* 2001; Bennett & Owens 2002), the driver behind this differential life history emphasis (i.e. to live longer or to produce more offspring each year) is still subject to debate.

A number of theories have been proposed to account for latitudinal variation in life history traits, from increased nest predation in tropical areas (Skutch 1949), food limitation (Lack 1948; Ashmole 1963; Martin 1987) and stable climates (Cody 1966; MacArthur 1972), however the extent of the effect of each of these on life histories to a large degree remains unclear. It is perhaps more likely that each of these theories plays some part in the variation, and as outlined by Martin (1996), high adult survival may then be facilitated by low seasonality and further bolstered by high nest predation or unpredictable food availability thereby leading to a reduced reproductive effort. What is clear is that ecological conditions will influence an organism's evolutionary response (Cole 1954; Murphy 1968) such that animals in unpredictable environments are likely to have rapid rates of reproduction to compensate for low adult survival (Roff 1992) and those in more stable and predictable environments have higher adult survival and a reduced need to invest in reproduction. These two situations represent the extremes of a continuum in life history trade-offs (i.e. the *r*- and *K*- selection of MacArthur & Wilson (1967)).

Although levels of investment in life history activities can be readily measured through direct and obvious factors (e.g. determination of clutch size and egg mass during reproduction), there are numerous other, less obvious, potential ways in which species can vary resource allocation. For example, delayed breeding or extension beyond normal bounds results in a cost that must be passed on to other activities, most often resulting in a more rapid moult in temperate species (Dhondt 1973; Jenni & Winkler 1994). This has further costs in the form of reduced time available for foraging, reduced feather quality, and reduced flight capability, all of which are likely to be further expressed as reduced annual survival or reduced ability to breed in the subsequent season (Svensson & Nilsson 1997; Hemborg *et al.* 2001). All such processes are therefore interconnected through time and, in the seasonal environments of temperate areas, the timing and duration of essential life history processes tends to be reasonably tightly scheduled and performed according to the availability of resources either to feed young or maintain condition (e.g. whilst moulting).

The timing of life history stages such as moult may be more flexible in tropical areas, even those that are more strongly seasonal. Hormonal variation according to seasonal changes in light levels (i.e. photostimulation and photorefractoriness) plays an important role in regulating the start and finish of reproduction in temperate species (Nicholls *et al.* 1988; Wingfield & Kenagy 1991). This ensures that essential activities such as breeding occur during the most likely period of food abundance and finish in time to allow for preparation and undertaking of other important activities such as moult (Farner *et al.* 1983). The extent of these hormonal processes in species at equatorial latitudes is still open to question, however there is evidence (Hau *et al.* 1998; Beebe *et al.* 2005) that tropical species are similarly able to respond to the slight seasonal variation in photoperiod in tropical areas and use this to time annual reproductive schedules (Dittami & Gwinner 1990; Stutchbury & Morton 2001). The levels of hormones that serve to mediate the incompatibility between moult and breeding in temperate birds (Hahn *et al.* 1992) might not be sufficient to inhibit such overlap in tropical birds (as found in Spotted Antbirds – *Hylophylax n. naevioides* in Panama (Wikelski *et al.* 1999)) and this, alongside the apparent lack of photorefractoriness in tropical species (Beebe *et al.* 2005) may allow flexible adjustment of the end of the breeding period to allow exploitation of environmental conditions. Also, constraints on moult both in terms of its energetic requirement and timing may be less severe than in temperate species and may allow either the overlap of moult or its delay until other activities are finished. This is particularly apparent when considering the generally longer moult durations of tropical species (Fogden 1972; Gwinner *et al.* 1983; McGregor *et al.* 2007a; Chapter 2) and the increased prevalence of overlap of breeding and moulting in these areas (Foster 1974a; 1975b Savalli 1993; Tidemann & Woinarski 1994; Chapter 3).

Overall then there are numerous possible interrelationships between life history parameters. Their assessment along with the determination of their comparative importance is essential if we are to further advance our understanding of their relative roles in governing the life histories of animals. Here, empirically derived estimates of a variety of life history parameters were used to assess their relationships and trade-offs in tropical West African savannah bird species. The relationships between breeding, moult, the immature phase and survival were then explored across species, specifically:

1. Breeding period duration and timing
2. Moult duration, timing and variability in timing
3. Moult breeding overlap
4. Immature phase duration
5. Adult and juvenile survival

The first objective was to test how important life history traits such as moult and breeding characteristics covary. Traits such as duration of breeding and duration of the immature phase may be generally, across species, positively correlated, as with K selected species, or negatively correlated because they are subject to trade-offs, or there may be no general pattern because some species show negative, and others positive, correlations. Reduced seasonality in tropical areas (Martin & Karr 1986) should mean that activities such as breeding and moult are less temporally constrained than for temperate species. The timing and duration of moult and breeding should therefore show considerable variation and be mutually independent. Reduced constraints on timing of these activities, particularly the need for moult to be performed within a strongly defined time period, should result in more opportunistic exploitation of breeding opportunities and interruption or slowing of the lengthy moults performed by tropical species. The overlap of moult with breeding should therefore be common.

The second objective was to test the general prediction of life history theory:

6. that investment in clutch size, duration of breeding, moult or the immature phase covaries with adult survival.

Life history theory predicts that those species investing more on breeding, moult and the immature phase, and which have smaller clutch sizes, will be allocating fewer resources per unit time and therefore will have higher adult survival. Life history components are also constrained by body size (see Bennett & Owens 2002). Most life history processes have been shown to take proportionally more energy and time to complete in larger species (Walsberg 1983; Kozlowski & Weiner 1997). Positive correlations between body mass and traits such as survival (Sæther 1989; Dobson 1990), moult duration (Ginn & Melville 1983) and egg mass (O'Connor 1984) have all been identified in temperate species but few of such relationships have been thoroughly investigated in the tropics. Body mass could therefore operate as an important and confounding life history variable and was therefore compared directly with adult survival here, to assess this relationship. Analyses were, however, constrained by sample size (n = number of species) with only a small number of species with data available for all life history variables, so limiting the scope for powerful multivariate analyses.

Methods

Data collection

Field Methods

Birds were captured at the Amurum Community Forest Reserve using mist nets following the capture protocols outlined in Chapter 2. All birds were aged, sexed and ringed with unique metal rings.

Data analysis

Determination of life-history characteristics

Survival

Rates of both annual adult survival and first-year survival of juveniles were determined through analysis of recapture data using program MARK (White & Burnham 1999) – see Chapter 4. Apparent annual survival rates were determined for adults of 40 species and for first-years of 13 of these species.

Breeding characteristics

The timing of occurrence of brood patches in captured individuals was used to identify the breeding periods of 42 species – see Chapter 3. All individuals of each species sufficiently advanced in brood patch development were used to identify the boundaries of the start and end of the breeding season. Whilst this may overestimate durations for those few species thought to have two main breeding periods each year (e.g. *Camaroptera brachyura* (Elgood *et al.* 1994)) or make several consecutive attempts at regular intervals (e.g *Chalcomitra senegalensis* (Elgood *et al.* 1994)), the aim here was merely to provide a representative measure of the duration of the breeding season and of the mean date and season in which the species was most likely to be recorded to be breeding.

Where insufficient data were available to determine mean date and duration of breeding from brood patches, the timing of capture of juveniles was used. Comparison of mean dates and durations of breeding for species having both brood patch and juvenile capture data revealed that, generally, estimates derived from juvenile captures were around 30 days later than those from brood patch data. For comparisons of life-history characteristics the data derived from brood patch assessments was used preferentially, using the estimates based on juvenile captures (minus 30 days) only for those species where brood patch data were unavailable. All data derived from these estimates were compared with data from other sources (Elgood *et al.* 1994) to ensure that they were close to, or within, expected periods.

The mean date of breeding was also used to identify the primary breeding season, i.e. the season containing the highest proportion of breeding birds for each species (Table 4, Chapter 3). Seasons were identified as: Late dry (February–April); Early rains (May-July); Late rains (August-October); and, Early dry (November-January).

Data on clutch size was obtained from Birds of Africa (Keith *et al.* 1992; Urban *et al.* 1997; Fry *et al.* 2000, 2004). Where multiple estimates were given those having the largest sample size, which were geographically closest to the study area (Jos), were used. Where no location was given, those estimates obtained for savannah habitats were used. Mean estimates were used in all cases, however where only a range was given then the mid-point was used. Where no information was given for a species (*Cisticola guinea*) then data for the most closely related species that occurred in similar habitats was used.

Moult characteristics

Only data from moulting birds were used to derive species-specific estimates of the timing and duration of the complete moult in adults – see Chapter 2. The proportion of primaries in moult was plotted against date such that lowest scores (i.e. those at the start of moult) were at the start of the plot thereby ensuring a progression of moult (scores) with time. Extreme outliers and those data potentially the result of errors were removed from the plot and the residuals for the new plot analysed for normality. In cases where such actions failed to resolve breaches of the assumption of normality, the data were further examined for outliers and, if no further logical or biologically reasonable reduction could be performed, the species was excluded from analysis (see Underhill & Zucchini 1988). The pooled data were further examined for annual variation which, if found, resulted in data being analysed separately by year. Mean start date was identified from the intercept of the regression line with a proportion in primary moult value of 0, and completion date derived from the addition of mean duration to this (Pimm 1976; Summers *et al.* 1983).

The timing and duration of moult were used in the same manner as the data for breeding in determination of primary moult season, i.e. the season containing the highest proportion of the moult duration with seasons identified as above.

Other characteristics

As well as the duration of moult in adults, the duration of time that newly fledged birds retained their juvenile plumage was also determined. Successive recaptures of individuals were used to identify the latest dates that each species was recorded as a juvenile or immature and the earliest dates that they were recorded to have attained full adult plumage. The means of these dates was then subtracted from the mean date of breeding to identify duration of the immature phase. Such an approach worked well where periods between successive recaptures were short and the individual had not changed age category (i.e. 3-3, 5-5). Where successive captures occurred after a period of more than 4 months and the individual had changed from an immature to an adult plumage, only the date of the last known capture as an immature was used in determining period of immature plumage phase. Individuals recaptured as adults within 4 months of having been recorded with an immature plumage were included within the dataset. Here the point of change to adult plumage was considered to be the mid-point between the two captures. Overall the derived estimates of this period are believed to be reasonably representative of this immature phase, e.g. the estimate of 142 days duration in *Spermestes cucullata* is similar to that obtained for captive and free-living individuals of this species (ca. 160 days - in Restall (1996))

The mean mass of adults (regardless of sex) of all species for which other life-history characteristics were available was determined in order to give a measure of the specific variation in size.

Table 1. Summary of variables used in modelling relationships between life history traits in West African birds.

Variable	Summary	Total number of species	Number species in overall model
ADSURVIVE	Annual adult survival	40	19
JUVSURVIVE1	First year survival	13	0
BREEDTIME	Mean date of breeding – derived from mean date of brood patch occurrence or mean date of juvenile capture – 30 days	42	19
BRDDURN	Duration of breeding period – derived from 95% confidence intervals for BP period (or for juv capture dates – 30 days)	42	19
BRDSEASON4	Main breeding season – equates to: 1. Feb-Apr (Late dry) 2. May-Jul (Early rains) 3. Aug-Oct (Late rains) 4. Nov-Jan (Early dry)	42	19
MLTSTART	Start date of moult measured as day of the year	28	19
MTIMEVAR	Annual variation in timing of moult: 1/0	28	19
MLTDURN	Duration of moult in days	28	19
MDURNVAR	Annual variation in moult duration: 1/0	28	19
MLTSEASON4	Main moult season – equates to: 1. Feb-Apr (Late dry) 2. May-Jul (Early rains) 3. Aug-Oct (Late rains) 4. Nov-Jan (Early dry)	28	19
IMMPHASE	Time taken, in days, between hatching and attaining complete adult plumage	36	19
WEIGHT	Mean mass of the species regardless of sex	54	19

Modelling of relationships between life-history characteristics

The relationships between each of the various measured life history characteristics (Table 1) were tested using general linear models. Only those variables shown to be reasonably independent during analysis (see results) were used to test the overall model and the influence of various life-history characteristics on annual adult survival. Only those species for which data for 11 variables (i.e. all of those listed in Table 1 except first-year survival) were available were used in the initial tests of the overall model. All species that had a measure of the relevant characteristics were used for all other tests of relationships. Values for each life-history characteristic for each species are listed in Table 2.

Table 2. Specific values for each life-history characteristic used in general linear models assessing relationships. In variables identifying seasons: 1 – Late dry; 2 – Early rains; 3 - Late rains; 4 – Early dry.

Species	Adult Survival	1st Year Survival	Mean Breeding Date	Breeding Duration	Breeding Season	Moult Start Date MSD	Annual variation MSD	Moult Duration (MD)	Annual variation in MD	Moult Season	Immature. Phase	Mean Mass
Streptopelia hypopyrrha			54	86	1	63	0	84	1	1	372	158.5
Streptopelia senegalensis						45	1	138	0	1		93.5
Turtur abyssinucus	0.606					24	1	108	0	4	135	61.2
Pogoniulus chrysoconus	0.416		212	323	2	338	1	118	0	4	247	10.8
Lybius vieilloti	0.599		250	112	2							37
Colius striatus	0.619		236	155	3						47	52.1
Phoeniculus purpureus			249		3						134	46.1
Merops bullocki			78	97	1						375	23.9
Indicator indicator			249	291	3						134	46.1
Pycnonotus barbatus	0.668		213	314	2	117	0	146	0	1	204	38
Chlorocichla flavicollis	0.844											50.5
Camaroptera brachyura	0.636		284	54	3	268	1	100	1	3	179	10.9
Cisticola aberrans	0.650		273	42	3						41	13.4
Cisticola cantans	0.806		282	167	3	39	1	150	0	1	184	12
Cisticola guinea	0.510											9.4
Heliolais erythropterus			264	45	3						150	13
Prinia subflava						96	1	28	0	1		8.4
Eremomela pusilla	0.586					222	0	141	0	3		7.2
Sylvietta brachyura	0.875		284	44	3							8.5
Melocichla mentalis	0.948											33.5
Cossypha niveicapilla	0.779		253	80	3						174	36.9
Cercomela familiaris	0.539		216	212	2						187	17.3
Myrmecocichla cinnamomeiventris	0.657											40.1
Turdus pelios	0.799	0.261	244	157	3	248	1	58	0	3	190	65.1
Platysteira cyanea	0.700		327	70	4						100	13.8
Zosterops senegalensis	0.527		346	209	3	258	1	130	0	3	33	9.6
Cyanomitra verticalis	0.654	0.327	267	114	3	277	1	188	0	3	166	12.3
Chalcomitra senegalensis	0.769	0.789	252	255	3	245	1	193	1	3	160	10.4
Cinnyris venustus	0.534	0.002	161	342	2	24	0	263	0	4	299	6.2
Malaconotus sulfureopectus	0.923		202	267	2						260	28.5
Laniarius barbarus			294	12	4							48.8
Tchagra senegalus	0.660											51.1
Emberiza tahapisi	0.491		309	62	3	64	1	51	0	1	154	13.5
Petronia dentata			41	175	4							17.9
Ploceus luteolus	0.487		282	71	3						1	14.6
Ploceus vitellinus	0.726	0.876	290	42	3	291	1	124	1	3	72	20.4
Ploceus heuglini			358	203	4						48	23.6
Ploceus cucullatus	0.694	0.844	292	49	3	261	1	155	1	3	248	36.6
Ploceus nigricollis	0.786	0.186	277	200	3	289	1	39	0	3	150	26.2
Sporopipes frontalis	0.592											16.8
Euplectes hordeaceus	0.786		301	22	3						16	19.9
Euplectes franciscanus	0.720	0.763	303	76	3	296	1	73	1	3	32	15.2
Euplectes macrourus			287	25	3							21.3
Pytlia phoenicoptera			351	76	4							14.2
Estrilda caerulescens	0.566	0.581	292	139	3	283	1	149	0	3	123	9.4
Estrilda melpoda	0.571					235	0	198	0	3		7.4
Estrilda troglodytes			302	23	3	318	1	219	0	4	130	7.6
Uraeginthus bengalus	0.456	0.628	297	200	3	326	0	161	0	4	92	10.1
Ortygospiza atricollis			316	152	3	49	0	151	0	1	152	10.6
Lagonosticta rufopicta	0.564		301	135	3	348	1	117	1	4	124	9.4
Lagonosticta senegala	0.515	0.141	344	223	4						90	8.7
Lagonosticta sanguinodorsalis	0.559	0.547	320	225	4	384	1	80	1	4	98	10.5
Lagonosticta rara	0.528					24	1	90	0	4		9.8
Spermestes cucullata	0.269	0.093	299	40	3	89	1	240	1	1	142	8.9
Vidua chalybeata			289		4							12.1

All statistical procedures were performed using SPSS 17.0 (*www.spss.com*). Dependent variables were assessed for normality using Kolmogorov-Smirnov tests and for homogeneity between main effects using Levene's test for equality of error variances. Where necessary, variables were transformed using natural logarithms to achieve normality.

Results

1. Breeding period duration and timing

Duration of the breeding period was not dependent on any of the moult (timing, duration and variation), or breeding (timing) life history traits assessed here or the duration of the immature plumage phase (Table 3). There was a significant negative relationship with body mass, but this disappeared on removal of the outlier (*Streptopelia hypopyrrha*) (after removal, Body mass: $F = 1.0$, $p = 0.32$).

Table 3. Output of general linear model testing the relationship between duration of breeding period with moult characteristics, timing of breeding and body mass. Bold type indicates significant variables. Square brackets identify the factor value for which the parameter value is given.

Source	Parameter Estimate	S.E.	Sum of squares	df	F	Sig.
Corrected Model			104867.4	6	2.8	0.047
Intercept	748.705	254.18	61239.3	1	9.9	0.007
Timing of breeding	-1.505	0.76	24477.6	1	4.0	0.65
Variation in timing of start of moult [0]	80.399	49.13	16490.2	1	2.7	0.123
Timing of start of moult	-0.088	0.26	687.7	1	0.1	0.743
Moult duration	-0.694	0.45	14920.2	1	2.4	0.14
Length of immature phase	-0.081	0.44	212.5	1	<0.1	0.855
Body mass	**-3.371**	**0.99**	**71033.6**	**1**	**11.5**	**0.004**
Error			92376.5	15		
Total			711630	22		
Corrected Total			197243.8	21		

(Adjusted $R^2 = 0.344$, Levene's Test, $F_{1,20} = 3.6$, $p = 0.07$)

Duration of the breeding period was also not related to its scheduling during the year in the larger data set of 42 species available for univariate analysis ($F_{1,37} = 0.01$, $p = 0.94$; Levene's test, $F_{1,39} = 0.1$, $p = 0.83$). This was the case regardless of whether individuals were passerines or non-passerines ($F_{1,37} = 0.7$, $p = 0.43$) and there was no interaction between passerine status and timing of breeding ($F_{1,37}$ = 1.1, p = 0.31). Whilst there was no difference between the duration of breeding season for those species nesting in wet or dry seasons (*ANOVA*, $F_{1,39}$ = 0.2, p = 0.67; Levene's test, $F_{1,39}$ = 0.3, p = 0.6)), dividing this further into early- and late- dry and rainy seasons results in a significant relationship with season ($F_{3,37}$ = 7.4, p = 0.001; Levene's test, $F_{3,37}$ = 0.044). Mean duration of breeding season was longer for those species nesting predominantly in the early rainy season (May - July, mean ± se = 261 ± 35.5 days) than for any other season (mean ± se: early dry 126 ± 31.9 days; late dry 92 ± 5.5 days; late rains 102 ± 13.8 days). Significant differences in duration were identified between breeders in the late dry and early rainy seasons (Tamhane's T2, mean difference = 170.2 ± 35.94 days, p = 0.027) and the early and late rainy seasons (Tamhane's T2, mean diff = 159.3 ± 38.11 days, p = 0.028).

2. Moult duration, timing and variability in timing

Duration of moult was independent of all other moult characteristics and breeding variables (Table 4). Moult duration was, however, significantly negatively related to body mass with larger birds moulting more rapidly than smaller species (Figure 1). This relationship was still present after the exclusion of the two data points for species with largest body mass (*Streptopelia senegalensis*, mean body mass - 93.5g, and *S.hypopyrrha*, mean body mass - 158.5g) ($F_{1,14}$ = 6.7, p = 0.02).

Duration of the complete moult in adults was not influenced either by the season in which the species breeds, the season that it moults or in the interaction of these two factors (Table 5). Removal of the interaction from the model in Table 5 does not affect the results in any significant way. Furthermore, moult duration did not vary significantly between species that showed annual variation in moult timing and those that moulted around the same period each year.

Table 4. Output of general linear model testing the relationship between moult duration and various characteristics of moult and breeding. Bold type indicates significant variables. Square brackets indicate the factor for which the parameter estimate and standard error is given.

Source	**Parameter Estimate**	**S.E.**	**Sum of squares**	**df**	**F**	**Sig.**
Corrected Model			36909.3	6	2.4	0.084
Intercept	372.211	199.11	10704.5	1	4.1	0.061
Timing of breeding	-0.668	0.498	4708.2	1	1.8	0.2
Variation in timing of start of moult [0]	48.681	34.15	5317.4	1	2	0.174
Timing of start of moult	-0.008	0.11	12.5	1	<0.1	0.946
Breeding duration	-0.257	0.15	7253	1	2.3	0.117
Length of immature phase	0.136	0.28	596.7	1	0.2	0.64
Body mass	**-2.108**	**0.63**	**28935.3**	**1**	**11.1**	**0.005**
Error			39241.3	15		
Total			482247	22		
Corrected Total			76150.6	21		

(Adjusted R^2 = 0.279, Levene's Test, $F_{1,20}$ = 6.8, p = 0.017)

Figure 1. Relationship between mean body mass and duration of time to undertake a complete moult. (Linear regression line fitted for illustrative purposes only).

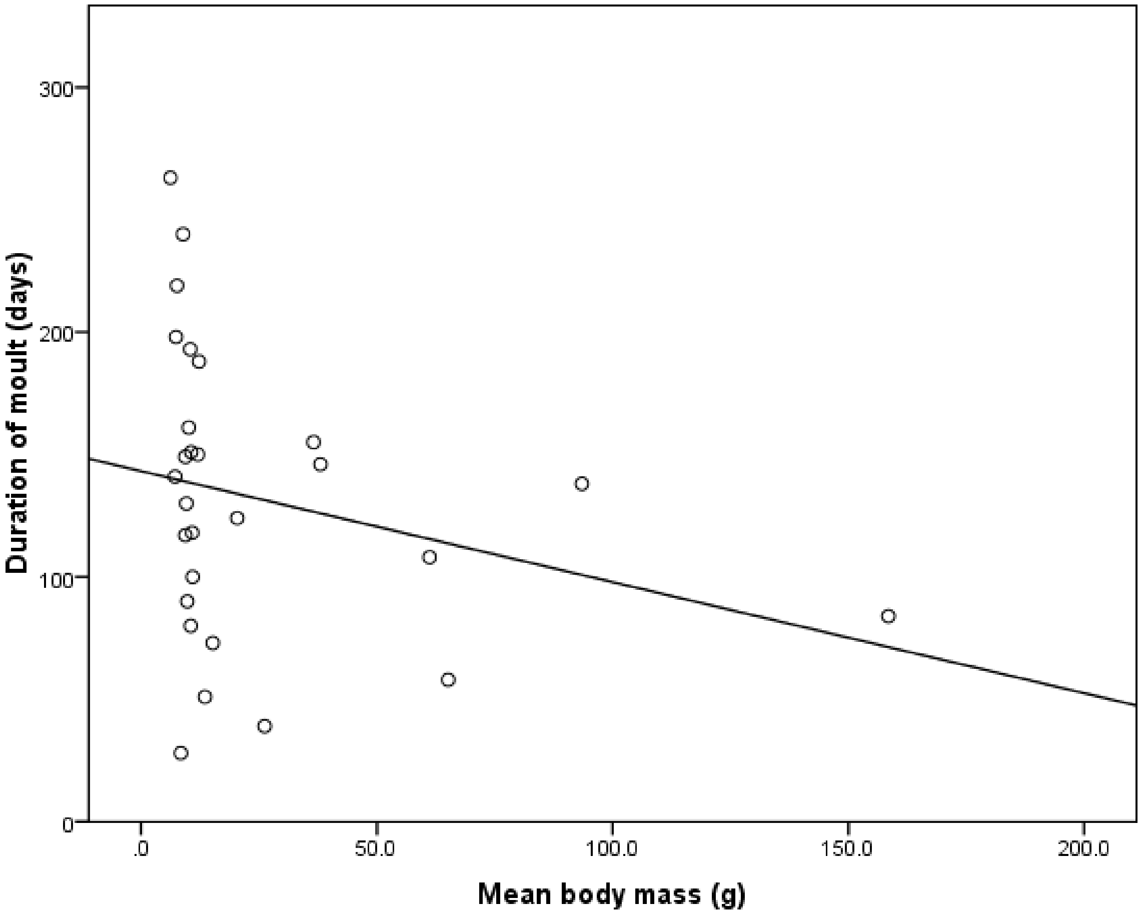


Table 5. Output of general linear model testing the relationship between duration of moult, seasonality and annual variability. Square brackets identify (combination of) factors for which parameter estimates and standard errors are given.

Source	**Parameter Estimate**	**S.E.**	**Sum of squares**	**df**	**F**	**Sig.**
Corrected Model			28006.8	8	0.9	0.514
Intercept	97.69	62.03	47743.6	1	12.9	0.003
Season of breeding			7808.8	3	0.7	0.567
[Season 1]	229	200.29				
[Season 2]	89.48	77.72				
[Season 3]	71.43	71.79				
Season of moulting			303	2	<0.1	0.96
[Season 1]	-10.99	46.69				
[Season 3]	-11.81	44.9				
Variation in timing of start of moult [0]	35.3	43.97	2387	1	0.9	0.437
Body Mass	-1.69	1.15	8012.5	1	2.2	0.165
Breeding season * Moulting season [2*1]	-1.47	96.91	0.8	1	<0.1	0.988
Error			48143.8	13		
Total			482247	22		
Corrected Total			76150.6	21		

(Adjusted R^2 = -0.021, Levene's Test, $F_{9,12}$ = 0.9, p = 0.56)

There was no evidence to suggest that timing of moult was dependent upon breeding duration or timing, or duration of the immature phase (Table 6).

Table 6. Output of general linear model testing the relationship between timing of moult and breeding characteristics. Square brackets identify factors for which parameter estimates and standard errors are given.

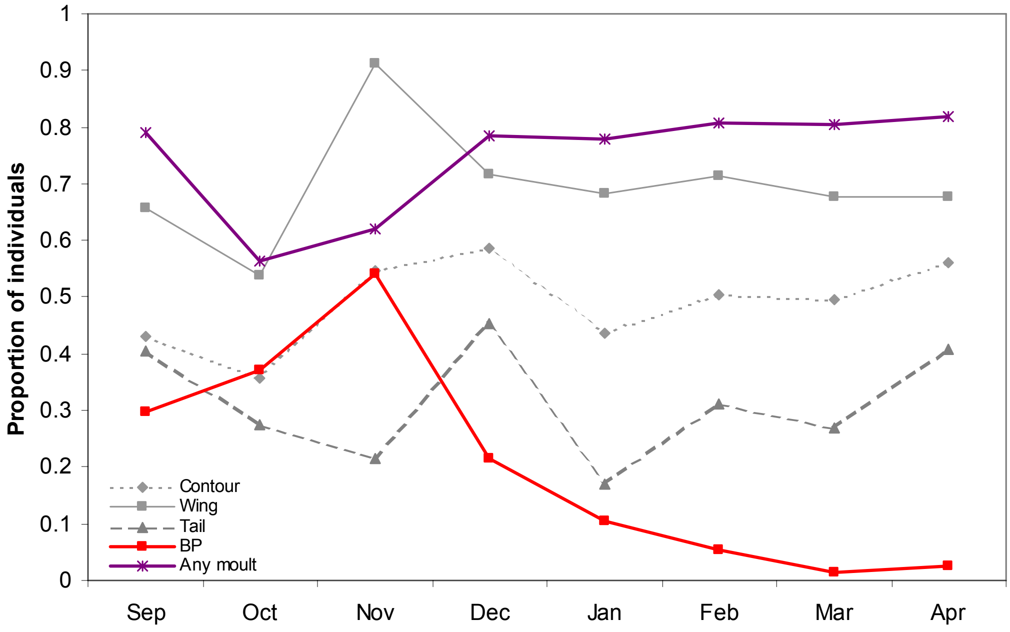
Source	**Parameter Estimate**	**S.E.**	**Sum of squares**	**df**	**F**	**Sig.**
Corrected Model			102995.6	7	1.1	0.424
Intercept	418.03	569.99	14385.1	1	1.1	0.321
Season of breeding			53846.1	3	1.3	0.307
[Season 1]	-84.76	409.41				
[Season 2]	164.86	197.51				
[Season 3]	208.02	134.09				
Timing of breeding	-0.93	1.49	5349.8	1	0.4	0.541
Duration of breeding	-0.09	0.43	579.1	1	<0.1	0.839
Duration of immature phase	-0.91	0.64	27657.6	1	2.0	0.176
Body mass	0.79	1.98	2136.2	1	0.2	0.698
Error			190410.4	14		
Total			1217956	22		
Corrected Total			293406	21		

(Adjusted R^2 = 0.027; Levene's Test, $F_{3,18}$ = 2.6, p = 0.08)

3. Moult breeding overlap

3491 records of 2983 individuals of 96 species belonging to 22 passerine families were available to assess the prevalence of moult-breeding overlap in passerines of West African savannahs. Active brood patches were recorded in 287 (17%) of 1674 individuals throughout the course of the year with a peak occurring during the late rains and early dry season (i.e. between September and December (Figure 2 and Table 7). Signs of reproductive activity were scarce in captured birds from February through until April.

Figure 2. Monthly frequencies of moult (of wing, contour (head and body), tail feathers and across all tracts) and brood patch (bp) presence in passerines of West African savannahs.



A high proportion (72%, *n* = 2514) of captured individuals were engaged in some form of moult (i.e. in either the wing feathers, tail or in the tracts of the head or body) and 21% of these (*n* = 524) were actively moulting in every major tract. Overall, the level of moult (of any tracts) showed an inverse of the pattern of brood patch occurrence. Moult of the main wing flight feathers (i.e. primaries and secondaries) was identified in 67% (*n* = 2999) of birds with a peak of occurrence during the period of peak reproductive activity (Figure 2). The proportion of individuals moulting these feathers remained high

(>50%) through every month suggesting a high incidence of overlap with breeding. Tail feather moult peaked in December, the month immediately following peak occurrence of breeding and moulting of wing flight feathers. In contrast, moult of contour feathers (reported from 48% of captured individuals) was reasonably constant throughout the year.

Table 7. Number of individuals of 32 West African bird species identified as having brood patches whilst also moulting. 'Contour' denotes active moult in head or body feathers; 'Flight' denotes moult in wing and tail feathers; *n* represents total number of individuals with brood patches assessed for moulting status. Guild represents predominant food only and granivore is also used to identify species feeding on plant parts other than seed. Several species here are known to be more generalist (e.g. weaver spp.) but here are recorded under the predominant foodstuff taken during the study period.

			Moult		
Common Name	Species	Guild	Contour	Flight	n
Common Bulbul	*Pycnonotus barbatus*	Frugivore	1	1	4
Grey-backed Camaroptera	*Camaroptera brachyura*	Insectivore	4	5	6
Rock-loving Cisticola	*Cisticola aberrans*	Insectivore	2	2	2
Singing Cisticola	*Cisticola cantans*	Insectivore	2	2	4
Moustached Grass Warbler	*Melocichla mentalis*	Insectivore	3	3	4
Red-winged Warbler	*Heliolais erythropterus*	Insectivore	1	1	2
Senegal Eremomela	*Eremomela pusilla*	Insectivore	3	2	3
African Thrush	*Turdus pelios*	Insectivore	1	1	1
African Yellow White-eye	*Zosterops senegalensis*	Frugivore	5	8	8
Yellow Penduline Tit	*Anthoscopus parvulus*	Insectivore	1	1	1
Variable Sunbird	*Cinnyris venustus*	Insectivore	2	0	3
Beautiful Sunbird	*Cinnyris pulchellus*	Insectivore	1	0	1
Yellow-crowned Gonolek	*Laniarius barbarus*	Insectivore	1	2	2
Black-crowned Tchagra	*Tchagra senegala*	Insectivore	2	2	2
Violet-backed Starling	*Cinnyricinclus leucogaster*	Frugivore	0	1	1
Cinnamon-breasted Bunting	*Emberiza tahapisi*	Granivore	1	1	5
Bush Petronia	*Petronia dentate*	Granivore	0	0	4
Vitelline Masked Weaver	*Ploceus vitellinus*	Granivore	2	3	7
Village Weaver	*Ploceus cucullatus*	Granivore	7	7	9
Black-necked Weaver	*Ploceus nigricollis*	Granivore	1	1	1
Northern Red Bishop	*Euplectes franciscanus*	Granivore	33	36	98
Yellow-shouldered Widow	*Euplectes macrourus*	Granivore	3	2	7
Red-winged Pytilia	*Pytilia phoenicoptera*	Granivore	0	3	3
Orange-cheeked Waxbill	*Estrilda melpoda*	Granivore	1	1	1
Black-rumped Waxbill	*Estrilda troglodytes*	Granivore	2	2	3
Lavender Waxbill	*Estrilda caerulescens*	Granivore	3	7	7
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	Granivore	2	3	16
African Quailfinch	*Ortygospiza atricollis*	Granivore	0	3	5
Bar-breasted Firefinch	*Lagonosticta rufopicta*	Granivore	3	0	5
Red-billed Firefinch	*Lagonosticta senegala*	Granivore	6	10	28
Rock Firefinch	*Lagonosticta sanguinodorsalis*	Granivore	4	10	11
Bronze Mannikin	*Spermestes cucullatus*	Granivore	4	10	10

The occurrence of overlap between moulting and breeding was high in the sample with 62% of individuals with brood patches also showing active moult in at least one feather tract. More individuals (n = 133, 49%) overlapped breeding with the replacement of feathers that were the most energetically costly to grow (i.e. the primaries and secondaries) than with the smaller contour feathers (38%, n = 138). The rectrices were the least likely feather tract to be replaced during breeding (20%, n = 55). 32 species were recorded moulting at the same time as having brood patches (Table 7), more than half of which (53%) were granivores. Overall however, there was no significant difference in proportions of species from each guild (granivores, insectivores and frugivores) that overlapped these activities ($X^2_2 = 1.4$, $p = 0.5$).

4. Immature phase duration

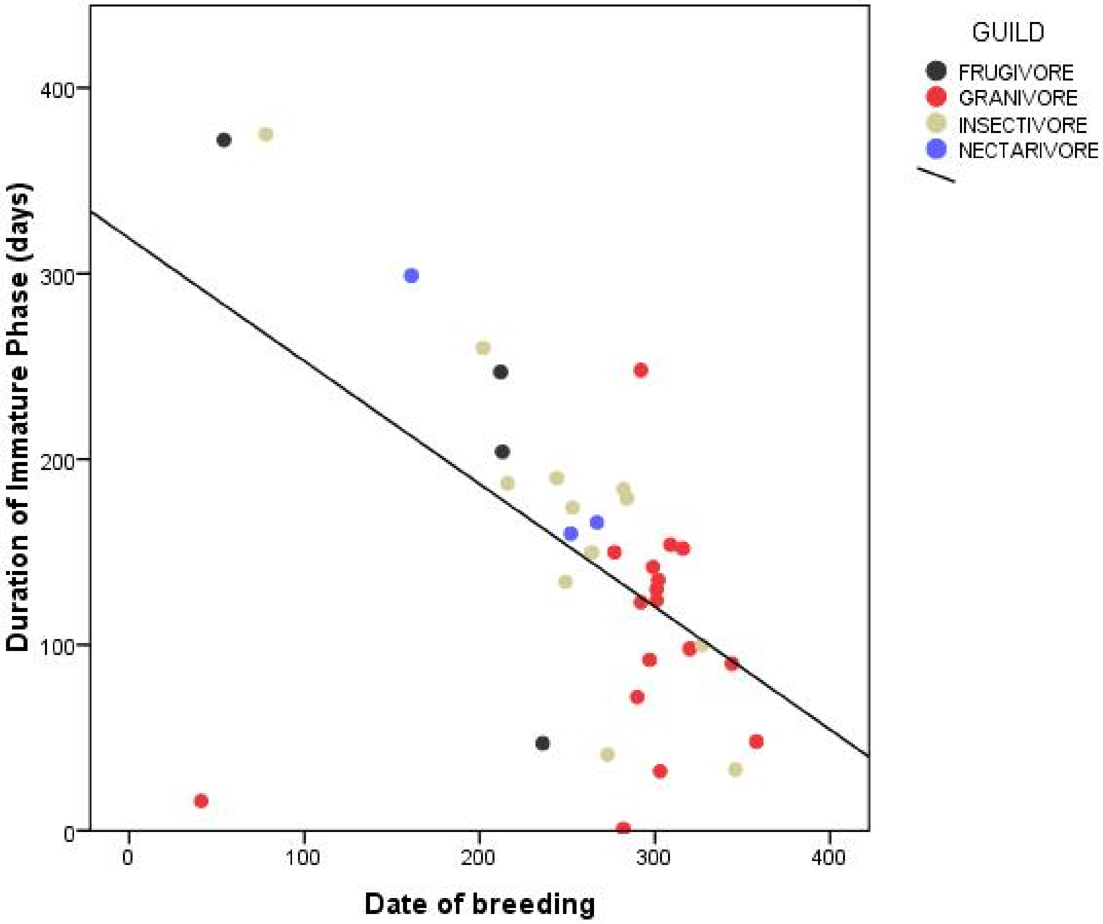
On average, birds in this study attained full adult plumage around five months after hatching (mean = 147 days, n = 36, 95% CI = 117 – 178 days). Duration of this immature phase was independent of any other moult characteristics and body mass, but did show a significant correlation with timing of breeding (Table 8). Therefore, species breeding later in the year (in the late rains and early dry seasons) moulted into full adult plumage more quickly after fledging than did species breeding earlier in the year (i.e. in the late dry season and early rains)(Figure 3). This relationship was apparent for all guilds (Figure 3) even though the duration of immature phase varied significantly between them (*ANOVA*, $F_{3,35} = 3.1$, $p = 0.039$; Levene's test, $F_{3,32} = 0.83$, $p = 0.49$; all Tukey HSD tests $p > 0.05$).

Table 8. Output of general linear model testing the relationship between duration of immature plumage and various characteristics of moult and breeding. Bold type indicates significant factors. Square brackets identify factors for which parameter estimates and standard errors are given.

Source	Parameter Estimate	S.E.	Sum of squares	df	F	Sig.
Corrected Model			104006.7	6	8.2	<0.001
Intercept	504.03	150.84	22116.3	1	10.4	0.006
Timing of breeding	**-1.17**	**0.37**	**21974.8**	**1**	**10.3**	**0.006**
Variation in start of moult [0]	-19.95	32.38	806.6	1	0.4	0.55
Timing of start of moult	-0.12	0.09	3542.7	1	1.7	0.22
Duration of breeding	-0.06	0.15	293.7	1	0.1	0.72
Duration of moult	0.11	0.23	484.5	1	0.2	0.64
Body Mass	-0.16	0.75	98.5	1	<0.1	0.83
Error			31860.3	15		
Total			710646	22		
Corrected Total			135867.1	21		

(Adjusted $R^2 = 0.672$, Levene's Test, $F_{1,20} = 1.3$, $p = 0.27$)

Figure 3. Relationship between length of time taken to attain full adult plumage and time of breeding period (Adjusted $R^2 = 0.304$).



5. Adult and juvenile survival

Although mean annual survival in adults (0.62 ± 0.15 SD) was higher than that for juveniles (0.46 ± 0.31 SD), this was not significant ($t(11) = 2$, $p = 0.08$). There was no significant relationship between survival of first years and adults (Table 9).

Table 9. Output of general linear model testing the relationship between adult and juvenile survival.

Source	Paramete Estimate	S.E.	Sum of squares	df	F	Sig.
Corrected Model			0.1	1	2.1	0.176
Intercept	0.53	0.08	1.1	1	48.2	<0.001
First Year Survival	0.2	0.14	<0.1	1	2.1	0.176
Error			0.2	1		
Total			5.3	13		
Corrected Total			0.3	12		

(Adjusted $R^2 = 0.083$)

6. Adult survival and other life history traits

Using only the 19 species for which there were complete datasets (i.e. of the 11 life history variables measured empirically in this study), no significant relationships were identified between any of those variables identified above as being reasonably independent (duration of immature phase, breeding and moult) and annual adult survival, when controlling for body mass (Table 10).

Table 10. Output of general linear model testing the relationship between adult survival and other life history characteristics. Bold type denotes significant relationships.

Source	Parameter Estimate	S.E.	Sum of squares	df	F	Sig.
Corrected Model			0.20	5	3	0.05
Intercept	0.939	0.16	0.47	1	34.4	<0.001
Duration of immature phase	<0.001	0.001	0.02	1	1.2	0.285
Duration of breeding	<0.001	<0.001	<0.01	1	<0.1	0.861
Duration of moult	<0.001	0.001	<0.01	1	0.1	0.818
Clutch size	**-0.092**	**0.035**	**0.1**	**1**	**7**	**0.02**
Body Mass	0.003	0.002	0.03	1	2.3	0.156
Error			0.18	13		
Total			7.5	19		
Corrected Total			0.38	18		

(Adjusted R^2 = 0.359)

Because of the lack of any significant relationship between adult survival and any of the variables measured in this study, data for all species having adult survival estimates were used to investigate the possible relationship with other, published, estimates of clutch size. Clutch size was significantly negatively correlated with adult survival, controlling for body mass, across all species in this study (Table 11, Figure 4).

Table 11. Output of general linear model testing the relationship between clutch size and adult survival. Bold type denotes significant relationships.

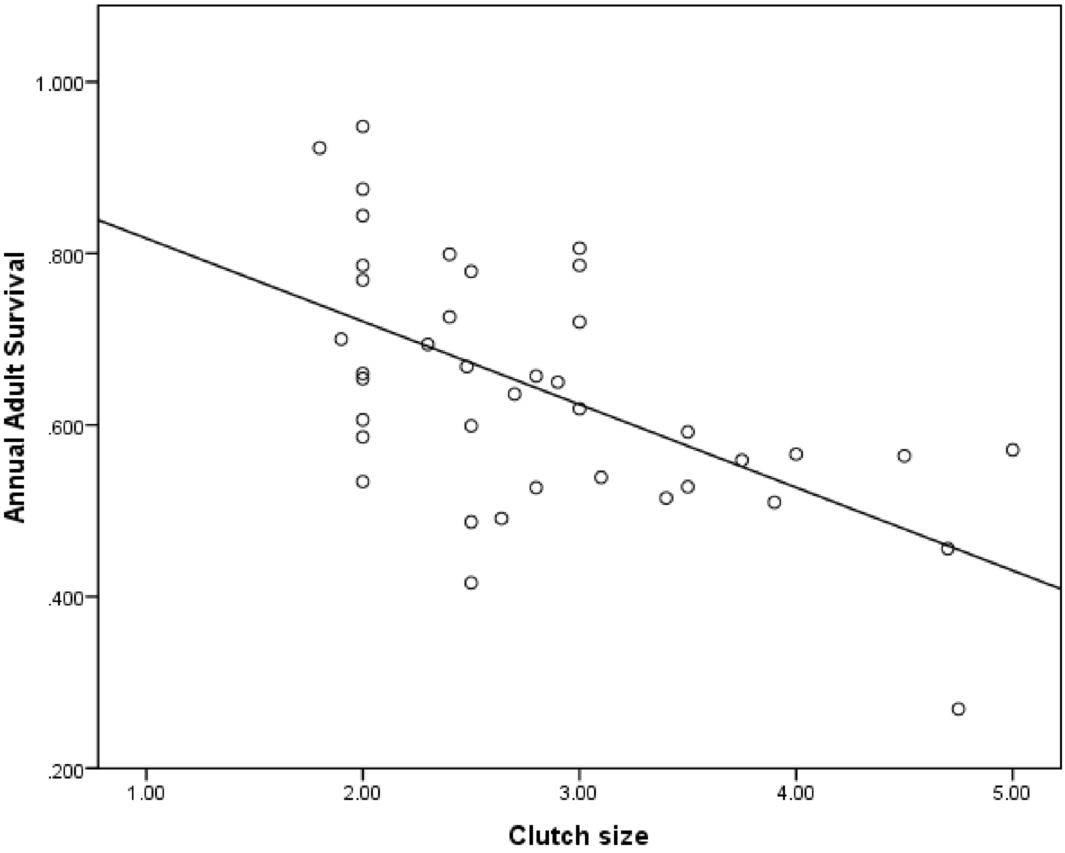
Source	Parameter Estimate	S.E.	Sum of squares	df	F	Sig.
Corrected Model			11.2	2	11.3	<0.001
Intercept	5.024	0.519	46.5	1	93.8	<0.001
Adult survival	**-3.059**	**0.859**	**6.3**	**1**	**12.7**	**0.001**
Body Mass	-0.011	0.007	1	1	2.1	0.159
Error			18.3	37		
Total			350	40		
Corrected Total			29.5	39		

(Adjusted R^2 = 0.346)

There was a negative relationship between clutch size and body size (body mass $F_{1,38}$ = 7.6, p = 0.009, B = -0.022 ± 0.008) and so a positive relationship between adult survival and body mass (body mass $F_{1,38}$ = 7.4, p = 0.010, B = 0.004 ± 0.001), when these variables were considered on their own.

Sample size was limited for analyses involving juvenile survival rate, however, with the caveat of limited power, no relationship between juvenile survival rate and clutch size ($F_{1,11}$ = 0.02, p = 0.89, Adj R^2 = -0.09) was identified. Similarly, although higher survival is generally linked to extended parental care there was no relationship in data from this study between juvenile survival and duration of immature phase ($F_{1,11}$ = 1.8, p = 0.21, B = -0.002 ± 0.001, Adj R^2 = 0.06).

Figure 4. Relationship of mean clutch size with annual adult survival in 40 tropical West African savannah passerines. (Adjusted R^2 = 0.346)



Discussion

The results of the study were, in summary:

- Breeding period duration and timing
  - Breeding duration and timing were independent of everything except duration of the immature phase and season
- Moult duration, timing and variability in timing
  - Moult duration and timing were independent of everything except body mass
- Moult breeding overlap
  - There was a high degree of overlap
- Immature phase duration
  - Species breeding earlier in the year had longer immature phase duration
- Adult and juvenile survival
  - Adults and juveniles have similar survival
- Adult survival and life history traits
  - No relationships found except between survival and clutch size; and both survival and clutch size covaried with body size

1. Breeding duration and timing

The lack of a fine scale linear relationship between the timing and duration of breeding in this study is most likely a result of the lack of severity in seasonal climate variation in the study area. Species in temperate areas are generally constrained to nest in the summer months because of a reliance on the seasonal abundance of food at this time for provisioning young etc (Cresswell & McCleery 2003). Often there are competitive advantages related to timing of breeding (e.g. early nesters obtaining the best territory (Perrins 1970; Verhulst *et al.* 1995; Nilsson & Svensson 1996)); however ultimately, food availability or other environmental conditions serve to constrain the scheduling of breeding and other activities (moult) which must be performed before the onset of unfavourable conditions (Orell & Ojanen 1980) or migration (Hemborg *et al.* 2001). In contrast, and because of their climatological characteristics, tropical environments tend to have much-reduced periods during which conditions are entirely unsuitable for breeding for all species (Martin & Karr 1986). Indeed some species may attempt to breed throughout the majority of the year (e.g. *Pycnonotus barbatus*).

Although wide variation in timing of breeding may prevent the determination of a fine-scale relationship between timing and duration of breeding (since species are breeding throughout the year) this study was able to identify whether the season in which the species breeds influences duration of breeding period. Mean duration of breeding season was much longer for those species nesting predominantly in the early rainy season. The reason for this is unclear but, as discussed in Chapter 3, methodological explanations are most likely. Firstly, fewer data were available to assess breeding periods during the early rainy season potentially affecting the accuracy of the estimates. Secondly, the level of reproductive synchrony is generally much lower in tropical bird species (Stutchbury & Morton 2001; Moore *et al.* 2005) and this inter-individual variation, along with annual variation, is likely to have resulted in much broader estimates of breeding duration. Lastly, a number of species are known to raise several consecutive broods in the same nest (Elgood *et al.* 1994; pers obs.) which, combined with asynchrony, will result in juveniles (and adults with brood patches) being present throughout much of the year and masking identification of the ‘true’ breeding season. On excluding these species, and the species having breeding durations longer than two seasons (since this duration implies no real seasonality), the relationship between season and duration was removed (ANOVA, $F_{3,36} = 2.1$, $p = 0.11$).

Although the above methodological explanations provide the most likely explanations for the finding of seasonal variation in duration of breeding season, these data may also reflect a true ecological difference. Reduced seasonality of climate will generally result in reduced constraints on timing of breeding since fluctuations in resources will be less predictable. Therefore, providing resources are available above some minimal threshold, then exploitation may be continuous. As a result, species occupying less seasonal tropical environments will tend to have long breeding seasons (Stutchbury & Morton 2008). The mean duration of breeding season here was only two months however, suggesting that the pattern of rainfall and drought (see Chapter 1) within the study area, and the consequent variation in environmental conditions, is sufficient to maintain reasonably well-defined and short breeding seasons. Longer durations in certain seasons might suggest increased nest predation since repeated nesting attempts will result in an increased range of dates of brood patch occurrence. Marchant (1960), Snow & Snow (1964) and Foster (1974) all report that the norm amongst tropical species was to renest after suffering nest predation. and that this cycle of breeding, nest predation and relaying may continue for prolonged periods. Alternatively, such predation may shorten the estimated length of breeding season if the individual does not attempt to renest, although this seems unlikely given the studies listed above. The stage of incubation or brooding at the point of predation will also influence the likelihood of, and timing between, relaying.

Nest predation studies in tropical environments have so far produced contrasting results when assessing seasonal variation in risk (e.g. Morton 1971; Gibbs 1991; Maina & Jackson 2003). The majority have been performed in forests where rates are believed to be lower than in more open, disturbed and fragmented habitats (Noske *et al.* 2008). Although few quantitative assessments have been performed, Brandt (2007) using the same study area as this study, found a high level of nest predation across the site with 50% of the nests of the small, ground-nesting, estrildid finch *Lagonosticta sanguinodorsalis* being predated. Unfortunately, because this species nests during the late rains and no assessments are available for species nesting in other seasons, it provides no further insight into the seasonal variation in nest predation levels throughout the year. Further investigation into the seasonal variation of risk of nest predation in more open tropical habitats is therefore necessary before its influence on timing of breeding by species, and the consequent life history impacts, can be properly assessed.

2. Moult duration, timing and variability in timing

No relationship between the timing and duration of moult could be detected for the species in this study although duration was related to body mass (see below). Seasonality generally governs the timing and duration of moult in temperate species through the general avoidance of those periods during which breeding occurs, and the need for feather replacement before periods of unfavourable conditions (Dhondt 1973; Kasparek 1980; Meijer 1991). Because there is a finite period of time during which breeding can occur in temperate zones (if breeding-moult overlaps are to be avoided), the available time left for moulting will usually determine the timing of moult. Timing of moult appears to be similarly linked to the timing and duration of breeding for a number of the synchronously breeding species in this study (e.g. *Euplectes franciscanus*) and occurs immediately after breeding. In general however, both the timing and duration of the two activities are unrelated (Table 6). In fact, a large majority of species were recorded to be moulting at the same time as breeding (see below). It therefore appears that the lack of strong seasonality reduces the level of constraint governing the periods that are (un)suitable for moulting allowing both its extension across seasons and co-occurrence with breeding. This may also explain why the season in which a species breeds or moults, or the annual variation in its timing, has limited effect on the variability in duration of these activities.

3. Moult breeding overlap

Data here supported the prediction that the overlap of moult with breeding is high in tropical species. Thirty-two species were recorded actively moulting whilst also incubating eggs in the study; the majority of these were moulting the most energetically demanding main flight feathers, rather than the smaller contour feathers. Although moult breeding overlap is commonly reported from tropical species (e.g. see Foster 1975b), few studies have reported such broad scale overlap across such a range of species or in such high proportions of the population as here. In other studies of tropical species rates of overlap are recorded at around 3-4% of the breeding population (Payne 1969; Ralph & Fancy 1996; Piratelli *et al.* 2000; Marini & Durães

2001) although Foster (1975) reported a 9% overlap. These studies were all performed in tropical forests or sub-tropical areas however and environmental differences between the two areas (such as restricted breeding periods, more pronounced seasonal food availability) may account for these observed differences. Overlap was also not restricted merely to adult males nearing the end of the brood-rearing schedule as in many temperate species (Hemborg *et al.* 1998). Instead individuals were recorded both starting and nearing completion of the main moult whilst undertaking breeding activities.

In most bird species, both in tropical and temperate areas, the complete moult of adults usually occurs shortly after breeding has finished (Payne 1969; Poulin *et al.* 1992; Jenni & Winkler 1994). In this study however, moult was recorded to occur throughout the year. And, although there was a decline in the proportion of individuals in moult during the peak period of breeding (the late rains), a large proportion of the individuals that were breeding were also moulting. This slight decrease in proportion moulting may represent the synchronous breeders in this study area. These species (e.g. *E. franciscanus*) exhibit a reduced tendency to overlap breeding and moult possibly because they must schedule activities more carefully and undertake a more rapid moult before moving away from the breeding area. Overall though, the proportion of the population in moult was high throughout the year (>70%) possibly reflecting the generally low synchrony in timing of essential activities in tropical birds (Scheuerlein & Gwinner 2002; Stutchbury & Morton 2008).

The reasons behind the high occurrence of moult breeding overlap may lie in the combined effect of reduced seasonality of tropical environments, competition and the increased risk of nest predation in these areas (Cody 1966; Ricklefs 1969b). In temperate species, timing of breeding and moult is generally constrained by food availability and periods of thermal stress such that both activities must occur during the summer months. In contrast, the reduced seasonality in tropical climates permits a longer breeding season (Ricklefs 1969b). Despite this, competition for food (Karr & Brawn 1990; Recher 1990; Poulin *et al.* 1992), low reproductive success (through high levels of nest predation) (Weidinger 2002; Scheuerlein & Gwinner 2006) and extended parental care (Russell *et al.* 2004a; Schaefer *et al.* 2004) may all combine to make the length of time required for the successful production of each offspring much greater than for temperate areas. It has therefore been argued that moult may be just as time constrained in tropical areas as temperate areas. For example, Foster (1974a) proposed that low reproductive success would make renesting throughout the course of a lengthy breeding season an efficient strategy since the probability of success will increase with increasing number of nesting attempts. She further suggested that repeated renesting may result in the individual exhausting the time available for moulting and that individuals in such a position should still moult as rapidly as resources would allow and schedule it to occur towards the end of the breeding period. However, since several of the species in this study had moult durations lasting in excess of 200 days (*Chalcomitra senegalensis*) it would appear more efficient to moult throughout the year, almost as a background activity, and interrupt (Snow & Snow 1964) or reduce the investment in this activity during periods of peak reproductive activity.

A number of physiological trade-offs will exist in adopting a strategy of performing moult and reproduction at the same time, not the least of which will be the conflict in demand for protein for the growth of feathers and production of eggs (Newton 1968; Lawrence & Schreiber 1974; Nilsson & Svensson 1996; Hemborg & Lundberg 1998). The result of this trade off may be that moult takes much longer to complete (Fogden 1972; Gwinner *et al.* 1983; Beebe *et al.* 2005) and that clutch sizes are smaller to allow both the performance of both activities in tandem and repeated renesting. Such a strategy may also account for the increased clutch sizes in those species that breed cooperatively (in this study, *Spermestes cucullata*), since the energetic costs will be shared amongst helpers. Similarly, those species suffering reduced nest predation or having strategies that spread the risk of such predation (i.e. polygynous) may have a reduced need to renest or are able to better schedule the end of breeding activities. In these species moult can be scheduled so that it has minimal impact on the resources necessary for breeding and occur immediately after breeding. These species are therefore likely to be typified by synchronous breeding and moult (e.g. *E. franciscanus*).

The increased incidence of overlap between breeding and moult could therefore be viewed as an adaptive strategy to cope with increased levels of nest predation. Further assessment and evaluation of this hypothesis could be achieved through comparative studies investigating the rate of renesting and the levels of nest predation between species that routinely overlap these two activities and those that do not.

4. Immature phase duration

The length of time taken to moult into complete adult plumage after fledging was shorter in those species breeding later in the year (i.e. in the months during the rains). Broadly speaking, this suggests that some factor (environmental, physiological or behavioural) influences the timing or rate of the complete post-juvenile moult such that it takes longer to reach full adult plumage for species whose young hatch during dry seasons (between December and April) than for those nesting during the rains. This relationship was apparent for all guilds (Figure 3) even though the duration of immature phase varied significantly between them. This suggests that, unless the availability or metabolism of some component for synthesis of the amino acids used in moult is seasonally restricted, diet is not driving this relationship. This is especially apparent when considering that the complete moult in adults generally occurs (at least in part) during the same period as the post juvenile moult yet its duration was not affected by seasonality (Table 5) and nor was it correlated with the duration of the immature phase ($r = 0.14$, $p = 0.54$, $n = 22$). This suggests that, unless the diet is markedly different for adults and young, some factor other than food or water availability is the cause of this relationship.

Prolonged breeding seasons (measured here as increased breeding duration) may reflect reduced nest success and increased re-nesting, possibly as a result of the increased level of nest predation thought to occur in tropical areas (Slagsvold 1982; Martin 1995). Increased nest predation has been linked to reduced nest-attentiveness (Skutch 1949; Fogden 1972) that may in turn lead to lengthened incubation and fledging periods (Lack 1968; Ricklefs 1968; Yom-Tov 1987). However, for many species assessed here (Chapter 3) these periods were quite uniform (see also Geffen & Yom-Tov 1999). It may be therefore, that juveniles of species suffering high levels of nest predation (and are consequently less attentive at nests) fledge at roughly the same age as those of other species but do so with a reduced body condition. Lack of sufficient physiological resources may therefore delay or slow moulting before the individual has attained suitable body condition. This may be further influenced by the colour of the adult plumage into which the individual will moult. Melanin-based colouration is reliant on amino acids usually obtained from the diet. Rate of accumulation of these amino acids is therefore likely to vary through the year and the ability to allocate these to feather production will vary according to body condition (Jawor & Breitwisch 2003; Norris *et al.* 2009). Each of these factors may lead to an increased need for prolonged parental care and result in the individual remaining within the parental territory. Prolonged retention of a sub-dominant plumage may facilitate this by enabling the individual to exploit the parental territory for longer periods without incurring agonistic interactions (Martin 1996). Also, because the cost of this to the parents may be minimal (if food is not limiting) there may be additional benefits for the territory holder (e.g. increased predator detection, co-operative assistance with breeding) that may further improve survival probability.

Alongside this, retaining juvenile plumage may provide other benefits for species that fledge in poor condition. This plumage is generally much drabber than that of adults and retaining this until such time that the individual is able to compete with adult conspecifics or become more experienced at predation avoidance, may provide a selective advantage and improve juvenile/immature survival rates.

Overall the duration of the immature phase was found to be long in tropical species. This follows the general pattern of slow growth rates and late maturation found in other studies of tropical birds (Ricklefs 1976; Bryant & Hails 1983; Russell *et al.* 2004b). Comparison of the measure here with the duration of the immature phase in temperate species however, is complicated by the variety of moult strategies, most notably the general lack of complete post-juvenile moults (Jenni & Winkler 1994). In species assessed here, individuals were considered to be ‘adults’ once they had moulted all traces of juvenile/immature plumage however, the majority of temperate passerine species undertake only a partial post-juvenile moult, moulting into the full adult plumage during the second year of life (Ginn & Melville 1983; Svensson 1992). Of the 20 or so European species that undertake a complete moult, most have finished moulting before migration or the start of the cold-weather period. This time restriction results in almost all of these species having immature phases of less than 100 days. Comparison with tropical species is therefore difficult and also prevents the further comparison of the adult survival/immature phase relationship between tropical and temperate areas.

Only when better information on the rate and causes of nest failure and some idea as to the number of breeding attempts made each year by a pair are available will it be possible to more clearly define the relationships discussed here. Also, further work assessing juvenile body condition and how juvenile and post-juvenile plumage types (i.e. whether drab/nonbreeding or bright/breeding) influence the duration of immature phase may help in further establishing whether the relationship between duration of breeding period and immature phase can be attributed to the costs of feather construction.

5. Adult and juvenile survival

No difference between estimates of adult and juvenile survival was identified in this study although estimates of the latter here are limited by small datasets for each species. Also, the power of the comparisons within species is limited by the very small sample size of species for which both adult and juvenile estimates were available.

On balance, it seems likely that there is a genuine difference in adult and juvenile survival rates and the lack of identification of a significant difference here may be a Type II error. In most bird species survival is generally considered to increase through each successive life stage (egg – chick – fledgling – immature – adult) until middle age, after which individuals start to senesce and survival decreases with age (Forslund & Part 1995; Newton *et al.* 1997; Rush & Stutchbury 2008; Low & Part 2009). This scenario has been well documented in temperate species and typical first-year survival rates in these areas is estimated to be around 10-30% (Lack 1954; Nolan 1978; Perrins 1980; Krementz *et al.* 1989; Sullivan 1989; Anders & Marshall 2005; Rush & Stutchbury 2008). In long-lived species, juvenile survival is of increasing importance in governing population dynamics (Lee *et al.* 2008). This has been proposed for large seabird species (e.g. Morrison *et al.* 2009) but may also apply to long-lived, small species in environments where mortality is low i.e. potentially also in tropical landbirds. This appears to be the case with the few other studies that have attempted to identify rates of juvenile survival in tropical species recognising rates similar to those of adults or at least proportionately higher than those of temperate juveniles (Covas *et al.* 2004; Schaefer *et al.* 2004; Sankamethawee *et al.* 2009). Here, estimates of mean first-year survival across species were found to be 46.4% (± 8.6%, *n* = 13). Although 15% lower than that for adults of the same species in this study (61.9% ± 4.3%) this value is nonetheless much higher than the estimate derived for juvenile survival in north temperate species in McGregor (2005) from published data.

But why should rates of juvenile, first year and post-fledging survival be higher than for similar temperate species? Young birds leaving the nest will usually lack the skills of their parents in finding food and water, and will also be more prone to depredation. This naivety should result in first year survival being considerably lower than annual survival in adults. Earlier in this chapter however, it was identified that duration of the immature phase was longer in this study than is likely for similar temperate species. It was proposed that reduced nest attentiveness by parents (in response to increased predation risk (Skutch 1949; Martin *et al.* 2000b; but see Cresswell 1997)) may account for this, with reduced attentiveness leading to lower provisioning rates and individuals fledging in poor condition. As a result, fledglings may require longer to gain sufficient condition to moult into adult plumage. The extended parental care frequently observed in tropical birds (Russell 2000; Schaefer *et al.* 2004; Styrsky *et al.* 2005) may therefore provide a compensatory mechanism to resolve the risks of young fledging in poor condition. Seasonal environmental restrictions prevent this prolonged extension of parental care in temperate species. In temperate species, adults are constrained to undertake the complete moult and gain body condition before the onset of harsh environmental conditions when risk of mortality is greater (Martin 1987; Ricklefs 1997) or to migrate (Ginn & Melville 1983; Underhill *et al.* 1992). Temperate species have adapted to these conditions by maximising output of young throughout the favourable summer periods to increase the probability of young reaching reproductive age during the following breeding season. Increasing investment in each offspring through extended parental care is unlikely to improve the chances of survival for the recently fledged individual given that over winter mortality is high even for experienced adult individuals.

Prolonged time spent with the parents after fledging may significantly improve the survival prospects of the juvenile past the risks associated with fledging at a lower mass. Although this has yet to be formally tested, I identified a difference in mean body mass between juveniles, immatures and adults such that mass of juveniles was around 4% less than that for adults (mean ± se: -3.99% ± 0.93, range: -25.53% - +8.33%, *n* = 45) and immatures 1% less (mean ± se: -1.34% ± 0.63, range: -11.9% - +10.83%, *n* = 44). It is important to note that it was not possible to determine the interval between fledging and measurement, and some of this difference may therefore relate to weight loss after fledging. Similarly, a proportion may be due to the smaller plumage mass of juveniles (Ginn & Melville 1983; Lindström *et al.* 1993) although such differences are likely to be small. Overall however, the suggestion from these results is that juveniles fledge with lower body mass than adults but gain it gradually over the following weeks. In contrast, fledglings of temperate passerine species frequently fledge with body mass larger than their parents (e.g. Gosler 1993), and this difference may indicate reduced nest attentiveness in response to higher nest predation in tropical species .

6. Adult survival and life history traits

Clutch size

The results of this study identify a variation in adult survival rates across tropical species that seems to be accounted for through a trade-off with clutch size. Jetz *et al.* (2008) suggest that the global pattern of variation in clutch size can be attributed to seasonality of food availability operating through adult mortality; a pattern that would fit with the data here. The results seem to confirm the established clutch size vs. adult survival temperate/tropical paradigm identified in other studies. For example, using 182 passerine species from north temperate and southern and subtropical areas, Ghalambor & Martin (2001) identified a strong negative correlation between clutch size and adult survival between phylogenetically related species; at the same time also demonstrating that southern species responded more dramatically to the risk of adult mortality.

Other investigations into the relative importance of the trade–offs between life history characteristics by McGregor (2005) however, suggest that the higher average adult survival in tropical species is insufficient to compensate for the smaller clutch sizes commonly found there. Instead, increased nest predation (Robinson *et al.* 2000), numbers of broods per year (Karr *et al.* 1990) and extended parental care (leading to increased juvenile survival) (Russell *et al.* 2004a) have all been proposed as additional constraints that may reduce the level of adult survival below that needed to compensate for reduced clutch sizes. At present however there are limited empirical assessments of these factors and those that have been performed suggest that nest predation rates are similar between tropical and temperate systems (Martin *et al.* 2000a). Similarly, tropical species have been shown to frequently have only one brood per year (König & Gwinner 1995; Jullien & Clobert 2000; but see Foster 1974a). Although these studies would suggest that neither of these factors are sufficiently variable to cause the observed differences in clutch sizes between the two areas, it seems more likely that there is greater interplay between them than has so far been demonstrated. Only when sufficient data for a variety of traits are available and for a range of species will the relationships be properly determined. Although such an approach was attempted here, no data were available relating to renesting attempts, levels of nest predation or quality (mass) of young fledging.

Duration of the breeding season

That no significant relationship between duration of breeding season and annual adult survival was found here suggests either that duration of breeding does not usefully represent reproductive investment, that there is no link between this and reproductive investment (in terms of renesting - Foster 1974a; Martin *et al.* 2000a) or that the method of assessing this variable used here was flawed.

It is possible that, despite the general presumption of increased numbers of broods during each breeding season (Foster 1974a), duration of the breeding season is more a function of the supposedly longer incubation and nestling periods of tropical species (Ricklefs 1969b). Indeed, the number of broods per year has been shown not to vary too greatly from that of temperate species (Fogden 1972; Martin 1996; Jullien & Thiollay 1998 – but see Elgood et al. 1994). Despite this, and as discussed above, a number of studies have shown that tropical species repeatedly attempt to renest after successive failures (Roper 2005). This suggests that duration of the breeding period should provide at least a starting measure of reproductive investment. The duration of the breeding season will however fail to account for the reproductive investment of individuals in polygynous systems. In such cases, synchrony of nesting should result in short breeding season durations and will fail to represent for the reproductive investment of the male.

Failure to identify a relationship between breeding duration and adult survival here is therefore likely to be a consequence of the crude method of estimating breeding duration (using brood patch occurrence and juvenile presence). As described above, this method is unlikely to be able to account for annual variation in timing of breeding due to inter-annual differences in environmental factors such as rainfall, and will underestimate durations in synchronously breeding species. Improved methods for assessing the level of renesting and the duration of the breeding season are necessary before further assessment of the role of breeding season duration can be properly made.

Duration of moult

If the time taken to complete the main moult is a reasonable indicator of investment in maintenance activities, then a failure to find any relationship between survival and moult duration here may indicate that tropical species invest less in ensuring their own condition and more in reproduction than predicted. As already discussed, the duration of moult of the species in this study varies widely (range: 28 – 263 days, mean ± se: 132 ± 11.16 days, n = 28), however the majority (20 of 28 species) have durations longer than 100 days (Figure 2, Chapter 2). Potentially, this may be because slower grown feathers are generally of better quality (Dawson *et al.* 2000; Hall & Fransson 2000) or because feathers of tropical species have a high melanin content and therefore take longer to grow than for temperate species (Krol & Liebler 1998; Roulin *et al.* 2008) – see Chapter 2. The most likely reason however, may be that many of the species in this study (that do not breed synchronously or have a short breeding period) perform moult as a background activity. Such a strategy would allow individuals to take advantage of suitable breeding opportunities or to permit repeated renesting in response to high levels of nest predation (see above). This appeared to be the case for a wide range of species regardless of their size and, as shown here, their annual survival rate. The results here suggestthat moult and feather maintenance are performed as long-running, low-level activities with no obvious trade-offs with specific life history variables.

Body size

The results here highlight a positive correlation between adult survival and body mass (though only when assessed without also considering clutch size). This is contrary to the findings of other studies of tropical birds (Johnston *et al.* 1997; Francis *et al.* 1999) including that of McGregor (2005). Using similar species and the same study site, he determined that there was no relationship between survival and body mass (also without considering clutch size). From this he argued that selection pressure, in the form of nest predation, may be more intense for larger species in tropical areas. He suggested that higher levels of nest predation (Martin & Clobert 1996; Mezquida & Marone 2001) may have greater impacts on the life histories of larger species in tropical areas since the cost of every breeding attempt is higher than for smaller species. Larger individuals should therefore delay investment until the latter stages of breeding, i.e. increasing parental care after the young have fledged. This would account for both the negative relationship between mass and fecundity and the positive correlation with fledging period / extended parental care. Although logical and based on the premise of higher nest predation and reduced seasonality, the reasons behind the difference may be somewhat more prosaic. McGregor's (2005) analysis was based on fewer species and, as mentioned earlier (Chapter 4), the estimates generated in his study were derived from fewer data than the estimates here and as a result, were somewhat different. Analysis of the data here suggests that a positive correlation between survival and body mass does exist and, as with temperate areas, that this may be predominantly driven by seasonality of the environment. Although increased nest predation in tropical areas may result in increased costs for larger species, the proportionally higher range and number of predators available to depredate the nests of smaller species may balance this. The rate of nest predation for these smaller species in such a system is therefore likely to be higher than for larger species, resulting in similar overall energetic trade-offs for both large and small species. Once again further investigation into these questions is hampered by the lack of precise data on nest failure and re-nesting rates.

Covariance of life history traits

Life history theory states that investment in an activity results in reduced availability of resources for another. This has led many researchers to suggest a mechanism linking reproductive investment to adult survival such that, as increasing time or resources are expended in attempting to reproduce, so the ability of the parent to maintain condition or avoid predation is compromised. As a result of this, I predicted that annual survival rates would be influenced by duration of breeding (one of the measures of reproductive investment), duration of immaturity in offspring (linked to intensity of breeding effort), and the level of investment in maintenance activities such as moult (here included as moult duration). I have already demonstrated that many of the predicted individual relationships between various life history characteristics and adult survival in this study are of little significance, and so do not appear to influence the survival rates of adults. Many of these factors may not work in isolation however, and their combined effects may play a more significant role in influencing survival. Testing of this however revealed that none of the variables here covaried in a general way to explain the variability of survival rates in the selection of species assessed.

Following on from work by Snow & Snow (1964); Rowley & Russell (1991); Faaborg & Arendt (1995); Peach *et al.* (2001) and McGregor *et al.* (2007b) I therefore returned to the use of clutch size as an estimate of reproductive effort. A model containing just adult survival, clutch size and body mass revealed the simple and strongly significant relationship between survival and clutch size suggested in other studies (Nur 1984,1988; Lima 1987; Martin 2002). This result suggests either that breeding duration, moult and duration of immaturity are limited in their impact on adult survival or that some other factor interacts with each of these to raise their importance and influence. Alternatively, it may be that the methods used here to measure these characteristics were in some way deficient and missed the significant factors associated with each activity.

Taking the result at face value, it appears that these life history variables (as measured here) do not have a general relationship with adult survival. Moult inevitably has implications for adult survival because of its impact on breeding (courtship and display), foraging ability and predator avoidance. In a tropical environment though, its direct impacts on adult survival may be somewhat masked by its co-occurrence (at least in this study) with other, more energetically demanding, tasks, such as breeding. In a similar manner, duration of breeding would be expected to influence adult survival particularly if it does relate to an increased tendency to renest. However, should it merely represent a lengthy phase associated with extended incubation and nestling phases then it is little surprise that this study did not identify any relationship. Without further information relating to renesting attempts and nest predation, the measure of duration of breeding seasons used here, and its variability, confounds many factors.

That clutch size is identified here as the only general trait to covary with adult survival is perhaps not surprising since the ability to optimise reproduction lies at the heart of life history theory and dictates a species' success and persistence. Natural selection operates such that individuals that maximise their fitness (lifetime reproductive success) tend to be most successful (Darwin 1859). In attempting to achieve this, the individual must identify the optimal rate of reproduction and, in so doing, weigh the comparative benefits of annual investment in young (clutch size and number of broods) with the potential impacts this investment will have on its long term survival (and therefore also its lifetime reproductive success)(Stearns 1992; Roff 2002). These trade-offs vary according to local conditions that, in strongly seasonal temperate environments, cause alternating periods of food abundance and shortage, and harsh and favourable climatic conditions. Under such conditions, compensation for the high potential risk of mortality by increasing investment in breeding makes evolutionary sense. Although species in such areas often have multiple broods, there is a finite period in which to raise young before conditions become unsuitable. As a result, evolutionary adaptation that maximises clutch size to parental ability both ensures maximum annual production of young that compensates for potential adult mortality and insures against low juvenile over-winter survival. In comparison, seasonal fluctuations in environmental conditions are generally less severe in tropical areas. Activities that are usually carefully timed in north temperate environments, such as reproduction, are often more fluid in tropical areas and can be performed across a much broader annual schedule. Why then do tropical species not have multiple broods to increase fecundity? Murray (1985) proposed that a female's annual fecundity (clutch size) should be the lowest required to replace herself since additional eggs are costly in terms of her survival. In a tropical environment where annual adult survival is high, a slower rate of reproduction represents the optimum strategy since it increases the possibility of further reproductive output during the female's longer lifespan.

In less markedly seasonal environments, although often focussed around periods when conditions are most suitable (e.g. food availability for feeding dependent young), reduced constraint may lead to greater individual, species-specific and niche-specific variation in trade-offs between life history activities (moult timing, duration, duration of breeding season). This variation ultimately renders identification of general patterns amongst those traits more difficult to achieve.

Life history trade-offs between survival, moult and breeding in a tropical seasonal environment

The aim here was to identifiy key relationships between a number of life history characteristics to determine which are the most important in explaining general patterns of variation between tropical and temperate species. Whereas tropical environments have traditionally been viewed as stable, aseasonal and predictable, we now understand better the seasonal pattern and annual fluctuations in rainfall and the influence this has on the wider tropical environment, more especially its role in determining food availability (Ashmole 1963; Ricklefs 1980; Lepage & Lloyd 2004). With this in mind, I assessed a range of life history characteristics in a tropical seasonal environment generating empirical assessments for survival, aspects of moult and various breeding variables. These were then compared to identify how variation in each influenced the range of potential values of a second, i.e. the life history trade-offs.

An important, though frequently overlooked, component of studies of life histories is the identification and examination of those characteristics governing self-maintenance (e.g. grooming, preening, resting). The most obvious of these characteristics in birds relates to the replacement of damaged or worn feathers, i.e. moult. Moult requires significant investment in resources in order to synthesize the necessary proteins for feather development (King 1981; Lindström *et al.* 1993), as well as avoid predation (Slagsvold & Dale 1996; Rivera *et al.* 1999; Lind 2001) and maintain the ability to forage efficiently (Adams & Brown 1990; Chai & Dudley 1999). Higher adult survival in tropical birds points to a reduced risk-taking nature of birds in these environments which, because of the need to balance the trade-offs associated with moult, would imply that individuals should reduce the starvation/predation risk by undertaking slow moults. Overall this strategy was observed for birds here with moult durations considerably longer than for similar temperate species. Although species appeared to preferentially select timing of moult according to seasonal constraints (e.g. in water and food availability), the degree of both inter-annual and inter-individual variation in timing was broad. This suggests that seasonal constraints in environmental conditions were not necessarily limiting.

Longer moult durations have consequences for the timing and success of both these and other activities though, since the coincidence of moult with other essential activities will inevitably result in fewer resources for both (Hemborg & Lundberg 1998; Siikamaki 1998). In temperate species, seasonal variability in both conditions and availability of resources has resulted in a well-established pattern of timing for the essential life history behaviours such as breeding and moult (Jenni & Winkler 1994). However for these species, breeding generally appears to predominate and is therefore carefully scheduled such that exploitation of time and resources occurs to maximise seasonal reproductive output. As a consequence, moult is essentially squeezed into the period between this concentration in breeding effort and upcoming periods of difficult environmental conditions or migration (Holmes 1971; Svensson & Hedenstrom 1999; Hemborg *et al.* 2001). The emphasis on current reproductive output therefore takes precedence over that from potential future attempts in species in environments where individuals face higher uncertainty in future survival.

In contrast, the seasonal predictability of tropical environments results in enhanced survival (Martin 1996; Stutchbury & Morton 2001) such that the value of each current breeding attempt is of less significance than the combined potential output of future attempts. Species in these environments are therefore likely to adopt a more conservative approach to risk taking resulting in the reduction in constraints affecting maintenance activities (i.e. moult). This was especially apparent from the level of overlap in essential activities (moult and breeding) in this study which suggests that, although breeding is obviously of importance, there is less need for an individual to risk its overall lifetime reproductive success (and therefore its current survival chances) by placing all of its emphasis on the current breeding attempt. The reduction in this constraint in the tropical species assessed here was evident from the finding that duration of moult and breeding showed a reduced linkage. Both of these activities were also seemingly independent of all other empirically measured life history characteristics derived here.

To summarise then, this study identified a general trade-off between clutch size and survival, and determined that the occurrence of small clutches/high survival is likely to be associated with the reduction of seasonal constraints on resource availability. In contrast, other life history traits such as duration of moult and breeding probably appear to have an optimum in areas where there are reduced seasonal constraints, and so do not covary with survival. The exact nature of breeding duration, number of broods and renesting potential for species remains to be discovered for tropical species generally. Moult duration however is clearly much longer than for temperate species and suggests that slow and steady moult always improves fitness in a non-seasonally constrained environment.

Chapter 7: References

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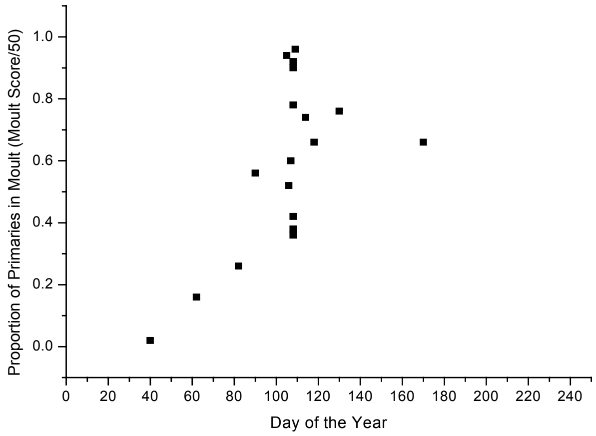
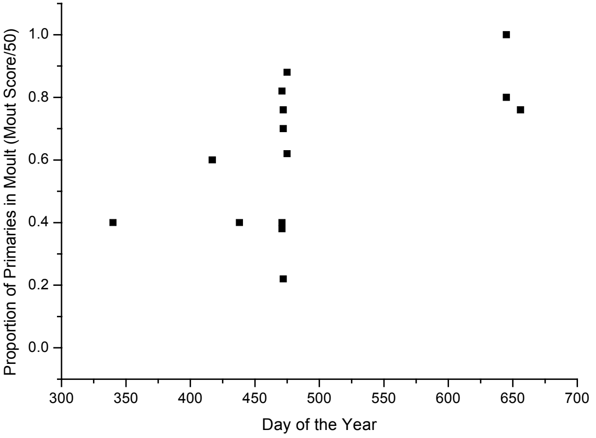
APPENDIX 1. Plots of primary moult versus date

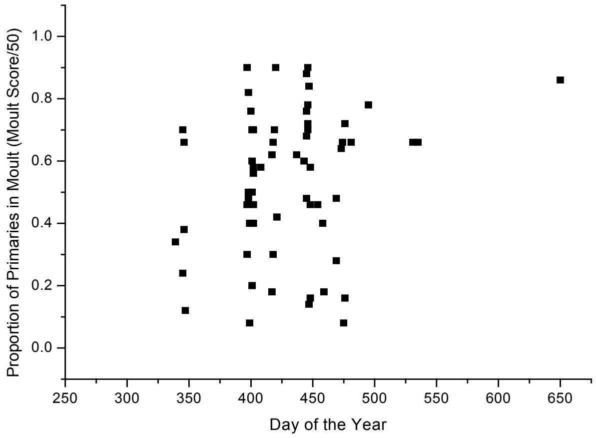
Adamawa Turtle Dove - ***Streptopelia hypopyrrha***



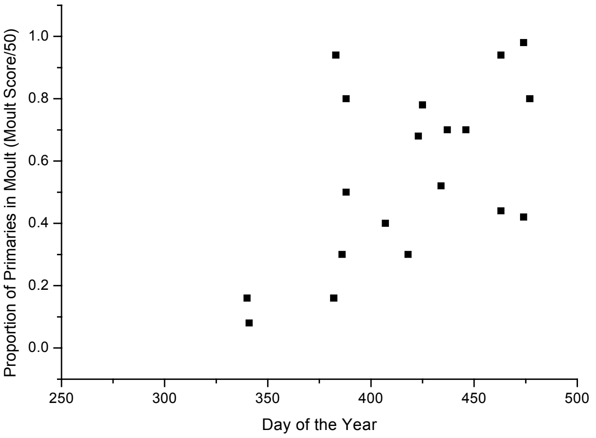
Laughing Dove - ***Streptopelia senegalensis***



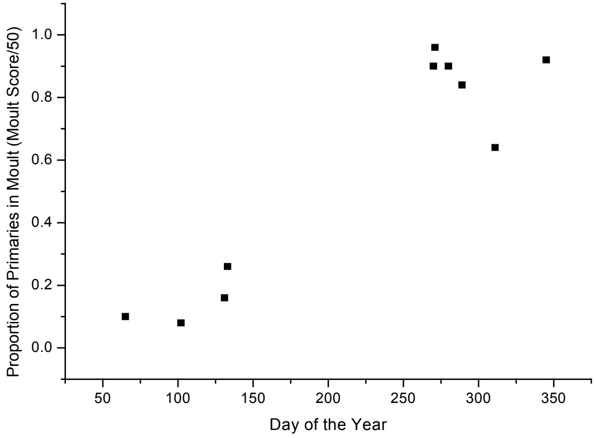
Black-billed Wood Dove - ***Turtur abyssinicus***



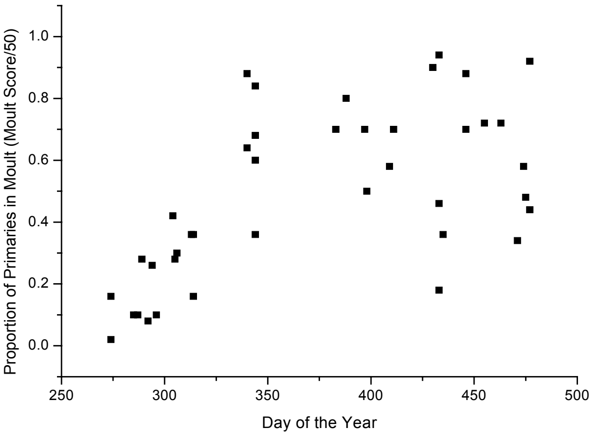
Yellow-fronted Tinkerbird - ***Pogoniulus chrysoconus***



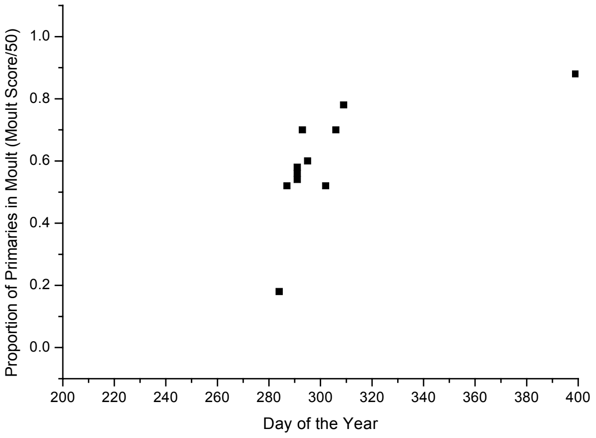
Common Bulbul - ***Pycnonotus barbatus***



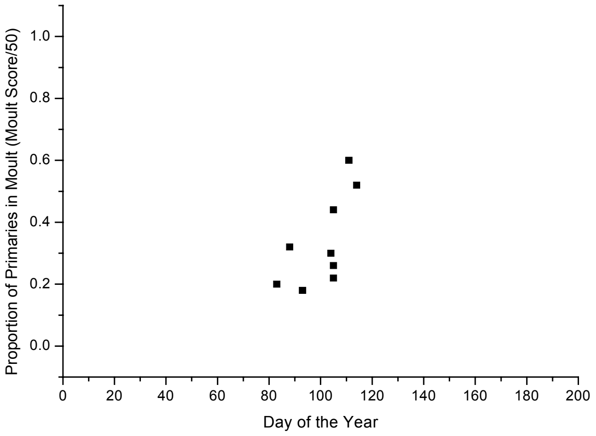
Grey-backed Camaroptera - ***Camaroptera brachyura***



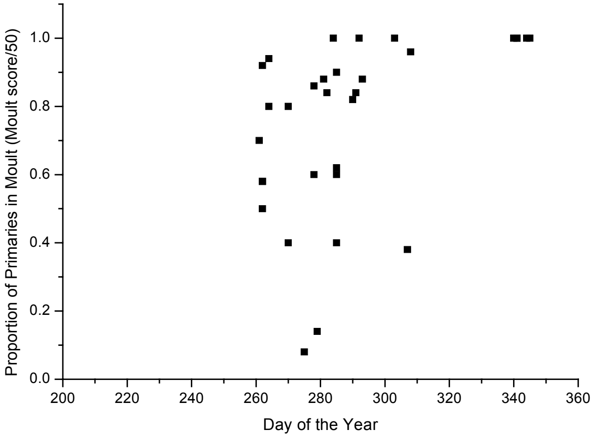
Senegal Eremomela - *Eremomela pusilla*



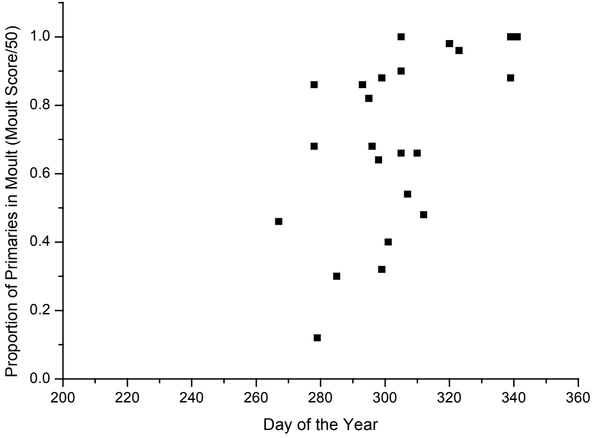
Tawny-flanked Prinia - *Prinia subflava*



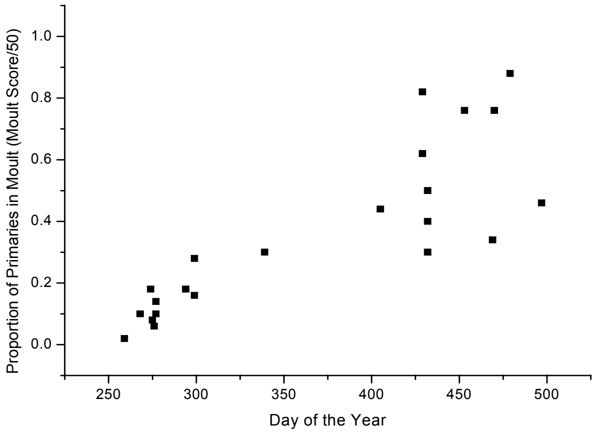
African Thrush - *Turdus pelios*



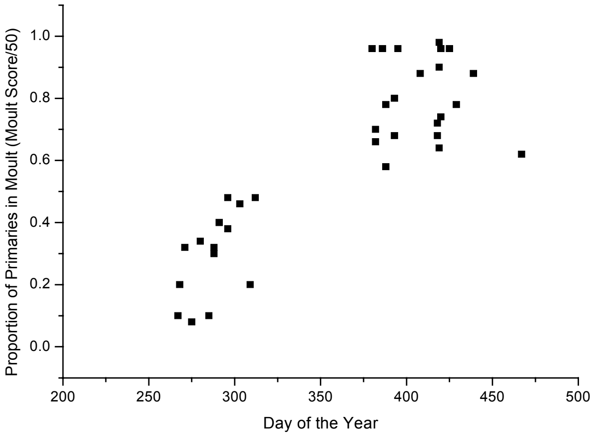
African Yellow White-eye - *Zosterops senegalensis*



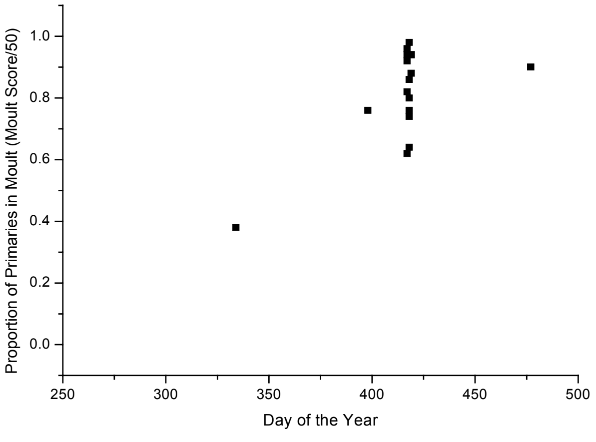
Green-headed Sunbird - *Cyanomitra verticalis*



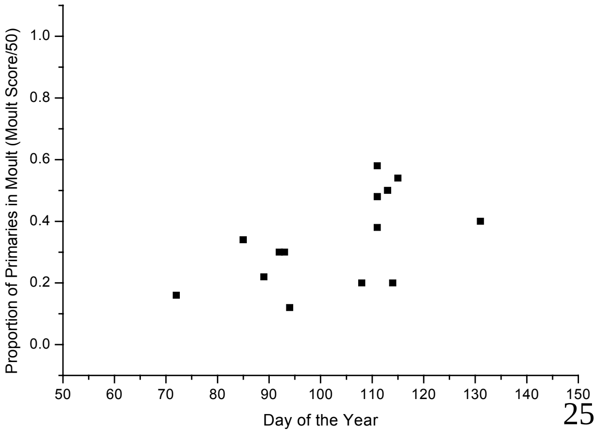
Scarlet-chested Sunbird - *Chalcomitra senegalensis*



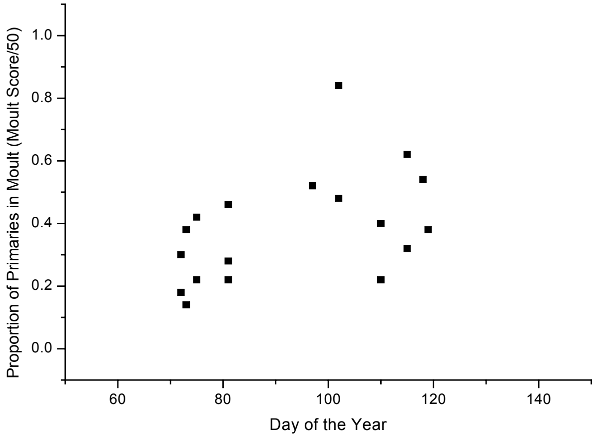
Beautiful Sunbird - *Cinnyris pulchellus*



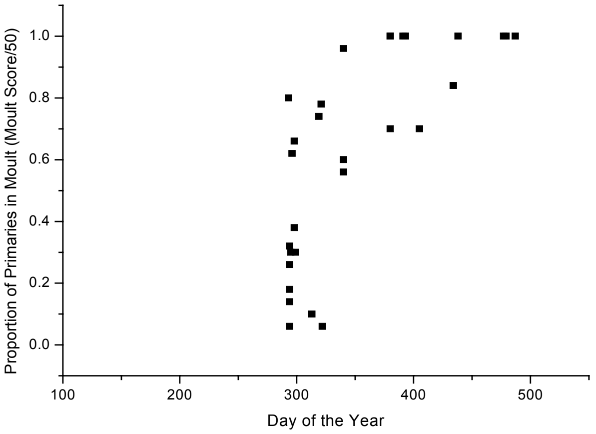
Variable Sunbird - *Cinnyris venustus*



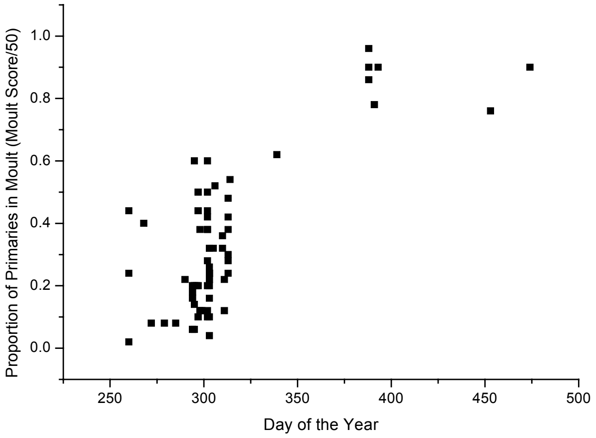
Cinnamon-breasted Rock Bunting - *Emberiza tahapisi*



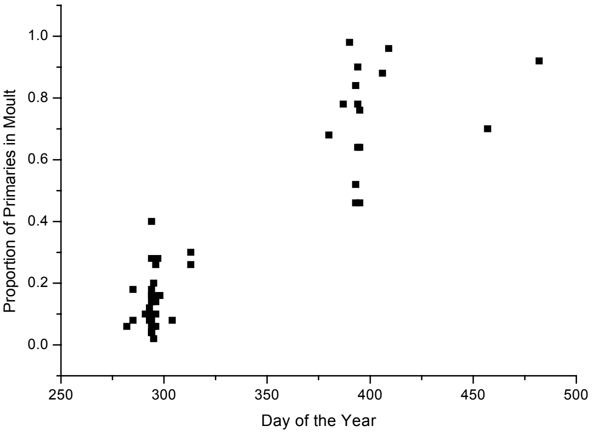
Black-necked Weaver - *Ploceus nigricollis*



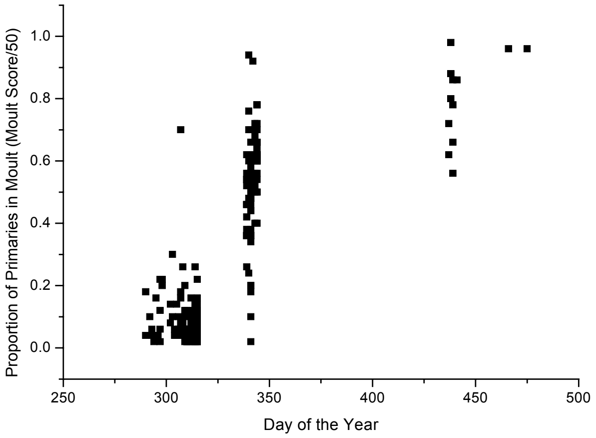
Village Weaver - *Ploceus cucullatus*



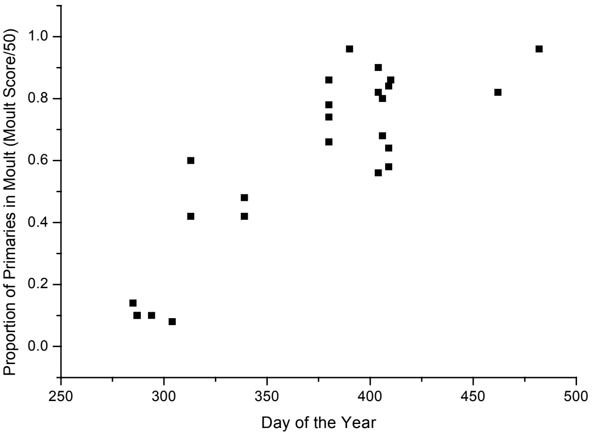
Vitelline Masked Weaver - *Ploceus vitellinus*



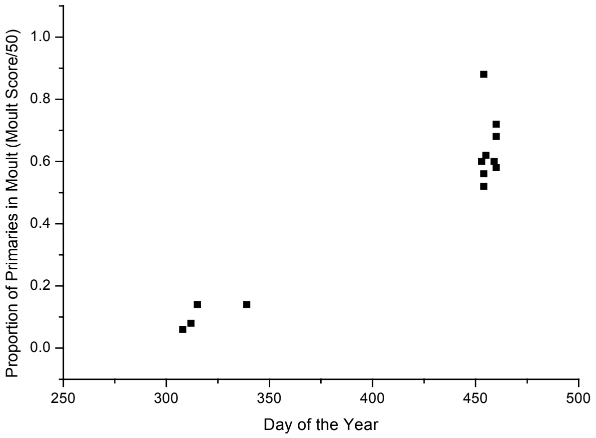
Northern Red Bishop - *Euplectes franciscanus*



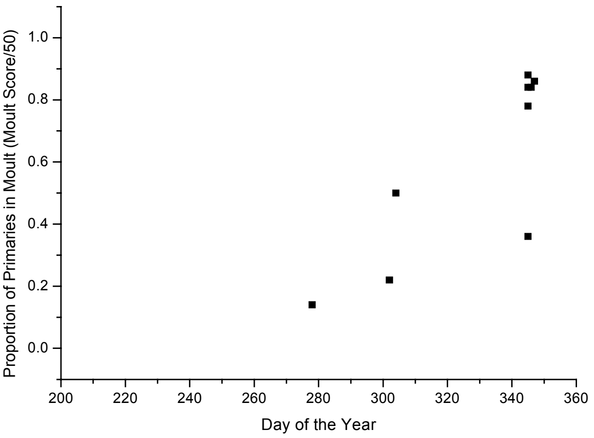
Lavender Waxbill - *Estrilda caerulescens*

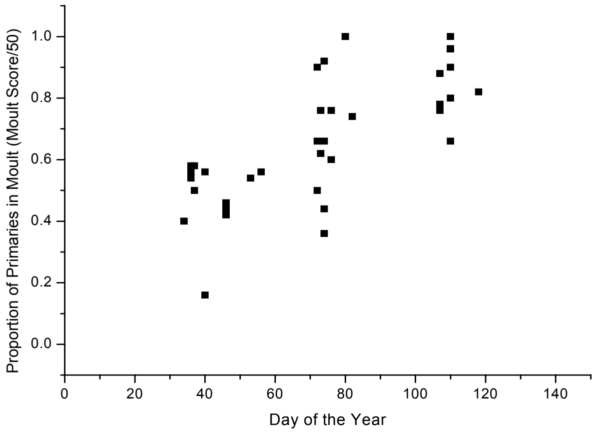


Black-rumped Waxbill - *Estrilda troglodytes*

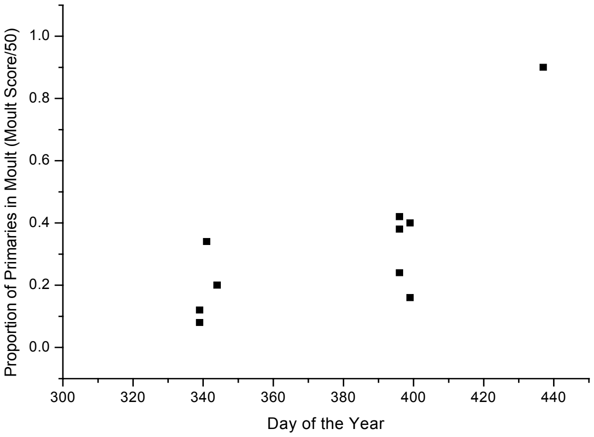


Orange-cheeked Waxbill - *Estrilda melpoda*

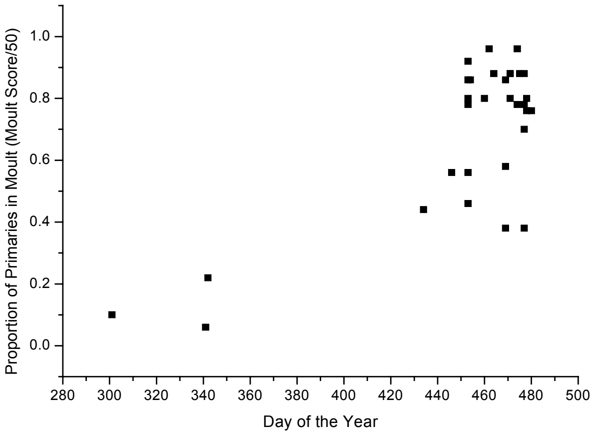




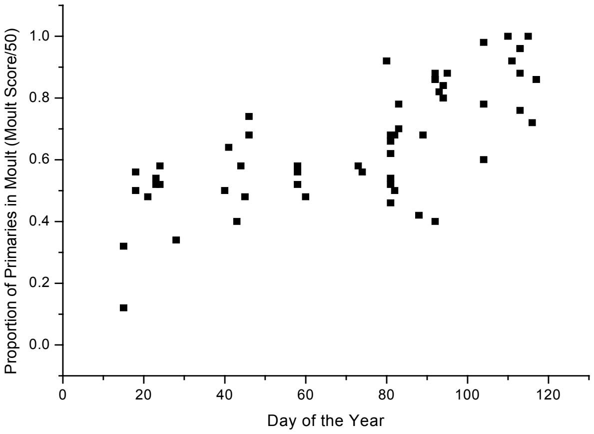
Red-cheeked Cordon-bleu - *Uraeginthus bengalus*



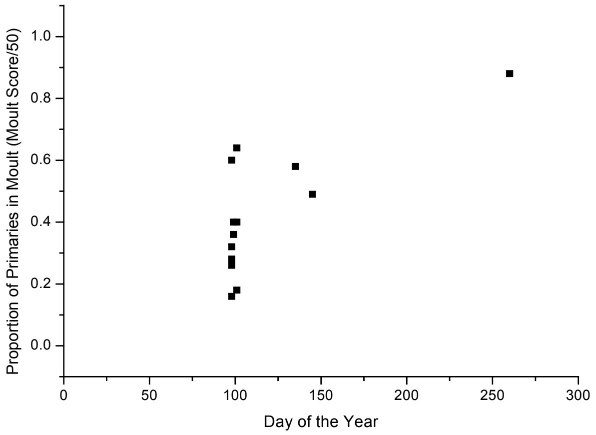
Bar-breasted Firefinch - *Lagonosticta rufopicta*



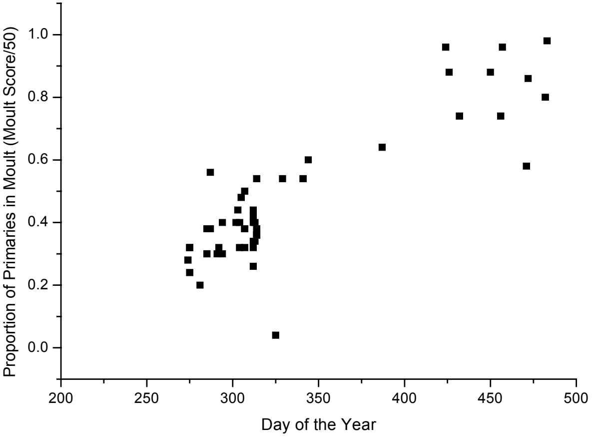
Black-bellied Firefinch - *Lagonosticta rara*



Rock Firefinch - *Lagonosticta sanguinodorsalis*



African Quailfinch - *Ortygospiza atricollis*



Bronze Mannikin - *Spermestes cucullatus*

APPENDIX 2

Changes in Sahelian bird biodiversity and tree density over a five year period in Northern Nigeria

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Bird Study (2010) **57**:

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Short title: Sahel bird and tree densities

Keywords: Sahel; climate change; deforestation; bird communities; bird densities; Palearctic migrant birds

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Capsule Two widespread censuses of already degraded woodland in the Sahel in Northern Nigeria separated by 5 years (2002 and 2007) showed relatively small further changes in tree and bird density

Aims To determine how change in tree density affects African and Palearctic migrant bird density in already degraded Sahelian woodland

Methods We compare differences in the number of bird species and their abundance with differences in the size and number of woody plants between two seasons separated by five years at 16 degraded woodland sites across 250 km east-west in Northern Nigeria.

Results Densities of large trees (> 5 m) decreased but densities of smaller trees and shrubs increased, partly as a consequence of growth and because larger trees have been preferentially removed or partly cut down: tree densities were, however, initially low. Of 37 common bird species, 16% had higher densities and 22% had lower densities, in the second study period. The density of Common Whitethroat, Northern Wheatear and Yellow Wagtail was correlated with the number and size of trees, but not that of Lesser Whitethroat and Subalpine Warbler. Overall there was relatively little turnover in species between the two surveys and if (the initially low) tree density was halved, only approximately 2.1% of the average total for number of bird species per 0.2 ha point would be lost.

Conclusion Few large changes in bird species' density were found possibly because:

1. all habitats sampled were already at relatively low tree density: initial reductions from high tree density or near removal of all trees may cause larger changes in local bird densities
2. reduction in the number of large trees was partially compensated by a more lush development of the vegetation as a whole in the second study period
3. the bird species remaining in degraded Sahelian woodland in Northern Nigeria are already well adapted to habitat change and low tree density

The Sahel of sub-Saharan West Africa is a semi-arid zone dominated by *Acacia* woodland (Maydell, 1986) that supports a distinct avifauna as well as a number of biome-restricted bird species (Fishpool and Evans, 2001). The Sahel is also an important wintering or staging area for approximately one-third of European breeding species (Moreau, 1972, Grimmett, 1987, Jones, 1995), many of which have declining populations (Berthold et al., 1998, Sanderson et al., 2006). There has been much anthropogenic habitat change in the Sahel, exacerbated by climate change (IUCN, 1991, Wickens, 1997, Hein and de Ridder, 2006), and climate change is predicted to intensify over the next fifty years (Held et al., 2006). Variation in climatic conditions in the Sahel have been correlated with the population declines of European birds that winter or stage there, such as Common Whitethroats *Sylvia communis* (Winstanly et al., 1974), Sedge Warblers *Acrocephalus schoenobaenus* (Peach et al., 1991, Foppen et al., 1999), Sand Martins *Riparia riparia* (Bryant and Jones, 1995, Szép, 1995, Cowley and Siriwardena, 2005), Barn Swallows *Hirundo rustica* (Robinson et al., 2003), Purple Herons *Ardea purpurea* (den Held, 1981) and White Storks *Ciconia ciconia* (Schaub et al., 2005). Despite the likely recent and also predicted climate and habitat change events and their suggested impacts on Afro-tropical migrant bird populations (Baillie and Peach, 1992, Newton, 2004), there is little baseline monitoring of bird populations with respect to habitat change directly within the Sahel: see Zwarts et al. (2009) for a review. This study presents data for changes in bird and woody vegetation density between two sampling periods separated by 5 years in the same region of the Sahel region of north Nigeria.

Deforestation has been rapid throughout the Sahel through human clearance for fuel wood, grazing, and conversion to intensive agriculture (Grimmett, 1987, IUCN, 1991, Odihi, 2003). For example, in Senegal the extent of *Acacia nilotica* woodland has declined substantially over a 40 year period (Tappan et al., 2004), with human deforestation leading to a reduction in tree species diversity and a shift southwards of more arid vegetation zones (Gonzalez, 2001). In north-east Nigeria, in Borno State there has been a 14% decline in woodland between 1976 and 1995 (Geomatics, 1998). Bird populations within the Sahel are probably greatly affected by habitat change, for example, at one Sahelian forest site in Nigeria tree density decreased by 82% from 1993-2001, and the number of birds counted per point, the total number of species recorded per point and diversity all declined, but not in adjacent farmland where there were no deforestation changes (Cresswell et al., 2007). However, after substantial deforestation, remaining densities of Palearctic migrants may then be relatively resistant to further deforestation, showing small changes in density across points that vary widely in tree and shrub densities (Wilson and Cresswell, 2006), at least within the Sahel of Northern Nigeria. Nevertheless, populations of Afro-Palearctic migrant birds are almost uniformly declining relative to non-migrant species suggesting that factors operating on their wintering grounds or during migration need to be studied to determine the causes of many of the species' declines (Sanderson et al., 2006).

The wintering distribution, habitat use, degree of residency and general ecology of European migrants in terrestrial habitats during the winter is poorly known (Bairlein, 2003). There are a limited number of studies that provide baseline densities of bird species in the Sahel (Jones et al., 1996, Nøhr and Jorgensen, 1997, Stoate, 1997, Vickery et al., 1999, Thiollay, 2006a, Thiollay, 2006b, Petersen et al., 2007). There are even fewer studies that have investigated relationships between habitat characteristics and bird densities (Wilson and Cresswell, 2006) and only one limited study to date that has specifically tested how deforestation in the Sahel might affect these densities (Cresswell et al., 2007). There have been several studies that have examined the ecological relationship between Palearctic migrant and Afrotropical "resident" birds in Africa. Early studies have concluded that Afrotropical species utilise more complex and dense habitats than their Palearctic counterparts (Lack, 1971, Bilcke, 1984, Rabøl, 1987), although later studies suggest that Afrotropical and Palearctic species may have similar ecological requirements (Salewski et al., 2003, Salewski and Jones, 2006, Wilson and Cresswell, 2007). Clarification of this is important because the former would suggest that habitat loss might impact upon the Afrotropical species to a greater degree. In any case, for Afrotropical resident species, deforestation may be more important because it will have a direct effect during both breeding and non-breeding periods. But despite few intensive local studies (Morel and Morel, 1992, and see Zwarts et al., 2009 for a review) , the likely result of deforestation in the Sahel would be lower densities of species reliant on woodland, or even disappearance of these species and replacement with desert or grassland species.

Here, we report changes in populations of Sahelian bird species, and in particular Palearctic migrant species (that are undergoing declines that may be related to conditions on the wintering ground), and associated vegetation, between surveys in Dec-Jan 2000-2002 and Jan 2007, collected over the same 625 point counts across 16 sites spread across a 250km east-west transect in northern Nigeria. It is important to note, however, that we survey only a limited time interval (5 years) in an area already heavily degraded prior to the first survey (e.g. Cresswell et al., 2007), and after the considerable habitat change due to the large scale Sahelian drought up to the 1990s (see Zwarts et al., 2009).

The aims of the study were to provide baseline data to monitor future changes in bird diversity in the Sahel and to determine if bird diversity has changed in the last 5 years in the already degraded woodland of the Sahel region of northern Nigeria. Specific aims were to:

1. Record change in tree density as a representative of long-term vegetation change.
2. Record change in species' densities, species richness and diversity.
3. Determine if changes in species richness, overall bird abundance and commonly occurring Palearctic species' abundance are related to changes in tree density.

Methods

Birds and vegetation density were estimated using point counts. Six hundred and twenty five point counts were conducted across 16 sites in Northern Nigeria in two periods: Survey 1 (S1) from December 2000/January 2001 to January 2002 and Survey 2 (S2) in January 2007 (Table 1, Figure 1). Sites were originally selected in 2001 as areas with Sahelian woodland that would have had relatively high densities of birds (in order to investigate bird/habitat associations), and in no way represent a random sample. However, densities from the sites in Survey 1 therefore represent densities from the least degraded habitat available at that time, and changes in densities between Survey 1 and Survey 2 are indicative of how habitat with initially relatively low levels of degradation have been affected by habitat change within 5 years. All possible points surveyed in December and January in Survey 1 as part of work by Wilson & Cresswell (2006) were repeated (N = 625), except in a small number of cases per site where difficulties such as human disturbance prevented a meaningful point count from being carried out at the time.

Bird point count methods are detailed in Wilson & Cresswell (2006), but in summary, bird counts were carried out at individual points located at 110m intervals along a transect placed at random through each of the 16 study sites. Between 28-57 points were covered per site (i.e. 3.1 to 6.3 km of transect). Individual point locations were recorded using a Garmin^{TM} 12 GPS, with the stated ‘Position Averaging Function’ giving an accuracy of c. 5m. On completion of each point count, the observer continued 110m along the transect line, using the GPS to give the distance to previous point (or to relocate the point), before stopping and repeating the count procedure. Counts were carried out during the 2.5-hour period immediately following local sunrise, with time since sunrise recorded for all points (called “time” in all models), and all individuals located by call or sight were recorded. Point counts were only carried out during still weather (wind speed less than Force 4 Beaufort Scale) and during days of good visibility – no rainfall was recorded in the area during the surveys.

Point count duration was three minutes, and was timed using a digital watch with countdown alarm. Counts began immediately upon reaching a point. Exact distances to individual birds were measured using a Bushnell Yardage Pro™ or a Leica laser rangefinder with a range of 10-700m and an accuracy of 1m. Distances less than 10m were estimated by eye, with regular calibration checks of estimated distances made using measured distances. All birds were identified to species (either by sight or call) during each point count. Where birds were clustered, the flock size was noted. Observations were carried out by Jared Wilson in Survey 1, and Matthew Stevens and Danaë Sheehan in Survey 2. Differences in observer ability, that might confound the results, were tested by comparing the distances at which a range of common species were detected. If observers are of similar ability in detecting and identifying birds then there should be no difference between the relative distances at which a species was seen and identified (and this comparison is robust even where the absolute frequency of occurrence may be different). There were no significant differences in the frequency distribution of detection distances for a range of species tested (e.g. Common Whitethroat χ^2_2 = 2.4, P = 0.30; Lesser Whitethroat *Sylvia curruca* χ^2_2 = 4.1, P = 0.25; Yellow Wagtail *Motacilla flava* χ^2_2 = 2.7, P = 0.27; African Collared Dove *Streptopelia roseogrisea* χ^2_2 = 5.7, P

= 0.06; Blue-naped Mousebird *Urocolius macrourus* $\chi^2_2 = 3.9$, P = 0.14; Olivaceous Warbler *Hippolais pallida* $\chi^2_2 = 5.2$, P = 0.08). Therefore it seems unlikely that intra and inter-survey differences in observer ability were significantly confounding the results (see also Wilson & Cresswell 2006 for further evidence of the lack of important inter-observer effects).

At each point count location, a 25m-radius vegetation plot was sampled during the late morning or afternoon of the day of the point count using methods described in Jones et al. (1996). In summary, stem counts were carried out within each plot: all trees and bushes were identified to species and counted, and their height (small 0.5-3 m; medium 3-5 m; large > 5 m high) estimated by eye. No categorisation of trees stunted by grazing or chopping of selected branches versus regenerating saplings was attempted. Tree species were identified using field guides (Maydell, 1986, Arbonnier, 2004): some identification was limited to genus (e.g. *Acaci*a) because of difficulties in identifying small individuals to species (Table 2).

Data analysis

There was uneven sampling across the 16 sites (Table 1: where 39 ± 2.3 points were sampled per site), so that any changes localised to Site 9, for example, would have a greater effect to those localised to Site 6. Analyses, therefore, accounted for the differences in sampling across sites by either considering site means (N = 16) or by specifying Site as a random factor in Generalised Linear Models and so adjusting the degrees of freedom accordingly.

Tree density changes (overall, for the three height classes separately and for individual species or Genera of tree), tree size ratio changes (density of trees > 3 m relative to density of trees 0.5 – 3 m) and tree diversity, were assessed using data from N = 625 points sampled twice, once in each survey, except for tree size ratio (N = 556 S1 and N = 600 S2) and diversity (N = 580 S1 and N = 592 S2) which excluded any points where there were no trees recorded, with GLMs including site as a random factor. Diversity of trees was calculated using the Weiner Index (Diversity = -(No. of species / total number of individuals) * (ln(No. of species / total number of individuals)).

The density of small, medium and large trees was also used to confirm vegetation change measurements on a larger scale recorded independently using remote sensing. Changes were again calculated as the simple arithmetic difference in densities between 2001/2002 and 2007, but pooled by assigning them to a 1 km grid square so that they could be related to satellite data. The satellite data used described parameters of the growing seasons of vegetation derived from annual variation in reflectance properties, measured by remote sensing. The indices were derived from Normalised Difference Vegetation Index (NDVI) data collected by SPOT – Vegetation sensor, which has a spatial resolution of approximately 1 km. This sensor uses daily passes to produce 10 day composite images that summarise the peak NDVI value over 10 day periods. These composite images reduce the potential effects of atmospheric interference, such as cloud. This produces 36 images for each year. These images were used to calculate the length and peak growth (NDVI) values for the preceding growing season. Changes were calculated as arithmetic difference between 2002 and 2007, expressed as a proportion of the 2002 value.

Changes in the number of bird species, the overall number of birds and diversity of birds were assessed using data from N =625 points sampled twice, once in each survey, except for diversity (N = 514 S1 and N = 513 S2) which excluded any points where there were no birds recorded, with GLMs including site as a random factor. Diversity of birds was calculated using the Weiner Index (see above).

Densities were calculated for any species with more than 20 sight records overall, and so where there was enough data to calculate meaningful estimates of density, using the DISTANCE program (Distance 5.0, University of St Andrews; (Buckland et al., 1993)). Density estimates were modelled based on observed clusters of birds (which for most species was 1), but densities were calculated for individual birds. All data were used, mostly without truncation, because half normal detection functions with cosine adjustments gave good fits to the observed data (see last column in Table 3): for three species right truncation was carried out until a good fit for the detectability function was obtained. A perceived problem of not truncating sightings is double counting: because individual points were located only 110m apart, a bird recorded at a second point at a large distance has some (very small) probability of already being recorded in an adjacent point. But double counting in this way does not violate any of the assumptions of density estimation using distance sampling (Buckland et al., 1993, Bibby et al., 2000) and so could be ignored.

A universal detection function per species was modelled in all cases (i.e. pooling Survey 1 and Survey 2 data) to increase the precision of the estimate of the detectability function. This assumes that the factors that affected detectability for a species were the same in both surveys. Considering the lack of any large change in vegetation (see results below), a similarity in detection distances between surveys (e.g. Common Whitethroat $\chi^2_1 = 1.4$, $P = 0.23$ and similar non-significant results for other species, Kruskall-Wallis 1-way ANOVA comparing the distribution of detection distances between the two surveys) and the lack of any negative relationship between the number of birds observed per point with tree density or vegetation complexity (see Table 4 below), this assumption seems to be valid. Differences in density were compared using t-tests using the standard errors generated by DISTANCE, at the 5% level throughout, and no correction was made for multiple tests. Some marginal differences may simply reflect Type I errors and so individual species' comparisons should be assessed in conjunction with their sample size and size of effect, but ignoring such marginal results may lead to an underestimate of any overall trends, particularly because the precision of density estimates from point counts is generally poor.

Bird numbers were related to vegetation density using Generalised Linear Models, using pooled data from all point counts (N = 1250). The number of bird species and the total number of birds (all records, sight or heard) recorded within a 25m radius of the point were used as dependent variables (both were normally distributed), with small, medium and large tree density, and number of tree species as potential predictor variables of interest; site number and year of survey were added as random effects to account for uneven and repeat sampling, and time since sunrise and Julian date to account for the potential confounding effects of differences in the time and season of sampling (see Table 4).

Changes in bird numbers were related to changes in vegetation by using Generalised Linear Models, using the difference in values for the same point between the two surveys. The change in the number of bird species, or the change in the total number of birds (i.e. their change in abundance within a 25m point count) were used as dependent variables (all were normally distributed). Change in small, medium and large tree density, and change in number of tree species were tested as potential predictor variables of interest. Site number was added as a random effect to account for uneven sampling, and difference in time since sunrise and Julian date to account for the potential confounding effects of differences in the time and season of sampling. Specific Palearctic migrant species that showed significant changes in densities between surveys were used to test the hypothesis that changes in vegetation result in changes in Palearctic migrant density. For Common Whitethroat, Lesser Whitethroat and Subalpine Warbler *Sylvia cantillans*, existing models from Wilson & Cresswell (2006) that were derived from Survey 1 data to predict species density from vegetation characteristics, were used to predict the abundance of a species based on the vegetation recorded in Survey 1 and for Survey 2. The difference in predicted abundance values for each point between surveys was then averaged for the 16 sites and then correlated with the average difference per site in observed abundance values: if vegetation changes lead to changes in numbers generally then these two sets of values should be positively correlated.

Statistical analyses were carried out in SPSS 12.0 (SPSS Inc. 2003). All tests were two-tailed. Means are quoted ± 1 standard error.). Non-linear relationships were tested by including squared main effects in models but there was no evidence that these improved models over the range of data analysed.

Results

Changes in trees

Mean tree density increased between the surveys (S1, 10.2 ± 0.4; S2, 13.5 ± 0.6 trees per point; $F_{1,1233}$=23.8, P < 0.001; site $F_{15,1233}$=17.4, P<0.001). Small trees increased in density ($F_{1,1233}$=6.3, P =0.012; site $F_{15,1233}$=14.7, P<0.001), medium trees also increased in density ($F_{1,1233}$=5.6, P =0.019; site $F_{15,1233}$=33.6, P<0.001) but tall trees decreased in density ($F_{1,1233}$=16.9, P<0.001; site $F_{15,1233}$=48.5, P<0.001): Figure 2. Consequently, the ratio of larger trees to small trees decreased between the surveys (1.5 ± 0.2 m S1 and 1.0 ± 0.1 M S2, $F_{1,1139}$=7.3, P =0.007; site $F_{15,1139}$=25.0, P<0.001). The diversity index of tree species per point did not change significantly between surveys (S1, 0.27 ± 0.004; S2, 0.26 ± 0.004; $F_{1,1155}$=0.1, P =0.77; site $F_{15,1155}$=2.5, P=0.001). The densities of most of the major plant species or groups (occurring in > 5% of points) increased (7 out of 11), but one decreased (*Calotropis procera*), and with the remaining 3 out of 11 not changing significantly between the surveys (Table 2).

Considering the remote sensing derived variables, there were increases between 2002 and 2007 in both the length of growing season (12.865 ± 0.408 vs. 16.519 ± 0.489; t_{50}=-8.36, P<0.001) and peak NDVI (139.82 ± 3.67 vs. 153.87 ± 3.35; t_{50}=-4.40, P<0.001). The change in the density of small and medium trees was positively correlated with the change in growing season length across the 51 one km^2 squares sampled (r = 0.394 and r = 0.307, P = 0.004 and P = 0.028 respectively), but not the density of large trees (r = -0.021, P = 0.88). The change in the density of medium trees was positively correlated with the change in peak NDVI across the 51 one km^2 squares (r = 0.400, P = 0.004), but the density of small and large trees was not (r = 0.243 and R = 0.100, P = 0.086 and P = 0.485 respectively).

Changes in birds

Overall 129 bird species were recorded (S1, 114; S2, 104), with 77 species recorded in more than 1% of points (S1, 74; S2, 72): Appendix Table 1. There was little change in species composition: of those species that were recorded in more than 1% of points (and therefore at a reasonably high frequency so that conclusions can be drawn about changes in presence between surveys not simply because of a low probability of recording at any time), two (relatively uncommon) species were recorded only in Survey 1 (Palm Swift *Cypsiurus parvus* 1% of points, Pied Crow *Corvus albus* 1.3% of points) and two species were recorded only in Survey 2 (Blue-cheeked Bee-eater *Merops persicus* 1.9% of points, Vinaceous Dove *Streptopelia vinacea* 1.6% of points): Appendix Table 1. The number of species recorded per point increased between surveys (S1, 2.0 ± 0.07; S2, 2.3 ± 0.08 species per point; $F_{1,1233}$=13.2, P < 0.001; site $F_{15,1233}$=17.6, P<0.001): Figure 3A. The number of birds counted per point increased (S1, 6.8 ± 0.8; S2, 15.1 ± 1.6 birds per point; $F_{1,1233}$=21.9, P < 0.001; site $F_{15,1233}$=5.9, P<0.001): Figure 3B. However, the diversity index of birds did not change significantly between surveys (S1 0.18 ± 0.01; S2 0.20 ± 0.01 birds per point; $F_{1,1010}$=3.7, P=0.053; site $F_{15,1010}$=2.2, P=0.004).

Of the 37 species that were recorded more than 20 times overall (thus providing enough data to calculate meaningful estimates of density), 14% increased (at the $P < 0.05$ level), 19% decreased whilst the densities for the remaining 67% of species showed no significant change (Table 3). Of the eight Palearctic species recorded commonly, the density of 4 decreased, 2 increased and 2 showed no significant change.

Changes in birds correlated with changes in tree density

The number of bird species was significantly positively correlated with the density of small, medium and large trees, and the total number of tree species (Table 4A). The change in the number of bird species recorded at a point between the two surveys was correlated with the change in medium and probably tall tree density at that point (medium tree density difference, $F_{1,596}$=11.7, P=0.001, B = 0.068 ± 0.020; large tree density difference $F_{1,596}$=3.6, P=0.059, B = 0.106 ± 0.056) but not small tree density difference ($F_{1,596}$=0.001, P=0.98) or difference in number of tree species per point ($F_{1,596}$=1.9, P=0.17): controlling for difference in Julian date and time, and with site as a random effect. The results are very similar if number of species recorded in the first survey is included in the model, so controlling for relative change in number of species, although the relationship with large tree density difference becomes significant ($F_{1,595}$=6.6, P = 0.010). The effect of change in medium tree density was similar when the number of Palearctic migrant species only was considered (medium tree density difference, $F_{1,596}$=5.4, P=0.021, B = 0.025 ± 0.011) or when number of African “resident” species only was considered (medium tree density difference, $F_{1,596}$ = 6.5, P = 0.011, B = 0.043 ± 0.017). Although tree density significantly affected the number of species, its biological effects within the study system were relatively small: if the mean density of medium and large trees halved (from an average of 13.2 and 5.9 per hectare respectively, N = 625 means for each point sampled twice, once for each survey), then the number of species per point would decrease by only 0.05, a decrease of approximately 2.1% of the average species total for a point (i.e. an average species total of 2.4 species as illustrated in Figure 3A).

The number of birds recorded per point was borderline significantly correlated positively with the density of medium trees and was significantly positively correlated with the total number of tree species, (Table 4B). The change in the number of birds recorded at a point between the two surveys did not correlate significantly with change in tree density or total number of tree species at that point (small tree density difference $F_{1,596} = 0.7$, $P = 0.40$; medium tree density difference, $F_{1,596} = 1.0$, $P = 0.32$; large tree density difference $F_{1,596} = 0.3$, $P = 0.56$, difference in number of tree species per point $F_{1,596} = 1.9$, $P = 0.17$): controlling for difference in Julian date and time, and with site as a random effect. The results are very similar if number of birds recorded in the first survey is included in the model, so controlling for relative change in bird numbers.

Five migrant species were examined in detail to determine the extent to which changes in vegetation were responsible for changing their densities. Common Whitethroat counts increased as densities of medium trees increased (Table 5): if the mean density of medium trees doubled (from an average of 13.2 per hectare), then the average density of whitethroats would increase by approximately 0.7 birds per hectare (Fig 4A). Northern Wheatear counts increased as the number of tree species declined (Table 5): if average tree species richness halved (from an average of 2.2 species per point) then Northern Wheatear density would increase by approximately 0.4 birds per hectare. Yellow Wagtail counts increased as the density of large and medium trees decreased (Table 5): if the mean density of medium and large trees halved (from an average of 13.2 and 5.9 per hectare respectively), then the density of wagtails would increase by approximately 10 per hectare. Changes in trees did not predict changes in Lesser Whitethroat and Subalpine Warbler counts. The observed changes in density of trees accurately predicted (from occurrence models derived from the first survey, see Wilson & Cresswell 2006) the observed changes in Common Whitethroat density (Fig 4B), but not for Lesser Whitethroat or Subalpine Warbler (Table 6).

Discussion

This study shows clear relationships between tree density and bird density for some species, confirming the results of previous studies carried out in the area (Jones et al., 1996, Vickery et al., 1999, Wilson and Cresswell, 2006). Additionally, the results of this study suggest that changes in tree density may be responsible for changes in the density of some species (Common Whitethroat, Northern Wheatear and Yellow Wagtail) but not others (Lesser Whitethroat and Subalpine Warbler). Where points have undergone substantial decreases in tree density, the density of some Palearctic migrant species was substantially affected (both positively and negatively depending on their ecological requirements). However, on average overall, changes in tree density between the two surveys were not large (being already low after much deforestation prior to the two surveys), and in essence reflected a change from more open woodland with mature trees to slightly denser, more scrubby habitat, thus resulting in little change in overall bird species richness. Even where tree density changed considerably, the same Palearctic and African species occurred.

Our results are limited in that they only sample two periods in a system which is well known for its seasonal variability in rainfall that is likely to affect the density of birds possibly independently of tree density (indeed our NDVI analysis results confirm that better growing conditions were present for the second survey). Also we only sampled areas that had a low tree density – that were largely already deforested before the *first* survey. Nevertheless we suggest that the African birds and wintering Palearctic migrant communities that remain in these degraded low density Sahelian woodland may show relatively little response to further decreases in tree density. The remaining species are already well adapted to low density woodland, although of course not to the removal of all trees.

Changes in vegetation

Although tree density did not change substantially, the structure of the vegetation changed, with large trees decreasing significantly, and smaller, more scrubby trees increasing. Much of this change can probably be attributed to selective removal of large trees for firewood, but also gradual reduction in the size of trees by gradual limb removal to provide grazing (large branches and stems are frequently chopped so that they can be bent within reach of domestic animals, pers. obs.). Large trees that form substantial bushes such as *Balanites* and *Salvadora* and even *Acacias* can be so chopped that several smaller trees result through a process equivalent to coppicing. As a result the increase in small tree density recorded in this study (which is simply a stem count), probably masks an overall decrease in the canopy density. Nevertheless 10 of the 11 of the major tree/shrub species recorded during this study, increased or maintained stem density between the surveys suggesting some regeneration. In recent years rainfall has improved in the Sahel (Held et al., 2006), so conditions for plant growth have improved; when rainfall is “normal” (i.e. not at the substantially lower than average rates that occurred in the 1970s and 1980s) primary productivity of Sahel plant communities will also be less affected by grazing (Hein, 2006). Our analysis of NVDI and growing season length also indicated that growing conditions were better for the Survey 2.

Contrary to what we expected on the basis of a previous single site comparison (Site 3, Watucal Forest Reserve, also surveyed again in this study), where tree density decreased by 82% from 1993-2001, with substantial negative effects on species richness and abundance (Cresswell et al., 2007), there was surprisingly little change in tree density. There are two likely explanations for this. Firstly, rainfall conditions have improved so allowing vegetation growth to keep pace with increasing deforestation and grazing pressure (Hein and de Ridder, 2006, and this study). Secondly, that all sites we surveyed are already well deforested, and sites such as Watucal (a “protected” forest reserve) no longer have a high tree density: we can only document substantial deforestation rates if there are high density sites remaining. In 1993 tree density at Watucal was about 84 trees per 25m point, and by 2001 this was down to about 15 trees (Cresswell et al., 2007) and by 2007 this was up to 22 trees (although these trees were smaller than 2001). Considering all 16 sites, tree density per point varied from 3 – 24 trees (15 – 123 trees/ha) in the 2007 survey: put simply, there are no high density Sahelian woodland sites remaining in our study.

Changes in birds

Although there was little change recorded in bird species richness and bird community, there were some changes in bird species’ density recorded. Six species (of 37, 16%) increased. Excluding species that were probably not recorded by chance, or the highly mobile Quelea, two species, African Collared Dove, and Common Whitethroat, on average, doubled their density (relative increase range 1.7-2.0). Seven species (of 37, 19%) decreased; again excluding species that were probably not recorded by chance, Blue-naped Mousebird, Vieillot's Barbet *Lybius vieilloti*, Yellow Wagtail, Black Scrub Robin *Cercotrichas podobe*, Lesser Whitethroat, and Subalpine Warbler, decreased on average by one third (relative decrease range 0.2 – 0.5). Some of these changes can be reasonably attributed to habitat change, for example, Common Whitethroat, Northern Wheatear and perhaps, Yellow Wagtail, because independently derived models of how species' density vary with vegetation density predicted the changes observed on the basis of vegetation density changes. These specific changes are not surprising: Common Whitethroats favour trees and bushes that have increased, whereas Northern Wheatears and Yellow Wagtails forage on the ground in open habitats that have decreased. Lesser Whitethroat and Subalpine Warbler declines were not predicted well by vegetation changes. Their apparent decrease may be simply a consequence of both species having large spatial variation in density in the area, which varies both within and between seasons (Jones et al., 1996, Vickery et al., 1999, Wilson & Cresswell unpublished), probably because of inter-annual variation in the timing and intensity of the pre-winter rainfall. Intra-African movement of species within and between years in response to rainfall (Jones, 1995) will confound any between year comparison of densities over a limited spatial scale. For example, rainfall varies between years – for example, the study sites in Survey 2 had higher NVDI index than Survey 1, so indicating higher and/or later rainfall in Survey 2, and so better foraging conditions, and so probably a more northerly distribution of birds.

The response of Sahelian bird species to tree density change in already degraded woodland

Although tree density changed little on average, some points showed considerable increases or decreases in tree density and these changes probably resulted in changes in some species' density (e.g. Common Whitethroat, see Figure 4), but not others (e.g. Lesser Whitethroat), and all species, more or less, occurred at reasonable densities even in sites with reduced tree density. Overall, species richness was little affected by changes in tree density (i.e. a halving of average tree density would result only in a reduction of 2.1% of species) and bird abundance was not significantly affected by changes in tree density, at least over the range of relatively low tree density sites that we surveyed. But please note that we surveyed sites with low tree density where it is likely that more than 80% of trees have already been removed prior to the first survey, so our predictions reflect changes in current low tree densities, rather than what would happen with deforestation in initially pristine areas of Sahelian woodland.

These results and earlier work in the same area (Wilson and Cresswell, 2006) suggest that the remaining Sahelian bird communities, in at least the north-east of Nigeria, may not change rapidly with tree density variation and therefore habitat change, after initial high levels of deforestation. There are two likely explanations for this. Firstly, Sahelian woodland may always have existed in some areas at low density, may be heterogeneous, and susceptible to great variation in productivity within and between years (Wezel and Schlecht, 2004) because of inter-annual rainfall variation (Moron, 1997, Held et al., 2006, Tilahun, 2006). Consequently many bird species may have already evolved to deal with anthropogenic habitat change, which simply mimics the existing natural heterogeneity and variation in rainfall. Secondly, we may already be observing a community post-habitat change (i.e. the major deforestation occurred before the first survey) and so we are recording the robust “survivors”.

Although the results of our study may appear to suggest that, at least at the present time, in a limited area of the Sahel bird populations are not being greatly affected by tree density change, and tree density change itself is not profound, two important points need to be made. Firstly, climatic conditions have been ameliorating since the 1990s in the Sahel (Held et al., 2006), yet conditions for birds have got worse in some sites (Cresswell et al., 2007) or remained similar (this study) suggesting that the underlying anthropogenic pressure on vegetation in the area has increased, compensating for any climate-mediated vegetation improvement (e.g. see Hein and de Ridder, 2006). The apparent lack of response of birds to change in tree density reported in this study may be being masked because of favourable rainfall and lusher vegetation of the second survey: tree density may be of secondary importance when rainfall is high, but should rainfall decrease tree density effects may be stronger. Secondly, although current Sahelian bird communities in degraded low density woodland appear not to be changing much in response to recent vegetation change, many species rely on at least some trees being present (e.g. Wilson and Cresswell, 2006) and with increased human population pressure, or lower rainfall in the future, many areas may lose trees entirely.

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Table 1: Location and dates of the two surveys, and the number of points surveyed (N) once during each survey. All dates in S2 were in January 2007. Sites 1,2 and 7-11 were located around the village of Alagarno, sites 3 – 6 were located around the town of Nguru. Site coordinates are given with latitude and longitude in the form of degrees, minutes and seconds expressed as a decimal fraction of minutes.

	Site Name			Survey 1			Survey 2	
		N	E	Day	Month	Year	Day	N
1	Reserve	13'04.062"	13'37.541 "	9	1	2002	9	35
2	Canal	13'09.719"	13'34.010 "	10	1	2002	12	35
3	Watucal Forest	12'48.785"	10'31.615 "	12	12	2001	24	34
4	Nguru A	12'53.337"	10'26.596 "	14	12	2001	23	48
5	Watucal In	12'53.684"	10'33.603 "	17	12	2001	25	29
6	Watucal De	12'52.552"	10'35.305 "	19	12	2001	26	28
7	School	13'09.018"	13'33.394 "	7	1	2002	11	44
8	Bore	13'11.354"	13'38.144 "	8	1	2002	15	28
9	Pratincole	13'08.822"	13'32.305 "	12	1	2002	13	57
10	Commiphora	13'11.061"	13'30.461 "	13	1	2002	14	36
11	Quail	13'02.539"	13'38.228 "	14	1	2002	10	28
12	W of Gashua	12'49.281"	11'0'7.311"	7	12	2002	22	37
13	Geidam	12'49.038"	11'47.404 "	8	12	2002	21	40
14	E of Damasak	13'01.821"	12'24.750 "	9	12	2002	20	48
15	W of Malamfatori	13'28.870"	13'00.497 "	10	12	2002	19	49
16	Malamfatori	13'36.892"	13'20.355 "	11	12	2002	18	49

Table 2: Mean number of the different tree species recorded in both surveys within the same 25m radius (0.196 Ha) point (N = 625). Species are ordered by percent change, significant increases in italics and significant decreases in bold. Changes were tested with a Generalised Linear Model controlling for uneven sampling across the 16 sites, with site specified as a random factor.

Species	Survey 1		Survey 2			
	Mean	SE	Mean	SE	$F_{1,1139}$	P
Prosopis africana	0.31	0.08	1.2	0.25	13.7	*<0.001*
Boscia senegalensis	0.45	0.09	1.1	0.24	9.3	*0.002*
Guiera senegalensis	0.46	0.14	0.94	0.26	3.3	0.07
Maerua sp.	0.52	0.08	1	0.13	12	*0.001*
Ziziphus sp.	0.2	0.03	0.33	0.06	0.7	0.41
Salvadora persica	1.1	0.15	1.7	0.28	4.9	*0.027*
Balanites aegyptiaca	2.1	0.18	2.7	0.22	6.2	*0.013*
Commiphora africana	0.12	0.04	0.12	0.04	0.1	0.72
Acacia sp.	3.9	0.31	3.6	0.25	1.1	0.28
Piliostigma reticulata	0.19	0.05	0.17	0.03	0.2	0.69
Calotropis procera	2.7	0.47	1.6	0.51	11	**0.001**

Table 3: Density estimates (birds/ha) for the 37 species that were recorded more than 20 times overall calculated using DISTANCE (i.e. taking into account detectability). Detectability was modelled pooling both surveys. Species marked ^{U} increased significantly in density between surveys and species marked with a ^{D} decreased significantly between surveys(* P < 0.05; ** P < 0.01, *** P < 0.001). Palearctic migrant species are marked in bold.

	Survey 1				Survey 2				Detect-
Species	Density	LCL	UCL	Obs[1]	Density	LCL	UCL	Obs[1]	ability[2]
Blackhead Plover	0.023	0.011	0.049	17	0.074	0.034	0.167	18	0.43
Vinaceous Dove^{U*}	0	0	0	0	0.059	0.029	0.122	20	0.76
African Collared Dove^{U*}	0.251	0.179	0.350	78	0.497	0.358	0.688	127	0.99
African Mourning Dove^{U**}	0	0	0	0	0.088	0.045	0.172	24	0.91
Laughing Dove	0.068	0.036	0.128	26	0.118	0.074	0.191	34	0.93
Namaqua Dove	0.156	0.104	0.232	42	0.316	0.204	0.487	69	0.89
Blue-naped Mousebird^{D*}	0.343	0.220	0.537	50	0.083	0.049	0.141	23	0.32
Blue-cheeked Bee-eater^{U**}	0.000	0.000	0.000	0	0.059	0.029	0.114	24	0.65
Hoopoe	0.045	0.025	0.083	19	0.032	0.017	0.057	17	0.59
Grey Hornbill	0.015	0.007	0.031	20	0.005	0.002	0.017	5	0.51
Red-billed Hornbill	0.078	0.050	0.122	39	0.058	0.033	0.100	44	0.16
Vieillot's Barbet^{D**}	0.022	0.011	0.041	28	0.004	0.001	0.011	5	0.20
Crested Lark	0.045	0.026	0.079	25	0.054	0.033	0.089	29	0.28
Chestnut-backed Sparrow Lark	0.316	0.203	0.488	50	0.196	0.124	0.308	35	0.86
Yellow Wagtail^{D***}	1.42	0.825	2.45	139	0.364	0.223	0.594	95	0.21[3]
Rufous Scrub Robin	0.015	0.007	0.031	20	0.005	0.002	0.017	5	0.51
Black Scrub Robin^{D**}	0.188	0.140	0.252	95	0.062	0.040	0.096	28	0.22
Northern Wheatear	0.226	0.099	0.515	204	0.124	0.055	0.284	113	0.20[4]
Bonelli's Warbler^{D*}	0.087	0.045	0.165	24	0.004	0.001	0.019	1	0.45
Common Whitethroat^{U**}	0.318	0.231	0.439	153	0.559	0.420	0.44	263	0.28[5]
Lesser Whitethroat^{D**}	0.347	0.251	0.481	98	0.131	0.089	0.193	37	0.24
Subalpine Warbler^{D***}	0.557	0.457	0.678	192	0.247	0.190	0.322	84	0.29
Cricket Warbler	0.287	0.173	0.477	63	0.170	0.098	0.296	34	0.95
Olivaceous Warbler	0.497	0.372	0.664	160	0.528	0.403	0.691	165	0.91
Yellow-bellied Eremomela	0.023	0.009	0.058	7	0.094	0.047	0.191	13	0.45
Pygmy Sunbird	0.147	0.088	0.245	34	0.083	0.042	0.167	13	0.79
Woodchat Shrike	0.023	0.013	0.042	21	0.020	0.011	0.036	16	0.78
Southern Grey Shrike	0.108	0.078	0.148	144	0.071	0.050	0.100	92	0.66
Chestnut-bellied Starling	0.212	0.143	0.314	65	0.137	0.080	0.234	45	0.28
Greater Blue-eared Starling	0.028	0.016	0.050	23	0.019	0.010	0.036	15	0.83
Red-cheeked Cordon Bleu	0.588	0.367	0.941	41	0.494	0.305	0.799	61	0.32
Red-billed Quelea^{U***}	1.37	0.52	3.61	29	16.1	11.6	22.5	279	0.64
Sudan Golden Sparrow	2.21	1.22	3.97	109	5.50	3.76	8.03	163	0.86
Grey-headed Sparrow	0.189	0.110	0.328	54	0.533	0.321	0.885	117	0.44
Speckle-fronted Weaver	0.092	0.051	0.164	22	0.250	0.145	0.432	40	0.61
Buffalo Weaver	0.277	0.159	0.481	57	0.239	0.132	0.435	52	0.53
Little Weaver	0.085	0.045	0.162	18	0.221	0.128	0.381	37	0.76

[1] Number of birds recorded in total

[2] P value of difference in modelled detectability function and observed data (Kolmogorov-Smirnov test)

[3] Right truncated at 150m

[4] Right truncated at 75m

[5] Right truncated at 120m

Table 4: How (A) number of species and (B) total number of birds seen or heard within a 25m radius point depends on tree density, controlling for time of day (minutes after sunrise) and year, with site and year specified as random effects (N = 1250 i.e. 625 points sampled twice in different years).

A. Dependent Variable: Number of species

Source		Type III	df	F	Sig.	B
Intercept	Hypothesis	311.0	1	22.5	0.007	2.2 ± 0.2
	Error	59.9	4.3			
Trees 0.5 - 3 m	Hypothesis	8.9	1	3.9	0.050	0.006 ± 0.003
	Error	2832.9	1226			
Trees 3 – 5 m	Hypothesis	123.7	1	53.5	<0.001	0.101 ± 0.014
	Error	2832.9	1226			
Trees > 5 m	Hypothesis	47.7	1	20.6	<0.001	0.132 ± 0.029
	Error	2832.9	1226			
No. tree species	Hypothesis	32.9	1	14.2	<0.001	0.150 ± 0.040
	Error	2832.9	1226			
Site no.	Hypothesis	366.7	15	10.6	<0.001	
	Error	2832.9	1226			
Year	Hypothesis	60.7	2	13.1	<0.001	
	Error	2832.9	1226			
Time	Hypothesis	10.4	1	4.5	0.034	-0.002 ± 0.001
	Error	2832.9	1226			
Julian date	Hypothesis	21.9	1	9.5	0.002	-0.015 ± 0.005
	Error	2832.9	1226			

B. Dependent Variable: Total number of birds

Intercept	Hypothesis	16037.5	1	4.1	0.10	9.0 ± 4.2
	Error	18277.7	4.7			
Trees 0.5 - 3 m	Hypothesis	2847.3	1	3.0	0.084	-0.099 ± 0.057
	Error	1164196.1	1226			
Trees 3 – 5 m	Hypothesis	3464.6	1	3.6	0.056	0.533 ± 0.279
	Error	1164196.1	1226			
Trees > 5m	Hypothesis	427.8	1	0.5	0.50	-0.397 ± 0.591
	Error	1164196.1	1226			
No. tree species	Hypothesis	5724.9	1	6.0	0.014	1.98 ± 0.807
	Error	1164196.1	1226			
Site no.	Hypothesis	95721.3	15	6.7	<0.001	
	Error	1164196.1	1226			
Year	Hypothesis	16485.4	2	8.7	<0.001	
	Error	1164196.1	1226			
Time	Hypothesis	3953.7	1	4.2	0.042	-0.044 ± 0.021
	Error	1164196.1	1226			
Julian date	Hypothesis	1828.6	1	1.9	0.17	-0.141 ± 0.101
	Error	1164196.1	1226			

Table 5: How changes in vegetation characteristics correlated with changes in counts at the same 625 points for five common Palearctic migrant species (note each point is 0.196 Ha). Change in count between the two surveys was the dependent variable, and difference in time of day and Julian date were included to control for confounding effects of different sampling times, and site was included as a random effect to control for uneven sampling across sites. Degrees of freedom = 1, 596 in all cases. Significant correlations are in bold.

	Common Whitethroat	Lesser Whitethroat	Subalpine Warbler	Northern Wheatear	Yellow Wagtail
	F value, p value, parameter estimates where significant				
Difference in:					
Large tree density	0.9, 0.35	0.9, 0.33	1.6, 0.20	0.02, 0.89	**13.5, <0.001** -1.56 ± 0.42
Medium tree density	**9.8, 0.002** 0.025 ± 0.008	0.04, 0.85	1.5, 0.21	2.4, 0.12	**29.5, <0.001** -0.82 ± 0.15
Small tree density	2.6, 0.11	2.9, 0.12	0.4, 0.52	0.001, 0.99	0.003, 0.96
No. of tree species	0.003, 0.96	0.3, 0.59	0.001, 0.97	**10.1, 0.002** -0.069 ± 0.022	0.4, 0.53

Table 6: Tests of how vegetation change predicted the change in counts for three common migrant species between the two surveys, using models originally derived from count and vegetation data in Survey 1 (see table numbers, and variables used as predictors as below for original models for each species in Cresswell & Wilson 2006). The original models were used to predict counts for the second survey on the basis of the observed vegetation change, and then the predicted counts were correlated with the observed counts for the second survey (see Figure 4 for further details). N = 16 site means in each case. Significant correlations are in bold.

	Common Whitethroat	Lesser Whitethroat	Subalpine Warbler
Model used	Table 3	Table 5	Table 4
Predictor variables:	Mean tree size *Balanites* density *Salvadora* density	Mean tree size *Balanites* density *Salvadora* density *Acacia* density Tree diversity	Mean tree size Overall tree density *Balanites* density *Salvadora* density *Acacia* density Shrub density
S1 Obs. vs Pred.	**r_s = 0.66, P = 0.006**	**r_s = 0.71, P = 0.002**	**r_s = 0.54, P = 0.032**
S2 Obs. vs Pred.	**r_s = 0.60, P = 0.015**	**r_s = 0.51, P = 0.042**	r_s = 0.11, P = 0.66
Diff. Obs. Counts vs. Pred. Counts	**r_s = 0.57, P = 0.022**	r_s = 0.04, P = 0.88	r_s = -0.04, P = 0.89

Figure Legends

Figure 1: Map of the location of study sites in north-east Nigeria (see Table 1 for key), and the location of the study area in West Africa (inset map).

Figure 2: Density of trees per 25m point (0.196 ha) in three height classes, for the two surveys (Survey 1, S1, 2001-2002, unshaded bars; Survey 2, S2, 2007, shaded bars). P values are to illustrate the single factor comparisons shown (for complete multivariate analysis see text).

Figure 3: Boxplots (median and interquartile ranges within the boxes) to illustrate how species richness (A) and bird abundance (B) varied within and between the two surveys.

Figure 4: How Common Whitethroat *Sylvia communis* density is a function of vegetation density. A. The change in the number of Common Whitethroats with change in the density of large and medium sized trees (> 3 m in height) at each of 625 points surveyed once in 2001-2 (Survey 1) and again once in 2007 (Survey 2). The positive relationship is highly significant (see text). Note that the low amount of variance apparently explained by this relationship is largely to do with the stochasticity of recording birds during point counts, where birds occur at low density and so have a low chance of occurring in the point during a point count, even if it has suitable habitat, and where, even if birds are present during the point count, there is a low chance of recording them because of low detectability. B. The correspondence between the predicted change in average counts per site (predicted from changes in vegetation between the two surveys) and the observed change in average counts per site. The predicted values for the counts for each point were obtained from a model of the relationship between count and vegetation density from data in Survey 1, and then the change for the predicted value between the surveys for each point was averaged across sites hence N=16 site mean differences. The observed values were simply the actual change in counts of Common Whitethroats for each point, averaged across sites. The positive relationship is significant (see text).

Figure 1:

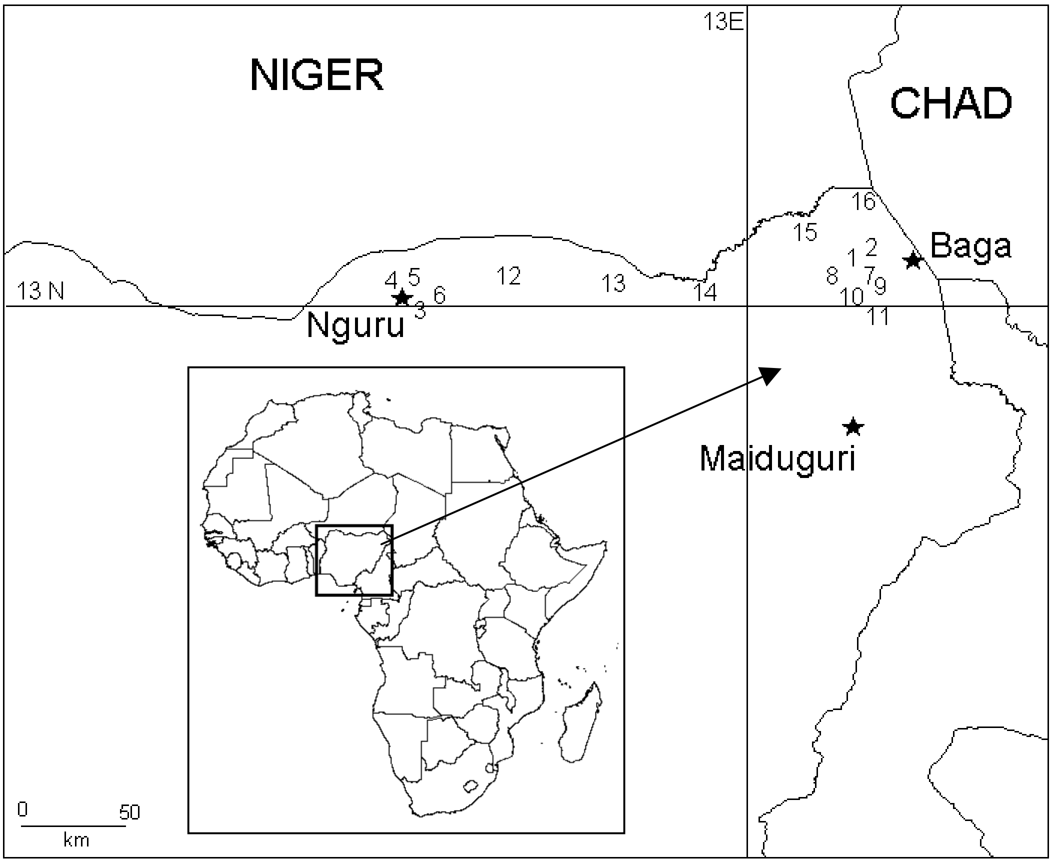

NIGER
CHAD
13E
13 N
Nguru
Baga
Maiduguri
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
0
50
km

Figure 2:

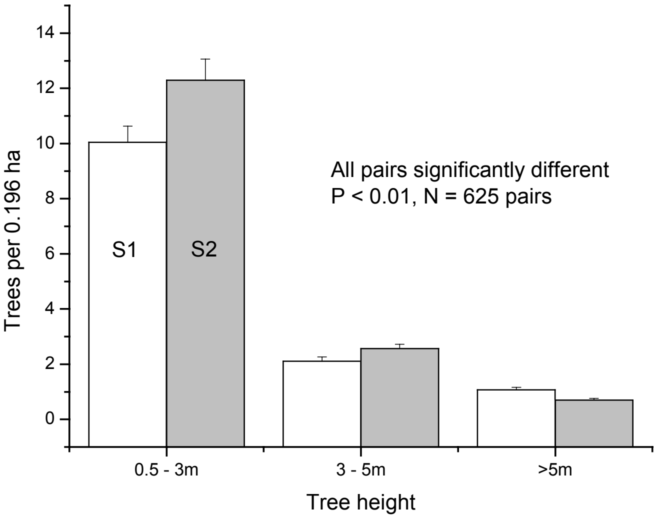

Trees per 0.196 ha
14
12
10
8
6
4
2
0
S1
S2
All pairs significantly different
P < 0.01, N = 625 pairs
0.5 - 3m
3 - 5m
>5m
Tree height

Figure 3:

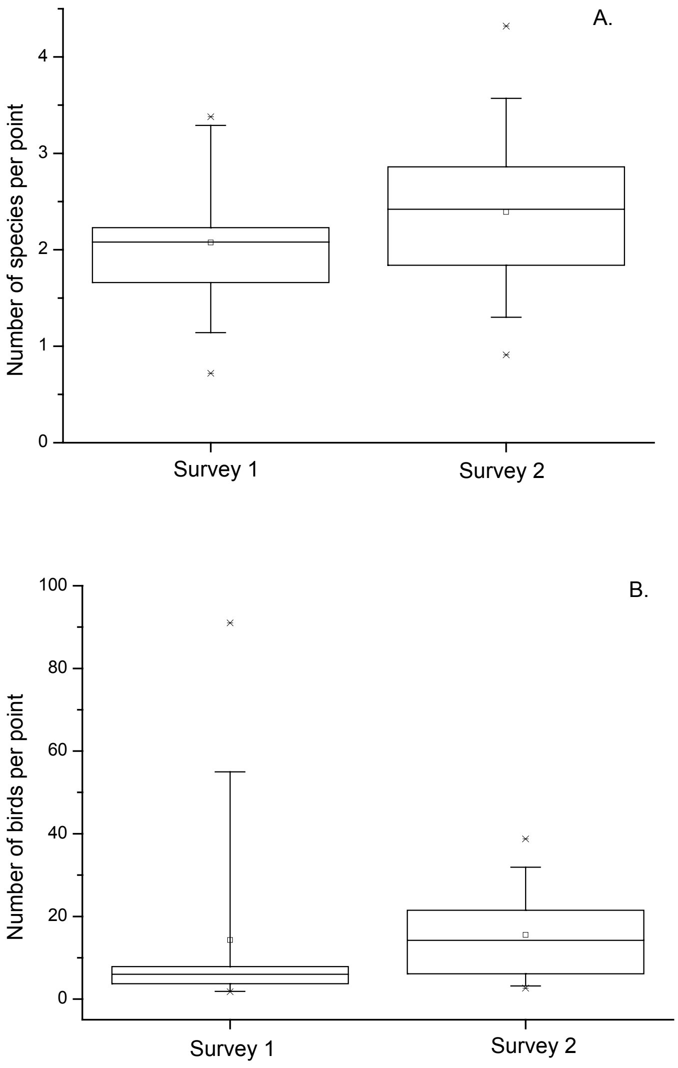
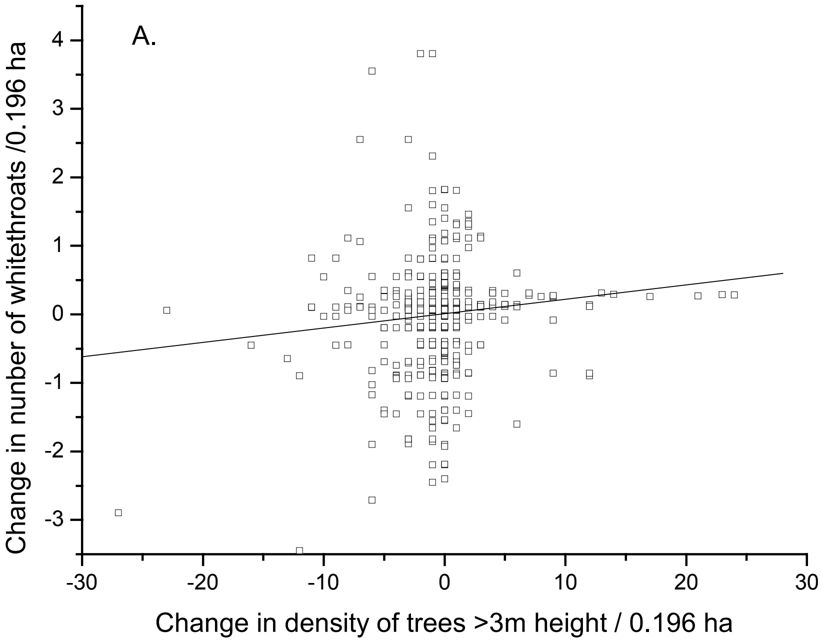
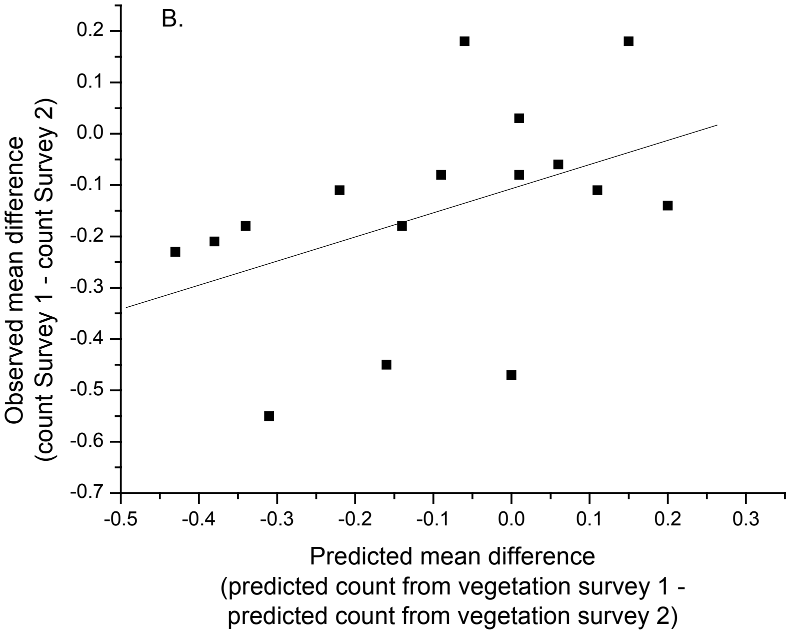

A.
Number of species per point
0
1
2
3
4
Survey 1
Survey 2
B.
Number of birds per point
0
20
40
60
80
100
Survey 1
Survey 2

Figure 4:


A.
Change in nunber of whitethroats /0.196 ha
Change in density of trees >3m height / 0.196 ha
4
3
2
1
0
-1
-2
-3
-30
-20
-10
0
10
20
30


B.
Observed mean difference
(count Survey 1 - count Survey 2)
Predicted mean difference
(predicted count from vegetation survey 1 -
- predicted count from vegetation survey 2)
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.5
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3

Appendix Table 1

Species		Survey 1 Total count	Total points	Survey 2 Total count	Total points
Grey Heron	*Ardea cinerea*	2	2	0	0
Black-headed Heron	*A.melanocephala*	1	1	0	0
Intermediate Egret	*Egretta intermedia*	1	1	0	0
Cattle Egret	*Bubulcus ibis*	23	6	16	3
Spur-winged Goose	*Plectropterus gambensis*	38	6	0	0
Osprey	*Pandion haliaetus*	3	3	0	0
Bateleur	*Terathopius ecaudatus*	1	1	0	0
Yellow-billed Kite	*Milvus migrans*	2	2	7	7
Marsh Harrier	*Circus aeruginosus*	7	7	0	0
Montagus Harrier	*C. pyargus*	4	4	2	2
Pallid Harrier	*C. macrourus*	18	18	6	6
Short-toed Eagle	*Circaetus gallicus*	1	1	1	1
Black-shouldered Kite	*Elanus caeruleus*	1	1	0	0
Gabar Goshawk	*Micronisus gabar*	3	3	0	0
Dark Chanting Goshawk	*Melierax metabates*	13	12	4	4
Tawny Eagle	*Aquila rapax*	1	1	0	0
Booted Eagle	*Hieraaetus pennatus*	2	2	1	1
Eurasian Kestrel	*Falco tinnunculus*	6	6	2	2
Lesser Kestrel	*F. naumanni*	26	9	0	0
Peregrine Falcon	*F. peregrinus*	5	3	3	2
Lanner Falcon	*F. biarmicus*	2	2	4	4
Red-necked Falcon	*F. chiquera*	1	1	1	1
Clappertons Francolin	*Francolinus clappertoni*	3	3	1	1
Quail-Plover	*Ortyxelos meiffrenii*	1	1	0	0
Common Quail	*Coturnix coturnix*	2	2	1	1
White-bellied Bustard	*Eupodotis senegalensis*	0	0	2	1
Black-headed Lapwing	*Vanellus tectus*	35	17	33	18
Green Sandpiper	*Tringa ochropus*	1	1	0	0
Ruff	*Philomachus pugnax*	7	1	0	0
Chestnut-bellied Sandgrouse	*Pterocles exustus*	14	5	1	1
Speckled Pigeon	*Columba guinea*	11	5	3	3
African Collared Dove	*Streptopelia roseogrisea*	133	78	212	127
African Mourning Dove	*S. decipiens*	1	1	33	24
Vinaceous Dove	*S. vinacea*	0	0	26	20
Laughing Dove	*S. senegalensis*	35	26	44	34
Namaqua Dove	*Oena capensis*	66	42	110	69
Black-billed Wood Dove	*Turtur abyssinicus*	0	0	2	2
Rose-ringed Parakeet	*Psittacula krameri*	20	6	6	2
Senegal Coucal	*Centropus senegalensis*	8	6	4	4
Palm Swift	*Cypsiurus parvus*	25	13	0	0
Blue-naped Mousebird	*Urocolius macrourus*	211	50	44	23
Striped Kingfisher	*Halcyon chelicuti*	0	0	2	2
Blue-cheeked Bee-eater	*Merops persicus*	0	0	39	24
White-throated Bee-eater	*M. albicollis*	0	0	2	1
Little Green Bee-eater	*M. orientalis*	17	17	14	11

Abyssinian Roller	*Coracias abyssinicus*	20	17	10	10
Black Wood Hoopoe	*Rhinopomastus atterimus*	2	2	0	0
Green Wood Hoopoe	*Phoeniculus purpureus*	1	1	0	0
Hoopoe	*Upupa epops*	22	19	22	17
Grey Hornbill	*Tockus nasutus*	35	20	7	5
Red-billed Hornbill	*T. erythrorhynchus*	73	39	172	44
Vieillots Barbet	*Lybius vieilloti*	48	28	6	5
Yellow-breasted Barbet	*Trachyphonus margaritatus*	13	8	0	0
Grey Woodpecker	*Dendropicus goertae*	3	3	6	3
Wryneck	*Jynx torquilla*	4	4	1	1
Singing Bush Lark	*Mirafra cantillans*	9	5	2	2
Crested Lark	*Galerida crisata*	28	25	34	29
Greater Short-toed Lark	*Calandrella brachydactyla*	0	0	11	5
Black-crowned Sparrow Lark	*Eremopterix nigriceps*	12	9	13	8
Chestnut-backed Sparrow Lark	*E. leucotis*	79	50	55	35
Common Sand Martin	*Riparia riparia*	216	8	1337	14
Ethiopian Swallow	*Hirundo aethiopica*	108	11	82	19
Tree Pipit	*Anthus trivialis*	0	0	9	1
Red-throated Pipit	*Anthus cervinus*	1	1	0	0
Plain-backed Pipit	*Anthus leucophrys*	1	1	10	7
Yellow Wagtail	*Motacilla flava*	1289	141	168	95
Common Redstart	*Phoenicurus phoenicurus*	3	3	3	3
Rufous Scrub Robin	*Cercotrichas galactotes*	20	20	12	12
Black Scrub Robin	*C. podobe*	96	95	32	28
Isabelline Wheatear	*Oenanthe isabellina*	2	2	6	6
Northern Wheatear	*O. oenanthe*	222	218	120	115
Black-eared Wheatear	*O. hispanica*	4	4	2	2
Nothern Anteater Chat	*Myrmecochicla aethiops*	5	2	2	1
Olivaceous Warbler	*Hippolais pallida*	160	160	169	165
Icterine Warbler	*H. icterina*	0	0	1	1
Lesser Whitethroat	*Sylvia curruca*	98	98	37	37
Common Whitethroat	*S. communis*	155	155	271	264
Orphean Warbler	*S. hortensis*	5	5	8	7
Subalpine Warbler	*S. cantillans*	193	192	86	84
Western Bonelli's Warbler	*Phylloscopus bonelli*	24	24	1	1
Wood Warbler	*P. sibilatrix*	0	0	1	1
Willow Warbler	*P. trochilus*	1	1	6	6
Yellow-bellied Eromemola	*Eremomela icteropygialis*	7	7	20	13
Buff-bellied Warbler	*Phyllolais pulchella*	0	0	21	11
Northern Crombec	*Sylvietta brachyura*	17	17	7	6
Grey-backed Camaroptera	*Camaroptera brachyura*	14	11	9	9
Tawny-flanked Prinia	*Prinia subflava*	3	3	1	1
Cricket Warbler	*Spiloptila clamans*	77	63	45	34
Desert Cisticola	*Cisticola aridulus*	2	1	6	6
Zitting Cisticola	*C. juncidis*	2	2	2	2
Yellow Penduline Tit	*Anthoscopus parvulus*	0	0	9	3
Sennar Penduline Tit	*A. punctifrons*	4	4	0	0
Pygmy Sunbird	*Hedydipna platura*	36	34	16	13
Beautiful Sunbird	*Cinnyris pulchellus*	18	16	4	3

Variable sunbird	*C. venustus*	0	0	2	2
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	3	3	0	0
Woodchat Shrike	*Lanius senator*	21	21	17	16
Masked Shrike	*L. nubicus*	1	1	1	1
Southern Grey Shrike	*L. meridionalis*	148	144	96	92
Brubru	*Nilaus afer*	5	5	9	9
Black-crowned Tchagra	*Tchagra senegala*	2	1	3	3
Fork-tailed Drongo	*Dicrurus adsimilis*	7	7	1	1
Pied Crow	*Corvus albus*	21	16	0	0
Brown-necked Raven	*C. ruficollis*	4	2	9	5
Long-tailed Glossy Starling	*Lamprotornis caudatus*	6	3	19	6
Great Blue-eared Glossy Starling	*L. chalybaeus*	45	23	23	15
Chestnut-bellied Starling	*L. pulcher*	187	65	197	45
Northern Grey-headed Sparrow	*Passer griseus*	90	54	263	117
Sudan Golden Sparrow	*P. luteus*	1489	109	1880	163
Bush Petronia	*Petronia dentata*	16	11	10	7
Chestnut-crowned Sparrow Weaver	*Plocepasser superciliosus*	5	3	0	0
Speckle-fronted Weaver	*Sporopipes frontalis*	38	22	94	40
Little Weaver	*Ploceus luteolus*	21	18	49	37
African Masked Weaver	*P. velatus*	21	12	41	8
Village Weaver	*P. cucullatus*	6	1	1	1
White-billed Buffalo Weaver	*Bubalornis albirostris*	599	57	469	52
Red-billed Quelea	*Quelea quelea*	875	29	26528	279
Northern Red Bishop	*Euplectes franciscanus*	0	0	10	5
Green-winged Pytilia	*Pytilia melba*	11	7	8	4
Lavender Waxbill	*Estrilda caerulescens*	1	1	0	0
Black-rumped Waxbill	*E. troglodytes*	18	1	0	0
Red-cheeked Cordon Bleu	*Uraeginthus bengalus*	107	42	81	61
Red-billed Firefinch	*Lagonosticta senegala*	4	3	11	9
African Silverbill	*Lonchura cantans*	57	17	1	1
Cut-throat Finch	*Amadina fasciata*	12	7	6	3
Sahel Paradise Wydah	*Vidua orientalis*	7	7	3	3
Village Indigobird	*V. chalybeata*	2	1	1	1
White-rumped Seedeater	*Serinus leucopygius*	17	11	15	8
African Golden-breasted Bunting	*Emberiza flaviventris*	0	0	1	1
Points with no species		0	48	0	64

APPENDIX 3

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Movements of Palearctic and Afrotropical bird species during the dry season (November-February) within Nigeria

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That wintering Palearctic migrants and Afrotropical bird species make migratory movements during the dry season within West Africa, and that Palearctic migrants are commonest at more northerly latitudes is well established, but there are actually very few studies that have quantitatively measured this change in the distribution of bird species within a season and with latitude. We recorded bird species in 25-40 point counts carried out at each of 17 sites spread from the Sudan savannah zone of northeast Nigeria to the forest zone of southeast Nigeria, in the early dry season in November 2007 and again in the late dry season in February 2008. Of the species recorded often enough to test distribution changes between the surveys, for 9 Palearctic migrant species, 22% (Subalpine Warbler and Woodchat Shrike) moved south, and 33% (Common Whitethroat, Tree Pipit and Willow Warbler) moved north, and for 63 Afrotropical species, 22% moved south, 14% moved north and 13% changed their distribution with no clear pattern of northward or southward movement. There was no significant difference in average latitudinal shift between terrestrial Palearctic and Afrotropical species. The number of terrestrial Palearctic migrant species decreased significantly with increasing tree density independent of latitude. Significantly fewer terrestrial Afrotropical species were recorded in the north and with increasing canopy height, and significantly more species in the east, and with increasing tree density. There was a significant difference in the relationship between latitude and number of Afrotropical species over the dry season, with relatively more species in the north in November. Consequently there was a significant increase in the proportion of species that were Palearctic migrants with latitude overall and this relationship was significantly steeper in the late dry season. The proportion of Palearctic migrant species also significantly decreased with tree density, controlling for latitude. The results confirm that some species move during the dry season, but that these movements are species specific rather than any general movement south in response to the greater degree of drying out and habitat deterioration generally accepted to occur at more northerly latitudes as the dry season progresses. The observed pattern of relatively more terrestrial Palearctic species being found in the north is driven by their preference for less dense habitats that occur there, and so Palearctic distribution is likely to become more southerly as deforestation in the region continues.

Introduction

Movements of birds within Africa in response to changing climatic conditions has been observed widely both within and between seasons (Moreau 1972, Sinclair 1978, Pearson and Lack 1992): rainfall patterns vary spatially and temporally in Africa and much bird distribution and movement can be predicted on its basis alone (Cheke et al. 2007, Saino et al. 2007, Willis et al. 2007, Wisz et al. 2007). Understanding such patterns is crucial because anthropogenic climate change is predicted to substantially alter rainfall patterns in Africa in the future (e.g. Held et al. 2006). The distribution and shifts of Palearctic migrants in particular are important because many have declining populations (Berthold et al. 1998, Sanderson et al. 2006) which may be dependent on climatic effects such as rainfall affecting wintering habitat quality, for example, Common Whitethroats *Sylvia communis* (Winstanly et al. 1974), Sedge Warblers *Acrocephalus schoenobaenus* (Peach et al. 1991, Foppen et al. 1999), Sand Martins *Riparia riparia* (Bryant and Jones 1995, Szep 1995, Cowley and Siriwardena 2005), Barn Swallows *Hirundo rustica* (Robinson et al. 2003), Purple Herons *Ardea purpurea* (den Held 1981) and White Storks *Ciconia ciconia* (Schaub et al. 2005) . How Palearctics use habitat and change distribution in response to rainfall was thought to be different to Afrotropical species (Lack 1971, Bilcke 1984, Rabol 1987), although later studies suggest that Afrotropical and Palearctic species may have similar ecological requirements (Salewski et al. 2003, Salewski and Jones 2006, Wilson and Cresswell 2007). Detailing any general similarities or differences between the two groups may help us better to predict how populations will change with further anthropogenic effects on habitat and climate in the area, particularly for Afrotropical species that lack the systematic breeding population monitoring typical for many Palearctic species.

There have been few quantitative studies of dry season movements in West Africa, but the general accepted pattern within Africa is that species that are “resident” (i.e. not migrants that follow the rains) may follow the rains in response to habitat degradation as habitats dry out (Moreau 1972, Sinclair 1978). By moving south in West Africa, a bird can move into wetter and so more productive areas, or where wetter areas remain, species can remain in more northerly areas throughout the dry season. This pattern is thought also to apply to Palearctic migrants that spend the dry season in West Africa (Morel and Morel 1992, Jones 1995). For example, great reed warblers have been shown to move further south in Ghana as the dry season progressed (Hedenstrom et al. 1993). This seasonal movement south may even be more pronounced for Palearctic migrants that are commonest in the drier, northerly areas (Wisz et al. 2007).

In this study we quantify specific and broad scale movement and distribution patterns with latitude over the dry season between November and February within Nigeria, over 7.5 degrees of latitude (825 km). During the dry season, bird species may move south from relatively dry, low rainfall areas of Sudan savannah, that may be more affected by the progressive effects of lack of rain through the dry season, to relatively moister areas of Guinea savannah or tropical rain forest , where the effects of the dry season will be less severe. We test whether:

1. Species generally tend to move south as the dry season progresses and whether this occurs to the same degree for Palearctic and Afrotropical species.
2. How the distribution of both Palearctic and Afrotropical species can be predicted by latitude and stage of the dry season (and therefore rainfall) independently of habitat characteristics such as tree density and canopy height.

Methods

Field methods

Two largely identical surveys were carried out to record bird species occurrence and relative abundance in November 2007 and February-March 2008. Standard point counts (Bibby et al. 2000) were carried out at 17 sites spread over an 825 km latitudinal spread, from the forest zone up into the northern limit of the Sudan savannah zone in the east of Nigeria (Table 1; Figure 1). Sites were chosen in advance (from prior experience of the area) so that they showed as little tree clearance as possible and so retained tree densities as high as possible for the latitude. The survey was therefore of forested (wooded) “natural” habitats rather than anthropogenically modified habitats, although in practice, most areas surveyed had some degree of recent tree removal. Survey 1 was carried out between 9th to 30th November 2007 and covered 15 sites (not sites 3 and 6) with a single observer, Matt Stevens. Survey 2 was carried out from 26th Feb 2008 to 15th March 2008, with the same points being repeat surveyed at the 15 sites by the same observer Matt Stevens, and new points at two additional sites. Additional point counts were carried out in Survey 2 by Will Cresswell at sites 2-5, and Mark Boyd at sites 5-17.

A new site was surveyed each day with point counts being carried out from dawn until about 09:30. The first point count of the day was selected haphazardly, and then subsequent points were carried out at 100m intervals along a fixed compass bearing measured using a GPS device. Points that occurred within anthropogenically modified areas where trees had been extensively removed (cleared fields, burnt areas etc.) were ignored and the observer moved on to the next point. During a point count single observers recorded all bird species seen or heard within about 2-3 minutes necessary to scan all areas, recording whether an individual bird was seen, heard, in flight and the distance from the observer if a bird was perched and seen (using a laser range finder). The location of the point was marked on the GPS device. After all the points for that morning had been surveyed (i.e. as many as could be fitted in before about 09:30) the observer retraced their steps and estimated tree density and mean modal canopy height for each point. Tree density was estimated by the observer noting a radius of 5-25m around them (using a laser range finder) and then counting all the stems or trunks of trees or shrubs >1m in height within the radius. Mean modal canopy height was the commonest maximum height of tree within a 25m radius of the observer, and so ignored emergents; heights were estimated with a laser range finder or by eye to the nearest 1m. A list of all bird species seen at a site was also kept, e.g. including sightings during transit between points and during the vegetation counting.

Analysis

Most species were recorded only a very few times and so changes in distribution between surveys are likely to simply represent the low probability of recording the species in any case. Therefore analysis was restricted to species that occurred in 10 or more point counts, except for Palearctic species which were of particular interest and relatively uncommon, where analysis was restricted to species that occurred in 2 or more point counts. Changes in distribution between surveys (i.e. dry season movements) were tested by comparing the relative frequency of counts across sites for a species using chi square tests (with continuity corrections for all test where expected values were low as appropriate). Analysis was restricted to the same points repeated by Observer 1 to keep the relative level of effort the same across the two surveys. This method of analysis is unaffected by the different levels of effort used across sites because it tests only whether the relative distribution (rather than absolute abundance) of birds within a survey was the same for the two surveys. This method of analysis also is unaffected by any changes in detectability of species between surveys (e.g. a species may be recorded more at one time of year because it is singing), as long as these detectability changes are uniform across sites. Site 3 (only surveyed in Survey 2) data were pooled with Site 4 data for these analyses because they had almost identical latitude.

Movement trends were compared between Palearctic migrant and Afrotropical species using a General Linear Model, from the data presented in Tables 2 and 3. The dependence of a species' average latitudinal movement on species group (Palearctic versus Afrotropical as a 2-way factor), and latitudinal range, and average latitude (as covariates) was tested. Average latitudinal movement was the mean number of sites moved from the most northerly and the most southerly sites for a species between surveys was calculated (e.g. Little Weaver, Table 2, moved 1 site north for both its northerly and southerly site, so giving an average movement of -1), with north movements being arbitrarily coded as negative, south as positive and no movement as 0. Latitudinal range was the mean of the difference in the site number for northerly-southerly site, for both surveys (e.g. Little Weaver, Table 2, had a span of 4 sites in Survey 1, and 4 sites in Survey 2, hence a mean of 4). Average latitude was the mean of the mid-point site number of a species' range for both surveys (e.g. Little Weaver, Table 2, had a mid latitude of 12.5 for Survey 1 and 13.5 for Survey 2 and so a mean of 13).

Factors influencing the distribution patterns for the total number of terrestrial Palearctic migrant species, terrestrial Afrotropical species and proportion of Palearctic migrant species were tested using Generalised Linear Models. The total number or proportion of species was calculated for each site (N=15 Survey 1 and N = 17 Survey 2). Its dependence on Survey (2-way factor), latitude, longitude, mean tree density (site mean) and mean modal canopy height (site mean) was then tested, including the number of points to control for the potential confounding effects of variable effort affecting the species accumulation curves (see Manu and Cresswell 2007; N = 17– 40 points in total for each site). Whether any relationship between the distribution of species and latitude was the same for both surveys (i.e. a change in north-south distribution over the dry season) was tested by adding the interaction between latitude*survey into the model. Any difference between the relationship between the distribution of species and latitude, that was dependent on whether the species were Palearctic or Afrotropical was tested by adding species group (2-way factor, Palearctic and Afrotropical) and the interaction species group*latitude to the model.

Analyses were carried out using SPSS 15 (www.spss.com). Means are presented as means ± 1 standard error. Note that Figures and the relationships illustrated are for bivariate relationships for simplicity and because they show the approximate biological relationships clearly: strict biological relationships should be taken from the parameter estimates presented in the tables, where the effects of confounding variables are fully accounted for. Species names follow Borrow & Demey (2001).

Results

Movement of species during the dry season

25 terrestrial Palearctic species were recorded: 9 species were recorded frequently enough on point counts to test for changes in distribution across sites. 22% (Subalpine Warbler and Woodchat Shrike) moved south, and 33% (Common Whitethroat, Tree Pipit and Willow Warbler) moved north, with the remaining 55% (Northern Wheatear, Yellow Wagtail, Montagu's Harrier, Tawny Pipit and Pied Flycatcher) not changing in distribution (Table 1). Overall several species were recorded only in Survey 1 (N = 3) or Survey 2 (N = 8), but at such low frequency (e.g. 7 species recorded on only one point count) that any lack of recording of the species in one or the other survey was likely purely to be because of the low chance of recoding rarer species in any case. If we consider species that were recorded in more than 1 point count, then Black Kite was recorded only in Survey 1, and Woodchat Shrike and Subalpine Warbler were only recorded in Survey 2. These species may then represent migrants that use the area surveyed for only part of the dry season. Whinchat was also only recorded on points in Survey 2, but was recorded incidentally during Survey 1 at sites outside of points.

246 species of Afrotropical species were recorded: 63 species were recorded frequently enough on point counts to test for changes in distribution across sites. 22% moved south, 14% moved north and 13% changed their distribution with no clear pattern of northward or southward movement, with the remaining 51% not changing significantly in distribution (Table 2). Overall many species were recorded only in Survey 1 (N = 29) or

Survey 2 (N = 78), but at such low frequency (e.g. 56 species recorded on only one point count) that any lack of recording of the species in one or the other survey was likely purely to be because of the low chance of recoding rarer species in any case. If we consider species that were recorded in more than 5 point counts, then Cinnamon-breasted Rock Bunting and Blue-Headed Wood Dove were recorded only in Survey 1, and Yellow-mantled Weaver, Copper Sunbird, African Palm Swift, Splendid Sunbird, Yellow-billed Kite, Red-throated Bee-eater, Yellow-bellied Hyliota, African Golden-breasted Bunting, and Sudan Golden Sparrow were only recorded in Survey 2. These species may then represent migrants that use the area surveyed for only part of the dry season.

Average movement in latitude during the dry season was not dependent on latitudinal range (Wald $\chi^2 = 0.002$, $P = 0.96$), average latitude (Wald $\chi^2 = 0.24$, $P = 0.62$) or group of species (Afrotropical versus Palearctic, Wald $\chi^2 = 0.42$, $P = 0.52$), and there was no difference between the effects of latitudinal range (range * species group, Wald $\chi^2 = 0.12$, $P = 0.73$) or average latitude (latitude * species group, Wald $\chi^2 = 0.56$, $P = 0.45$) on average movement comparing Afrotropical versus Palearctic species. Therefore, although species may vary in movement patterns during the dry season, there were no clear differences in movement patterns dependent on whether species were Afrotropical or Palearctic.

Distribution patterns

More terrestrial Palearctic species were found in the first survey and there was a trend for the number of Palearctic species to decline with increasing tree density, but there were no significant effects of latitude, longitude or canopy height, controlling for survey effort (Table 4). Both tree density and canopy height were strongly positively correlated and showed a very strong negative relationship with latitude (i.e. denser taller woodland or forest in the south: Fig. 2). There was no difference in any relationship between latitude and number of Palearctic species over the dry season (survey * latitude added to the model in Table 4, Wald $\chi^2 = 1.4$, $P = 0.23$, δAIC = 0.6). A reduced model containing only tree density, survey and number of points resulted in a substantial model improvement (δAIC = -4.8; overall model Likelihood ratio $\chi^2 = 22.0$, $P < 0.001$; survey 1

B = -1.2 ± 0.6, $P = 0.050$, tree density B = -9.2 ± 2.4, $P < 0.001$, number of points B = -0.03 ± 0.05, $P = 0.55$). Tree density remains a significant predictor in this model even if latitude is then added (Wald $\chi^2 = 5.8$, $P = 0.015$, $\delta AIC = 1.9$) so that a clear negative relationship between number of Palearctic species and tree density, independent of latitude, is demonstrated (Fig. 3A).

The number of terrestrial Afrotropical species recorded did not differ between the surveys but significantly fewer species were recorded in the north and with increasing canopy height, and significantly more species in the east, and with increasing tree density (Fig. 3B), controlling for survey effort (Table 5). There was a significant difference in the relationship between latitude and number of Afrotropical species over the dry season, with a weaker relationship during the early dry season, i.e. relatively more species in the north in November (survey * latitude added to the model in Table 5, Wald $\chi^2 = 6.9$, $P = 0.009$, Survey 1 B = 1.8 ± 0.6; overall model Likelihood ratio $\chi^2 = 51.6$, $P < 0.001$, model improvement compared to the model in Table 5 $\delta AIC = -3.3$): Fig. 4A. The decrease in species with latitude for Afrotropical species was significantly different from the lack of any relationship between latitude and number of Palearctic species (group * latitude added to the model structures of Tables 4 and 5, but with total number of species as the dependent variable, with two groups added to the model as a 2-way factor, Palearctic and Afrotropical species, Wald $\chi^2 = 27.7$, $P < 0.001$, Palearctics B = 2.6 ± 0.5; overall model Likelihood ratio $\chi^2 = 158.8$, $P < 0.001$)

Because of the change in Afrotropical species with latitude dependent on the time during the dry season there was a significant increase in the proportion of species that were Palearctic migrants with latitude overall (Table 6) and this relationship was significantly steeper in the late dry season (survey * latitude added to the model in Table 6, Wald $\chi^2 = 4.4$, $P = 0.036$, Survey 1 B = -0.014 ± 0.007; overall model Likelihood ratio $\chi^2 = 29.7$, $P < 0.001$, model improvement compared to the model in Table 5 $\delta AIC = -2.1$): Fig. 4B. The proportion of Palearctic migrant species also significantly decreased with tree density, controlling for latitude (Table 6: Fig. 5).

Discussion

The results of this study indicate that most species remain within their latitudinal range during the dry season and although some species do change distribution significantly during the dry season there is no general southward movement. There is no real evidence for any difference between Palearctic and Afrotropical species in terms of general patterns of dry season movement, although our results confirm that Palearctic species are commonest at higher latitudes in sub-Saharan West Africa. We show that this relationship is, however, driven by Palearctic species' association with habitats of lower tree density that occur more commonly in the North rather than latitude itself.

Limitations of the study

Before discussing the general implications of our results it is important to outline the limitations of this study. Firstly the survey only covered the start and end of the dry season – major movements may have occurred within the two survey period that were not recorded. Some species that exploit northerly latitudes for breeding during the rainy season may not also have migrated by the first survey, so confounding our aim of examining how dry season "residents" change their distribution as the effects of the dry season intensify. Only two species, recorded relatively infrequently on the first survey fitted this pattern however suggesting we can ignore this potential confounding effect. Similarly, the timing of the second survey was sufficiently late that any Palearctic movements north may simply be because migrants may have already started their spring migration. Therefore Common Whitethroat, Tree Pipit and Willow Warbler may actually be largely resident during the dry season. However two well known early migrants , the Subalpine Warbler (see Vickery et al. 1999) and Northern Wheatear, were observed to probably move south and not to move at all respectively, suggesting that large scale northerly movement by Palearctic migrants had not started during the second survey.

Another major limitation of the study is the limited amount of effort: because there is a low probability of recording even common species in any one point count, many less common species were recorded too infrequently to examine changes in distribution. Observer effort is clearly important to get sufficient data: on the second survey there were 2-3 observers compared to the single observer for the first survey. Consequently many more Afrotropical species were recorded in the second survey (78 species only in Survey

2 versus 29 only in Survey 1) and we made many more incidental records of Palearctic migrants (see Table 1, pale grey boxes). Our analysis methods ensured that the confounding effects of observer effort did not bias our detection of changes in distribution for those species where we had sufficient records, but the subset of species analysed is of course biased towards those which were relatively common. Species with low density may be particularly itinerant and be very mobile and/or localised during the dry season: we cannot draw any conclusions about the proportion of the over 100 Afrotropical species and 14 Palearctic species recorded only once or twice during the survey that may have not been “resident” during the dry season.

A final very important limitation of this study is that we have ignored the effects of variation in detectability of species between sites that may have changed between surveys. For example, if trees lost their leaves progressively during the dry season, then bird species at more densely forested southerly sites might become more visible and so be recorded more on the second survey. The species would then appear to be more common in southerly sites in the second survey because of detectability changes not movements. Although such a systematic bias is plausible, we regard it as unlikely. If detectability was a confounding factor in a comparison of counts across sites between surveys, we would predict that within a survey, at some sites, detection distances would change differently to other sites, i.e. a significant interaction between survey and latitude in a model to predict detection distances. This did not appear to be the case. For example, of three species recorded frequently in both surveys and across several sites and so where this idea is testable (see Table 3), there was no significant variation in the distances at which the birds were detected and latitude, dependent on survey (GLM of detection distance by survey with latitude with interaction of survey*latitude included: Vinaceous Dove across 7 sites, survey*latitude, $F_{1,154}$=2.1, P = 0.15; Bush Petronia across 6 sites, survey*latitude, $F_{1,234}$=1.8, P = 0.18; Scarlet-chested Sunbird across 4 sites, survey*latitude, $F_{1,111}$=0.2, P = 0.64). This means that where we could test for any changes in counts across surveys that could be accounted for by detectability changes, we found no evidence to support any change in detectability across sites that *differed* between surveys that would therefore bias our counts.

General implications

Our study has three main results which have general implications for the distribution of West African birds: (i) the lack of any general movement response to the effects of the dry season, (ii) no real difference in movement patterns with latitude between Palearctics and Afrotropical species, and (iii) an association of Palearctic species with habitats with a lower tree density in contrast to more Afrotropical species being found in areas of high tree density.

The lack of any general movement response to the effects of the dry season is counter to previous ideas of southward movement in response to the greater degree of drying out and habitat deterioration generally accepted to occur at more northerly latitudes as the dry season progresses, particularly for Palearctic migrants (Morel and Morel 1992, Jones 1995). Part of this discrepancy may be because our survey did not include the Sahel which has the greatest number of Palearctic migrant species, and also which has the longest dry season: movement south of species from the north of the Sahel during a worsening dry season would not be detected. There is some evidence for this: Subalpine Warblers and Woodchat Shrikes, both Sahelian dry season birds were only found in the most northerly sites in Survey 2, suggesting that their populations had shifted south during the dry season. Nevertheless, such southward shifts were not seen in Common Whitethroat, Tawny Pipit, Northern Wheatear and Yellow Wagtail that are also mainly Sahelian dry season species, although in our survey, recorded in Sudan savannah. Our results suggest, therefore, that movement south during the dry season by Palearctics may be limited to species or individuals that spend the dry season in the Sahel zone, and that most Palearctics are sedentary from November to February. There is emerging evidence that many Palearctic species may be very site faithful during the winter, maintaining winter territories within and between winters (Sauvage et al. 1998, Salewski et al. 2000, 2002). A notable exception in West Africa might however be the Willow Warbler (Salewski et al. 2000, 2002), the Palearctic species that we also found to be the least “resident”, occurring at 2 sites in Survey 1 and an additional 8 sites both north and south in Survey 2.

We found no real difference in movement patterns with latitude between Palearctics and Afrotropical species. This provides further evidence that Palearctic species are not particularly distinct as a group from “resident” Afrotropical species, except that they spend the rainy season in the Palearctic. Whether Palearctic and Afrotropical species are ecologically similar, and in particular how they respond to rainfall within a season, is important if we are to understand how anthropogenic climate change will affect bird populations between seasons. There have been several studies that have examined the ecological relationship between Palearctic migrant and Afrotropical “resident” birds in Africa. Early studies have concluded that Afrotropical species utilise more complex and dense habitats than their Palearctic counterparts (Lack 1971, Bilcke 1984, Rabol 1987), although later studies suggest that Afrotropical and Palearctic species may have similar ecological requirements (Salewski et al. 2003, Salewski and Jones 2006, Wilson and Cresswell 2007). Clarification of this is important because if Afrotropical and Palearctic species are ecologically similar as recent work suggests, and our study provides some additional evidence for this, then Afrotropical and Palearctic species on average may be affected in the same way by climate change acting in the dry season.

Finally, we found an association of Palearctic species with habitats with a lower tree density in contrast to more Afrotropical species being found in areas of high tree density. Neither of these results are surprising: denser tropical forest habitats have the highest bird diversity (Gaston 2000) and Palearctic species are found most commonly in northerly more open woodland habitats (Wisz et al. 2007). What is of greater interest is our result that the commonly observed negative relationship between the number of Palearctic species and latitude between the Sahel and the forest zones of sub-Saharan Africa (Fry 1992) is a function of tree density rather than latitude (and therefore rainfall) per se. Although rainfall primarily determines habitat type, there are strong anthropogenic effects so that, for example, cleared tropical forest may end up as Guninea Savannah. Replacement of dense forest habitat with more open savannah should provide more available habitat for Palearctic species regardless of its latitude. Deforestation within West Africa at lower latitudes may then be promoting Palearctic populations, while reducing Afrotropical forest bird populations. However, deforestation occurs throughout all latitudinal zones in West Africa, and deforestation has been rapid throughout the Sahel through human clearance for fuel wood, grazing, and conversion to intensive agriculture (Grimmett 1987, IUCN 1991, Odihi 2003). For example, in Senegal the extent of *Acacia nilotica* woodland declined by 90% between 1954-1986 (Morel and Morel 1992), with human deforestation leading to a reduction in tree species diversity and a shift southwards of more arid vegetation zones (Gonzalez 2001). In north-east Nigeria, in Borno State there has been a 14% decline in woodland between 1976 and 1995 (Geomatics 1998). Such deforestation coupled with our observation that Palearctic migrants are associated with tree density rather than latitude suggest that there may be a shifting southward in the dry season ranges of Palearctic migrants. It is entirely possible that such shifting has already occurred, so that we now observe less southwards movement during the dry season because Palearctics now winter further south already.

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Table 1: List of survey sites arranged from North to South. Note that Sites 3 & 4 were approximately at the same latitude and so were pooled into a single Site (4) for Tables 2 & 3.

Site name	Site no.	Degrees North	Minutes North	Degrees East	Minutes East
Wauru	17	13	47.12	5	24.2
Sutti	16	13	18.319	5	7.349
Tsamia	15	12	44.497	5	44.673
Kagara	14	12	18.244	6	5.954
Zugu	13	11	52.244	5	20.04
Zuru	12	11	32.181	5	1.716
Zente	11	10	59.621	5	5.881
Karuni	10	10	27.392	3	52.651
Mah	9	9	57.773	4	1.976
Boriya	8	9	21.807	3	10.119
Tumbaya	7	8	55.285	3	19.018
Old Oyo	6	8	36.037	3	48.772
Igbojaya	5	8	16.114	3	14.62
Maya	4	7	29.658	3	22.071
IITA	3	7	29.583	3	53.154
Omo	2	6	55.109	4	19.166
Okomu	1	6	21.357	5	20.228

Table 2: Distribution of Palearctic species across 17 sites from the north to south of Nigeria at the start (Survey 1, November) and the end (Survey 2, February) of the dry season. The table is arranged in order of decreasing latitude from left to right. The final column shows the significance of changes in distribution (chi-square tests of counts by site): * P < 0.05, ** P < 0.01, *** P < 0.001; S moving South and N moving North on average, 0 "resident", - insufficient data. The numbers within the grey boxes represent the total counts within the repeated points by Observer 1 and so are directly comparable.

Species and survey		NORTH													SOUTH			Move-ment
		17	16	15	14	13	12	11	10	9	8	7	6	5	4	2	1	
░ Subalpine Warbler	1												☐					S
	2	2			░													-
Booted Eagle	1	░											☐					-
☐ Black Kite	1	8											☐					-
Europ. Bee-eater	1	░	░										☐					-
Northern Wheatear	1		2	░									☐					0
	2	3	1	░	░	░	░											
Yellow Wagtail	1		3	░									☐					0
	2		1															
░ Woodchat Shrike	1												☐					S
	2	2	3	3			░											*
Marsh Harrier	1		░		░	░						░	☐					
	2		1															-
Isabelline Shrike	1		1										☐					-
Montagu's Harrier	1		░	1									☐					0
	2		5		░										░			
Tawny Pipit	1		░	4	░								☐					0
	2	░	1	6	2													
Short-toed Eagle	1			░									☐					-
Pallid Harrier	1			░									☐					-
☐ Barn Swallow	2			1														-
▓ Common Whitethroat	1		11	░	2	1							☐					N
	2	9	3	░	1	1	░	░	░	░	░	░	░					**
Bonelli's Warbler	2				1													-
Redstart	2						1						☐					-
European Roller	1									░								-
▓ Tree Pipit	1					░			2		8	1	☐					N
	2					3				░	1	1	8	░	░			*
Pied Flycatcher	1								1				☐	2				0
	2									░	1		1	1	░			
▓ Willow Warbler	1												☐	░	3			N
	2							░	2	1	1	░	1	5	2	░	░	*
Spotted Flycatcher	1												☐	2				-
	2												░	2				
Icterine Warbler	2													░				-
Wryneck	2													░				-
Whinchat	1											░	☐					-
	2													░	1			
Garden Warbler	1														1			-

☐ Migrant	*Recorded during points*	▓	*Additional records*	░
▓ Moving north	*Nov 2007 survey*	1	*Feb 2008 survey*	2
░ Moving south	*Not surveyed*	☐		

Table 3: Distribution of Afrotropical species across 17 sites from the North to South of Nigeria at the start (Survey 1, November) and the end (Survey 2, February) of the dry season. The table is arranged in order of decreasing latitude from left to right. The final column movement shows significance of changes in distribution (chi-square tests of counts by site): * P < 0.05, ** P < 0.01, *** P < 0.001; S moving South and N moving North on average, 0 "resident". The numbers within the grey boxes represent the total counts within the repeated points by Observer 1 and so are directly comparable.

		NORTH													SOUTH			Move-
Species and survey		17	16	15	14	13	12	11	10	9	8	7	6	5	4	2	1	ment
Northern Grey-headed Sparrow	1	20	1	1	7													S
	2	13		5	12	6												*
Eurasian Kestrel	1	1	1															0
	2	19	3															
Pied Crow	1	1					3											M
	2	388	377															***
African Silverbill	1	5		2														S
	2	1	5			6												***
Sudan Golden Sparrow	1																	S
	2	23	197		129													***
Rufous Scrub Robin	1			1	3													0
	2	2	2	6	1													
Chestnut-bellied Starling	1		4	11	14		6											N
	2	7	8	12	36													**
Laughing Dove	1	3			12	1	3	4										0
	2	7	2		7	1		3		3		1						
Northern Red Bishop	1	15	45	19			8											S
	2					9												***
Abyssinian Roller	1		1															S
	2	2	10		5		6	3	3	1	1	2						***
Namaqua Dove	1		2	4	2		1											0
	2		1		4		1	2										
Chestnut-backed Sparrow Lark	1		1	1	4	3	8											S
	2		2		2	3	1	7										*
Speckle-fronted Weaver	1		1		20		3			2								N
	2	2			32	4												*
Little Weaver	1				2		4	1										N
	2			4		5	2											**
Red-billed Hornbill	1		2	8	12	6		4	1		1							0
	2		3	1	7	5		3	1									
Yellow-crowned Gonolek	1			21	2	5			2									M
	2																	**
Cinnamon-breasted Rock Bunting	1					1	12	13										N
	2																	***
Yellow-billed Shrike	1		6	4	1	2					6	5						M
	2				1						8							*
Senegal Eremomela	1			2			6	7		4	3							S
	2			8		12	43	6	3	14			5					***
Vieillot's Barbet	1					3	3		1	2								0
	2					3	1			2								
Vinaceous Dove	1		3	15	17	5	12	13	14	8	3	7						S
	2	1	7	4	8	10	25	47	16	12	1	1	6	3	8			***
Red-cheeked Cordon-bleu	1			2		17	8	1	6									0
	2				1	7			6						1			
Brubru	1						4		2	1								0
	2					1			3	3								
Pygmy Sunbird	1			1	1	1	15	2	4	27								S
	2					16	4	4	8	37	5	7	2					***

Lesser Blue-eared Glossy Starling	1			1					2	7								0
	2									7								
Rufous-crowned Roller	1				5			1										S
	2						1		1				1					*
Tawny-flanked Prinia	1		1	1					5	2	7	6			7			N
	2	2			1	1	7	░	3	1	4	2	2		4			*
Black-crowned Tchagra	1		1	12			4	1	1	4		1		1	4			0
	2		1	░				░		1			2		2			
Black-billed Wood Dove	1				1	5	2	2	9		1	2		1	2			0
	2				░	2	░	3		1								
Yellow-fronted Tinkerbird	1					3	1	6	4		1	2						0
	2			1		9		1	3					1				
Fork-tailed Drongo	1			3	3	3	1	8	2	4				1				0
	2			12	1	3	9	9	6	5			3	░	3			
Grey-backed Camaroptera	1		2	11	1	6	2	3	14	2	4			9	5			S
	2				1	5		2	8		1		4	2	10	░		*
African Grey Hornbill	1			2	3	5		3	6			16		3	5			0
	2			2	1	5		6	2	1	2	7	3	7	9	░		
Bush Petronia	1			1	44	17	24	81	19	62	20	16			3			N
	2			2	95	9	3	56		6	5	17	6		1			***
Senegal Parrot	1					7	4	1	4	5		1						S
	2					5	8	1		15	3	░		2				*
Green Woodhoopoe	1					2	2				7				1			N
	2			░	10		3		3		3	11	3					***
Variable Sunbird	1		1	1			1		3						8			M
	2						2				7		4	3	2			**
Common Bulbul	1			2		8	1		15	6	9	12		12	39			S
	2					1	░		20	2	1		6	35	37	░		***
White Helmetshrike	1					9								11	4			M
	2					6	7	9	10			3		1				***
Senegal Batis	1									2		1						0
	2					5		░		3	1		4					
Scarlet-chested Sunbird	1					19	5	1	13	7	34	8		1	6			M
	2					15	░	18	27	5	10	2	9	░	3			***
Senegal Coucal	1				2				1	1	2	2			2			0
	2									1			3	2	░	░		
Cattle Egret	1											2						N
	2					3					17	5	1	1	░			*
Western Grey Plantain-eater	1					2					1	1		2	1			0
	2								2	2	2	6			3			
Double-spurred Francolin	1					4	1		2	3	8	7		3				S
	2										3	7		░	16			***
Short-winged Cisticola	1										3			1	2			0
	2							1	1	1			3					
African Thrush	1										2			1	1			0
	2					3					1		1	4	3			
African Golden Oriole	1					2			5	1	1				2	2	1	N
	2						░	8	1	2	6	2	2	1	5		1	**
Splendid Sunbird	1																	M
	2											4	5	12				***
Red-eyed Dove	1								3		1	2		4	7			M
	2														2			*
African Paradise Flycatcher	1								3					6	1			0
	2													2			1	
Square-tailed Drongo	1													8	2			0
	2													3	4			
African Green Pigeon	1														7	3	4	0
	2										2	2			3	6	1	
African Pied Hornbill	1													1		1	1	0
	2											░		4	5	1	░	
Collared Sunbird	1													1		1	1	0

	2			6	6	1		
Yellowbill	1		☐	1		1	2	0
	2			1	2		4	
Red-bellied	1		☐			1	2	0
Paradise Flycatcher	2			1	5	4	2	
Piping Hornbill	1		☐		2	4		0
	2				░	12		
Yellow-throated	1		☐			16		0
Tinkerbird	2					1		
Western Nicator	1		☐			4	4	0
	2				2	1	5	
White-thighed	1		☐			4	17	0
Hornbill	2						3	
Tambourine Dove	1		☐			8	2	0
	2					░	1	
African Grey Parrot	1		☐				13	0
	2						2	

☐ Migrant	*Recorded during points*	▓	*Additional records*	░	
▓ Moving north	*Nov 2007 survey*	1	*Feb 2008 survey*	2	
░ Moving south	*Not surveyed*	☐			

Table 4: A Generalized Linear Model to test the effects of latitude on the number of Palearctic species recorded across 17 sites in Nigeria during the dry season, controlling for survey (two surveys, Nov and Feb), longitude, mean tree density and mean modal canopy height. Sample unit is the site mean (N = 15 Survey 1, N = 17 Survey 2) calculated from 17 – 40 individual points per site. Variable effort across sites and surveys was controlled for in the model by including the number of point counts undertaken at each site. Significant (or near significant) effects are in bold.

Dependent variable: No. of Palearctic species

Source	Type III			Parameter estimates	
	Wald χ^2	df	Sig.		
(Intercept)	0.31	1	0.58		-2.2 ± 2.9
Survey	**3.8**	**1**	**0.052**	**Survey 1**	**-1.2 ± 0.6**
Latitude	0.43	1	0.51		0.2 ± 0.3
Longitude	0.58	1	0.44		-0.3 ± 0.4
Tree Density	2.5	1	0.11		-6.5 ± 4.1
Canopy Height	0.001	1	0.97		0.002 ± 0.06
No. of Points	0.31	1	0.57		0.03 ± 0.05
				Scale	1.2 ± 0.3

Overall model significance likelihood χ^2 = 23.1, P < 0.001

Table 5: A Generalized Linear Model to test the effects of latitude on the number of Afrotropical species recorded across 17 sites in Nigeria during the dry season, controlling for survey (two surveys, Nov and Feb), longitude, mean tree density and mean modal canopy height. Sample unit is the site mean (N = 15 Survey 1, N = 17 Survey 2) calculated from 17 – 40 individual points per site. Variable effort across sites and surveys was controlled for in the model by including the number of point counts undertaken at each site. Significant effects are in bold.

Dependent variable: No. of Afrotropical species

Source	Type III Wald □^{2}	df	Sig.	Parameter estimates	
(Intercept)	14.9	1	<0.001		45.3 ± 12.8
Survey	0.7	1	0.38	Survey 1	2.3 ± 2.7
Latitude	**21.2**	**1**	**<0.001**		**-5.5 ± 1.2**
Longitude	**5.5**	**1**	**0.019**		**4.1 ± 1.8**
Tree Density	**11.3**	**1**	**0.001**		**59.7 ± 17.7**
Canopy Height	**16.8**	**1**	**<0.001**		**-1.1 ± 0.3**
No. of Points	**15.8**	**1**	**<0.001**		**0.8 ± 0.2**
				Scale	22.5 ± 5.6

Overall model significance likelihood □^{2} = 45.3, P < 0.001

Table 6: A Generalized Linear Model to test the effects of latitude on the proportion of Palearctic species recorded across 17 sites in Nigeria during the dry season, controlling for survey (two surveys, Nov and Feb), longitude, mean tree density and mean modal canopy height. Sample unit is the site mean (N = 15 Survey 1, N = 17 Survey 2) calculated from 17 – 40 individual points per site. Variable effort across sites and surveys was controlled for in the model by including the number of point counts undertaken at each site. Significant effects are in bold.

Dependent variable: Number of Palearctic species/total number of species

Source	Type III			Parameter estimates	
	Wald $\square^2$	df	Sig.		
(Intercept)	0.004	1	0.95		0.023 ± 0.1
Survey	**6.1**	**1**	**0.014**	**Survey 1**	**-0.062 ± 0.02**
Latitude	**5.3**	**1**	**0.022**		**0.026 ± 0.01**
Longitude	2.1	1	0.15		-0.024 ± 0.01
Tree Density	**5.1**	**1**	**0.024**		**-0.37 ± 0.16**
Canopy Height	2.0	1	0.16		0.003 ± 0.002
No. of Points	1.3	1	0.24		-0.002 ± 0.002
				Scale	0.002 ± 0.001

Overall model significance likelihood $\square^2$ = 25.6, P < 0.001

Figure Legends

Figure 1: A map of the location of study sites (1-17) in Nigeria. The shaded scale on the right indicates the approximate location of the major habitat divisions (darkest – forest zone, mid tone – Guinea savannah, light tone – Sudan savannah).

Figure 2: The relationship between mean modal canopy height ($y = -3.2x + 42.6$, $F_{1,16} = 24.7$, $P < 0.001$, adj. $R^2 = 0.60$) and tree density ($y = -2.7x + 41.7$, $F_{1,16} = 14.8$, $P = 0.002$, adj. $R^2 = 0.46$) with latitude. Both measures are highly correlated ($R = 0.84$, $P < 0.001$). Note that the axes are reversed so that the effects of latitude can be seen, with up and down equivalent to north to south.

Figure 3: The relationship between the number of (A) Palearctic species ($y = -8.7x + 3.2$, $F_{1,16} = 8.1$, $P = 0.012$, adj. $R^2 = 0.31$) and Afrotropical species ($y = 44.6x + 24.4$, $F_{1,16} = 4.5$, $P = 0.050$, adj. $R^2 = 0.18$) with mean tree density.

Figure 4: The relationship between the number of (A) Afrotropical species, controlling for survey effort (Nov: $y = -0.08x + 2.1$, $F_{1,14} = 12.6$, $P = 0.004$, adj. $R^2 = 0.45$; Feb: $y = -0.12x + 2.3$, $F_{1,16} = 21.9$, $P < 0.001$, adj. $R^2 = 0.57$) and (B) the proportion of Palearctic species (Nov: $y = 0.012x – 0.073$, $F_{1,14} = 4.6$, $P = 0.052$, adj. $R^2 = 0.20$; Feb: $y = -0.023x – 0.15$, $F_{1,16} = 15.2$, $P = 0.001$, adj. $R^2 = 0.47$) with latitude, showing the differences in the relationships with time during the dry season (both pairs of lines are significantly different, see text). Note that the axes are reversed so that the effects of latitude can be seen, with up and down equivalent to north to south.

Figure 5: The relationship between the proportion of Palearctic species ($y = -0.42x + 0.12$, $F_{1,16} = 9.3$, $P = 0.008$, adj. $R^2 = 0.34$) with mean tree density.

Fig. 1

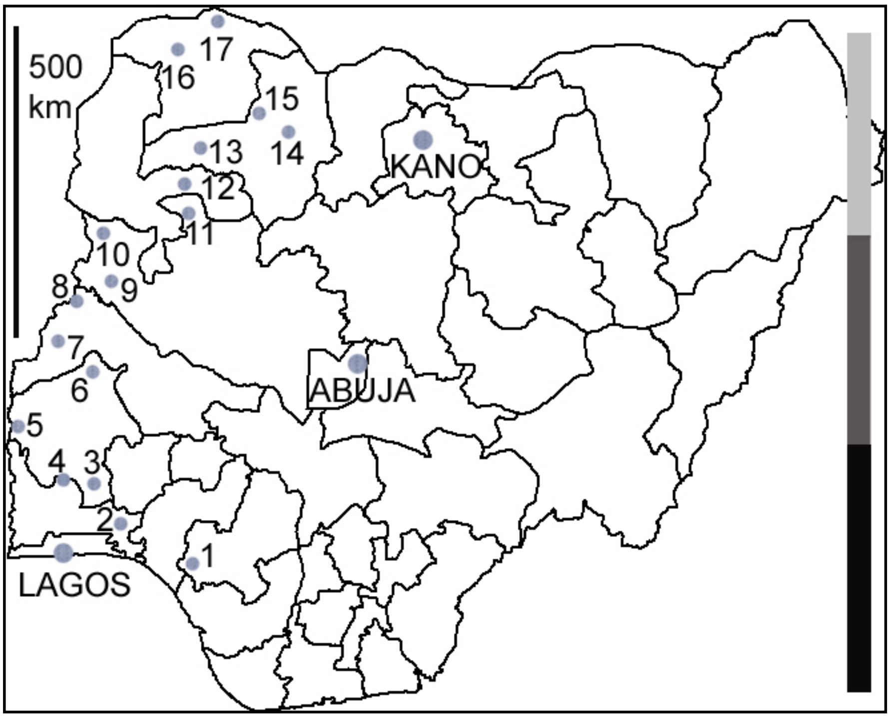


Fig. 2:

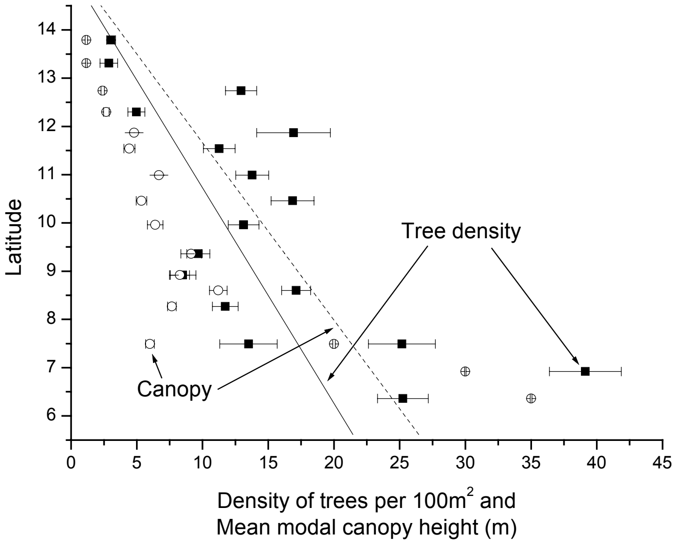
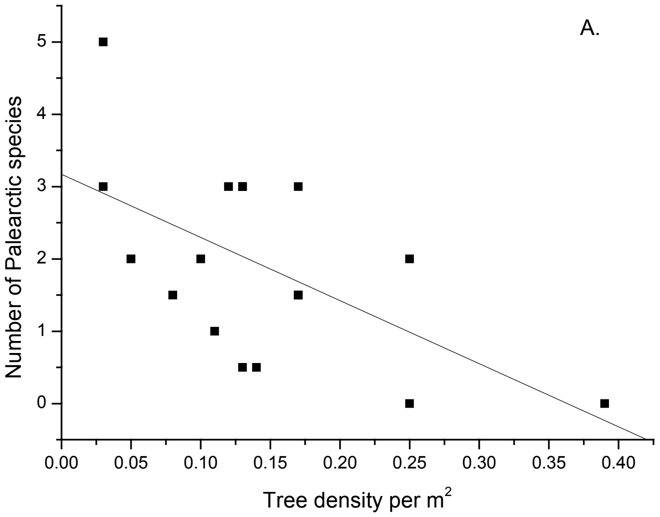

Tree density
Canopy
Latitude
14
13
12
11
10
9
8
7
6
0
5
10
15
20
25
30
35
40
45
Density of trees per $100m^2$ and
Mean modal canopy height (m)

Fig. 3:


A.
Number of Palearctic species
0
1
2
3
4
5
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
Tree density per m^2

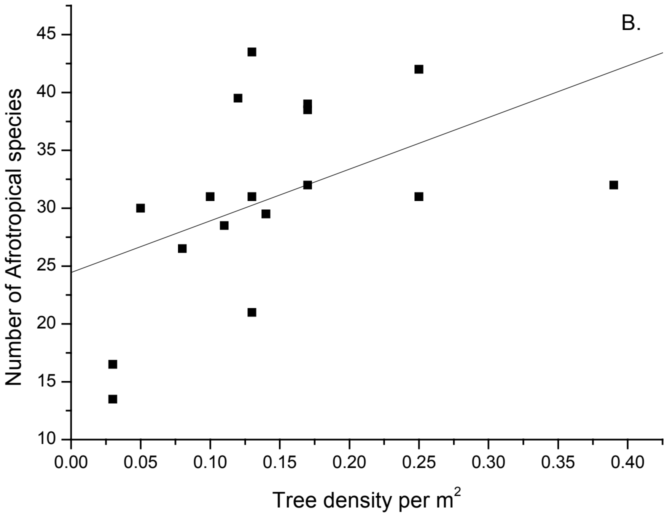

B.
Number of Afrotropical species
10
15
20
25
30
35
40
45
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
Tree density per m^2

Fig. 4:

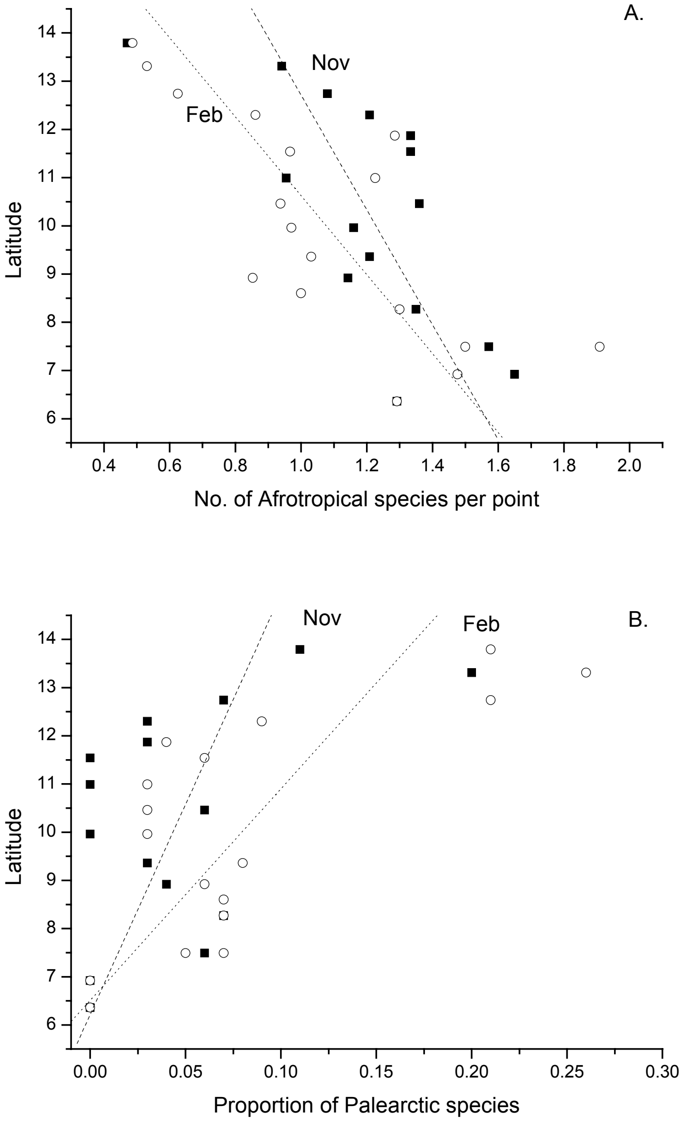
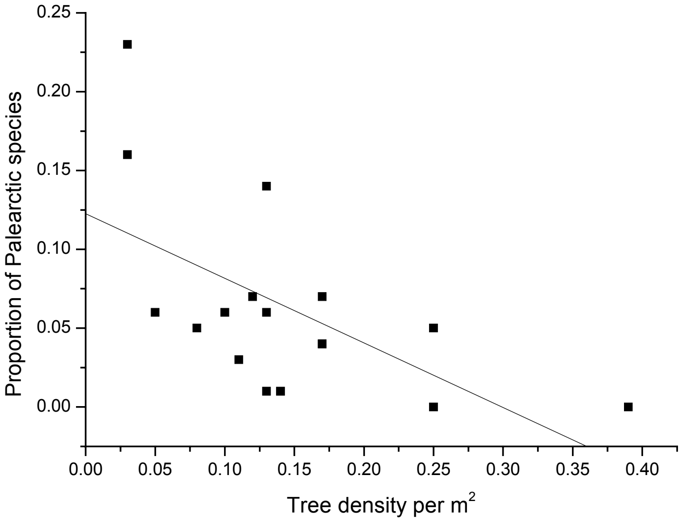

A.
Nov
Feb
Latitude
No. of Afrotropical species per point
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
6
7
8
9
10
11
12
13
14
B.
Nov
Feb
Latitude
Proportion of Palearctic species
0.00
0.05
0.10
0.15
0.20
0.25
0.30

Fig. 5:


Proportion of Palearctic species
0.25
0.20
0.15
0.10
0.05
0.00
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
Tree density per m2