TRADE-OFFS BETWEEN THE RISKS OF PREDATION AND STARVATION IN SUBTROPICAL GRANIVOROUS FINCHES

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Trade-offs between the risks of predation and starvation in subtropical granivorous finches

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Submitted for the degree of Doctor of Philosophy
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for my mum

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Summary

Animal community structures, life histories and individual foraging behaviour are all an outcome of a trade-off between competition for resources (and thus the risk of starvation) and survival (and thus the risk of predation). The relative importance of these factors however, differs between ecosystems, and especially when comparing temperate to tropical ones, we usually find marked differences. The seasonality of tropical ecosystems is much reduced compared to temperate ones, and weather conditions are less extreme. Accordingly tropical systems are characterised by higher species diversity, and different life history traits have been found between temperate and tropical birds. However, how the different environmental factors interact, and how predation and starvation risk vary to cause these differences still remains largely unknown.

We studied the feeding behaviour of several granivorous Estrildid finches in scrub savannah habitat in central Nigeria to test, how they respond to varying degrees of starvation and predation risk. During field observations and aviary experiments we investigated whether there is seasonal variation in the birds' foraging behaviour correlating with the abundance of grass seeds and tested how they respond to different group sizes and differing distances from cover (representing a difference in predation risk). Further we also carried out field observations on the natural feeding behaviour of several closely related sympartic Estrildid finches to investigate inter-specific and seasonal differences in competition and microhabitat choice to see if this could explain their coexistence. Finally we studied habitat choice, movement behaviour and breeding biology of the potentially threatened endemic Rock Firefinch (*Lagonosticta sanguinodorsalis*) between the wet and the dry season via radio-tracking to establish its habitat requirements and gain the first information in its life history traits and population trends.

We found little seasonal variation in the species' foraging behaviour, and parameters that varied did not do so in a consistent manner. Thus, we found little evidence for a seasonal change in the risk of starvation. However, the abundance of several bird species varied widely between seasons and species leaving during periods of food shortage might have released competition for remaining resources. Birds did not show a strong response in their feeding behaviour with respect to cover in either intake rate or timing of feeding. However, intake rate increased with group size, which we believe to be due to scramble competition rather than risk dilution. We therefore conclude that predation did not shape the foraging behaviour of tropical granivorous passerines as markedly as that of temperate ones.

Rock Firefinches were found to breed between the late rainy and the early dry season. They selected inselberg habitat, where most nests were found between rocky boulders. During the dry season, when water sources in inselberg habitat had dried out, they had to fly distances of up to 700 m to the gallery forest to get water and this lead to the inclusion of more scrub savannah and gallery forest within their home ranges. Daily egg survival was 0.89 ± 0.03 calculated after the Mayfield analysis and most failing nests were depredated probably mainly by lizards. We suggest that in addition to nest predation, water availability might limit breeding time and thus reproductive output of Rock Firefinches.

Predation risk did not seem to be of high importance in shaping the birds' feeding behaviour because there was no seasonal variation in the risk of starvation. We found some suggestive evidence that competition might be important and it is likely that bird populations constantly stay close to carrying capacity. In contrast to temperate regions the need to conserve water might be of higher importance in shaping the birds' feeding behaviour. High adult survival rates might be due to reduced seasonality in the risk of starvation thereby leading to reduced predation risk on adult birds. High nest predation might also be of higher importance in shaping the life history traits of tropical passerines, but at present this suggestion remains speculative. The results fit into the general framework that there is a trade-off between starvation and predation risk, and in the absence of starvation risk for some species in tropical areas, predation risk is also relatively unimportant.

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Chapter 1: General introduction

Natural selection favours those individuals that leave the highest number of reproducing offspring, as their genes will be transmitted into the next generation and thus proportionally increase in the population. Life long reproductive success of an individual depends on its breeding output within each season and its survival rate. However, breeding has been shown to be costly in terms of energy expenditure as well as predation risk and thus compromises survival (e.g. Nilsson & Svensson, 1996; Murphy, 2000; Tavecchia et al., 2001; Orell & Belda, 2002). The balance between the energetically conflicting demands of reproducing and surviving is what we refer to as an animals' "life history" (Bennett & Owens, 2002).

While each living organism is constantly faced with the need to acquire enough resources to maintain itself and to reproduce, it has to decide what, when, where and how long to feed, and thereby most organisms are constantly trading off the risk of starvation versus the risk of predation as part of their life history. This is because foraging and avoiding predation are usually mutually exclusive activities. A classic example is the trade-off between foraging and watching for predators, where foraging is usually incompatible with maintaining a high probability of detecting an approaching predator. An animal that forages constantly may not starve but it will almost certainly not detect an approaching predator. Conversely an ever-vigilant animal that may never be surprised and caught by a predator will eventually starve. Therefore all animals have to resolve this conflict and maximise gaining resources while minimising their chance of being depredated.

Following Darwin's theory of evolution we generally assume that natural selection has favoured individuals that have solved such trade-offs in an optimal way so as to maximise their lifelong reproductive success (Perrins & Birkhead, 1983; Krebs & Davies, 1993). Behavioural ecologists have therefore investigated foraging behaviour in terms of optimisation, for example "optimal foraging", which assumes that individuals will maximise gains of energy and nutrients per unit time. If individuals then have complete information and are free to go anywhere this would lead to an "ideal free distribution" (Fretwell and Lucas 1970 cited in Sutherland, 1996), where individuals distribute themselves over food patches so that energy gain will finally be equal in all patches. However, factors such as interference competition and predation risk might change this outcome and have to be added to this model to make it realistic (Sutherland, 1996). Furthermore individuals will differ in competitive ability and susceptibility to predation, such that the optimal solution is not the same for each individual (Sutherland, 1996). By studying individual behavioural components and how they are traded off to optimise fitness, and how these optima change dependent on ecological constraints, it should therefore be possible to better understand how evolution occurs. Conversely, by assuming optimality and determining how the trade-offs are resolved it should also therefore be possible to understand ecological constraints.

As behavioural foraging decisions are usually highly flexible, their prevailing patterns might also provide us with an indication of how strong the relative risks of starvation (and with it the extent of competition) and predation might presently be and allow us to extrapolate onto population levels to deduce what factors might be limiting population densities and determining the structure of animal communities. As Sutherland (1996) pointed out, the knowledge of the behavioural basis of population ecology enables extrapolation to novel conditions like predicting population responses to habitat loss. Incorporating behavioural studies into population ecology should thus increase its overall explanatory and perhaps also predictive power (Sutherland, 1996). Therefore an understanding of how individuals trade-off starvation and predation risk should allow us to better understand and predict the dynamics of populations.

This thesis attempts to measure how tropical birds trade-off the risk of starvation with the risk of predation. Such measurements will allow us to draw conclusions with respect to the evolution of adaptations that reduce predation risk (e.g. flocking behaviour and vigilance) and starvation risk (e.g. competitive foraging interactions and foraging morphology). From this we might be able to infer how selection may act to limit population growth and to promote particular life-history traits. Such measurements will also allow us, under the framework of optimality, to draw conclusions about prevailing ecological conditions that are difficult to measure directly, such as the level of overall predation and starvation risk and its seasonal variation. This is particularly relevant to our understanding of why life-history traits such as clutch size and survival appear to differ fundamentally between temperate and tropical areas.

1.1 Avian life histories

Unlike other vertebrates, birds show a remarkably consistent basic life cycle (Bennett & Owens, 2002). They all lay eggs, deposit them in nests, and with the exception of *Megapodes* all eggs require incubation of an adult bird before chicks hatch. However, there is great variability in the size and number of eggs laid, breeding attempts per year, time required for incubation, developmental state of hatched chicks, time to independence and age at maturation with most diversity occurring between bird families and orders (Bennett & Owens, 2002), but there also is great variability between some closely related species (Martin, 1995; Martin, 2004). The diversity of avian life histories is an outcome of the selective forces of competition and predation. Some of these life-history measures co-vary in a consistent manner: female body weight, egg weight, incubation period, fledging period, age at first breeding and adult survival are positively correlated with each other while adult survival is negatively correlated with annual fecundity and clutch size (Bennett & Owens, 2002). From this results a continuum of life history strategies between two extremes: high adult survival, slow development, delayed breeding, low annual reproductive output on one end (birds living in the slow lane) and low adult survival, fast development, early breeding and high annual reproductive output on the other end (birds living in the fast lane). These two extremes are also frequently referred to as r- and k-selected life histories respectively (Pianka, 1970).

It was hypothesised that this variation in life history traits is simply a by-product of selection primarily acting on body size (Kozlowski, 1996; Kozlowski & Weiner, 1997). However, it has been shown that body size was not correlated with other measures of survival and that life history relationships can be demonstrated independently of body size (Bennett & Owens, 2002). It is therefore more likely that selection is operating on a number of closely linked traits, of which body size is only one factor (Bennett & Owens, 2002). Lack (1948, 1968 cited in Bennett & Owens, 2002) proposed that food limitation is the main selective factor shaping avian life histories and this theory has received support form studies showing that changes in food availability can lead to changes in clutch size (reviewed by Martin, 1987). More recent evidence however, suggests food limitation might be a proximate factor influencing clutch size but nest mortality is the prevailing ultimate factor shaping life histories, and so age-specific mortality schedules are probably the main selective force promoting life history diversity (Cole, 1954 cited in Bennett & Owens, 2002; Charlesworth, 1994). Bennet & Owens (2002) found that the different life histories among ancient bird lineages are linked to different nesting habits such that those with high fecundity and low survival are nesting in relatively risky places such as on the ground and in open nests, whereas low fecundity and high adult survival is linked to nesting in relatively safe places such as in tree holes or bird colonies. Martin (1995) also found that among 123 North American representatives of woodpeckers and passerines high chick mortality is associated with an increase in annual fecundity.

The correlation between measures of fecundity and adult survival may not, however, only be a consequence of reproduction compromising survival, but instead high adult mortality might cause high fecundity as animals with low chances to survive until the next breeding season maximise their current reproductive effort, a phenomenon known from other taxa (Roff, 1992). It has not yet been disentangled in avian life history studies what the relative importance of reproductive costs and extrinsic factors such as predation are in determining adult mortality, but this is an important aspect if we are to understand cause and effect (Martin, 2004). Further, if nest predation mainly acts so as to reduce nest but not adult survival, this may cause birds to spread their reproductive effort over several breeding attempts resulting in smaller clutch size. Martin (1995) found the number of broods to be negatively correlated with clutch size and stated that this was possibly due to an energy trade-off. Re-nesting ability was also found to be the main factor determining annual fecundity in areas with high nest predation (Foster, 1974; Roper, 2005). Crucial to this all is adult survival and therefore we need to understand how predation risk operates in tropical systems.

1.2 Population dynamics

The factors that shape the life history of birds can be, but are not necessarily, the same factors that limit populations. While factors promoting life history diversity have acted over long evolutionary time spans and are thus ultimate factors, those, which presently limit populations can act quite temporarily, might frequently be changing and thus represent proximate factors. Charles Darwin already observed in the “origin of species” 1884: “Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks. … Climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food”. Lack (1954) also suggested that competition for food should be the main factor limiting population. He based this suggestion on the observations that bird numbers and breeding performance frequently correlate with food abundance, that coexisting species differ in their feeding habits and that fighting over food can frequently be observed. However, as Darwin also observed ("... very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species"), predation on adult birds or nests can also act as a factor limiting populations. Accordingly several studies found breeding densities or breeding success to be limited by food abundance, nest predation or nest site availability (reviewed by Newton, 1994), which might point to the fact that population growth could indeed be limited by these factors. Other factors influencing the population dynamics of birds might be disease, parasites and brood parasitism in some cases. However, little evidence for a significant role of these factors in limiting bird populations exists so far.

A species' population size is thus most likely to be limited by competition for food often mitigated by severe weather conditions, or in some cases by predation on adults or nests. If populations are limited by competition for food, the extent of competition naturally depends not only on food abundance and availability but also on the abundance of other species feeding on similar food resources, leading to inter-specific differences that reduce the extent of inter-specific competition. A complex pattern will then evolve from how competition for food is acting or has acted on bird populations in the past, resulting in the diverse range of foraging adaptations that can be observed in coexisting species, and these inter-specific differences in turn will determine the present structure of bird communities. Information on levels of competition and its relative importance with respect to predation is therefore crucial to understanding avian population dynamics in tropical areas.

1.3 Bird communities

As competition for food is the most likely factor limiting the population size of bird species, community patterns are most likely a result of inter-specific competition acting concurrently or in the past (Wiens, 1989). Following the "competitive exclusion principle" (Grinnell, 1904), if two species are feeding on the same food resource, the chances that they are equally well adapted is negligible and thus one species will out compete the other. Therefore species have to differ in some essential way in order to coexist, and a diverse pattern of the food resources species use and where they use them results. Many field studies have demonstrated the importance of inter-specific competition (e.g. Connell, 1983; Schluter et al., 1985) and especially two commonplace observations point to the importance of competition in bird communities: differences among similar species are accentuated where they coexist (“character displacement”) (Lack, 1947a; Schluter et al., 1985), and the absence of one species might lead to the invasion of an ecologically similar species that is otherwise absent (Lack, 1954).

Competition for food differs between seasons and is most likely to act as a limiting factor during winter when food is scarce and the birds’ energy demands are raised or during the breeding season when the demand for food increases as parents have to provision young. It is essential therefore that studies investigating the importance of inter-specific competition consider all seasons.

Many studies have attempted to define the differences in resource use between coexisting species and tried to find corresponding inter-specific differences in morphology (Schluter & Grant, 1984a; Schluter & Grant, 1984b). Inter-specific differences in dominance or escape behaviour and patch specific predation risks may further lead to species-specific foraging patterns or is an axis along which food is partitioned as competition is active (Pulliam & Mills, 1977; Harris, 1984; Kotler, 1984; Lima, 1990; Lima, 1992; Lima, 1993; Suhonen et al., 1993; Krams, 1996; Carrascal & Alonso, 2006). If competition is an active factor shaping bird communities, species should diverge in their resource use as food becomes limiting as, for example, Smith (1978) and Feinsinger (1985) observed in avian communities. Some studies however, found the opposite: species were segregated in their resource use when food was plenty but converged in their resource use when food became scarce (Pulliam, 1985). It must then be concluded that differences between these species might not result from competition being presently active, however, they could be a result from competition in the past. Convergence in resource use also does not prove the absence of competition, bearing in mind that evolution is a dynamic process, because competition might be acting on a trait that has not yet changed.

Predation also might have important implications on community structure. Some species despite being highly competitive might be more susceptible to predation. If a dominant species is limited by predation, the competitive pressure on a less competitive species might decline enabling it to coexist (Wiens, 1989). In such cases predation might promote species diversity and ecologically similar species might be able to coexist as competition for food is released (Ciros-Perez et al., 2004). In other cases however, predation could also decrease species diversity if competitive inferior and therefore rare species are heavily depredated (Wiens, 1989). Clearly, if we are to better understand avian community structure in tropical areas we need to consider both competition for resources and predation risk.

1.4 Foraging behaviour

To understand the selective pressures that currently limit populations, that have resulted in community structure and that might have caused differences in life history traits, it is essential to understand the relative importance of the risk of predation and starvation in determining adult survival rates. This might be inferred from an animal's foraging decisions, as these also are an outcome of the same trade-off between the prevailing risks of predation and starvation. Investigating behavioural responses of individuals to different degrees of competition and predation could therefore enhance our overall understanding of underlying evolutionary processes.

Starvation risk

Starvation risk arises because there are limited resources and other individuals are therefore competing for them: competition is therefore a crucial component of the starvation-predation risk trade-off. Competition occurs where there is a demand of two or more organisms for a resources that is in limited supply such as food, nest sites or living space (Begon et al., 1996). There are two kinds of competition acting on foraging individuals. One type of competition is "depletion competition", where a resource is simply removed by the use of other individuals thus reducing intake rate in that patch. This type of competition will lead to ideal free distribution. "Interference competition" on the other hand, is where intake rate declines because individuals affect each other's foraging success temporarily in ways dependent on the animals' density rather than as a result of simple depletion. Interference competition may occur as individuals defend a resource and fight as one extreme form or simply as disturbance of prey items or hindering each other when crossing each others search pass as a more subtle form (Krebs & Davies, 1993). In the first case the outcome will be an "ideal despotic distribution" where the distribution of individuals over patches depends on the competitive ability of individuals (more dominant ones occupying the more profitable food patches) (Krebs & Davies, 1993).

Predation risk

Predation risk arises because competition for resources means that insufficient time or resources can be allocated to anti-predation behaviours (Lima & Dill, 1990). Variation in predation risk arises because competition varies spatially and temporally and also because the distribution, density and capture success of predators vary spatially and temporally. Even though intake rate between patches might theoretically be equal, a higher predation risk might cause this not to be the case because animals feeding in patches of higher predation risk have lower intake rates when being vigilant (Pulliam, 1973). A high predation risk might completely prevent birds from feeding at otherwise profitable food patches as the need to avoid predation and foregoing future chances to reproduce outweighs the need to maximise energy gain. Predation is therefore a strong factor shaping an animals' foraging decisions and among other things has been shown to have influences on animals' intake rate (Barnard, 1980; Lazarus & Symonds, 1992; Hogstad, 1988; Caraco et al., 1980), patch choice (Hilton et al., 1999; Jones et al., 2001), timing of feeding (van der Veen & Sivars, 2000; Macleod et al., 2005) and fat deposition (Gosler et al., 1995; Piersma et al., 2003). This is not only because longer feeding times increase time exposed to predators but also because carrying high mass may increase predation risk due to reduced escape probabilities (mass dependent predation risk) (Lima, 1986; McNamara & Houston, 1990; Houston & Mcnamara, 1993; Witter & Cuthill, 1993; Brodin, 2001). Increases in the risk of starvation such as during severe weather periods however, might cause individuals to accept a higher predation risk. The outcome depends on the relative importance on the risks of starvation and predation (Hilton et al., 1999).

The feeding and breeding habits of a species as well as the proximately prevailing predation risk on adults and nests and competition for food will determine the population size of a species. Together with the population size of other coexisting species and the extent of differentiation (determining the amount of competition and being a consequence of it) this will then determine the structure of the bird community (Fig. 1).

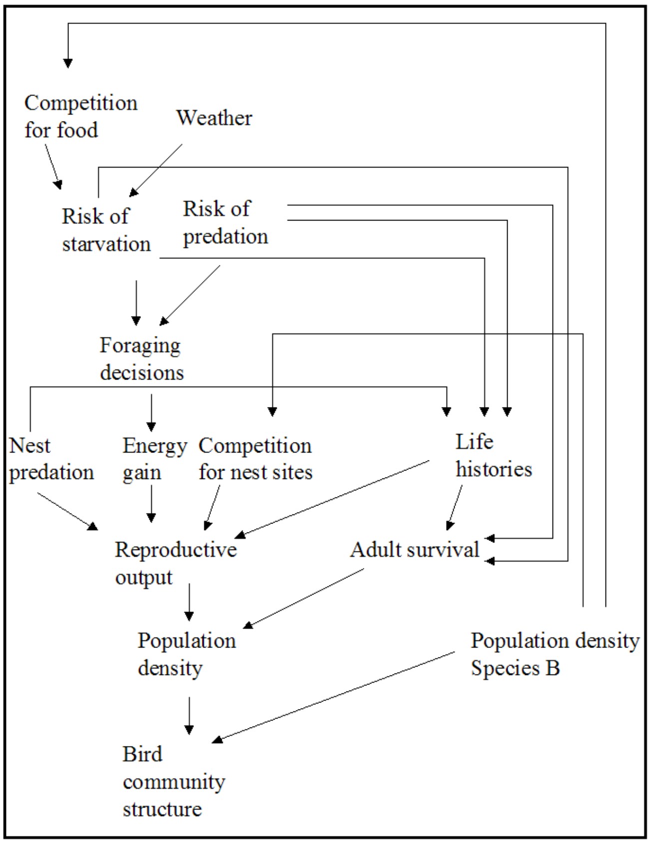

Fig. 1. Simplified flow chart illustrating the connections between individual foraging behaviour, life history strategies, population dynamics and community structure in avian communities.

1.5 Tropical ecosystems

Tropical bird populations and communities

Tropical ecosystems are characterised by much more stable climatic conditions than temperate ones. In temperate regions organisms are faced with severe weather conditions during the winter period and many individuals die during harsh winters due to hyperthermia or starvation. These environmental constraints are largely lifted in the tropics even though the change between the wet and the dry season in the subtropics might pose other seasonally changing demands. However, Dobzhansky (1950) already noted that severe winter conditions in temperate and arctic regions usually destroy great masses of individuals of a species and that this occurs irrespective of individual traits apart from those which enhance coping with such climatic conditions. In the tropics, on the contrary, selection might act on much more detailed differences in traits, because rather than mainly having to cope with climatic conditions, interrelations between competing, symbiotic and parasitic species are a more pronounced adaptive problem.

Dobzhansky (1950) stated that while competition between organisms is usually pronounced, food limitation is less frequent in tropical systems, but he did not state what exactly animals are competing for, other than food. On the contrary Martin (1996) stated that competition for food should be more pronounced in the tropics as populations constantly stay near carrying capacity due to reduced seasonality, such that competition for resources ought to be constant. As a much higher diversity of plants and insects might provide more opportunities for bird species to specialise on particular food resources, higher speciation and diversity might occur. We still know little about levels of competition in tropical avian communities; and to what extent predation might influence community structure in the tropics also still remains largely unknown.

Life histories of tropical birds

Our knowledge of avian life history is largely confined to temperate systems despite the fact that most species actually occur in the tropics (Martin, 2004). From the few studies of avian fecundity and survival in the tropics we have learned that adult survival seems to be higher than in temperate counterparts (Yomtov et al., 1994; Johnston et al., 1997; Geffen & Yom-Tov, 2000; Peach et al., 2001; McGregor et al., in press), clutch size (Lack, 1947b; Cody, 1966; Ricklefs, 1980; Murray, 1985; Skutch, 1985; Cardillo, 2002; Schaefer et al., 2004; for review see Martin, 1996) and annual fecundity (Schaefer et al., 2004) seem to be lower, while there is a longer period of post fledging care (Geffen & Yom-Tov, 2000; Russell, 2000; Russell et al., 2004; Schaefer et al., 2004). So tropical species seem to be living in the slow lane. Adult survival in the tropics might be higher due to reduced fluctuations in starvation risk, less extreme weather conditions and maybe also lower predation risk on adult birds in addition to the possible influence of reduced fecundity. The causes of adult bird mortality in the tropics have seldom been studied and so the relative importance of extrinsic and intrinsic mortality is not known. However, this is crucial to understanding the differences in life history traits (Martin, 2004).

Lower clutch size in tropical birds have been attributed to food limitation during the breeding season (Ashmole, 1963), or higher rates of nest predation (Skutch, 1994; Roper, 2005). However, the latter is contradicted by the above reasoning that high nest predation also decreases adult survival and should thus lead to increased fecundity. If however, nest predation mainly concerned eggs and chicks without effecting adult survival, birds might reduce clutch size in order to enhance re-nesting ability. Roper (2005) indeed found that re-nesting ability was of great importance in the Western Slaty Antshrike (*Thamnoplilus atrinucha*) in central Panama if they are to successfully reproduce. However, Martin (2004) recently stated that nest predation alone can not explain broad latitudinal variation in life-history traits and pointed to the importance of understanding the influence of age-specific mortality as already mentioned above. Studying the differences of these and its correlation with life history traits of birds in the tropics and comparing it to those in temperate regions, where very different mortality schedules will prevail, might hold the key to understanding the evolutionary basis of avian life history traits. We may start by trying to understand why adult survival seems to be higher in tropical areas, and studying the predation – starvation risk trade-off in foraging individuals might help to understand the relative importance of these factors in natural selection.

Foraging behaviour of tropical birds

If there really are major differences in the relative importance of predation and competition in tropical ecosystems, this should also be reflected in an individuals' behavioural adaptations. If competition is strong and the risk of predation relatively light, one would expect birds to react much stronger to the presence of other individuals and react less to differences in predation risk. How tropical passerines respond in their foraging behaviour to differences in predation and competition has rarely been studied. For example, there are only a few studies investigating how intake rate differs with group size (Lazarus, 1979; Hamed & Evans, 1984; Beauchamp & Livoreil, 1997; Slotow & Coumi, 2000) but only Slotow & Coumi (2000) also considered predation risk by considering the influence of distance from cover. It is also unclear if tropical birds respond to changes in food abundance between the dry and the wet season by putting on mass to insure against unpredictable foraging conditions like temperate passerines do in winter, or whether the difference in starvation risk is not large enough to cause this behaviour as expected from reduced seasonality. If predation risk is of little importance, birds might also gain mass earlier in the day in the tropics. If populations really stay close to carrying capacity such that competition for food is important throughout the year, species should be well specialised to what and where they feed, and there should be little overlap in terms of microhabitat choice between species. A reduction in the overlap of resource use should be most pronounced during times when food resources decline.

There are two other factors prevailing in subtropical savannah habitat, which might further influence a birds' foraging behaviour: relatively high midday temperatures and a seasonal difference in the availability of water. Tropical birds might have several physiological adaptations to reduce water loss (Macmillen, 1990; Weathers, 1997; Tieleman & Williams, 1999), nevertheless they largely rely on behavioural adaptations (Weathers, 1997). It might thus be expected that avian foraging behaviour has evolved so as to avoid water loss and overheating. Habitat choice might also be quite different between the dry and the wet season in granivorous birds, that rely on preformed water to a great extent. It would be interesting therefore to investigate if the behavioural outcome of the starvation – predation risk trade-off is different from that of temperate birds that are relatively unconstrained by the availability of water.

1.6 This study

We studied a granivorous bird community in subtropical savannah habitat in central Nigeria (9.87°N 8.98°E) near the city of Jos (Fig. 2), where a marked change between the wet and the dry season, each lasting approximately six months, occurs. The study was carried out in a reserve consisting of patches of scrub savannah, gallery forest and inselberg (rocky outcrops up to 30 m high and covered with grass and scrubs) habitat. Human disturbance within this reserve is minimised and a high bird species diversity exists. The granivorous bird community consists of mainly eight abundant species: five Estrildid finches, two Euplectes weavers, and one Embrezia bunting. However, many less common granivorous species also occur. This provides us with an excellent opportunity to study species interactions and food partitioning and inter-specific differences in the predation – starvation risk trade-off.

During this study we investigated how the density of granivorous food changes seasonally and if several parameters of the birds' foraging behaviour reflect this change. We further investigated how individual birds trade-off the risk of starvation and predation behaviourally by observing their foraging behaviour when feeding at different distances from cover presenting differing predation risks and under different group sizes and food densities that represent different degrees of competition. In temperate birds a marked decline in intake rate with greater distance from cover and lower group size has been observed, both these situations representing increased predation risk. We also investigated whether birds will delay feeding towards later in the day when under higher predation risk as observed in some temperate species. From this we hope to infer the prevailing overall level of predation and competition for food resources and its relative importance in limiting populations and maybe affecting life history traits.

We further investigated food partitioning between closely related coexisting granivorous Estrildid finches, testing whether differences in microhabitat choice are an outcome of inter-specific differences in response to predation risk and competition and whether they are correlated with species-specific bill shapes and dominance. If competition really is more pronounced in tropical ecosystems, little overlap in resource use should occur and species should diverge in resource use if food abundance declines.

Finally we studied habitat choice, movement patterns and breeding behaviour of Rock Firefinches (*Lagonosticta sanguiodorsalis*), between the late wet and the early dry season to test if water availability influences their behaviour and to gain information on their general habitat requirements and life history parameters. The Rock Firefinch is a recently discovered and potentially threatened Estrildid species probably endemic to central Nigeria, which is brood parasitised by the Jos Plateau Indigobird (*Vidua maryae*) (Payne, 1998) and about which little is known in terms of behaviour until today. It is one of the species found to have relatively higher survival rates compared to temperate counterparts (McGregor et al., in press) and by studying its behaviour in more detail we might be able to gain clues about the causes for this. Furthermore we intended to gain more information on its breeding behaviour to test whether its high adult survival rate correlates with relatively low fecundity as is generally assumed, and to see if they also have relatively low clutch sizes as reported for many other tropical passerines.

Summarising we asked the following general questions during this study:

1. Is there a seasonal change in the abundance of granivorous food and if so, will this be reflected in the birds' foraging behaviour (as evident from the extent of feeding, timing of feeding and response to competition and predation)? (Chapter 2)
2. How do bird species respond in their foraging behaviour (patch choice, intake rate and timing of feeding) to increasing group sizes and different distances from cover (presenting differences in predation risk)? (Chapter 2, 3 and 4)
3. Do species differ in how they trade-off the risks of starvation and predation and is this reflected in their choice of feeding microhabitat? (Chapter 3 and 5)

4. Do species segregate in their resource use and microhabitat choice and is this more pronounces during times of lower food availability as expected if it was an outcome of inter-specific competition for food resources? (Chapter 5)
5. What are the habitat requirements of Rock Firefinches and do they change between the wet and the dry season? (Chapter 6)
6. Does the breeding behaviour of Rock Firefinches follow the expected traits typically associated with high adult survival? (Chapter 6)

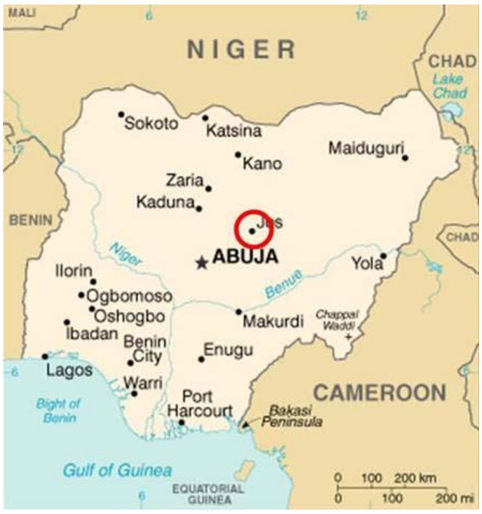

Fig. 2. The circle indicates the approximate location of the study area in Nigeria.

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Chapter 2: Are seasonal constraints on subtropical, granivorous birds evident from variation in feeding behaviour?

Abstract

An animal’s life history traits and its underlying management of resources are an outcome of competition for resources and risk of predation and how this might change over time. Because tropical birds are not subject to a severe cold winter period with low food availability, they were assumed to have life history traits differing from that of temperate birds. However, tropical climates are characterised by a strong seasonality of rainfall, which in turn might be associated with fluctuations in food abundance, especially granivorous food. It is thus not clear that tropical birds are freed from the constraints of seasonal variance in the risk of starvation.

Studies carried out on birds in temperate regions have revealed that during periods of increased starvation risk birds (i) gain more mass as a result of depositing fat reserves, (ii) feed earlier in the day, (iii) show more risk taking behaviour by feeding more often in risky areas (iv), show higher levels of competitive interactions as individuals converge on limited remaining food patches and use provided food more readily and (v) show strongly seasonal periods of breeding and moult coincident with high availability of food resources. If there is seasonal variability of starvation risk in tropical areas, this should then be reflected in similar patterns of resource management and behaviour. We tested these predictions in tropical granivorous bird species inhabiting savannah habitat in central Nigeria.

We predicted fat reserves and mass, risk taking behaviour, use of provided food patches and competitive interactions to peak, group size to be smallest and breeding and moult not to occur during the rainy season when food availability is expected to be lowest.

During the early rainy season birds (i) deposited more fat and gained more mass but this was lost during the late rainy season and remained at roughly similar levels throughout the dry season in most species. Depletion rates of artificial feeding patches differing in predation risk revealed that birds (ii) fed more in the morning than in the afternoon during the late dry season but (iii) did not show seasonal variation in risk taking behaviour (feeding with respect to cover). There was (iv) no consistent seasonal variation in competitive interactions, group size was smallest during the late dry season and consumption of provided food was relatively even during all of the dry and the early rainy season but declined considerably during the late rains. Birds (v) bred during the late rainy season and early dry season and moulted during the early to late dry season.

Results show that although there is significant seasonal variation in some variables, they do not coincide consistently, and there is therefore no strong evidence for seasonal unpredictability in foraging. However, seasonal mass gain and timing of breeding and moulting suggest that tropical granivores may be subject to some seasonal foraging constraints in the early rainy season, however, these might not be strong enough to cause compensation in other behaviours. Furthermore, using depletion rates as indicators of feeding behaviour might not be appropriate in areas of high species diversity and its potential problems and suggested solutions are discussed.

Introduction

An animals’ life history traits and its underlying management of resources are an outcome of competition for resources and risk of predation and how this might change over time. As a consequence, much variation in the life history of animals stems from the extent of seasonality of climate and associated fluctuations in food abundance. Accordingly differences in life history traits of tropical birds from that of temperate birds were attributed to a more stable climate such that birds are not subject to a severe cold winter period when food availability is unpredictable and limited and thermoregulatory costs are raised (Ashmole, 1963). However, even though tropical climates do not undergo extreme temperature changes, they are characterised by a strong seasonality of rainfall, which in turn might be associated with fluctuations in food abundance. In particular tropical granivores may face strong seasonal variation in the risk of starvation as a consequence of a pronounced rainy season resulting in a period between existing seed germination and production of new seed.

Temperate, resident passerines are subject to a strong seasonal climate and adult mortality during winter is high in many species. The time of high food availability and favourable temperatures is short and so the time for reproduction is limited to a few summer months (Stutchbury & Morton, 2001). For tropical and subtropical birds, on the contrary, it was assumed that the constraints of seasonal climate are largely lifted and that this explains their differing life history traits such as higher survival rates (Yomtov et al., 1994; Johnston et al., 1997; Peach et al., 2001; Geffen & Yom-Tov, 2000), lower clutch sizes (Lack, 1947; Cody, 1966; Ricklefs, 1980; Murray, 1985; Skutch, 1985; Cardillo, 2002; Schaefer et al., 2004; for review see Martin, 1996), lower annual fecundity (Schaefer et al., 2004) and a longer period of post fledging care (Geffen & Yom-Tov, 2000; Russell, 2000; Russell et al., 2004; Schaefer et al., 2004). However, low clutch size in temperate birds might be caused by seasonal food limitation (Ashmole, 1963), higher rates of nest predation (Skutch, 1994; Martin, 1996; Roper, 2005) or simply be a consequence of selection for high adult survival (Murray, 1985; Martin, 2002). It thus remains largely unclear to what extent a lack of strong seasonality in temperature and / or food abundance might be responsible for these differing life history traits, and we know little about the importance of these factors in tropical and subtropical ecosystems.

Even though temperature changes in the subtropics might not be that extreme, there is a strong seasonal pattern of rainfall. This is often associated with seasonal variability of food abundance. Insects for instance will be more abundant during the rainy season (Poulin et al., 1992) while granivorous food will be highly abundant during the beginning of the dry season (Crowley & Garnett, 1999) but with the beginning of the wet season seed production ceases and seeds fallen to the ground will germinate or decay. This means that tropical birds experience some seasonal changes and many tropical species have indeed been observed to have distinct breeding seasons (e.g. Cruz & Andrews, 1989; Poulin et al., 1992) as a consequence.

Seasonal variation in food resources or unpredictability in foraging, manifests itself in a number of aspects of an individuals resource management. Studies carried out on birds in temperate regions have revealed that during periods of increased starvation risk birds (i) gain more mass as a result of depositing fat reserves, (ii) feed earlier in the day, (iii) show more risk taking behaviour by feeding more often in risky areas and so deplete these areas to a higher degree, (iv) show higher levels of competitive interactions as individuals converge on limited remaining food patches and use provided food more readily and (v) show strong seasonal periods of breeding and moult coincident with high availability of food resources. If there is seasonal variability of starvation risk in tropical areas, this should then be reflected in similar patterns of resource management and behaviour.

(i) Mass gain

While high mass and fat deposition insures against periods of food shortage, it also carries a cost in terms of mass dependent metabolism (McNamara & Houston, 1990; Witter & Cuthill, 1993; Brodin, 2001) and mass dependent predation (Lima, 1986; McNamara & Houston, 1990; Houston & Mcnamara, 1993; Witter & Cuthill, 1993; Brodin, 2001). This is because a larger body mass is energetically more costly to maintain (Witter & Cuthill, 1993) and as a result a bird has to spent more time exposed while feeding to compensate (Lima, 1986; Brodin, 2001). High mass and fat were also shown to reduce a birds ability to escape predators due to reduced take off speed and manoeuvrability and / or lowered escape angle (Witter et al., 1994; Metcalfe & Ure, 1995; Lee et al., 1996; Lind et al., 1999; but see Kullberg, 1998; Kullberg et al., 1998; Veasey et al., 1998; Van der Veen & Lindstrom, 2000; MacLeod, 2006). Many theoretical studies have demonstrated that reduced food availability or predictability and / or higher energy demands and thus a higher risk of starvation will result in increased mass and fat deposition (Lima, 1986; McNamara & Houston, 1990; Houston & Mcnamara, 1993; Bednekoff & Houston, 1994a; Bednekoff & Houston, 1994b; McNamara et al., 2004). Several empirical studies indeed found that during winter in temperate and arctic regions birds gained more mass (e.g. Rogers, 1987; Haftorn, 1989; Haftorn, 1992; Cresswell, 1998; Macleod et al., 2005a), usually by depositing more fat**,** due to shorter day length and / or low overnight temperatures. Birds also gained more mass in response to unpredictable feeding opportunities (Ekman & Hake, 1990; Bednekoff & Krebs, 1995; Cuthill et al., 2000) and unpredictable temperatures (Bednekoff et al., 1994), while they reduced mass in response to increased overall natural predation risk (Gosler et al., 1995; Piersma et al., 2003) and also to experimentally increased predation risk (Lilliendahl, 1997; Carrascal & Polo, 1999; van der Veen, 1999; Lilliendahl, 2000; van der Veen & Sivars, 2000; Gentle & Gosler, 2001; Rands & Cuthill, 2001; but see Fransson & Weber, 1997; Lilliendahl, 1998; Pravosudov & Grubb, 1998; Bautista & Lane, 2000; andMcNamara et al., 2005).

If granivorous birds in African savannah habitat are faced with a heightened risk of starvation during the rainy season and predation risk remains reasonably constant they should therefore gain more mass and carry higher fat reserves during this time than during the dry season when food is plenty. We tested this by capturing birds and measuring mass and how it varied through the year. It is not enough, however, to only measure mass gain, as mass can be due to several factors such as fat deposition, pectoral muscle, crop content, gut content, water-deposition and also egg production. When capturing birds during the different seasons we therefore measured not only mass but also fat, pectoral muscle and crop content to see how much each of these factors contributes to potential mass changes. We also controlled for sex differences to account for mass changes due to egg production.

(ii) Daily feeding pattern

The relative importance of starvation and predation risk may further influence the daily pattern of mass gain in birds. McNamara (1994) showed that under relatively poor foraging conditions, foraging activity should peak early in the day and then decrease steadily, while under poor foraging conditions a bimodal foraging pattern might occur with peaks at dawn and dusk. Bednekoff & Houston (1994a) also demonstrated that under unpredictable foraging conditions foraging activity should be concentrated early in the day. Blackbirds indeed gained mass early in the morning during winter, while in summer the majority of mass gain occurred at the end of the day (Macleod et al., 2005a). Yellowhammers (van der Veen & Sivars, 2000) and great tits (Macleod et al., 2005b) exposed to a predator postponed mass gain towards later in the day.

If food is limiting during the rainy season, granivorous birds in African savannah habitat would therefore be expected to feed more during the morning hours compared to the afternoon hours, while during the dry season this should be more equal. We tested this by comparing seed depletion rates of birds during the morning and afternoon between the different seasons.

(iii) Risk taking behaviour

As pointed out above, a bird’s mass gain and foraging decisions are an outcome of the relative importance of the risks of starvation and predation. It then follows that when food resources become limiting, birds should show more risk taking behaviour in order to avoid starvation. This might not only show in birds gaining more mass but also in their choice of feeding patches differing in predation risk. Hilton et al. (1999) and Yasue et al. (2003) indeed found that redshanks were more willing to choose feeding patches of higher predation risk when starvation risk was increased due to bad weather conditions.

If there is seasonal variation in food availability for tropical granivorous birds, depletion rates with respect to distance to cover should vary seasonally. We predicted depletion rates to generally be higher next to cover than away from cover but expected this difference to decrease during the rainy season as birds become more willing to accept a higher predation risk in order to avoid starvation.

(iv) Extent of competition and use of provided food

As the risk of starvation and with it the extent of competition for available resources increases, birds are expected to utilise patches of remaining food more and show more aggressive behaviour and / or be less tolerant towards con- and heterospecific birds. Large group sizes decrease predation risk via risk dilution (Hamilton, 1971) and shared vigilance (Pulliam, 1973), but also incur a cost in terms of interference and depletion competition (Cresswell, 1997; Beauchamp, 1998; Cresswell et al., 2001).

If there is seasonal variation in food availability for tropical granivorous birds, they should be expected to trade off the safety of feeding in large groups for decreased competition as the risk of starvation increases. Smaller group sizes and stronger negative associations between species on feeding tables should therefore arise during the rainy season. We tested this by observing the number of birds and their species affiliations on artificial feeding tables at different times of the year.

We also predicted that depletion rates of provided food would vary seasonally. We therefore compared depletion rates between the different seasons to test whether birds fed more on provided food during the rainy season. Competition for small grass seeds, however, is not restricted to birds only. Rodents and ants might also make a considerable contribution to seed depletion. If we want to understand the extent of competition at different times of the year we should also get an idea of how much each of these guilds might contribute to seed depletion. We therefore compared seasonal seed depletion rates between artificial feeding places that were manipulated so that only rodents, ants or birds could access them.

(v) Timing of breeding and moulting

Several studies demonstrated various costs associated with reproduction (Walsberg, 1983; Gustafsson & Sutherland, 1988; Norris et al., 1994; Nilsson & Svensson, 1996; Golet &

Irons, 1999; Tavecchia et al., 2001; Veasey et al., 2001; Orell & Belda, 2002) and moult (Payne, 1973; Walsberg, 1983; Hedenstrom & Sunada, 1999; Hemborg, 1999). Theses activities should therefore be timed to coincide with times of highest food abundance and the least energetic constraints. Accordingly many species of temperate birds were reported to time their breeding and moulting to coincide with the time of the highest food abundance (Payne, 1973; Vannoordwijk et al., 1995; Cresswell & McCleery, 2003).

If there is seasonal variation in food availability for tropical granivorous birds we expect seasonal breeding coincident with the peak of food availability. We thus expected tropical granivorous birds to start breeding during the early dry season when granivorous food becomes abundant and to avoid breeding and moulting during the rainy season.

In summary, assuming that the rainy season is a time of limited food availability, our predictions are that:

(i) Birds will gain more mass (by depositing fat) during the rainy season.
(ii) Depletion rates will be relatively higher during the morning during the rainy season.
(iii) Depletion rates will be relatively higher at the safe patch close to cover but this difference will be less during the rainy season.
(iv) Negative associations between bird species will be strongest and group sizes will be the smallest during the rainy season. Overall depletion rates will be highest during the rainy season.
(v) Birds will time breeding and moult out with the rainy season.

Methods

Data collection

Weather data

Weather data were collected by a Davis Vantage Pro2 weather station within the study area from 08/02/2005 - 13/02/2005 and the 15/04/2005 - 21/02/2006. The period of gathering weather data does not entirely coincide with the time during which data were gathered for depletion rates because the weather station was unavailable in the early stages of the project. We therefore do not use them for detailed investigations but only to show the mean rate of rain and the mean temperature curve for the different months to establish weather differences between the seasons and to verify our categorisation into the four different seasons. Even though slight differences will exist, average rain and temperature for each month will be fairly similar between years such that they can give an impression on what the yearly cycle of these weather parameters is like.

Seed sampling

Seed samples were collected by walking a transect through the study area along the same path that was used to check depletion rates (see below). Two samples were taken 10 m beyond each of the seven feeding sites by randomly throwing a round wire 30 cm in diameter and collecting the top soil within it. The ground was generally very solid and the top layer not very deep (1 - 2 cm deep) such that all seeds within the top layer should be available to the birds. Samples were then checked for all seeds less than 3 mm in their smallest diameter and seeds in each sample were counted. This procedure was repeated every month (except during June for logistic reasons).

Bird trapping and handling

Birds were caught in mist nets at four different places within Amurum Forest reserve, central Nigeria (9.87°N 8.98°E). Nets were checked every 45 min during the morning and afternoon but at a more frequent interval during midday hours when temperature was high. We measured body mass to the nearest 0.1g using a Pesola spring balance and wing length by measuring the flattened, straightened wing chord using a stopped wing rule (Svensson, 1992). Fat score was estimated from a scale of 0 - 8 (Bairlein, 1995), pectoral muscle on a scale from 0 - 3 (Bairlein, 1995) and crop content on a scale from 0 - 3 (with 0 being totally empty, 1 filled up to one third, 2 filled up to two thirds and 3 totally filled). Moult was determined as active or not active wing moult. In birds undergoing main moult each primary and secondary was scored from 0 (old un-moulted feather) to 5 (new feather completely re-grown) in 6 increments. The sum of the score of the first nine primaries (the tenth is often hard to score in the field due to its small size and was therefore excluded) was then regressed against the date of capture with date entered as the dependent variable following (Pimm, 1976) to estimate the mean individual moult from the sampling population. Data were collected from the four most commonly occurring Estrildid finches in the reserve, which are: Rock Firefinch (*Lagonosticta sanguinodorsalis*), Red-billed Firefinch (*Lagonosticta senegala*), Red-cheeked Cordon Bleu (*Uraeginthus bengalus*) and Lavender Waxbill (*Estrilda caerulescens*).

Seed depletion

At seven sites in the reserve we placed two bird feeding places between June 2004 and July 2005, one next to cover and one 3 - 5 m away from cover. Cover was defined as being a bush at least 1.5 m high and 1 m wide. Each feeding place consisted of a feeding table (30x30x50 cm) on which we placed a plastic plate 30 cm in diameter that was filled with a mixture of 500 g of sand and 100 g of acha (*Digitaria exilis*) seeds. Sand grains used were larger than acha-seeds such that sieving could separate them. To get the birds used to feeding places, seeds were put in place on a Wednesday and left in the field until the following Monday during week 1. They were then collected and replaced on a daily basis from Monday until Saturday at 8:00 during week 2. They were then replaced again at 6:00 on Monday and during this week 3 they were collected and replaced at 11:30 and collected again at 17:00. After this week followed a week without seeds in the field until the whole procedure was started again. Collection of seeds took about one hour and was always done starting at the same location. Thus seeds were out during approximately 5.5 hours in the morning and in the afternoon. During collection seeds were separated from sand by sieving and weighed. If seeds were wet they were taken home, dried and weighed when dry.

At each of the seven sites we also placed a feeding plate for rodents filled with 300 g of sand and 100 g of acha seeds on the ground next to cover that was covered with a wooden box (50x50x50 cm) to exclude birds. From May 2005 we also placed feeding places for ants at six of the seven sites. This was done by using a plate of the same dimensions as for the other feeding places that was covered by another plate of the same dimensions. The two plates were attached by five bull clips placed over the plates’ rims, and five small pieces of rubber between the plates’ rims served as separators leaving a gap of about 0.1 cm between the plates. The plate was buried in the ground up to its rim to provide easy access to ants and then covered with a larger plate to prevent rain from entering. Seeds were placed starting on a Wednesday and left in the field for 5 consecutive days. This procedure was then repeated three times followed by one week without seeds. The collection of seeds for rodents followed the bird feeding place procedure during week 1 and 2 but during week 3 they were placed overnight from 17:00 until 6:00 as rodents are assumed to be mainly nocturnal.

Observations

Observations were carried out at the two of the seven feeding places that offered the best viewing conditions without disturbing the birds. The observer sat about 20 - 30 m away from the feeding site and used a telescope. Observations were made for five days during week 3 alternating between site 1 and 2, always starting at site 1. Thus we observed place 1 for 3 days and place 2 for 2 days during week 3. Observations were carried out between 06:30 - 10:00 in the morning and between 14:00 - 17:00 in the afternoon. Every five minutes we recorded the number and species of birds on each of the two feeding tables starting with the one next to cover. We also noted colour-ringed birds whenever possible to get an idea of how many different individuals were sampled.

Data analyses

In all cases where seasonal differences were tested, the seasons were grouped as follows: early dry season: November - January, late dry season: February - April, early rainy season: May - July, late rainy season: August - October.

Mass changes

To investigate seasonal and daily mass changes we calculated a general linear model (GLM) with a mixed factorial design entering sex and season as factors and hour and wing length as covariates. ID was specified as a random factor without including it in the model to control for repeated measures from the same individual. We also entered the interactions of sex with hour and sex with season but only retained the interaction of sex with season in the final model, because sex with hour was never significant. We also tested for influences of moult status but did not include this variable in the final model, as moult data did not exist for each bird and would thus have reduced sample size considerably. However, moult was not found to have a significant effect in any species, so not controlling for this factor in final models was unlikely to have affected the results. The same GLM model was used to test for the pattern of seasonal and daily change in fat, pectoral muscle and crop content except that wing length was not included.

Seed depletion

To test for the influences of time of day and distance from cover on seed consumption in birds, data were log transformed to achieve normal distribution and a GLM with a mixed factorial design was applied. Seeds remaining was entered as a dependent variable, season, time of day and cover were entered as factors and location was entered as a random factor. We also tested for the interaction of season with time of day, season with cover and cover with time of day, but only retained significant interaction terms in the final model.

To test for differences in seed depletion between birds, rodents and ants and for seasonal variation within each guild, data from when food was out for a whole week (week 1) were used. Since neither normal nor Poisson distribution could be achieved by applying transformations, non parametric Friedman test for several related samples and Wilcoxon test for two related samples was used to test for differences between guilds. Kruskal-Wallis test for several unrelated samples was used to test for seasonal variation within guilds. Simple Bonferroni-correction was applied to correct for carrying out multiple tests on the same data set.

Competitive interactions and group size

To investigate the nature of inter-specific relationships we calculated a logistic regression where the absence or presence of the species of interest was entered as the dependent variable and presence / absence of other species entered as independent variables. We also controlled for distance from cover, time of day and season.

To test for seasonal differences in intra- and inter-specific group sizes, we calculated a GLM fitted to a Poisson-distribution with group size entered as the dependent variable and season, distance from cover and time of day (afternoon or morning) entered as factors.

GLMs fitted to a Poisson-distribution (group size data) or GLMs where a random factor was specified that was not included in the model (data for mass, fat, pectoral muscle and crop content) were carried out using the statistical software-package SAS 9.1 All other statistical procedures were carried out using the software-package SPSS 12. A significance level of 0.05 was considered for all statistical tests applied. Data were tested for normal distribution using Kolmogorov-Smirnov test and for homogeneity of error variances over main effects using Levenes test for error variances.

Results

Weather

As seen in Fig. 1a, rainfall started in May, reached its peak in July and August and ceased in October. Based on this we divided the seasons into early dry (November - January), late dry (February - April), early rainy (May - June) and late rainy season (August - October). More rain usually fell in the afternoon than in the morning, while rain only occasionally fell overnight (Fig. 1b). The form of the daily temperature curve was similar during the dry and rainy season (Fig. 2): mean temperature was at its low between 06:00 - 07:00, increased steeply until reaching a peak between 12:00 - 15:00, decreased again relatively steeply until 19:00 and then stayed relatively stable with only a slight decrease until reaching its minimum at 06:00. This decrease however was more pronounced during the dry season. The minimum of mean overnight temperatures did not differ greatly between rainy and dry season (17.5°C as opposed to 18.5°C), however, since temperatures decreased more steeply during the dry season these periods of minimum temperatures were of shorter duration during the dry season. Midday temperatures on the contrary were considerably higher during the dry season (30°C as opposed to 23°C) so that the temperature range was greater. Minimum temperature recorded was 11.6 °C on the 27/12/05 at 07:00 and maximum temperature was 34 °C recorded on the 15/04/05 at 14:00.

Natural seed abundance

Seed availability on the ground was high but very variable during all of the dry season. It was still high during the beginning of the rainy season in May (note that data were not collected during June). During the late rainy season (August - October) there were almost no seeds left on the ground (Fig. 3). Grasses started to produce seed at the beginning of the dry season in November. At about the beginning of March almost all seeds have fallen to the ground, and no more seeds were available on the grasses.

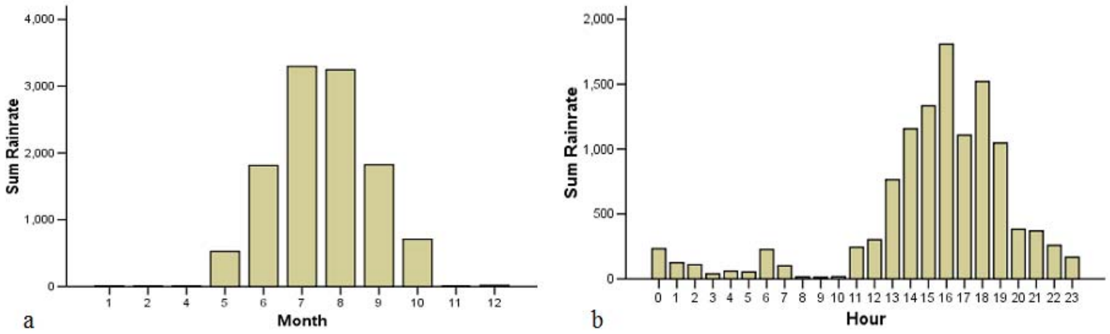


Fig. 1 a-b. Total rain in mm a) fallen at different months and b) fallen by hour of day pooled over all months.

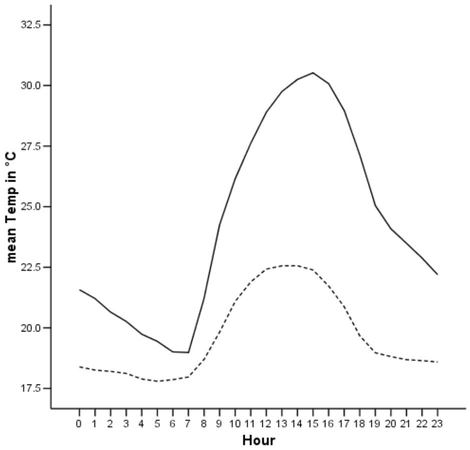


Fig. 2. Temperature curve during February (mid dry season, solid line) and August (mid rainy season, broken line) estimated as means over all days.

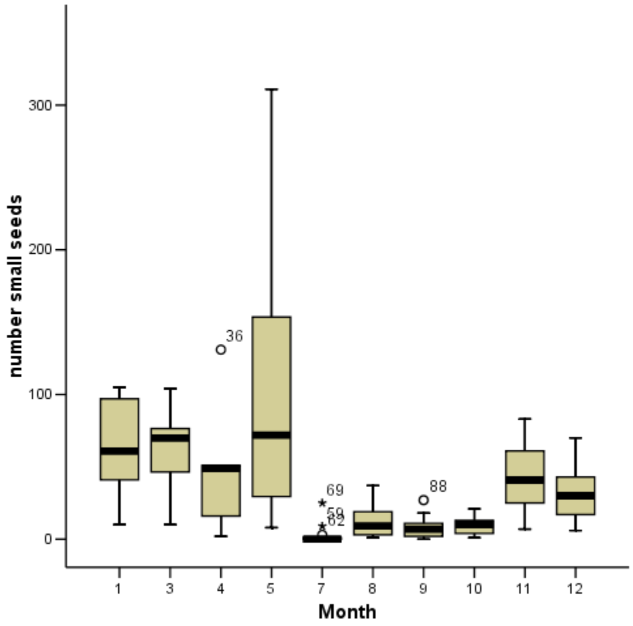


Fig. 3. Means of the number of small seeds occurring on the ground (mean per sample) for the different months. Note that no data were collected for February and June.

(i) Seasonal pattern of mass gain

All of the four granivore species under investigation showed seasonal differences in mass gain (Table 1a-d). In all three species in which sex could be determined (all apart from Lavender Waxbills) there was a significant influence of sex on this relationship. When only males were considered season had a significant influence on mass in Rock Firefinches ($F_{3,240}$=3.22, $p<0.05$, controlling for wing length, time of day and ID) and Red-billed Firefinches ($F_{3,985}$=4.82, $p<0.01$, controlling for wing length, time of day and ID) but not in Red-cheeked Cordon Bleus ($F_{3,51.4}$=1.07, p=0.37, controlling for wing length, time of day and ID). In both sexes of Rock Firefinches and Red-billed Firefinches body mass was relatively low during the early and late dry season but increased considerably during the early rainy season. During the late rainy season, however, body mass of females stayed high while body mass of males decreased again (Fig. 4a-b). Females of Red-cheeked Cordon Bleus were also heavier during the late rainy than during the other seasons (Fig. 4c). In Lavender Waxbills a similar seasonal pattern was found (Fig. 4d), however, body mass remained high during the late rainy season with much more variance (but note that the confounding effects of sex could not be considered in this species as sex can normally not be determined). The increase body mass in males of both Rock Firefinches and Red-billed Firefinches from the early dry to the early rainy season was 9.8%. There was also a significant influence of time of day on mass in Rock Firefinches, Red-billed Firefinches and Lavender Waxbills with time of day having a slight linear positive effect, however, no effect of time of day was found in Red-cheeked Cordon Bleus. This did not change when time of day was entered as a factor instead of a covariate. The increase from 06:00 to 18:00 was about 15.9 % in Rock Firefinches, 11.1 % in Lavender Waxbills and 4.7 % in Red-billed Firefinches.

In three species there was a significant seasonal difference in fat and pectoral muscle and in two species there was also a significant seasonal difference in crop content (see Table 2 for summary of results). In contrast to the effects on mass there was no influence of sex on this relationship in any of the three species where sex could be determined. In three species time of day had a linear positive effect on fat, in one species on pectoral muscle, and in all four species on crop content. It thus appears that seasonal mass changes are largely due to differences in fat deposition and changes in pectoral muscle but also partly due to differences in crop content. The pattern of seasonal changes in all these three parameters did indeed follow the same pattern as seasonal mass changes in males (see Fig. 5a-c for an example with Rock Firefinches). Increasing mass with time of day appears to be largely due to crop content but also to increasing fat depositions, while daily differences in pectoral muscle appear to be less important.

Table 1 a-d. GLM results testing for seasonal variation in mass gain in Rock Firefinches (a), Lavender Waxbills (b), Red-billed Firefinches (c) and Red-cheeked Cordon Bleus (d). ID was specified as a random factor.

a.	**Body mass in g of Rock Firefinches**			
	B	df	F	p
sex		1,176	3.91	<0.05
season		3, 234	3.48	<0.05
wing	0.02	1, 209	21.50	<0.01
time of day	0.01	1, 224	47.43	<0.01
sex*season		3, 241	5.72	<0.01

b.	**Body mass in g of Lavender Waxbills**			
	B	df	F	p
season		3, 293	12.20	<0.01
wing	0.007	1, 283	5.37	<0.05
time of day	0.007	1, 256	80.66	<0.01

c.	**Body mass in g of Red-billed Firefinches**			
	B	df	F	p
sex		1, 219	0.03	0.86
season		3, 197	4.64	<0.05
wing	0.016	1, 209	10.56	<0.01
time of day	0.003	1, 164	5.37	<0.05
sex*season		3, 200	7.73	<0.01

d.	**Body mass in g of Red-cheeked Cordon Bleus**			
	B	df	F	p
sex		1,143	9.19	<0.05
season		3, 124	1.52	0.21
wing	0.004	1, 155	1.55	0.21
time of day	0.001	1, 96.8	2.24	0.14
sex*season		3, 124	5.45	<0.01

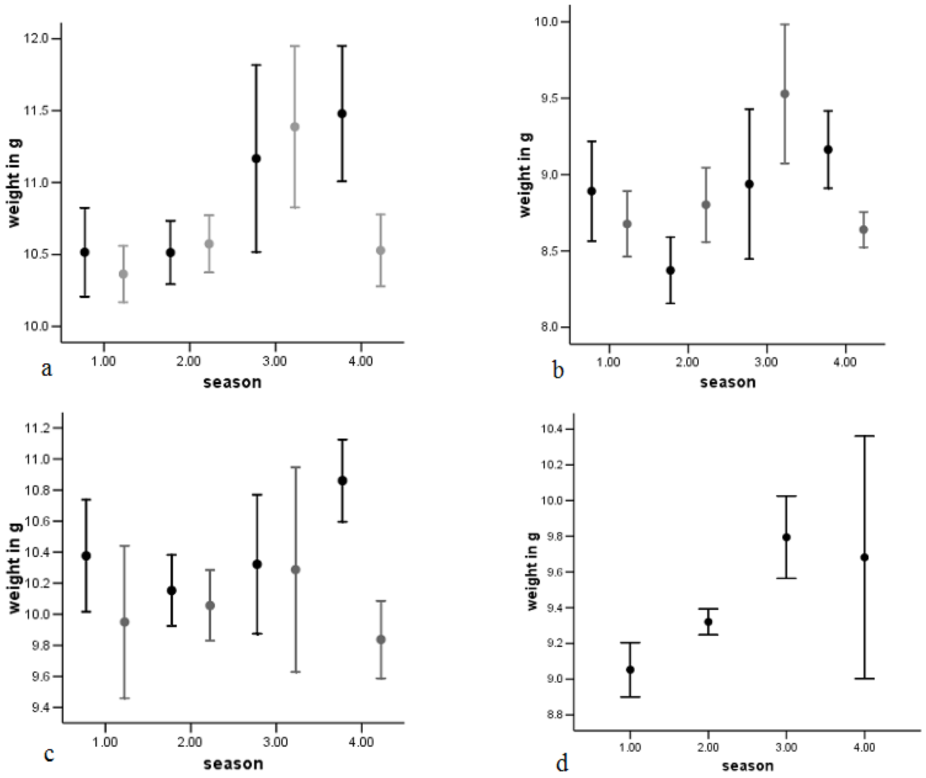


Fig. 4 a-d. 95% confidence intervals for body mass (in g) of female (dark bars) and male (light bars) a) Rock Firefinches, b) Red-billed Firefinches, c) Red-cheeked Cordon Bleus and d) Lavender Waxbills (not discriminated between sex in this species) at the different seasons (1 = early dry season Nov-Jan, 2 = late dry season Feb-Apr, 3 = early rainy season May-July, 4 = late rainy season Aug-Oct).

Table 2. Results from GLM testing for the influences of season and time of day on mass, fat, pectoral muscle and crop content in four species of Estrildid finches. The symbols ∗∗ and ∗ represent significance levels of p≤0.01 and p≤0.05 respectively and n.s. refers to non significant effects (p>0.05). For detailed results on mass see Table 1 a-d. When testing for the effects on the other three parameters we also controlled for the effects of ID. If the interaction of season and sex was not significant, the model was run without this interaction to test for the effects of season and time of day.

Species	**independent variable**	**dependent variable**			
		mass	*fat*	*pectoral muscle*	*crop content*
Rock Firefinch	*season*sex*	∗∗	n.s.	n.s.	n.s.
	season	--	∗∗	∗	n.s.
	sex	--	∗∗	n.s.	n.s.
	time of day	∗∗	∗∗	∗∗	∗
Lavender Waxbill	*season*	∗	∗	∗	∗∗
	time of day	∗∗	∗∗	n.s.	∗∗
Red-billed Firefinch	*season*sex*	∗∗	n.s.	n.s.	n.s.
	season	--	∗∗	∗∗	∗∗
	sex	--	n.s.	n.s.	n.s.
	time of day	∗∗	∗∗	n.s.	∗∗
Red-cheeked Cordon Bleu	*season*sex*	∗∗	n.s.	n.s.	n.s.
	season	--	n.s.	n.s.	n.s.
	sex	--	n.s.	n.s.	n.s.
	time of day	n.s.	n.s.	n.s.	∗∗

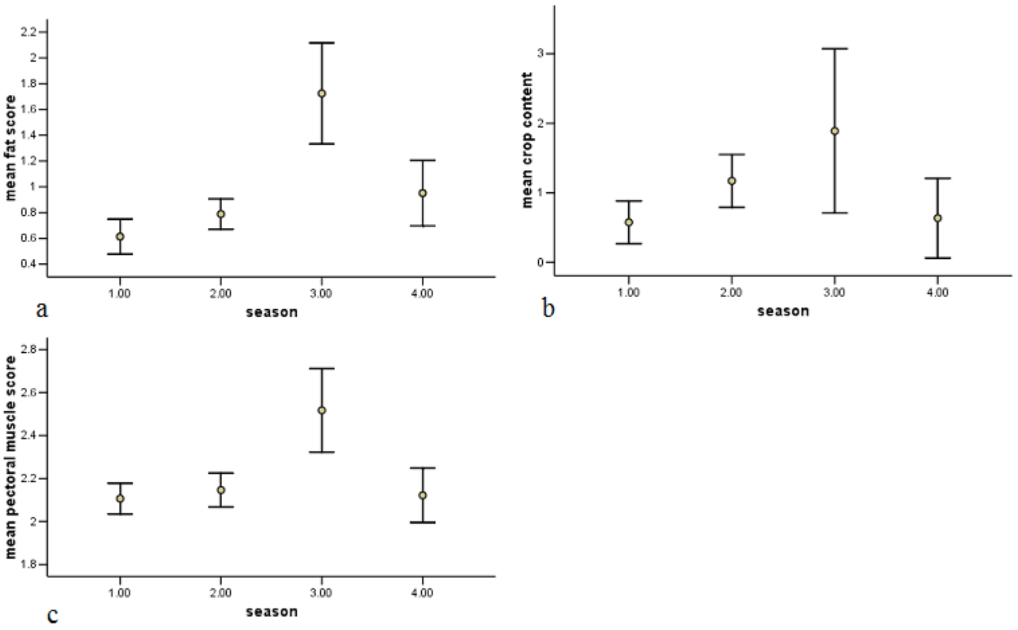


Fig. 5 a-c. Seasonal variation in a) fat deposition, b) crop content and c) pectoral muscle in Rock Firefinches (1 = early dry season Nov - Jan, 2 = late dry season Feb - Apr, 3 = early rainy season May - July, 4 = late rainy season Aug - Oct).

(ii) and (iii) The effects of season, time of day and distance from cover on depletion rates in birds

There was a significant interaction of season with time of day on bird depletion rates (Table 3): birds fed more in the morning than in the afternoon during the late dry season, during the other seasons there was no difference. Relatively more food was consumed during the whole dry season as well as during the early rains while during the late rainy season seed consumption was considerably less (Fig. 6a). During all seasons birds consumed more seeds at the patch next to cover than at the patch away from cover (Table 3, Fig. 6b). Neither the interaction of cover with time of day ($F_{1,1836}$=0.89, p=0.35) nor the interaction of cover with season ($F_{1,1836}$=1.6, p=0.19) were significant and therefore were not included in the final model.

Fifteen different species were regularly observed on feeding tables (probability of the species occurring during any of the observation sample greater than 0.01). However, eight species made up the majority of observations with each of these species occurring with a probability of greater than 0.1 during at least one season. All of these species apart from Indigobirds (*Vidua sp.*) were of the family Estrildidae. For all species where sample size was sufficient for meaningful tests there were seasonal differences in the probability of presence on the feeding tables (see results of logistic regression on presence in Table 4). As can be seen in Fig. 7a, of the eight most common species all apart from Red-billed Firefinches and Indigobirds occurred least often during the late rainy season. However, at what time of the year a species occurred most commonly differed greatly between species. Red-billed Firefinches, Rock Firefinches and Red-cheeked Cordon Bleus occurred most often during the early dry season, Black-rumped Waxbills (*Estrilda troglodyte*), Lavender Waxbills and Indigobirds during the late dry season and Bronze Mannikins (*Lonchura cucullata*) during the early rainy season. Even though each of these species was present during every season it is also clear that species differed in their abundance on feeding tables between season and thus group composition on feeding tables was different depending on time of the year. Of the species that were observed less commonly (with a probability of <0.1) there is even more seasonal variation with some species only being present on feeding tables during some seasons (Fig. 7b).

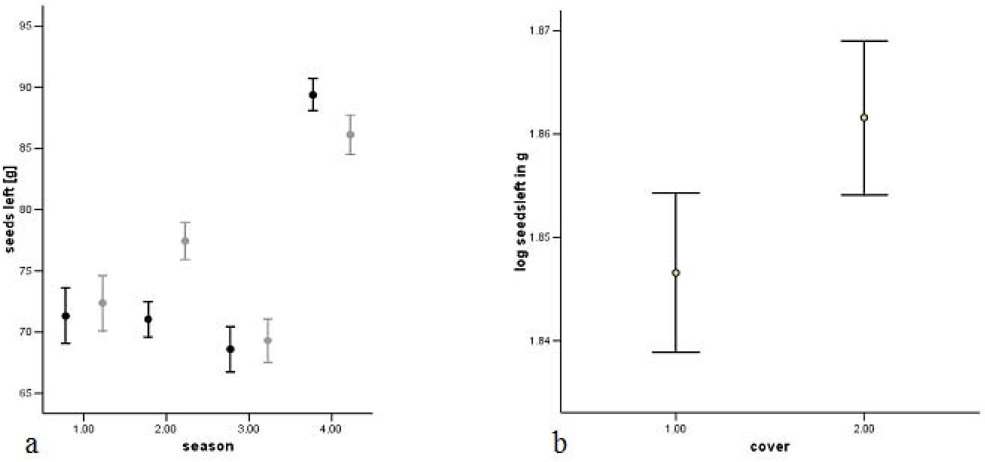
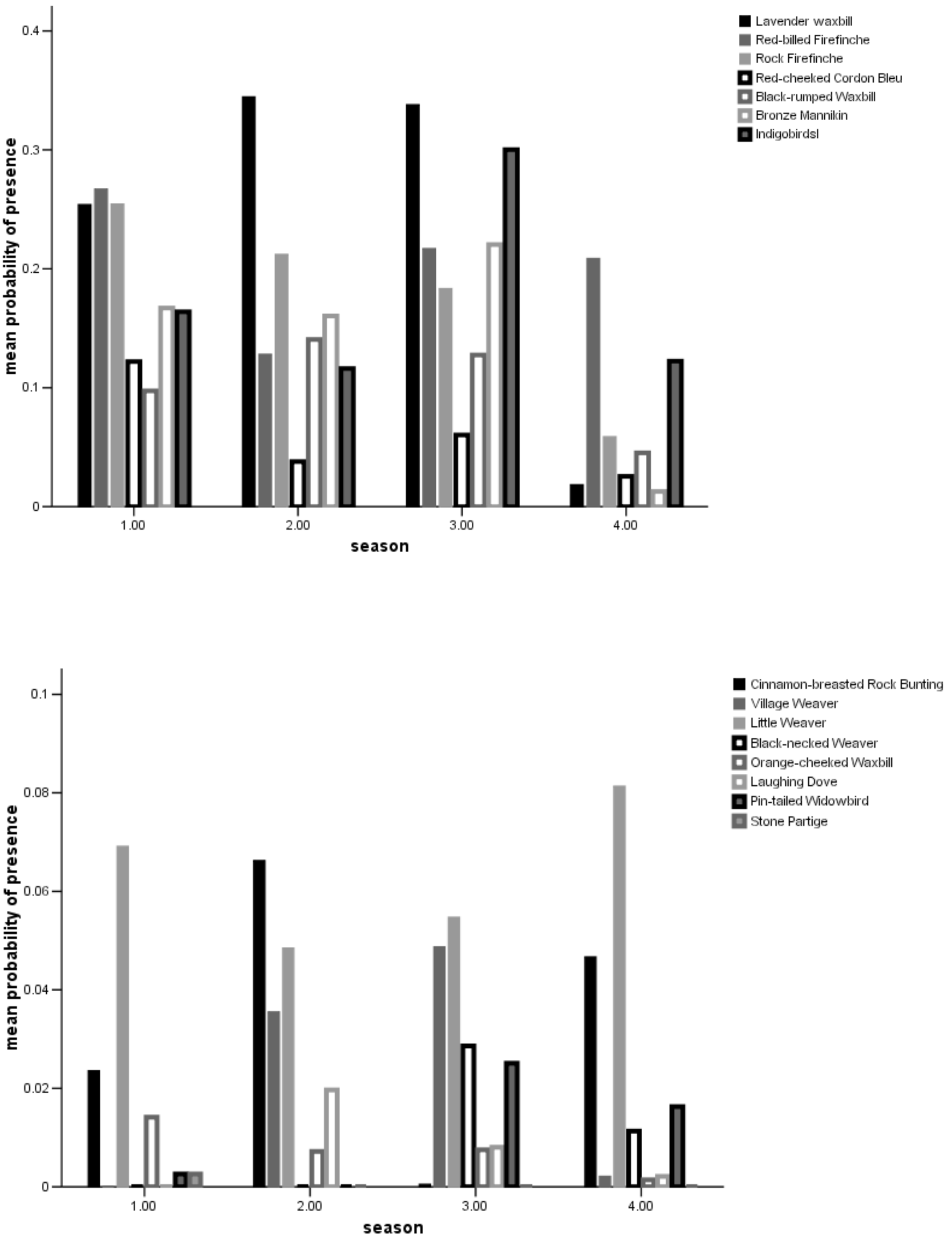


Fig. 6 a-b. Seeds left by birds at provided feeding patches a) during the morning (dark bars) and during the afternoon (light bars) at the different seasons (1 = early dry season Nov-Jan, 2 = late dry season Feb-Apr, 3 = early rainy season May-July, 4 = late rainy season Aug-Oct) and b) next to cover (cover = 1) and away from cover (cover = 2).



a

b

Fig. 7 a-b. Mean probability of a) common species and b) less common species being present at a given season averaged over all observations during one season.

Table 3. Results of GLM testing variables influencing depletion rates of birds

Dependent variable		Log seeds left on feeding place [g]			
		Type III Sum of Squares	df	F	p
Cover	Hypothesis	0.11	1	8.93	<0.01
	Error	21.57	1840		
Time	Hypothesis	0.02	1	1.88	0.17
	Error	21.57	1840		
Season	Hypothesis	3.01	3	85.59	<0.01
	Error	21.57	1840		
Location	Hypothesis	0.87	6	12.41	<0.01
	Error	21.57	1840		
Season*Time	Hypothesis	0.16	3	4.64	<0.01
	Error	21.57	1840		
Intercept	Hypothesis	5785.07	1	43990.59	<0.01
	Error	0.80	6.11		

Table 4. Results from logistic regression testing for species associations. Dependent variables are presented in rows, independent variables in columns. Symbols indicate the following: + : a positive significant effect, - : a negative significant effect, 0 : no significant effect (p>0.05), *: a significant effect for season which was entered as a factor. Double and single symbols indicate a significance level of p≤0.01 and p≤0.05 respectively. A positive effect of cover means birds occurred more often next to cover.

	LAVWB	**REBFF**	**ROCFF**	**RECCB**	**BLRWB**	**BROMA**	**IB**	**Cover**	**Hour**	**Season**
LAVWB		0	+ +	+ +	+ +	+ +	+ +	+ +	0	**
REBFF	0		0	+ +	+	- -	+ +	+ +	+ +	**
ROCFF	+ +	0		-	+ +	- -	- -	+ +	0	**
RECCB	+ +	+ +	-		+ +	0	0	+ +	+ +	**
BLRWB	+ +	+ +	+ +	+ +		+ +	+ +	- -	+ +	**
BROMA	+ +	- -	- -	-	+ +		-	- -	+ +	**
IB	+ +	+ +	- -	+	+ +	- -		0	+ +	**

(iv) Inter-specific relationships, group sizes and seasonal use of feeding patches

Most species pairs showed a positive association (12 cases) when testing for the influence of the presence of one species on the presence of another (Table 4). Two species relationships were neutral while five were negative. In two cases analyses for one species pair yielded different results with one species having a negative or positive effect on the other, while the other did not effect the first: in all other cases results matched (Table 4). In all species pairs that showed negative associations it was either Rock Firefinches or Bronze Mannikins involved. We then re-ran the model for these two species and tested for the influence of season on this negative association. In Bronze Mannikins season had a significant effect on the negative influence of Indigobirds and Red-billed Firefinches but not on the influence of Rock Firefinches. In Rock Firefinches season had a significant effect on the influence of Indigobirds and Red-billed Firefinches, but not on the influence of Bronze Mannikins. Thus in only three of the five species pairs with negative associations did the extent differ seasonally. The negative association of Rock Firefinches and Indigobirds was least pronounced during the early dry season, while the negative relationship of Bronze Mannikins with Indigobirds and of Bronze Manninkins with Red-billed Firefinches was least pronounced during the early and late rainy season.

There was a significant seasonal difference in both intra- as well as inter-specific group size for all species tested apart from Red-billed Firefinches, for which seasonal differences in intra-specific group size were not significant. For all cases were there was a significant seasonal difference, group size was smallest during the late dry season. Group size during the other seasons did not differ greatly and not in a consistent manner across species (Table 5).

There was a significant difference between seeds consumed by birds, ants and rodents (Friedman test, $chi^2=73.52$, df=2, n=58, $p<0.01$). Birds ate most seed with an overall mean of 73 ± 23 g out of 100 g of seeds per week, while ants consumed 25 ± 22 g per week and rodents ate least seed with an average of 17 ± 16 g of 100 g seeds consumed per week. There were significant differences between all the guilds (Wilcox, birds-ants: $Z=-6.66$, $p<0.01$; birds-rodents: $Z=-6.85$, $p<0.01$; rodents-ants: $Z=-2.87$, $p<0.01$; Fig. 8).

There was strong seasonal variation in bird consumption (Kruskal Wallis-test, $chi^2=24.92$, df=3, $p<0.01$) with most seeds consumed in the late dry season and fewest in the late rainy season (Fig. 8). Ants also showed significant seasonal variation (Kruskal Wallis-test, chi²=34.78, df=3, p<0.01) with much higher seed consumption during the whole dry season while this was much reduced during the whole rainy season (Fig. 8). In rodents there was no significant seasonal variation (Kruskal Wallis-test, chi²=5.28, df=3, p=0.15, Fig. 8).

Table 5. Mean intra- and inter-specific group sizes of species at the different seasons. The smallest group size per species is highlighted in bold script. Stars indicates significant seasonal differences in group sizes with a double and single symbols indicating a significance level of p≤0.01 and p≤0.05 respectively.

	Intra-specific group size by season 1-4					**Inter-specific group size by season 1-4**				
Species	**1**	**2**	**3**	**4**	**sig.**	**1**	**2**	**3**	**4**	**sig.**
Rock Firefinch	1.59	1.51	1.44	**1.10**	∗∗	4.97	4.12	4.11	**1.84**	∗∗
Red-billed Firefinch	1.69	**1.63**	1.64	1.67	n.s.	3.82	3.98	4.91	**2.54**	∗∗
Red-cheeked Cordon Bleu	1.35	1.53	1.53	**1.19**	∗∗	5.03	4.68	4.90	**3.67**	∗∗
Lavender Waxbill	2.30	1.86	1.73	**1.31**	∗∗	6.33	4.89	4.60	**3.04**	∗∗
Bronze Mannikin	7.13	7.66	3.93	**2.33**	∗∗	9.56	9.53	6.47	**4.00**	∗∗
Black-rumped Waxbill	1.67	2.54	2.32	**1.67**	∗∗	7.69	5.89	6.21	**4.09**	∗∗
Indigobird	1.06	1.24	1.37	**1.05**	∗∗	4.21	3.96	4.39	**2.11**	∗∗

(v) Time of moult and breeding

The times during which juvenile birds and adult birds in active wing moult were caught are given in Table 6 and Table 7. We have pooled data over the seasons in Table 6 to make them comparable to results from feeding behaviour but give the actual dates in Table 7 as well as the amount of days during which moult and breeding (as derived from juvenile birds caught) overlapped. We give more detailed data on juvenile birds caught of each species below.

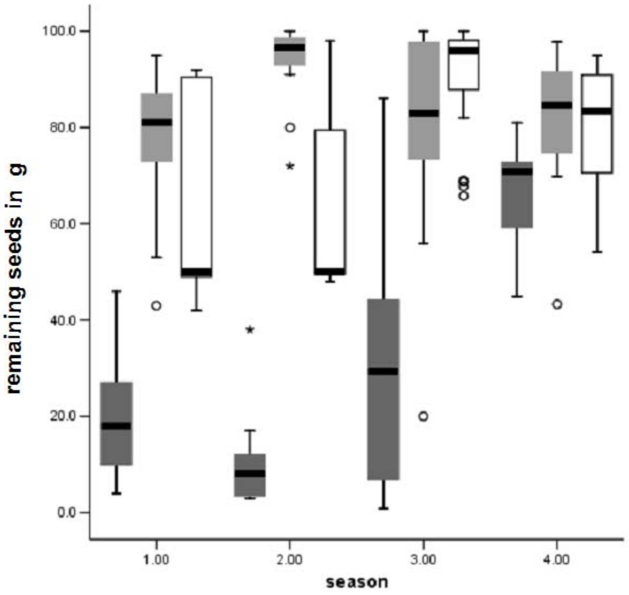


Fig. 8. Seeds remaining (in g) after seeds have been out for 5 days for the different guilds: dark filled plots = seeds left by birds, light filled bars = seeds left by rodents and open bars = seeds left by ants at the different seasons (1 = early dry season Nov-Jan, 2 = late dry season Feb-Apr, 3 = early rainy season May-July, 4 = late rainy season Aug-Oct).

During the years 2004 and 2005 we caught a total of 11 juvenile Rock Firefinches, ten between 22/11 - 14/12 (6 in Nov. and 4 in Dec.) and one on the 12/02. Nine subadult Rock Firefinches moulting into adult plumage were caught between November and March. Eleven juvenile Red-cheeked Cordon Bleus were caught between 10/10 and 7/12 (3 in Oct., 5 in Nov. and 3 in Dec.) and seven subadult birds in December and March. Eight juvenile Lavender Waxbills were caught between 13/10 - 14/12 (1 in Oct., 2 in Nov. and 5 in Dec.) and nine subadults between November and April. We caught a total of 19 juvenile Red-billed Firefinches, nine between 19/10 - 14/12 (1 in Oct., 5 in Nov. and 3 in Dec.) and ten between 4/3 - 5/5 (8 in Mar., 1 in Apr. and 1 in May). A total of 80 subadult Red-billed Firefinches was caught between December and May.

Considering that it takes about four weeks from the first egg until juvenile birds fledge, the breeding season for all four species probably started during the late rainy season between September and October when rains started to decrease. For Rock Firefinches, Red-cheeked Cordon Bleus and Lavender Waxbills breeding was probably mainly finished in December while in Red-billed Firefinches there was either a second breeding season between March and May, or more likely the species had a much extended breeding season. As seen in Table 7 in all species, apart from Lavender Waxbills, the moulting period overlapped with more than 30% of the breeding season and in Red-billed Firefinches almost completely overlapped with the breeding season. Moulting was timed to mainly coincide with the dry season but slightly extended into the first month of the rainy season.

Table 6. Breeding and moulting times for four Estrildid-species. Calculated are the percentage of birds caught during each season (including recaptures) that were juveniles and moult is calculated as the percentage of adult birds caught (including recaptures) during each season that were in active moult. Sample sizes do not exactly match because moult information was not available for each bird. Note that during season 2 data were only available for May but not June or July.

		season			
		1	**2**	**3**	**4**
% juvenile birds	Rock Firefinch	14%, n=92	1%, n=138	0%, n=29	0%, n=40
	Red-billed Firefinch	13%, n=63	8%, n=113	4%, n=23	0%, n=44
	Red-cheeked Cordon Bleu	21%, n=39	0%, n=63	0%, n=18	4%, n=71
	Lavender Waxbill	11%, n=64	0%, n=212	0%, n=37	8%, n=12
% birds in main moult	Rock Firefinch	39%, n=57	85%, n=82	62%, n=26	0%, n=37
	Red-billed Firefinch	4%, n=55	50%, n=104	95%, n=22	7%, n=59
	Red-cheeked Cordon Bleu	11%, n=31	68%, n=63	50%, n=18	0%, n=68
	Lavender Waxbill	32%, n=57	14%, n=212	21%, n=37	18%, n=11

Table 7. Actual time periods when juveniles were caught and moulting period calculated as individual moult and number of days during which breeding and moult overlapped. One juvenile Rock Firefinch caught in February was not considered as assumed to be an exception.

	juveniles caught	**moult**	**overlap**
Rock Firefinch	22/11 - 14/12 (n=11) 23days	23/11 - 22/04 (n=98) 150 days	21 days
Red-billed Firefinch	19/10 - 05/05 (n=19) 210 days	10/01 - 18/05 (n=47) 138 days	197 days
Red-cheeked Cordon Bleu	10/10 - 07/12 (n=11) 59 days	15/11 - 18/04 (n=32) 154 days	23 days
Lavender Waxbill	13/10 - 14/12 (n=8) 63 days	01/12 - 03/03 (n=93) 93 days	14 days

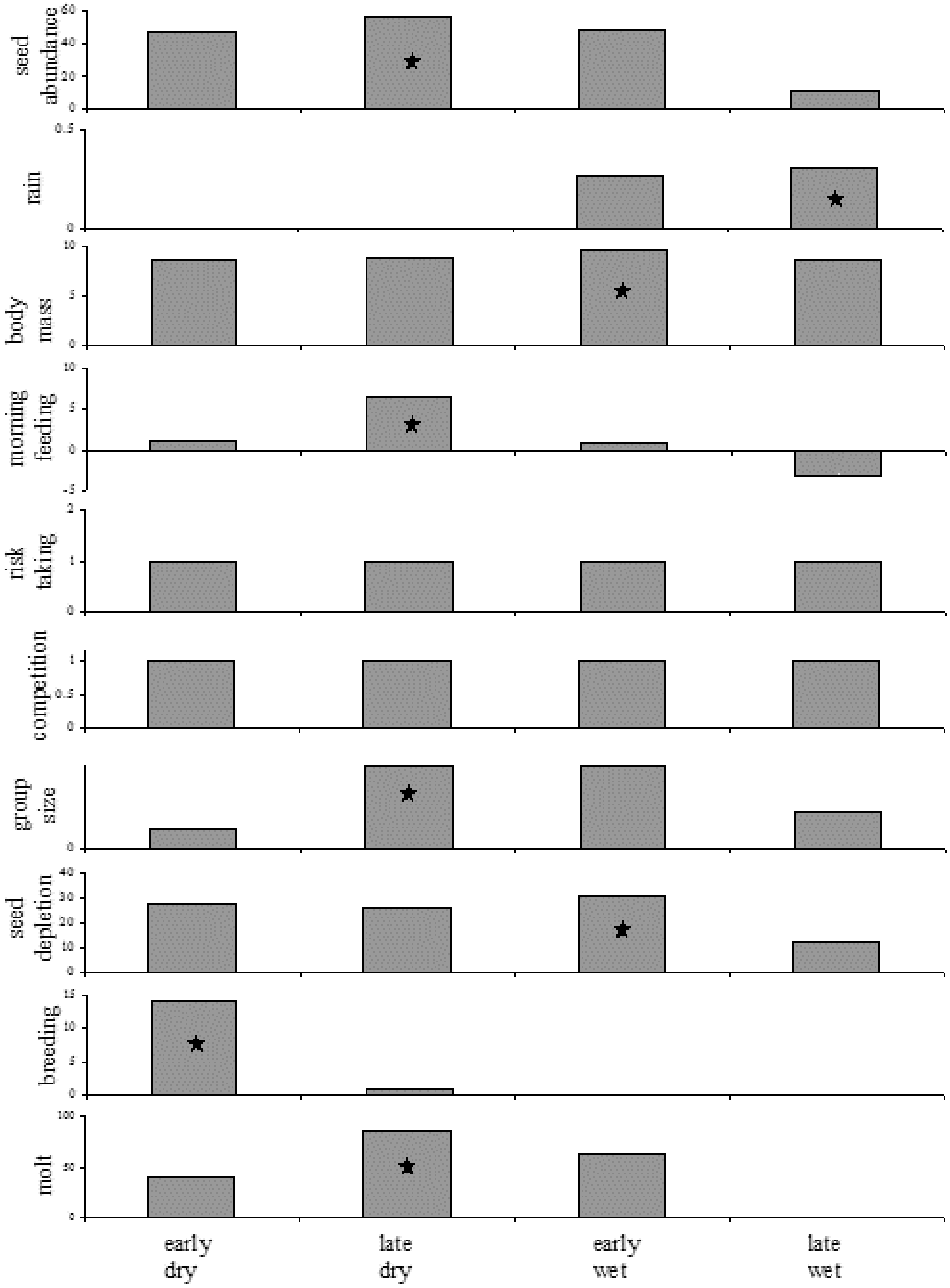


Fig. 9. Overview of results of parameters predicted to vary seasonally. Rainfall is given as mean mm per month, mass as mean body mass of Rock Firefinches, morning feeding as the difference between depletion rates in the morning and afternoon, seed depletion as mean amount of seeds eaten in g, group size is shown as mean intra-specific group size of Rock Firefinches, breeding as % of juvenile Rock Firefinches caught and moult as % of Rock Firefinches caught in main moult. In risk taking and competition there was no statistical seasonal difference so all values equal one. Peaks of each parameter are indicated with a black star.

In Summary (Fig. 9) results show that seed density was highest during the late dry season and declined during the early rainy season, mass was highest during the early rainy season and did not differ during other times (i). Morning feeding peaked in the late dry season (ii). There was no seasonal variation in risk taking behaviour (iii). There was also no seasonal variation in the strength of negative associations between bird species, group size was smallest during the late rainy season and seed consumption peaked during the early rains (iv). Breeding started during the late rainy season and peaked during the early dry season, while moult happened mainly during the dry season with a peak in the late dry season (v). It is thus obvious that, contrary to our predictions, parameters did not peak at the same time and some did not even show any seasonal variation at all.

Discussion

Seasonality and seed abundance

Seed density on the ground was relatively stable during all of the dry season but decreased during the rainy season. Seed density was still relatively high in May, however, two months later in July it was almost nil. Crowley & Garnett (1999) found that rains of about 50 mm in Australia resulted in seed-bank germination of about 93% and that wide spread seed depletion occurred at the start of about 8% of the wet season. With rainfall of just over 50 mm in May and about 200 mm in June in our study area it is thus reasonable to assume that seed density on the ground declined markedly in June. However, we did not check if seeds contained kernels and considering that Crowley & Garnett (1999) found the proportion of kernels in seeds to decline over the dry season due mainly to predation by granivorous it is likely that we overestimated the availability of food during the late dry and early rainy season by only counting seeds.

Minimum temperature recorded was 11.6 °C at one morning in December and it is unlikely that this temperature would place significant thermoregulatory costs on birds in our study area (Walsberg, 1983). However, high midday temperatures of up to 34 °C maximum might cause thermoregulatory costs and restrict feeding activity during this time.

Mass changes

The patterns of seasonal mass gain only partly fitted the predictions. Mass increased during the early rainy season in three out of four species and this was mainly due to increased fat deposition and pectoral muscle. The increase of about 9% of average body mass is indeed comparable to the increase that some temperate passerines of a similar body mass show in winter (Bednekoff & Krebs, 1995; Haftorn, 1989). This would support the assumption that birds undergo a period of higher starvation risk during the rainy season due to either lower food availability or interruptions of feeding by rain. However, male mass decreased again in the late rainy season when weather conditions were still the same and the abundance of granivorous food on the ground was even lower. Higher mass of females during this time was almost certainly due to egg production, since fat deposition was not higher than during the dry season and did not differ from that of males. This also fits the observation that the first juveniles appeared in the very early dry season. Energy demands during breeding should be higher for females while producing eggs. For both sexes the time available for feeding is further reduced during incubating as both sexes of all three species studied, in which sex could be determined, contribute to incubation (pers. obs.).

It is surprising therefore, that birds deposited fat during the early rainy but not the late rainy season and that they timed the onset of breeding to coincide with low abundance of granivorous food on the ground. This suggests that there is no increased starvation risk during the late rainy season. Alternative food resources might become available during this time or seeds are already available from the crop of grasses directly. Lavender Waxbills were observed to feed on alternative food resources such as figs, pollen or insects (Chapter 5) and Red-billed Firefinches and Red-cheeked Cordon Bleus have also been reported to feed on insects (Fry et al., 2004). Despite more than 50 hours of feeding observations in the field and high bird density we never found the most frequently encountered Rock Firefinches to feed on anything but seeds (Chapter 5) and we never observed anything other than seeds in their crops (pers. obs.). We thus believe that seeds comprise the main food resource for at least Rock Firefinches and possibly also Red-billed Firefinches and Red-cheeked Cordon Bleus. These three species were also observed to feed on seeds from the ground rather than from the crop itself (Chapter 5). Our measurement of seed density should therefore correctly indicate food availability to these species. Alternatively, even though seed abundance was still low, competition for remaining seeds might have been released due to many birds leaving the area. A considerable decrease of feeding activity on the feeding tables might indicate this and we believe this to be related to the onset of breeding. When birds start breeding they seem to disperse as maybe a result of other resources (such as nest sites) becoming relatively more important. This might have caused lower bird density in our study area reflected in lower seed depletion and group size on the feeding tables.

Time of feeding and risk taking behaviour

Seasonal differences in the timing of feeding did not follow the predicted pattern and thus did not support the existence of higher starvation risk during the rainy season. Feeding activity was higher in the morning during the late dry season, higher in the afternoon during the late rainy season and equal during other times. This pattern is unlikely to be caused by seasonal differences in food abundance or predictability since seed density was high during all of the dry season. Weather conditions are also unlikely to be the cause because otherwise a consistent pattern should probably be observed during the whole dry and the whole rainy season. Rain was heavier in the afternoon so feeding activity should have been higher in the morning if interruptions by rain were to cause observed feeding patterns. Following models presented by Bednekoff & Houston (1994a) and McNamara et al. (1994) delayed feeding in the late rainy season might reflect an increase in predation risk. This could also explain why birds decreased mass again during this time. However, females did not compensate for an increase in mass dependent predation risk caused by egg production (and associated higher mass) by increasing pectoral muscle. This should be expected if mass dependent predation risk mattered (unless low food availability does not enable them to do so). If the risk of predation really varies with season one would also expect differences in risk taking behaviour. Contrary to our predictions, the extent of risk taking behaviour did not undergo any seasonal differences and did not yield evidence for seasonal variation in either starvation or predation risk. We therefore believe that observed daily feeding patterns are not a result of seasonal differences in the extent of either starvation or predation risk. We believe that they are an outcome of some variable that shows a diurnal variation but are presently unable to say what this factor might be.

It should be noted, however, that there might be several problems associated with measuring risk taking behaviour via depletion rates in an area of high species diversity. Species composition on the feeding tables differed between the seasons and we found that species differed in their response to distance from cover (Chapter 3). Despite all Estrildid-species flying into cover when disturbed, some actually preferred to feed away from cover and these species also tended to form larger intra-specific groups. It follows, that if risk taking behaviour increases, species might respond in opposite directions such that effects mask each other and no overall effect is found. A simple change in species composition might also change the observed overall pattern, even though that of each single species did not change. If this occurs we would have to concentrate on just one species if we are to investigate seasonal variation in risk taking behaviour. As this is impossible when measuring depletion rates in the field (unless one can design a feeder only accessible by one species) this would have to be done via direct observations and possibly in an aviary to account for confounding effects of competition with other species.

Competition

Observed competitive interactions also did not support the existence of seasonal variation in starvation risk. We have shown that most associations between bird species were positive and the few that were negative did not follow a consistent seasonal pattern. Group size was relatively equal between seasons apart from the late rainy season when it declined substantially in all species. However, as overall depletion rates also decreased, this is more likely to be the outcome of lower bird abundance in the study area rather than an indication of less tolerance towards con- and hetero-specifics.

It might be questioned whether the parameters we measured are good indicators of the strength of competition in granivorous birds. Most species associations were positive and this raises the question whether there really are disadvantages via interference competition associated with forming larger groups. We showed (Chapter 3) that intake rates in the field increased with group size and concluded that interference competition in granivorous birds is of little importance in our study system. Unlike invertebrates (e.g. see Minderman et al., 2006), granivorous food is not mobile and would thus not be disturbed by birds feeding nearby. Competition in granivorous birds is therefore more likely to occur as depletion rather than interference. A more appropriate response to increased competition might thus be to increase intake rate, a phenomenon known as “scramble competition” (Elgar, 1989; Lima et al., 1999). If this occurred the extent of competition would have less of an effect on species association because in the absence of direct interference competition one species would not exclude another. The extent of competition and its potential seasonal variation might thus better be assessed by studying seasonal variation in the response of the birds’ intake rates to increased group size. Assuming that predation risk is equal, a higher risk of starvation should then result in a stronger positive response of intake rate to increased group size.

Comparing seed depletion between the different guilds it appears that birds clearly are the most dominant seed consumers, which is in line with findings for a semi-arid desert in South Africa (Kerley, 1991), a woodland savannah in Zimbabwe (Linzey & Washok, 2000), and a semi-arid region in Chile (Kelt et al., 2004). However, it contrasts findings for desert regions in North and South America, where birds were found to be of minor importance compared to rodents and ants (Morton, 1985). Rodents only contributed a minor part to total seed consumption during this study, and there was no seasonal variation in seed depletion. Whether the relatively low intake of rodents was due to them being generally less abundant, consuming other resources to a greater extent than grass seeds or whether they have higher giving up densities due to being less efficient in separating seeds from sand remains unclear. Seed depletion by ants showed strong seasonal variation. There was much depletion during the whole dry season but only minor depletion during the whole rainy season. This might be related to seasonal differences in above-ground activity in ants. Harvester ants in Argentina and epigaeic ants in South Africa were shown to decrease above-ground activity during winter (Lindsey & Skinner, 2001; Pol & de Casenave, 2004) and this might also apply to the rainy season in Nigeria. They thus might have a competitive effect on birds during the dry season but not during the rainy season. However, seed abundance during the dry season was generally quite high such that it is more likely that seed abundance is limiting during the early and late rainy season. During this time however, ant depletion was low, while bird depletion was still high. It thus follows that competition within the bird guild is probably more important. In general birds made up the majority of seed consumption during all seasons with consumption only decreasing during the late rainy season, while rodents seem to be of little importance and ants being of importance during the dry season only. The hypothesis that all guilds show higher seed depletion during the rainy season when natural seed abundance is less was therefore not met. In ants at least, this might be due to reduced activity during the rainy season. Birds however, showed the highest seed depletion during the early rainy season which might be in line with the assumption that birds are faced with a higher risk of starvation during this time and thus are more willing to feed on artificial feeding patches. However, seed depletion declined markedly during the late rainy season when seed abundance on the ground was still low. This was also found by Molokwu *et al*. (in press) who studies giving up densities of birds feeding on the larger millet seeds in the same study area. This might indicate that birds rely on different food resources during this time and feed on seeds to a lesser extent. However, dispersion of birds due to the onset of breeding or birds migrating away from the study area could also be a reason. Until we have more information on seasonal variation in diet choice and bird densities the reason for less seed depletion during the late dry season remains unclear.

Timing of breeding and moult

The timing of breeding did not follow the pattern we predicted. Birds started to breed during the late rainy season (when seed density was lowest) as indicated by female mass and capture of juvenile birds. This was at a time when seed density on the ground was still low. However, it might be more crucial that seed abundance is high when juvenile and inexperienced birds fledge. Young (1994) also did not find tropical house wrens to time breeding to coincide with high food availability and suggested that reproduction is timed to facilitate post-breeding activities such as moulting. It is surprising nevertheless, that breeding followed a strong seasonal pattern even though other parameters did not. However, Barta (2006) showed that only a small extent of seasonality in food availability is sufficient to cause a relatively distinct breeding season. The seasonal variability in food availability might have been great enough to cause a distinct breeding season in our study species but not enough to cause other behaviours to change. Alternatively time needed for moulting might constrain time for breeding.

The timing of moult followed the predicted pattern to some extent. It mainly occurred during the dry season but lasted into the beginning of the rainy season. However, it was terminated in June in most species when rain increased substantially and when we assume seed density to decline markedly and when heavy rains started. Moult therefore coincided with the time of highest food availability but occurred over a relatively long period. We probably overestimated the duration of overlap with moult and breeding as we assumed the breeding season to end with the last juvenile bird caught. As juvenile birds might not moult into adult plumage for three weeks after hatching, breeding in Rock Firefinches, Red-cheeked Cordon Bleus and Lavender Waxbills might have been finished breeding by the time moult started, and overlap in these species compared to Red-billed Firefinches was much shorter anyhow. In Red-billed Firefinches however, overlap between moult and breeding was extensive and this has often been reported for tropical passerines (Foster, 1974; Foster, 1975; Moreno, 2004). It has been suggested that this long moulting period and the overlap with breeding might serve to enable an extended breeding season with more breeding attempts (Foster, 1974) or might be due to high demands on the immune system in a tropical environment because of a likely higher abundance of parasites and higher risk of disease (Moreno, 2004). This would allow only a small amount of energy to be allocated to moulting at one time so that immune response does not substantially decline (Moreno, 2004). Alternatively predation risk on adult birds is high such that moulting follows a pattern that minimises impairment of the ability to escape predators. However, survival rates of the bird species we studied were high compared to temperate birds (McGregor et al., in press) and birds also did not strongly respond to differences in predation risk in their feeding behaviour (Chapter 2) rendering this explanation as unlikely.

Conclusions

We considered several parameters of the birds’ behaviour that were shown to indicate a seasonal variation in starvation risk in temperate birds. However, these parameters did not follow a consistent pattern that would indicate an increased starvation risk during one particular time. Fat deposition and seed depletion peaked during the early rainy season, morning feeding peaked during the late dry season and risk taking behaviour and competitive interactions did not show any seasonal differences. Breeding started during the late rains and continued during the early dry season, while moult occurred during the dry season but extended into the early rainy season.

Even though there might be some problems associated with how we attempted to measure the extent of risk taking behaviour and competition in our study system (which we have discussed), we believe that our results show that there is little evidence for a strong seasonal variation in the risk of starvation in our study area. Unlike in temperate regions where most variables that potentially impose constraints on birds (low temperature, low food availability, short day length, high predation risk) peak at the same time, in subtropical and tropical regions these factors might be more diverse and might peak at different times. Likely constraining variables in the tropics are the availability of several food resources which peak at different times (e.g. insects during the rainy and seeds during the dry season), extent of rainfall (peaking at the middle of the rainy season), high temperatures (generally being higher during the dry season), sun exposure (being higher during the dry season), predation on adults and eggs by a wider range of predators than in temperate regions (several reptile, mammal and birds species) with a corresponding wider range in seasonal activity, extent of competition with other bird species and other guilds feeding on the same food resources, parasite density and so on. We still know far too little to be able to predict how each of these variables might effect the behavioural patterns we investigated. As they might have different consequences for different behavioural patterns, this makes it difficult to assess at what time constraints might be highest. Not surprisingly a more complicated pattern than in temperate regions emerges and remains to be investigated in much more detail before we will be able to understand it. Nevertheless results suggest that there is little food limitation and other factors might regulate population growth.

Ashmole (1963) invoked relative differences in food availability during and outside the breeding season to explain low cutch size in tropical oceanic birds and this hypothesis has also been adopted to explain this phenomenon in tropical passerines. The hypothesis states that due to slight seasonal differences in food availability and adult mortality, food only becomes limiting during the breeding season and then restricts reproductive investment and success. Our results support one prerequisite of Ashmole's hypothesis, which is that there is little evidence of food limitation of adult birds during any time of the year. It is possible that due to high adult survival and little seasonality of adult mortality, food or alternatively high nest predation may actually limit reproductive output regulating population growth.

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Chapter 3: Do tropical granivores modify their foraging with respect to distance from cover?

Abstract

The trade-off between predation risk and starvation risk is crucial in determining the fitness and life history evolution of animals. Relatively little is known about how animals in tropical areas trade-off predation and starvation risk, where life history traits, such as low annual fecundity and high adult survival, imply that levels of predation and starvation risk may be fundamentally different from well studied temperate regions.

We investigated the importance of predation risk by determining how distance from cover affected flocking and foraging behaviour in seven co-flocking African granivorous bird species (Rock Firefinches *Lagonosticta sanguinodorsalis*, Red-billed Firefinches *L. senegala*, Red-cheeked Cordon-Bleus *Uraeginthus bengalus*, Lavender Waxbills *Estrilda caerulescens*, Black-rumped waxbills *Estrilda troglodytes*, Bronze Mannikins *Lonchura cucullata* and Cinnamon-breasted Rock Buntings *Emberiza tahapisi*) in both the field and aviary experiments. In the field, predator encounter rate was low (0.06 escape responses per hour into cover to avian predators, N = 47 hours) and birds escaped into cover apart from Cinnamon-breasted Rock Buntings.

Species differed in their feeding patch choice with respect to cover and this was possibly linked to different predator escape and flocking behaviour. In the field, all species showed an increase in intake rate with increasing group size but there was no effect of distance to cover on this relationship suggesting, that the increase was due to scramble competition not dilution of risk effects. Intake rate itself also was independent of distance to cover. In the aviary, intake rate in Lavender Waxbills also increased with group size but only away from cover (>2m): intake rates decreased with group size next to cover, and intake rates were lower overall next to cover, a result largely inconsistent with predation risk determining intake rate. Intake rate declined with prey dilution, but there was no effect of group size on this relationship, which suggests that interference competition is not important. In the aviary, Rock Firefinches also did not show an increase in intake rate with distance to cover, but had significantly shorter feeding bouts further from cover. The

results suggest that despite an apparent low avian predator encounter rate, some African finch species show specific patch preferences with respect to distance from cover, and Rock Firefinches, at least, also compensate when feeding away from cover by reducing foraging bout length, consistent with distance to cover representing higher predation risk. However, birds did not compensate by increasing vigilance or reducing total foraging time away from cover, and scramble competition effects seemed to be the relatively important determinant of feeding rate, not risk of predation. While distance to cover does represent predation risk in the tropics, its effects probably play a relatively weaker role in subtropical ecosystems in shaping birds' feeding behaviour than in temperate systems, and competition is possibly relatively more important in determining group size effects than risk dilution.

Introduction

The trade-off between predation risk and starvation risk is crucial in determining the fitness and life history evolution of animals. Since feeding usually means that an animal is exposed to a higher predation risk than when resting, each individual is faced with a trade-off between predation and starvation risk. Relatively little is known about how animals in tropical areas trade-off predation and starvation risk, where life history traits, such as low annual fecundity and high adult survival, imply, that levels of predation and starvation risk may be fundamentally different from well studied temperate regions. Tropical birds have been shown to have higher survival rates (Johnston et al., 1997; Peach et al., 2001) and it is assumed that this may be partly due to a much lower predation risk of adult birds in these regions (Johnston et al., 1997). If this is the case, then tropical birds should forage under less constraint from predation risk and so respond to factors that influence predation risk in a different way or less strongly. In this study we investigate this trade-off in tropical granivorous bird species.

How birds trade off the risk of predation and starvation has been studied in many bird species in temperate regions. A common approach is to examine how intake rate and vigilance varies with group size and distance to cover because predation risk should vary as a function of both, decreasing as group size increases (the dilution effect, Hamilton, 1971) and increasing as distance from cover increases (as escape distances to cover that acts as a refuge increases) (Ydenberg & Dill, 1986). Intake rate may also vary with group size because the time available for foraging may increase with group size due to vigilance benefits (Pulliam, 1973). Both observational and experimental studies have aimed to investigate this issue. Although several patterns can be observed, the prevailing effect found is that time spent vigilant decreases with increasing group size (Hogstad, 1988; Elgar, 1989; Lima & Dill, 1990; Lima, 1995; Roberts, 1996; Beauchamp, 2003) and decreasing distance from protective cover (Barnard, 1980; Lazarus & Symonds, 1992; Hogstad, 1988; Caraco et al., 1980). However, Elgar (1986) found no such effect in House Sparrows (*Passer domesticus*) and Lima (1987) even reported that House Sparrows decreased vigilance levels further from cover, demonstrating that other factors may influence these relationships. For example, flocking disadvantages through competition, such as more aggressive interactions or indirect interference as individuals become more vigilant towards con-specifics (Cresswell, 1997; Beauchamp, 1998) may outweigh the benefits gained through dilution of predation risk and group vigilance. Overall the strength of competition and dilution effects will result in different shapes of the relationship between intake rate and group size (Beauchamp, 1998). Acting in opposition the effects could be masked and so no overall effect would be found (Beauchamp, 1998). Therefore, competition must also be considered when examining whether there are group size effects on vigilance.

Even in case of a positive relationship of intake rate with group size, predation risk may not be the only driving factor. As Elgar (1989), Roberts (1995) and Beauchamp (2003) pointed out, reduced vigilance or higher intake rate might also be caused by scramble competition, when animals compromise time spent vigilant in an attempt to increase their share of a resource. Thus even if intake increases with group size the direction of causation remains unclear. Recent work has focused on modelling the effects of risk dilution and scramble competition on intake rate under a factorial design where the effect of group size was studied under different predation risk (Bohlin & Johnsson, 2004). A recently published model predicts no effect of an interaction between group size and level of predation risk on intake rate if only competition is involved. If, however, dilution and competition or dilution alone determine the animals’ vigilance levels (Grand & Dill, 1999; Bohlin & Johnsson, 2004), such an interaction would be expected, with intake rate increasing faster in the low risk habitat (Bohlin & Johnsson, 2004). Higher intake rate might also be a result of increased predation risk because animals may trade-off overall time exposed to predation risk with vigilance. Animals may then have high intake rates and low vigilance and consequently shorter feeding bouts. They could thus minimise exposure time, which under certain situations (for example when predator attacks are not very frequent) might be a better strategy. Alternatively, if a bird increases vigilance while feeding in more risky areas, bout length and overall time spent feeding in a day may increase. Clearly if we are to disentangle the effects of predation risk on foraging behaviour we need to measure a variety of factors.

In this study we investigated how predation risk affects small tropical birds by determining how distance from cover and group size (and their interaction) affected foraging behaviour in seven co-flocking African granivorous bird species (Rock Firefinches *Lagonosticta sanguinodorsalis*, Red-billed Firefinches *L. senegala*, Red-cheeked Cordon-Bleus *Uraeginthus bengalus*, Lavender Waxbills *Estrilda caerulescens*, Black-rumped Waxbills *Estrilda troglodytes*, Bronze Mannikins *Lonchura cucullata*, and Cinnamon-breasted Rock-buntings *Emberiza tahapisi*) in both the field and aviary experiments. To our knowledge there are only four studies investigating intake rates or vigilance levels in tropical seed eating passerines (Lazarus, 1979; Hamed & Evans, 1984; Beauchamp & Livoreil, 1997; Slotow & Coumi, 2000). They all investigated intake rates or vigilance with respect to group size but only Slotow & Coumi (2000) also considered how distance from cover influenced feeding behaviour. We investigated whether birds preferred feeding patches close to or away from cover both in the field and the aviary, and recorded escape responses from avian predators in the field. We manipulated predation risk at artificial feeding sites in the field by varying the distance from cover and also observed the effects of natural variation in group size. In a controlled aviary experiment we manipulated predation risk by varying distances from cover and the extent of competition by providing seeds undiluted or diluted with sand.

We predicted that, if predation risk is an important constraint on foraging, then:

(i) Birds will prefer to feed closer to cover (and respond to predators by flying into cover).

(ii) Intake rate will decrease with distance to cover because more time may be allocated to vigilance as predation risk increases.

(iii) Intake rate will increase with increasing group size because of the “group-size” effect on vigilance. Intake rate may also increase with group size through scramble competition, but if scramble competition is the dominant effect, then the group size effect on intake rate should be independent of distance to cover (Bohlin & Johnsson, 2004).

(iv) Bout length and total feeding time will change with distance to cover because shorter bout lengths and less total feeding time may minimise exposure to predation risk or because longer bouts and longer total feeding time may result from birds being more vigilant.

However, any one of these predictions depend on there not being any compensation via another behaviour, for example intake rates being maintained with increasing distance to cover, because of increasing group size or shortened bout length. We therefore consider several behaviours simultaneously so that such compensation is more likely to be detected (Lind & Cresswell, 2005).

Methods

Data collection

Study area

This study was carried out in Amurum Forest reserve located on the Jos plateau in central Nigeria (9.87ºN 8.98ºE). The habitat consists of mainly bushy savannah with many inselbergs and granite outcrops, interspersed with small patches of gallery forest. Birds were caught with mist nets at feeding sites baited with acha (*Digitaria exilis*) seeds. They were ringed with individually numbered aluminium rings and individual colour-ring combinations.

Field experiments and observations

Five feeding tables were set in bushy savannah habitat at varying distances from cover and with at least 5 m between tables. Feeding tables were made from wood and measured 40×40×40 cm. 100 g of acha seeds were distributed evenly over the feeding table. Seed density was thus very high and seeds were replaced every 3 hours such that the effects of depletion were minimised. Observations were carried out from a location on an inselberg nearby from a distance of at least 20 m and from a higher position than the feeding tables, such that the influence of the observer on the birds’ behaviour was minimised. All observations were carried out by one person with a telescope equipped with a 20 - 60x zoom lens. After recording the number of birds on the feeding table, intake rates of identified individuals were counted using a tally counter. Recording was terminated once the number of birds changed, an aggressive interaction occurred or 1 min had passed. Only feeding bouts of a minimum of 20 sec were included in analyses. Intake rates were calculated as successful pecks / min. Additionally we recorded every instance where a predator occurred within a 100 m radius of the feeding sites. Raptors were only counted if at an altitude of less than 50 m. The predator species and its distance from the feeding sites were recorded and the response of birds feeding on the table observed. We noted whether birds started to obviously scan the environment more extensively than usual and whether they left the feeding table.

To gain data on feeding patch preferences identical feeding tables were set up at two sites, with one table next to cover and one 4 - 6 m away from cover (and also from the other table) at each site respectively. Sites were about 30 m apart. On each table 100 g of acha seeds mixed with 500 g of sand were placed in a plastic plate (30 cm in diameter). Observations were carried out from a point as described above in alternation between the two sites over periods of 1 - 4 hours. The number of birds and their species affiliation were reported for both sites (the one with a table next to cover and the one with a table away from cover) every 5 min.

Aviary experiment 1: Lavender Waxbills

Six adult Lavender Waxbills were caught and placed into an aviary in April 2004. The aviary measured 6×1×2 m and consisted of a concrete floor, a metal frame, wire mesh and a thatched roof made from grass mats to provide shelter. A bush was positioned in one end of the aviary to serve as cover. The type of aviary available to us (entrance on one site only) prevented us from being able to change the site at which cover was placed, so it had to remain in the same position throughout the experiment. Food and water were provided *ad libitum*. Acha seeds mixed with sand were provided on a plastic plate measuring 30 cm in diameter that was placed on a wooden table measuring 40×40×40 cm. Birds were held in the aviary 5 days prior to the experiments, allowing them to habituate to the aviary and to feeding from the plates. During trials food was given at 6 different dilutions: 100 g seeds without sand, 100 g seeds + 500 g sand, 100 g seeds + 1000 g sand, 50 g seeds + 750 g sand, 50 g seeds + 1000 g sand and 50 g seeds + 1250 g sand giving a seed dilution of 0, 5, 10, 15, 20 and 25 respectively. The feeding table was placed at 0 m, 2.5 m and 5 m from cover so as to vary the birds' perception of predation risk. Birds responded to an approaching observer by flying into cover and the same behaviour was also noted in the field. Thus we considered the placement of feeding tables at differing distances from cover as varying the predation risk of the feeding patch. A video camera was placed on a tripod in front of the feeding table at a 0.5 m distance and the feeding behaviour of birds was filmed. Trials lasted for one hour between 06:00 - 10:00 in the morning and 16:00 - 18:00 in the evening to avoid the midday heat. For each combination of food density and distance from cover we conducted two trials. During some trials birds did not feed at all or only very briefly. Therefore we choose that trial for each combination that yielded more time periods with birds feeding and analysed these for intake rates. Only for the treatment of undiluted seeds we analysed both trials, as birds regularly fed during both trials and because this gave us more power to detect possible effects of distance from cover and group size. This yielded a total of 25 hours of video recordings that were analysed.

Intake rate was analysed from videos in the following way: Videos were replayed and the number of birds and their identity recorded every 30 sec. If the birds present over the preceding 30 sec period had not changed, i.e. no bird left or arrived at the plate, this period was included for the recording of the intake rate of all birds present. Intake rates were recorded for identified birds using a tally counter and the time of the day, the number of birds on the feeding plate and their identity was noted.

An additional food patch choice experiment was conducted in the aviary. Birds were given the choice of three feeding tables placed at a distance of 0 m, 2.5 m and 5 m from cover. During four sessions, three lasting 60 min and one lasting 15 min (terminated due to the onset of rain) we noted the number of birds on each table and their ID in 30 sec time intervals.

Aviary experiment 2: Rock Firefinches

One male Rock Firefinch fitted with a PIT-tag glued onto a plastic colour-ring around its leg (c.f. Macleod et al., 2005) and one untagged Rock Firefinch female were placed in the aviary one to two days prior experiments started. Ten pairs in total were tested. For part one of the experiment 30 g of acha seeds were provided on a wooden table (30×30×30 cm) next to cover for the whole day. For part two of the experiment this table was moved to a distance of 5 m from cover. The order of the two parts of the experiment was alternated. Food was presented within a PIT tag detecting antenna (30 cm in diameter), that was placed on the feeding table. This antenna was attached to a data-logger, which took a reading every 1 / 16 of a sec. The data logger was powered by a 12 V car battery, which together with the data logger stood on the ground of the aviary beside the feeding table. Food and data loggers were set at 06:00 during sunrise, data were downloaded and food removed at 18:30 after sunset. To gain data on intake rates, feeding places were filmed from 06:00 - 07:30 and 16:30 - 18:00 avoiding the midday heat when birds were usually found to be less active in the field (pers. obs.). A Sony digital camcorder was placed on a tripod 0.5 m from the feeding table and the table was videoed for 1.5 hours during each part of the experiment. Birds were kept in the large aviary for a maximum of 4 days and then released at the place where previously caught.

From videotapes we recorded the times during which each of the two birds fed. The beginning and end of a feeding bout were defined by the first and the last peck a bird made on one of the plates respectively. From this we obtained data for feeding bout length and feeding bout frequency. Feeding bout frequency was determined as number of feeding bouts that occurred during the three hours of filming during a day (06:00 - 7:30 and 16:30 - 18:00). For analyses of intake rate, all feeding bouts during which a bird fed for at least 60 sec were considered and its pecks during the whole feeding bout were counted and then transformed into pecks per min.

Data analyses

Field experiment

A Box-Cox transformation was applied to normalise intake-rate data collected in the field. Transformed intake rates were analysed using a general linear model (GLM) with species and cover entered as a factor and group size entered as a covariate. We also entered the interaction terms of species with distance from cover, species with group size, and group size with distance from cover, but only retained significant interactions in the final model. Only data from known individuals were used except for Bronze Mannikins, for which we included intake rates of unknown individuals due to the lack of enough colour-ringed individuals on the tables: group size of Bronze Mannikins was often up to 14 individuals and colour ringed individuals were only occasionally re-sighted. Hence we assume a high turnover of individuals at feeding sites and a large population. Thus it can be assumed that samples come from many different individuals.

When calculating a species-specific GLM, ID was entered as a random factor, cover as a factor and group size (note that also large group sizes of more than ten individuals are included in analysis of field data unlike for the aviary experiments where we could only consider group sizes of up to three individuals) as a covariate. We also included the interaction of group size and distance from cover but only retained it in the model if it was significant. Analyses were restricted to the three species for which there were sufficient data for meaningful analysis.

To investigate patch choice we compared the number of birds of each species on the table away from cover with the table next to cover at the same time, for each sample, by using a matched-pairs Wilcoxon signed rank test. We also compared presence and absence of birds on the tables with a matched pair for each sample, using only samples where at least one of the focal species was present, to allow a test of preference that would not be swamped by multiple pairs of zeros when no birds were present. For these analyses we only included data points at times when sun exposure was the same at both tables to avoid testing the effects of sun exposure rather than distance from cover on birds' patch choice.

Aviary experiment 1

To analyse intake rates in the first aviary experiment we calculated the means for each individual under each treatment and entered these as the response variable in a GLM. Food density, distance to cover and group size were entered as covariates and bird ID was entered as a random factor. We also included the interactions of group size and distance from cover, group size and food density and distance from cover and food density, but only retained significant interactions in the final model. Only data for group sizes of one to three individuals were included, as there were few data for group sizes four to six.

Data from the feeding patch choice experiment in the aviary were tested for serial autocorrelation and re-sampled until no autocorrelation was found. This was achieved after only including every fourth data point. Data were then analysed for differences of the number of birds between feeding patches using the non-parametric Friedman's U-test for multiple dependent samples.

Aviary experiment 2

The total time spent feeding by male Rock Firefinches was obtained from PIT-tag data. Data were analysed by pooling all readings per second and calculating the total time spent feeding as the sum of these seconds in which a bird was recorded. From comparing logger data to video data it became obvious that each reading actually did not always represented a bird feeding, because when hopping around on the table outside the antenna occasional readings were also taken. However, this problem is expected to be equal between treatments and should thus not bias the effect of the treatments. For analyses of bout length and frequency however, the data from videotaping were considered as more accurate and thus used for analyses.

The number of seconds a bird was recorded on the feeding plates was entered into a GLM as the dependent variable with distance from cover entered as a fixed factor and ID entered as a random factor. Data for feeding bout length were log transformed before data were entered into a univariate general linear model, with trial, time of day (morning or afternoon) and day (1 or 2) entered as random variables and distance from cover and sex entered as fixed factors. Feeding bout frequency was calculated for each individual for each filming period and divided by the number of minutes filmed, then log transformed. Bouts per min were then entered into a GLM as the dependent variable, with hour, trial number (as only one individual was used per trial this also controls for ID) and day entered as random factors, and distance from cover and sex entered as fixed factors.

All statistical procedures were carried out using software package SPSS 11. All dependent variables were tested for normality using a one sample Kolmogorov Smirnov test and for homogeneity over main effects by using Levene’s test for homogeneity of error variances: where necessary variables were then transformed to achieve normal distribution.

Results

(i) Patch choice and response to predators

In the field Rock Firefinches and Red-cheeked Cordon Bleus preferred feeding next to cover; Bronze Mannikins, Black-rumped Waxbills and Red-billed Firefinches preferred feeding at the patch away from cover, and Lavender Waxbills showed no preference (Table 1). Tests on the number of birds and on presence / absence of birds on feeding tables yielded the similar results except for Bronze Mannikins where there was a preference detected with the second but not with the first method.

Table 1. Results of Wilcoxon matched-pairs tests testing patch preference with respect to distance from cover. We tested for differences in the total number of birds and in the probability of the presence/absence of birds of a species, if one or more birds of any species were present.

	Number of birds on feeding tables			Presence / absence of birds in feeding tables		
Species	Z	p	preferred	Z	P	preferred
Lavender Waxbills	-4.80	0.63	_	-1.40	0.16	_
Red-billed Firefinches	-3.90	<0.01	Open	-2.51	0.01	Open
Rock Firefinches	-11.15	<0.01	Cover	-11.67	<0.01	Cover
Red-cheeked Cordon Bleu	-4.20	<0.01	Cover	-3.96	<0.01	Cover
Black-rumped Waxbill	-5.31	<0.01	Open	-3.49	<0.01	Open
Bronze Mannikin	-0.62	0.54	_	-1.99	<0.05	Open
Cinnamon-breasted Rock Bunting	-5.72	<0.01	Open	-5.50	<0.01	Open

In the first aviary experiment with Lavender Waxbills there was a significant difference between the number of birds on each table (Fig. 1) (Friedman-test, Chi^{2}=27.95, n=50, df=2, p<0.01) with an mean of 1.06 ± 1.43 birds on the table at 0 m distance to cover, 0.30 ± 0.71 birds on the table at 2.5 m distance from cover and 0.14 ± 0.45 birds on the table at 5 m distance from cover. When comparing tables pair wise, the differences between the tables at 0 and 2.5 m distance and between the tables at 0 and 5 m distance were significant (Friedman-test, Chi^{2}=16.67, n=50, df=1, p<0.01; Chi^{2}=16.67, n=50, df=1, p<0.01), however, the difference between tables at 1.5 m and 3 m distance was not significant (Friedman-test, Chi^{2}=1.3, n=50, df=1, p=0.25).

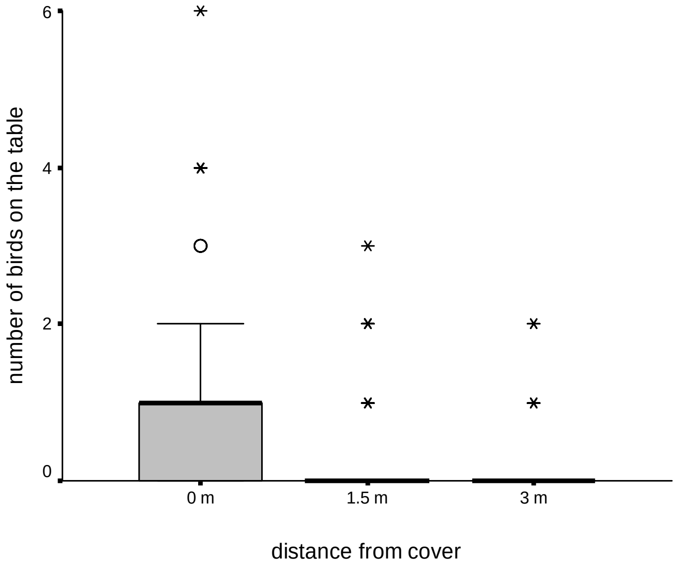

Fig. 1. Box-plots represent the number of Lavender Waxbills (n = 50 observations) at tables with three different distances from cover during the aviary experiment averaged over all observations.

During 47 hours of feeding observations we did not witness a single predator attack on passerines on the feeding tables. However, birds did respond to the presence of Lanner-Falcons (*Falco biarmicus*) at feeding sites. In three out of ten instances at least some of the birds responded by escape flights, however there seemed to be differences between species. All Estrildid finch species escaped in three out of five instances, when several species were present, whereas Cinnamon-breasted Rock Buntings, which were present during all ten over-flights, left the table only once. In the other cases they remained on the table even if all other species left (four cases), but they usually became more alert. All species flew into cover when disturbed, if they flew. Observations are summarised in Table 2.

Table 2. Summary of passerine response to the presence of a raptor less than 100 m away from feeding tables and less than 50 m above ground. ROCFF = Rock Firefinch, REBFF = Red-billed Firefinch, LAVWB = Lavender Waxbill, BROMA = Bronze Mannikin, BLRWB = Black-rumped Waxbill, INDBI = Indigobird, CIBBU = Cinnamon-breasted Rock-bunting.

Date	**Raptor at feeding site**	**Birds on feeding table**	**Response**
09/03/04	Lanner	1 ROCFF, 1 CIBBU	all more alert but remain on table
09/03/04	Lanner	2 REBFF, 1 CIBBU	2 REBFF escape, CIBBU more alert but remains on table
12/03/04	Lanner	1 CIBBU	more alert but remains on table
16/03/04	Lanner	1 CIBBU, 1 REBFF	all no response
16/03/04	Lanner	2 CIBBU, 1 LAVWB	1 LAVWB escapes, 2 CIBBU more alert but remain on table
22/03/04	Lanner	3 REBFF, 2 CIBBU	all escape
23/03/04	Lanner	6 LAVWB, 7 REBFF, 1 ROCFF, 1 BLRWB, 2 VIIBI, 10 BROMA, 1 CIBBU	all escape, apart from CIBBU that becomes more alert and remains on table
24/03/04	Lanner	1 CIBBU	no reaction
24/03/04	Lanner	1 CIBBU	more alert but remains on table
25/03/04	Lanner	2 REBFF, 1 CIBBU, 1 ?	all escape, except for CIBBU that becomes more alert and remains on table

(ii)+(iii) Intake rates at different distances from cover and different group sizes

Field data

There was a significant positive influence of group size on intake rate, but intake rate was independent of distance to cover; and there was a significant effect of species on intake rate (Table 3). Neither the interaction of group size and distance from cover nor of species and group size were significant and thus not included in the final model (Table 3). There was also, however, a significant difference in the relationship between intake rate and cover with species. Therefore we re-ran the analyses individually for each of three species where we had sufficient data. In the species-specific analyses of intake rates, we found no significant interaction between group size and cover for any of the species and therefore did not retain this interaction term in the final model. All three species showed significantly higher intake rates with increasing group size and none of the species was found to show any response of intake rate to distance from cover (Table 4).

Table 3. Results of GLM testing variables influencing intake rate of all bird species combined. There was no significant influence of cover*group-size ($F_{1,605}$=1.95, p=0.16) or of species*group-size ($F_{2,605}$=2.08, p=0.13).

Dependent variable	**Intake rate of all bird species combined**				
	Type III Sum of Squares	B	df	F	p
Corrected Model	937.70		6	43.52	<0.01
Species	544.16		2	75.77	<0.01
Cover	7.67		1	2.14	0.14
Group-size	172.11	0.19	1	47.93	<0.01
Species*Cover	21.81		2	10.90	0.05
Intercept	37659.01		1	10488.04	<0.01
Error	2183.13		608		
Corrected Total	3120.81		614		

Table 4. Results of GLM testing variables influencing intake rates of Bronze Mannikins (A), Rock Firefinches (B), and Lavender Waxbills (C). The term Cover*Group-size was not significant in any of the three species (Bronze Mannikins: $F_{1,76}$=0.18, p=0.67; Rock Firefinches: $F_{1,177}$=0.46, p=0.50; Lavender Waxbills: $F_{1,300}$=0.06, p=0.82).

A. Dependent variable		**Intake rate of Bronze Mannikins**				
		Type III Sum of Squares	B	df	F	p
Corrected Model		104.03		2	6.73	<0.01
Cover		14.80		1	1.92	0.17
Group-size		103.54	0.28	1	13.39	<0.01
Intercept		6886.40		1	890.84	<0.01
Error		595.23		77	7.73	
Corrected Total		699.25		79		
B. Dependent variable		**Intake rate of Rock Firefinches**				
Cover	Hypothesis	1.79		1	0.66	0.42
	Error	485.16		178		
Group-size	Hypothesis	43.66	0.20	1	16.02	<0.01
	Error	485.16		178		
Bird ID	Hypothesis	277.53		20	16.02	<0.01
	Error	485.16		178		
Intercept	Hypothesis	10506.11		1	5.09	<0.01
	Error	321.74		69.6		
C. Dependent variable		**Intake rate of Lavender Waxbills**				
Cover	Hypothesis	2.36		1	1.14	0.29
	Error	323.25		301		
Group-size	Hypothesis	49.86	0.17	1	23.97	<0.01
	Error	323.25		301		
Bird ID	Hypothesis	183.91		30	2.95	<0.01
	Error	323.25		301		
Intercept	Hypothesis	9160.12		1	3675.75	<0.01
	Error	630.65		253.1		

Lavender Waxbills in aviary experiment 1

There was a significant interaction of group size and cover (Fig. 2 and Table 5) with a stronger increase of intake rate with group size furthest away from cover but a decrease next to cover. When splitting analyses by distance from cover, the decrease of intake rate with group size when next to cover was significant ($F_{1,54}$=5.30, B=-1.79, p<0.05) and so was the increase with group size 5 m away from cover ($F_{1,53}$=8.91, B=1.70, p<0.01). However, the relationship between intake rate and group size was not significant when birds were feeding 2.5 m away from cover ($F_{1,54}$=2.90, p=0.10). Intake rate significantly decreased with decreasing food density (Table 5) but there was no effect of distance from cover or group size on this relationship (Table 5).

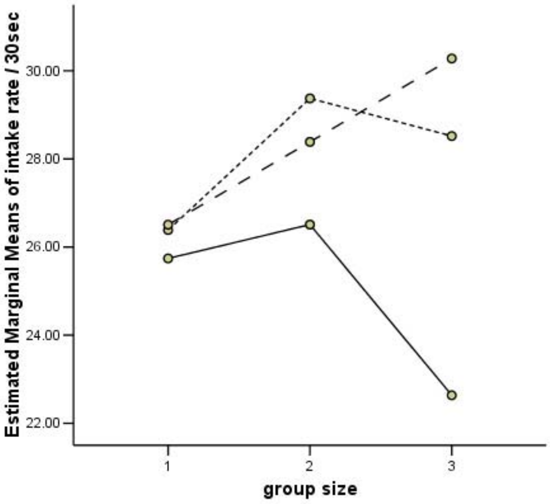

Fig. 2. The estimated marginal means of intake rate / 30 sec in Lavender Waxbills during the aviary experiment for different group sizes (number of birds on the feeding table) with separate lines for different distances from cover. The continuous line represents 0m distance from cover, the dotted line 2.5m from cover and the broken line 5m from cover.

Table 5. Results of GLM testing variables influencing intake rate of Lavender Waxbills in the aviary. There was no significant interaction of group-size*food-dilution ($F_{1,175}$=0.95, p=0.33) or cover*food-dilution ($F_{1,175}$=0.17, p=0.68, controlling for cover, group size, food dilution and ID in both cases).

Dependent variable		**Intake rate**			
		Type III Sum of Squares	df	F	p
Cover	Hypothesis	26.68	1	1.81	0.18
	Error	2584.91	175		
Group-size	Hypothesis	113.55	1	7.69	<0.01
	Error	2584.91	175		
Food-dilution	Hypothesis	546.71	1	37.01	<0.01
	Error	2584.91	175		
Bird ID	Hypothesis	313.86	5	4.25	<0.01
	Error	2584.91	175		
Group-size*Cover	Hypothesis	148.84	1	10.08	<0.01
	Error	2584.91	175		
Intercept	Hypothesis	3968.87	1	250.28	<0.01
	Error	2500.15	157.7		

Rock Firefinches in aviary experiment 2

There was no influence of distance from cover or group size on intake rate (Table 6). However, intake rate significantly differed between the sexes (Table 6) with females (74.9±15.3 swallows per minute, n=63) having lower intake rates than males (80.9±13.2 swallows per minute, n=43).

Table 6. Results of GLM testing variables influencing intake rates in Rock Firefinches in the aviary. Note that only one bird was used for each trial number, so by controlling for trial number we also controlled for ID.

Dependent variable		**Length of feeding bouts**			
		Type III Sum of Squares	df	F	p
Sex	Hypothesis	1915.32	1	14.35	<0.01
	Error	12547.13	94		
Cover	Hypothesis	214.65	1	1.61	0.21
	Error	12547.13	94		
Group size	Hypothesis	0.30	1	0.00	0.96
	Error	12547.13	94		
Trial number	Hypothesis	8855.43	8	8.29	<0.01
	Error	12547.13	94		
Intercept	Hypothesis	400567.73	1	491.26	<0.01
	Error	7211.39	8.84		

(iv) Bout length and total feeding time

Rock Firefinches in aviary experiment 2

Feeding bout lengths were shorter further from cover (Table 7, Fig. 3a). Males had significantly longer feeding bouts than females (Table 7). There was an indication that the influence of distance to cover on bout length was greater for males (sex*cover term added to the model in Table 7, $F_{1, 402} = 3.66$, $P = 0.06$). The number of feeding bouts was similar at different distances from cover ($F_{1, 56} = 0.38$, $p = 0.54$; model including sex $F_{1,56} = 2.12$, $p = 0.15$ and trial number).

The average of 132 ± 45 minutes birds spent feeding per day under the situation with food provided next to cover did not significantly differ from the average of 110 ± 35 minutes birds spent feeding under the situation with food 5 m from cover (t-test, t=2.09, df=9, p=0.07, Fig. 3b). There was a trend, however, for birds to spend overall less time feeding further from cover.

Table 7. Results of GLM testing variables influencing feeding bout length in Rock Firefinches.

Dependent variable		**Length of feeding bouts**			
		Type III Sum of Squares	df	F	p
Sex	Hypothesis	4.33	1	13.19	<0.01
	Error	132.29	403		
Cover	Hypothesis	1.36	1	4.15	0.04
	Error	132.29	403		
Trial number	Hypothesis	16.85	8	6.42	<0.01
	Error	132.29	403		
Intercept	Hypothesis	999.64	1	515.05	<0.01
	Error	16.03	8.26		

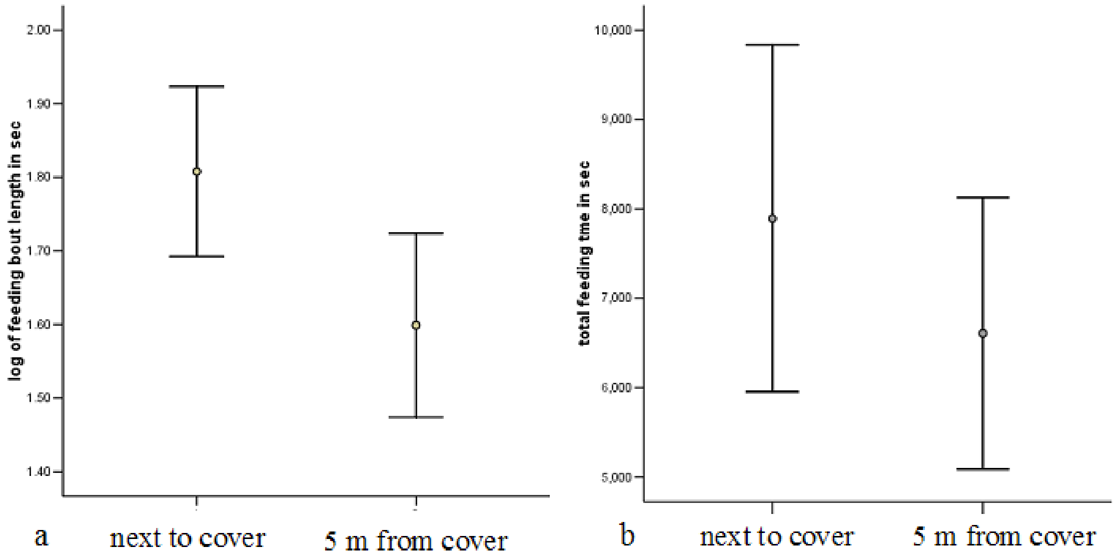

Fig. 3a-b. a) log of feeding bout lengths (in sec) and b) total daily feeding time (in sec) of male Rock Firefinches when present with food next to and 5 m from cover. Horizontal bars show 95% confidence intervals.

Discussion

(i) Patch choice and response to predators

All bird species we investigated apart from Cinnamon-breasted Rock Buntings responded to predator encounter by fleeing into cover. This is in line with the many studies investigating the escape behaviour of several temperate finch species, which were also found to flee into cover (Lima, 1990; Lima, 1993). Cinnamon-breasted Rock Buntings, however, responded differently. They stayed on the feeding patch and became more vigilant. They thus seem to exhibit different predator avoidance behaviour and to monitor a situation more closely before taking flight. Not surprisingly Cinnamon-breasted Rock Buntings preferred feeding away from cover, where they can possibly spot and monitor an approaching predator more easily. This result is in line with Limas study (1990), who found that Lark Buntings (*Calamospiza melanocorys*) did not flee into cover upon predator encounter and preferred feeding at patches with less cover. This supports the suggestion that inter-specific differences in predator escape behaviour lead to differing habitat preferences (Lima, 1990; Lima, 1992; Lima, 1993). However, despite fleeing into cover, only two of the finch species actually preferred feeding next to cover (Rock Firefinches and Red-cheeked Cordon Bleus) and Lavender Waxbills showed a preference for cover in the aviary but not in the field. Red-billed Firefinches, Black-rumped Waxbills and Bronze Mannikins on the contrary preferred feeding in the open. In Black-rumped Waxbills and Bronze Mannikins we believe this to be related to the different flocking behaviour of these species. Rock Firefinches and Red-cheeked Cordon Bleus were both observed to mainly feed in pairs when feeding on natural food resources, while Bronze Mannikins were observed to form large flocks (Chapter 5) and similar observations are reported for Black-rumped Waxbills (Fry et al., 2004). Feeding in large flocks naturally makes these birds more conspicuous to predators and rather than feeding in the safety of cover these species might gain an advantage from feeding in the open where a predator can be spotted earlier. A generally larger flock size minimises the risk of predation via dilution (Hamilton, 1971; Calvert et al., 1979; Duncan & Vigne, 1979) and possibly shared vigilance (Caraco, 1979; Barnard, 1980; Bertram, 1980). In contrast, for species mostly feeding in pairs these benefits usually do not exist and so they may prefer feeding in or next to cover because here they are less conspicuous and less likely to be detected by a predator. Red-billed Firefinches, however, prefer feeding in the open despite feeding mainly in pairs. Our hypothesis that birds prefer feeding next to cover was therefore only partly supported. However, this might partly be explained by inter-specific differences in predator escape tactics or flocking behaviour.

(ii) Intake rates at different distances from cover

Based on the species patch preferences, one would assume at least Rock Firefinches, Red-cheeked Cordon Bleus and Lavender Waxbills to show decreased intake rates away from cover due to a trade-off with increased vigilance levels. For Red-cheeked Cordon Bleus this could not be investigated due to low sample size, however, neither Rock Firefinches nor Lavender Waxbills showed any difference in intake rates with different distances to cover. In Bronze Mannikins, which preferred feeding away from cover, intake rates also did not vary with distance from cover. Our second hypothesis that birds should have decreased intake rates at greater distances from cover was therefore not supported. This suggests that, either birds have not evolved a behavioural mechanism to adjust vigilance to the extent of predation risk (which seems unlikely), compensate via a different behaviour that was not measured, or distance from cover does not actually represent different degrees of predation risk.

One might speculate that feeding away from cover does not actually increase predation risk as predation by ground predators and snakes might be higher next to cover. Lima et al. (1987) and Lazarus & Symonds (1992) pointed out that cover can be both protection for passerines and concealment for predators, and they demonstrated that birds show different behavioural responses depending on which factor prevails. Under field condition during our study, cover could indeed have been both. However, in the aviary we used a bush with dry twigs and leaves that was densest 0.5 - 2 m above ground where the first 50 cm above ground only consisted of a trunk and a few twigs, which is very similar to the one Lazarus & Symonds (1992) used as protective cover. That most species showed patch preferences with respect to cover does further support the assumption that they do indeed perceive differences in predation risk with differing distances from cover. It is therefore more likely that the absence of adjustments in intake rate means that birds do not perceive overall predation risk as important enough to adjust vigilance levels or compensate for predation risk in a different way. Nevertheless, we clearly need more data on predator abundance and the birds' response to different predator types before rejecting that birds show plasticity in their intake rates in response to differences in predation risk. Slotow & Coumi (2000) indeed found a tendency for Bronze Mannikins to increase vigilance and decrease intake rates away from cover, but they used hanging feeders, which might further change the perception of predation risk. Bronze Mannikins in their study also formed larger groups next to cover whereas we found no difference in group size and Bronze Mannikins preferred feeding away from cover.

(iii) Intake rates at different group sizes

Despite not responding to distance from cover, all species showed increasing intake rates with increasing group sizes, which is in line with other findings for tropical granivores (Lazarus, 1979; Hamed & Evans, 1984; Beauchamp & Livoreil, 1997; Slotow & Coumi, 2000). This was unlikely to be due to risk dilution or shared vigilance because there was no effect of distance from cover on this relationship, which according to Bohlin & Johnsson (2004) indicates that scramble competition rather than risk dilution is causing this effect. However, we did not find any effect of distance from cover on intake rate per se showing that our manipulation of predation risk might not have been sufficient to alter the birds' perception of it. The absence of an effect of the interaction of group size and distance from cover on intake rate can therefore not be taken as strong proof for the absence of an effect of risk dilution in our study.

Intake rate did not decrease again with high group sizes, showing that interference competition was also probably not an important factor. Considering the resource that birds feed on, this is not surprising. Minderman et al. (2006) found redshanks to show much stronger interference competition when feeding on mobile invertebrate food. Birds in our study were presented with high seed abundance on the feeding tables and as a result do not have to move much to locate food. Interference due to crossing of another forager's search path or disturbance of prey is therefore unlikely. Even though intake rate decreased with higher seed dilution in Lavender Waxbills in the aviary, there was no effect of group size on this relationship, again suggesting that interference competition is of no or only little importance. As competition in granivorous birds is therefore much more likely to occur as depletion rather that interference it might be a better strategy to respond to increasing group size by increasing intake rate rather than by wasting time by being vigilant towards con- or hetero-specifics. However, despite intake rate increasing at large group sizes, a high amount of inter-specific aggression occurred on feeding patches because of birds pecking or chasing others off the table. This suggest that the time lost because of increased vigilance towards con- and heterospecifics might be masked by the time gained by reducing vigilance for predators because of scramble competition.

However, if scramble competition occurs, following a model about risk dilution by Bohlin & Johnsson (2004), one might predict that there should be an interaction of group size and food dilution, with intake rate increasing faster with group size under high food abundance than under low food abundance. We did not find this effect and therefore our conclusion that scramble competition is causing the relationship we observed in tropical granivorous birds remains speculative. We further found distance from cover to influence the relationship between intake rate and group size in captive Lavender Waxbills. Intake rate decreased with group size next to cover but increased away from cover. This result is opposite that predicted by Bohlin & Johnsson (2004) if risk dilution occurs and its explanation is unclear. Distinguishing the effects of dilution and competition does not seem to be as straightforward as it might appear from current models.

In summary, our hypothesis that intake rate increases with group size was supported, however, against predictions this was probably an effect of scramble competition rather than risk dilution. However, more research has to be done to clarify this.

(iv) Bout length and total feeding time

As Lima (1987) suggested, birds might minimise exposure time under a high risk situation and as a result might even increase intake rate. Despite not adjusting vigilance levels birds might therefore reduce bout length and total daily feeding time to reduce predation risk. Rock Firefinches in the aviary did indeed slightly decrease foraging bout length away from cover, however, total feeding time did not significantly differ when only presented with food away from cover. It is possible that under natural situations Rock Firefinches simply avoid feeding away from cover and are rarely forced to do so, such that the development of such a behavioural response is only of little adaptive value.

Conclusions

We found relatively little behavioural variation in feeding of subtropical granivorous finches in response to apparent variation in predation risk, and the three main species under investigation did not follow the usual pattern observed in most temperate granivores. Due to such weak behavioural responses we believe that predation plays a relatively weaker role in subtropical ecosystems in shaping the birds’ feeding behaviour than in temperate systems, however, further studies are needed to clarify this. Increasing intake rates with group size seem more likely explained by scramble competition than risk dilution, and competition might thus be relatively more important in subtropical granivorous birds, but again further studies need to clarify this. We further showed that granivorous bird species, despite showing the same predator escape behaviour, choose different feeding patches with respect to cover, and this is likely to be a result from differences in predator escape and flocking behaviour. Rather than adjusting individual behaviour to predation risk, species might have evolved relatively fixed inter-specific behavioural strategies to avoid predation such that feeding in small flocks next to cover or feeding in large flocks away from cover reflect different trade-offs with the same result. This might be an outcome of strong inter-specific competition resulting in birds feeding at different locations and as a result adopting differing anti-predator strategies. A wider range of species would have to be investigated to confirm this. Our results are, however, broadly consistent with the idea that predation risk may be relatively low for tropical birds when foraging, leading to high survival rates and lower clutch sizes and other life-history characteristics typical for tropical passerines.

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Chapter 4: Do subtropical Rock Firefinches (*Lagonosticta sanguinodorsalis*) modify their daily feeding pattern under different predation risks?

Abstract

An animal’s foraging decisions are an outcome of the relative importance of the risk of starvation and predation. High mass and fat deposition insures against periods of food shortage but it also carries a cost in terms of mass dependent predation risk due to reduced escape probability and extended exposure time. Accordingly birds have been observed to carry less mass and delay feeding towards later in the day under high predation risk and predictable food resources, and models further predict a bimodal foraging pattern with peaks at dusk and dawn to emerge under these conditions.

We tested this hypothesis in a tropical granivorous finch, the Rock Firefinch (*Lagonosticta sanguinodorsalis*), in an outdoor aviary experiment during which food was provided *ad libitum* and the risk of predation was varied by providing food only next to or 5 m away from cover. We predicted Rock Firefinches to exhibit a stronger bimodal feeding pattern with more feeding activity in the afternoon under the high risk situation when food was provided only away from cover.

Rock Firefinches showed a bimodal foraging pattern regardless of the risk of predation at which they fed. We believe temperature to be relatively more important in shaping the daily feeding pattern of subtropical birds in that high midday temperatures prevent birds from feeding during this time. Relatively warmer temperatures during the afternoon than during the morning may further prevent birds from delaying feeding towards later in the day. Alternatively birds did not perceive a great difference in the risk of predation, either because in the tropics adult mortality is relatively low anyhow or because our manipulation of predation risk did not suffice to achieve a difference in the birds’ perception of it. Further experiments to clarify this are suggested.

Introduction

An animal’s foraging decisions are an outcome of the relative importance of the risk of starvation and predation. Even though high mass and fat deposition insures against periods of food shortage, it also carries a cost in terms of mass dependent predation (Lima, 1986b; McNamara & Houston, 1990; Houston & Mcnamara, 1993; Witter & Cuthill, 1993; Brodin, 2001). This is because high mass reduces a birds’ ability to escape predators due to reduced take off speed and manoeuvrability and / or lowered escape angle (Witter et al., 1994; Lee et al., 1996; Lind et al., 1999; but see Kullberg, 1998; Kullberg et al., 1998; Veasey et al., 1998; Van der Veen & Lindstrom, 2000; MacLeod, 2006). Therefore, birds exposed to a higher risk of predation are expected to carry smaller fat reserves, spent less time feeding and delay feeding towards later in the day. McNamara (1994) showed that under relatively poor foraging conditions, foraging activity should peak early in the day and then decrease steadily while under good foraging conditions a bimodal foraging pattern might occur with peaks at dawn and dusk. Bednekoff & Houston (1994) also demonstrated that only under unpredictable foraging conditions should foraging activity be concentrated early in the day. Accordingly several temperate bird species reduced mass in response to increased overall natural predation risk (Gosler et al., 1995; Piersma et al., 2003) and also to experimentally increased predation risk (Lilliendahl, 1997; Carrascal & Polo, 1999; van der Veen, 1999; Lilliendahl, 2000; van der Veen & Sivars, 2000; Gentle & Gosler, 2001; Rands & Cuthill, 2001; but see Fransson & Weber, 1997; Lilliendahl, 1998; Pravosudov & Grubb, 1998; Bautista & Lane, 2000; andMcNamara et al., 2005). Blackbirds gained mass early in the morning during winter while in summer the majority of mass gain occurred at the end of the day (Macleod et al., 2005a) indicating that only in summer is the risk of predation relatively more important than the risk of starvation. Yellowhammers (van der Veen & Sivars, 2000) and great tits (Macleod et al., 2005b) exposed to a predator also postponed mass gain towards later in the day. If a bird can only feed under a high risk situation it might therefore delay feeding towards later in the day as long as feeding is relatively predictable because high mass decreases the chances of escaping a predatory attack.

We tested the hypothesis that the diurnal feeding pattern would change with increased predation risk in a tropical granivorous finch, the Rock Firefinch (*Lagonosticta sanguinodorsalis*). We kept the finches in an aviary in which food was provided ad libitum and the risk of predation was varied by providing food only next to or 5 m away from cover during a full day. We predicted Rock Firefinches to exhibit a stronger bimodal feeding pattern with more feeding activity in the afternoon under the high risk situation when food was only provided away from cover as compared to the situation when food was provided next to cover.

Methods

Bird trapping and handling

Rock Firefinches were caught in mist nets at four different places within Amurum Forest reserve on the Jos Plateau in central Nigeria (9.87°N 8.98°E). Nets were checked every 45 min during the morning and afternoon but at a more frequent interval during midday hours when temperature was high. Birds were aged, sexed and ringed with a uniquely numbered metal ring.

Experimental set up

Ten pairs of one Rock Firefinch male fitted with a PIT-tag glued onto a plastic colour-ring around its leg (Macleod et al., 2005b) and one untagged Rock Firefinch female were placed in the aviary one to two days prior experiments started between 23/03/2005 - 12/05/2005. For part one of the experiment 30 g of acha (*Digitaria exilis*) seeds were provided on a wooden table (30×30×30 cm) next to cover for the whole day. For part two of the experiment this table was moved to a distance of 5 m from cover. The order of the two parts of the experiment was alternated. Food was presented within a PIT tag detecting antenna (30 cm in diameter) placed on the feeding table. This antenna was attached to a data-logger, which took a reading every 1 / 16 of a sec. The data logger was powered by a 12 V car battery, which together with the data logger stood on the ground of the aviary beside the feeding table. Food and data loggers were set at 06:00 before sunrise, data were downloaded and food removed at 18:30 after sunset. Birds were kept in the large aviary for a maximum of four days and then released at the place where previously caught.

Weather data

Weather data were collected by a Davis Vantage Pro2 weather station within the study area between 15/04/2005 - 11/05/2005. The period of gathering weather data does not entirely coincide with the time during which the aviary experiment was conducted because the weather station was unavailable in the early stages of the project. However, temperature during March are very similar to those in April and May so that available data can give a good impression of what the daily temperature curve is like during the time when this experiment was conducted.

Data analyses

Daily feeding patterns of male Rock Firefinches were obtained from PIT-tag data. Data were analysed by pooling all readings per second and calculating the time spent feeding per hour as the sum of these seconds in which a bird was recorded during that hour.

To test for differences in the daily feeding pattern we calculated a GLM including feeding time as the dependent variable, time of day and distance from cover as fixed factors and bird-ID as a random factor. We also tested for a difference in the interaction of distance from cover with time of day. To analyses the shape of the daily feeding pattern we ran a curve estimation fitting a linear, quadratic and cubic curve to each of the two scatter plots (one for the low risk and one for the high risk situation) to test which curve best represents the pattern of daily feeding under each situation. Before parametric tests were applied data were tested for normal distribution using Kolmogorov Smirnov test and for homogeneity of error variances over main effects using Levene’s test for error variances. All statistical procedures were carried out using the software package SPSS 11.

Results

A GLM revealed a significant influence of time of day on the feeding activity of Rock Firefinches, while neither distance from cover nor its interaction with time of day were significant (Table 1). Birds showed a bimodal foraging pattern under both situations, food provided next to and 5 m away from cover (Fig. 1a-b). Foraging was concentrated early in the day with a peak at dawn between 06:00 - 07:00 (Fig. 2). Foraging then declined and was lowest during the early morning and midday hours between 09:00 - 14:00. A second foraging peak occurred during the afternoon between 14:00 - 18:00 but this was lower than the morning peak. No feeding occurred after sunset at 18:00. Under both situations a linear fit was not significant ($R^2=0.02$, $F=2.45$, $df=118$, $p=0.12$ and $R^2=0.01$, $F=0.81$, $df=118$, $p=0.37$ respectively). The quadratic fit ($R^2=0.18$, $F=12.86$, $df=117$, $p<0.01$ and $R^2=0.12$, $F=7.82$, $df=117$, $p<0.01$ respectively) as well as the cubic fit ($R^2=0.21$, $F=10.02$, df=116, $p<0.01$ and $R^2=0.12$, $F=5.48$, df=116, $p<0.01$ respectively) were significant and provided similarly good fits under both situations (Fig. 1).

Table 1. Results of GLM testing variables influencing total feeding time (in sec) per hour of male Rock Firefinches.

Dependent variable		**Log seeds left on feeding place [g]**			
		Type III Sum of Squares	df	F	p
Cover	Hypothesis	687582	1	2.28	0.13
	Error	62495900	207		
Time of day	Hypothesis	19679884	11	5.93	<0.01
	Error	62495900	207		
Cover*time of day	Hypothesis	3228161	11	0.97	0.47
	Error	62495900	207		
Bird-ID	Hypothesis	7481991	9	2.75	<0.01
	Error	62495900	207		
Intercept	Hypothesis	87601750	1	105.4	<0.01
	Error	7481991	9		

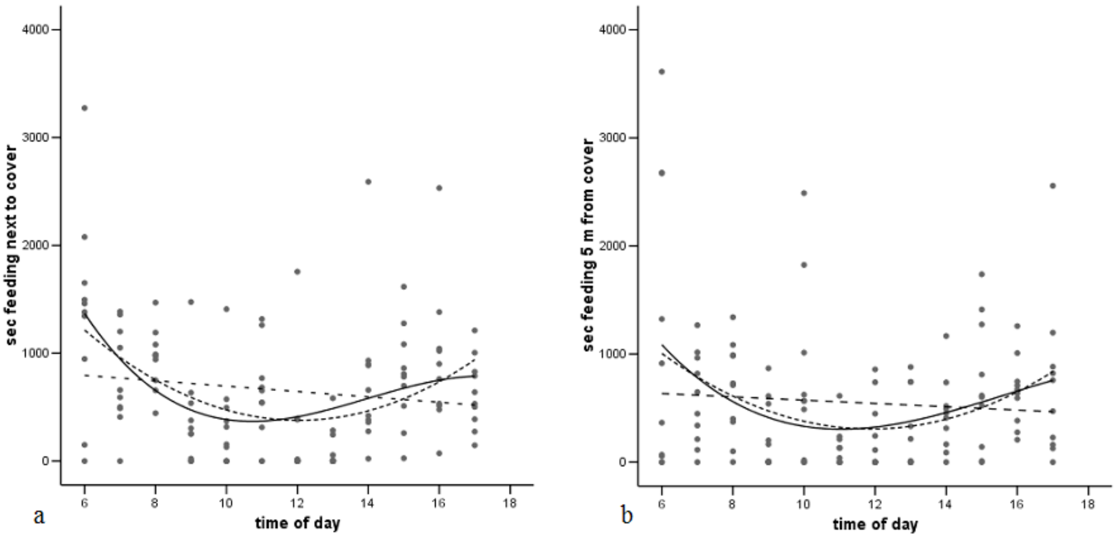

Fig. 1 a-b. Scatter plot and line fits for the number of seconds male Rock Firefinches spent feeding per hour with food provided next to cover (a) and 5 m away from cover (b). Numbers on the x-axis represent the starting hour for this period (i.e. 6 = 06:00 – 07:00). Broken line = linear fit, dotted line = quadratic fit, solid line = cubic fit. The best fit was provided by a cubic fit but the quadratic fit was also significant while the linear fit was not.

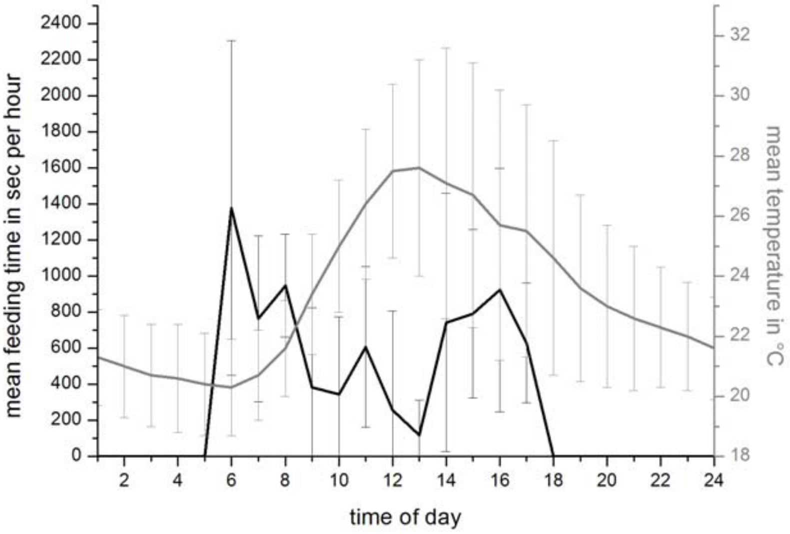

Fig. 2. Mean feeding time in sec per hour of male Rock Firefinches when food was provided next to cover (black line) and daily temperature curve showing average temperatures for each hour between 14/04/05 - 12/05/05 (grey line). Error bars denote standard deviation for mean feeding time and mean temperature.

Temperatures steadily climbed from about 20°C at 06:00 until reaching a peak of about 27°C between 12:00 - 14:00. They then slightly declined again until reaching about 24.5°C at 18:00. Temperatures were thus a lot cooler during the morning than during the afternoon and rose more steeply than they declined (Fig. 2). During the night temperatures dropped slowly from about 24°C at sunset to the minimum of about 20°C at 06:00.

Discussion

Our data did not support the hypotheses that Rock Firefinches delayed feeding towards later in the day when presented with food 5 m away from cover representing a higher predation risk. This might indicate that birds did not perceive a difference in the risk of predation; however, we suggest that temperature plays a more important role in shaping the birds’ daily feeding pattern than the risk of predation.

One possible explanation for our negative result might simply be that birds perceived predation risk to generally be low overall so that feeding away from cover did not represent a significant increase in risk, or that our manipulation of predation risk was not sufficiently large to cause a change in the birds' perception of it. Adult mortality has been shown to be lower in the tropics than in temperate regions (Yomtov et al., 1994; Johnston et al., 1997; Geffen & Yom-Tov, 2000; Peach et al., 2001) and survival rates of adult birds within our study area were indeed found to be high compared to temperate birds of similar sizes (McGregor et al., in press). Birds might therefore not be under great enough constraints from predation risk to alter their feeding patterns when food is provided at different distances from cover. However, survival rates of Rock Firefinches (0.66 ± 0.18) were still relatively low when compared to those of closely related species such as the Red-billed Firefinch (0.89 ± 0.39) (McGregor et al., in press). Despite not altering intake rate with distance from cover (Chapter 3), Rock Firefinches were observed to feed relatively close to cover in the field (Chapter 5) and they preferred artificial feeding patches in the field next to cover over those 3 m away from cover (Chapter 3), suggesting that avoidance of predation risk is of some importance. They also responded to the appearance of a predator by flying into cover (Chapter 3), rendering it unlikely that they would perceive the place 5 m away from cover in the aviary as less risky, as one might argue if birds were at relatively more risk from terrestrial predators or because cover obstructs their view of an approaching predator (Lima, 1986a; Lima et al., 1987).

We suggest that temperature rather than predation risk may be the over-riding factor in determining the observed bimodal feeding pattern in Rock Firefinches. The birds' feeding pattern seemed to reflect temperature changes over the day. The majority of feeding occurred during the relatively cool morning hours and feeding steeply declined as temperature increased until almost ceasing at midday when it was hottest. A second peak of feeding occurred during the afternoon when temperatures decreased slightly, however, this peak was lower than during the morning. Even though birds have to replenish energy that was lost during the night, which might in part explain more extensive feeding during the morning, it is unlikely that this should be the sole cause for the feeding pattern of Rock Firefinches. Temperatures during the night were between 20 and 22 °C, and this is unlikely to cause extensive thermoregulatory costs for small passerines. The thermo neutral zone of Rock Firefinches is not known, but the smaller Black-rumped Waxbills (*Estrilda troglodytes*) and Silverbills (*Lonchura malabarcia*), which occur in the same habitat and feed on similar food resources, were reported to have a lower critical temperature (T_{LC}) of 28°C (Lasiewski et al 1964 in Macmillen, 1990) and 33 °C (Willoughby 1969 in Macmillen, 1990) respectively.

Diurnal temperature variation may affect diurnal feeding patterns through the need for birds to conserve water. Somewhere below the T_{LC} for Rock Firefinches occurs a point up to which a positive water balance can be maintained, but above which respiratory water loss exceeds metabolic water production so that birds rely on external water sources (Macmillen, 1990). In the zebra finch with a relatively high T_{LC} of 36 °C this point lies somewhere around 22 °C (Macmillen, 1990). It is likely therefore that a positive water balance without external water can only be maintained by Rock Firefinches up to an ambient temperature (T_A) of somewhere below 22 °C. Under field conditions some Rock Firefinches had to fly over 0.5 km to get water during the dry season (Chapter 6), so gaining water is expensive and conserving water might become a necessity. Even though small bird species conserve water by allowing their body temperatures (T_B) to rise so that a positive gradient of T_B-T_A can be maintained (up to temperatures of over 40 °C in some species) to allow thermal conductance and minimise evaporative water loss (Weathers, 1997; Tieleman & Williams, 1999), most species probably rely on behavioural adaptations (Weathers, 1997). Rock Firefinches might therefore avoid high midday temperatures and consequent water loss by resting in the shade rather than being active foraging at sun exposed places, resulting in a feeding pattern inversely linked to temperature.

The high density of seeds provided to Rock Firefinches in the aviary and practically no search time associated with such a food resource might enable birds to fill their crop relatively quickly and therefore digestive constraints might have prevented them from feeding for longer in the morning, resulting in the bimodal pattern. For example, Ward (1978) suggested that higher feeding activity during the morning than during the afternoon in Red-billed Queleas (*Quelea quelea*) is linked to them having to wet their crop contents to aid digestion, which they mainly do during the midday hours, and Bednekoff & Houston (1994) stated that digestive constraints may cause feeding to be spread more evenly through the day. Rock Firefinches might therefore use the late morning and midday to digest food before more seeds can be stored in the crop during the afternoon. Digestive constraints were also found to limit feeding time in hummingbirds (Diamond et al., 1986), and finches caught in our study area during the late morning hours often had their crop completely filled with seeds (Chapter 2). Costs associated with thermoregulation and water loss and daily drinking schedules might therefore outweigh the importance of predation risk and prevent birds from delaying feeding towards later in the day, when thermoregulatory costs and water loss are higher, while digestive constraints prevent birds from feeding longer during the morning.

Most likely the lack of a change in the feeding pattern of Rock Firefinches in response to different distances from cover at which food was provided was a result of a combination of a relatively high importance of temperature and a relatively low importance of predation risk for adult granivorous passerines in tropical and subtropical areas. Further experiments to test and disentangle the relative importance of these causes are needed. An indoor aviary experiment could be conducted during which birds are presented with different temperature regimes during the daylight period to establish the role of temperature in shaping the birds feeding pattern in more detail and test whether there is an interaction of temperature with distance from cover. It would also be useful to present the birds with a model predator in addition to changing the distance from cover at which food is provided to establish if birds change their feeding pattern in response to immediate danger.

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Chapter 5: Coexistence of granivorous bird species in savannah habitat: enabled by differing microhabitat choice?

Abstract

Competition has long been recognised as a strong factor shaping animal communities, because selection favours any adaptation that reduces inter-specific competition and therefore differentiation between species. Microhabitat segregation has been well documented in temperate insectivorous bird communities inhabiting woodland areas. However, relatively little information exists for tropical granivorous bird communities, which are characterised by a particularly high species diversity and abundance.

We examined competitive coexistence by studying microhabitat segregation in a granivorous bird community in savannah habitat in central Nigeria, where several closely related Estrildid finches are sympatric. We examined whether differences in inter-specific microhabitat choice might arise from differences in the choice of feeding area with respect to predation risk, facilitated by different feeding abilities due to different bill morphology and different dominance or competitive abilities. We recorded the feeding behaviour and feeding locations of several sympatric finch species during transects. We further carried out an aviary experiment to test whether dominant Rock Firefinches exclude subdominant Red-billed Firefinches from the more profitable food patch and to test whether the species with a longer bill is more efficient in extracting seeds mixed with sand.

Species partly segregated in their microhabitat choice. Lavender Waxbills and Bronze Mannikins were generalists, switching between different microhabitats, while Red-cheeked Cordon Bleus, Red-billed Firefinches and Rock Firefinches were specialised to feed on seeds from the ground. Microhabitat choice of Bronze Mannikins converged with the other ground feeding species during the late dry season when few seeds were available on grass ears, and thus competition may be higher during these times. However, differences in microhabitat choice compared between other species did not show a clear seasonal direction. No clear relationship was found between a species' dominance and the profitability or likely predation risk of a feeding patch. Despite being dominant over Red-

billed Firefinches, Rock Firefinches were found to feed at similar distances from cover and at places with a lower percentage of bare ground. However, during the aviary experiment we found that although Rock Firefinches were capable of excluding Red-billed Firefinches from the more profitable food patch, they were more efficient in extracting seeds from sand and this is probably related to their longer bill shape. Results suggest that dominance plays only a minor role in determining feeding patch choice and that species-specific adaptations to feed at different microhabitats exist.

Introduction

Competition has long been recognised as a strong factor in shaping animal communities (Wiens, 1989). Many communities are composed of species differing in their spatial distribution, morphology and / or behaviour more than expected by chance, and inter-specific competition is often the most likely explanation for this pattern (Brown, 1995). Nevertheless a large number of ecologically similar species co-occur to form local communities (Wiens, 1989). According to classical competition theory these species have to differ in some essential ways in order to coexist (Wiens, 1989) as otherwise one species would out compete the other. Species occurring in the same habitat and feeding on the same food resource therefore might avoid competition by using these food resources in differing microhabitats. One well documented example for this are insectivorous bird communities in woodland areas, where species partition resources by using them at different trees or different parts of a tree (Balda, 1969; Edington & Edington, 1972; Noske, 1979; Alatalo, 1980; Alatalo, 1981; Saether, 1982).

Such differences in microhabitat usage might be related to species differing in their anatomy leading to different foraging efficiency at separate microhabitats (Jones et al., 2001) or they might be a result of a species' ability to exploit a resource changing with environmental conditions (Lawler & Morin, 1993). A universal variable environmental condition is predation risk, and differing degrees of anti-predation behaviour and / or vulnerability will cause species not to perceive predation risk equally in the same area (Lima, 1993). Different behavioural adaptations or vulnerabilities to predation risk might then serve to spatially segregate species in their feeding habitats as reported for rodents by Harris (1984) and Kotler (1984). For example, Pulliam & Mills (1977) and Lima (1990) reported different finch species to feed at differing distances from cover and this may have been due to different predator escape tactics or vulnerability. Another factor altering microhabitat use are the inter-specific dominance relationships which might force subdominant species to forage at places or at times of higher risk or lower food profitability in order to avoid inter-specific competition (Suhonen et al., 1993; Krams, 1996; Carrascal & Alonso, 2006).

Most examples of habitat segregation in avian communities stem from temperate regions. However, only very little information exists on the community patterns and feeding habits of tropical granivorous bird species. Animal and plant populations in tropical ecosystems have long been thought of as staying closer to carrying capacity due to reduced seasonality in climate and associated low mortality such that higher inter-specific competition leads to greater specialisation and diversity (Dobzhansky, 1950). There should therefore be little overlap between species in resource use. The relationship between bill morphology and diet choice has been well studied in Galapagos finches (Price et al., 1984; Grant, 1986), but such island populations are probably subject to much different selective forces than continental populations (Schluter, 1988). One of the few studies on continental tropical granivorous birds has been carried out by Schluter (1988), who studied the granivorous finch community in Kenya and found that little inter-specific differences exist in bill shape, and rather than partitioning resources by seed size, species segregated in their microhabitat use. However, similar studies are rare so that little is known overall on tropical granivorous finches, and about how their microhabitat preferences relate to bill shape and how this might reduce competition. In savannah habitat of Amurum forest reserve in central Nigeria several closely related granivorous Estrildid finch species, two species of Euplectes weavers and one Embrezia species are commonly observed in the same habitat and are thought to feed on the same food resources. They thus provide a good opportunity to investigate microhabitat usage and its relation to morphology and vulnerability to predation of the different species in a subtropical system and to test the hypothesis that subdominant species feed at places of higher risk and lower food profitability.

If inter-specific competition is important in shaping the birds feeding behaviour, inter-specific differences in diet choice or microhabitat use should be most pronounced during periods of food limitation (Lack, 1947; Smith et al., 1978) and birds should also respond numerically by migration, death or reduced reproduction (Smith et al., 1978). If however, intra-specific competition is relatively more important, species should broaden their habitat use and increase diet breaths during times of food shortage (Smith et al., 1978), which might lead to larger inter-specific overlap. If competition is not active, populations should not show shifts in diet or microhabitat use other than those directly dictated by changes in the nature of available food (Smith et al., 1978). Only if species diverge in diet or microhabitat choice during food limitation, can competition for food lead to species divergence in behavioural and morphological traits related to the obtaining of food. Assuming that inter-specific competition is important we therefore predict finch species in Nigeria to diverge in their microhabitat use during the late dry season when the abundance of grass seeds is expected to decline.

One of the most abundant species in the reserve is the Rock Firefinch (*Lagonosticta sanguinodorsalis*), which has been described only recently and is probably endemic to the Jos Plateau in central Nigeria (Payne, 1998). Little information exists on the biology of this potentially threatened species such that any data on its feeding patterns and interactions with other species would be useful for assessing its potential status.

In this paper we provide novel information on the feeding habits, microhabitat choice and microhabitat segregation of several granivorous bird species in savannah habitat in Nigeria and how they change between the early and late dry season when considerable differences in food availability are expected. We investigated the following species: Lavender Waxbills (*Estrilda caerulescens*), Bronze Mannikins (*Lonchura cucullatus*), Red-billed Firefinches (*Lagonosticta senegala*), Rock Firefinches (*Lagonosticta sanguinodorsalis*), Red-cheeked Cordon Bleus (*Uraeginthus begalus*), Northern Red Bishops (*Euplectes franciscanus*), Black-winged Bishops (*Euplectes hordeaceu*) and Cinnamon-breasted Rock Buntings (*Emberiza tahapisi*), chosen due to their high abundance within the study area. We carried out both field observations of microhabitat choice and dominance interaction as well as aviary experiments with Rock Firefinches and subdominant Red-billed Firefinches. We investigated how foraging with respect to predation risk, dominance interactions, bill-shape and foraging efficiency interacted to result in any microhabitat choice differences between species that may then result in reduced inter-specific competition. We also examined whether subdominant species feed at places of higher risk. We tested the following specific hypotheses:

1. Birds will segregate in their microhabitat use and this will be more pronounced during the late dry season when food resources are expected to decline.
2. Species feeding further from cover (where predation risk is higher) will form larger groups (so as to compensate for a higher predation risk by dilution of risk effects and shared vigilance), and the same pattern should be found between groups within species.
3. Dominant species will feed closer to cover (representing places of lower predation risk) and at places with less ground cover (where food is easier to obtain).
4. Species will differ in their bill morphology and this will be linked to differences in microhabitat choice.
5. Dominant Rock Firefinches will exclude subdominant Red-billed Firefinches from more profitable food patches.
6. Rock Firefinches having a longer bill will be more efficient than Red-billed Firefinches in separating seeds from sand.

Methods

Field observations

Data collection

Study area

This study was carried out in the Amurum Forest reserve (9.867ºN 8.983ºE) located on the Jos Plateau in central Nigeria. The rainy season in this region lasts from May until October and the dry season lasts from November until April. Mean daily temperatures vary between 20 - 25°C and annual rainfall is about 146 cm. The altitude of the reserve is about 1200 m and the habitat is characterised by scrubby grass savannah (northern guinea savannah) located between granite outcrops about 30 m in height and interspersed with patches of gallery forest.

Food availability

Data on seed availability were obtained by taking 12 randomly located soil samples around the area where transect 3 (see below) was located by throwing a wire-circle with a diameter of 30 cm and taking the top layer off within this circle. The ground was generally very solid and the top layer not very deep (1 - 2 cm deep) such that all seeds within the top layer should be available to the birds. Twelve samples were taken both in November 2004 and in April 2005. The number of grass seeds within each sample was counted and a mean was calculated for each month. The amount of seeds available on the grass crops was estimating by recording the percentage of grasses that were in crop in a 10 m radius around each of the 12 points.

Observations on feeding behaviour

To gain data on the natural foraging behaviour of granivorous finches three transects through the reserve were repeatedly walked between 6:00 - 10:00 and 16:00 - 18:00. Transects were between 800 - 1300 m long and took approximately one hour to complete. Thirty-four transects were walked between 12/11/2004 - 12/12/2004 during the early dry season and 50 transects were walked between 09/03/2005 - 27/04/2005 during the late dry season. All feeding observations were carried out by M. J. Brandt to avoid observer biases.

For each single bird or flock of birds encountered feeding, the following parameters were noted: species, group size, resource the birds fed on, feeding position, height above ground, nearest distance from cover (defined as a bush at least 1×1×1 m) and time of day. For birds that fed on the ground the following parameters were recorded in a 0.5 m radius around the birds’ position: percentage bare ground, percentage vegetation litter, percentage vegetation below 30 cm in height and vegetation higher than 30 cm. These parameters were recorded in 5% intervals, distance from cover in 0.5 m intervals. Six different feeding positions were distinguished: 1: feeding on seeds from the ground, 2: perched on a grass stem feeding on seeds from the grass ear, 3: perched on bush-twigs feeding on seeds from the grass ears, 4: feeding on a resource in a tree (insects, pollen or figs), 5: taking insects in flight from the air, 6: standing on the ground feeding on seeds from the grass-ears. When a flock of birds was encountered the feeding position of the majority of birds was recorded and the height at which most birds fed was estimated. For distance from cover and vegetation composition the centre of the flock was chosen as a reference point. The distance at which birds were flushed was estimated in 1m intervals and their subsequent escape behaviour noted.

Dominance hierarchies

To establish data on dominance hierarchies in the observed species, replacement rates at artificial feeding places in the reserve were observed. Each feeding site consisted of a wooden table (30x30x50 cm) on which an orange plastic plate was placed (30 cm in diameter), which was filled with 100 g of acha (*Digitaria exilis*) seeds and 500 g of sand. Eight different feeding places were videoed for 1.5 hours each, four of which were close to cover and four of which were between 3 - 5 m away from cover. The camera was placed 4 m away from the feeding table. From video the first replacement that occurred during each 30 sec interval was recorded and the species, sex and if possible identity of the replacing and the replaced bird were noted. From this a dominance matrix was created. Data are unlikely to be confined by different abundances of species on the feeding table as all fife species for which dominance interactions were analysed readily used provided food and are the most commonly observed species on the feeding table (Chapter 2).

Anatomical measurements

Data on weight and bill shape were obtained during mist netting in the same area. Birds were weighted to the nearest 0.1 g using a spring balance, bill length was measured from the tip of the bill to the feathering and bill height was measured in a vertical line through the centre of the nostrils. Bill measurements were to the nearest 0.1 mm. Analysis on differences in bill-shape were restricted to the Estrildid species only to avoid interpreting differences which are simply a result of phylogeny alone.

Data analyses

Only single-species flocks and species with a minimum of ten observations in total were considered for analyses of microhabitat differences. For investigations on differences in microhabitat choice between birds feeding on grass-seeds from the ground, data were split by season as seasonal differences were expected. When testing for differences in microhabitat use between seasons, only species with a minimum of five observations during each season were considered. Data were tested for significant deviation from normal distribution using a one sample Kolmogorov Smirnov test. Where data significantly deviated from normal distribution non parametric tests were applied. Regression analyses were performed to test whether group size correlated with the distance from cover at which birds fed. For all these analysis of microhabitat differences and group sizes only single species flocks (which were the majority of flocks encountered) were considered. Bonferroni-corrections were applied where several tests were performed on the same data set.

Aviary experiment

Data collection

Experimental set up

Birds were captured in Amurum forest reserve on the Jos Plateau in central Nigeria using mist nets between 06:00 - 11:00 and 15:00 - 18:00 between September and December 2005. Nets were checked every 45 min. Captured birds were ringed, sexed and aged, weighted to the nearest 0.1 g and then placed in a holding cage. Only adult male birds were used in experiments. We used a total of ten adult Rock Firefinches and ten adult Red-billed Firefinches during aviary experiments.

Birds were kept in a small holding cage (50×30×30 cm) for no more than three days before being transferred into the aviary for experiments. Water and food were always provided ad libitum apart from one hour before experiments started (when food was removed). The aviary measured 6×1.5×2 m and was divided into two equal sections by a removable door in the middle such that experiments could be carried out on both sides simultaneously. On the side of the removable door a bush was placed inside the aviary on either side to provide cover and shelter. The aviary consisted of a metal frame over which small meshes was spanned and was covered with a slightly tilted thatched roof to serve as protection from sun and rain.

Birds were placed in the aviary one day prior to when experiments started. For part one of the experiment during which birds were tested singly for feeding parameters, one Rock Firefinch and one Red-billed Firefinch were placed on either side of the aviary. They were given food in two identical 13 cm radius plates next to the bush. One plate contained 30 ml of acha, the other contained 3 ml of acha and 30 ml of sand later referred to as high and low density seeds respectively. For part two of the experiment the two birds were placed in the aviary together and the experiment carried out as before. Sides of the aviary, arrangement of the two feeding plates and order of the two parts of the experiment were alternated. Experiments were carried out for 1.5 hours between 06:30 - 10:30 and 16:00 -

18:00 to avoid the midday heat when birds were usually less active (Chapter 4). A Sony digital camcorder was placed on a tripod 1.5 m from the feeding plates and the feeding site was filmed for 1.5 hours. If one bird did not feed during this time the trial was repeated.

After the two parts of the experiment were finished each of the birds was again placed in one side of the aviary separately and provided with low density seeds only for 1.5 hours to record intake rate of each species feeding on low density seeds. Again the feeding place was filmed for 1.5 hours. This was not repeated if a bird did not feed during the trial. After the 1.5 hours trial birds were again given food ad libitum.

Birds were kept in the large aviary for a maximum of seven days and then released at the place caught. One Rock Firefinch and one Red-billed Firefinch died in the aviary for unknown reasons (these birds are not included in the ten species pairs used in analysis), apart from that no problems with holding the birds in captivity were encountered.

Video analyses

Tapes were analysed by connecting the camcorder to a TV and recording the times each bird fed. A feeding bout was defined as the time between a bird's first peck after hopping on to the plate and its last peck before leaving the plate. Bird ID and seed density it fed on were noted.

For intake rate analyses, the first feeding bout where a bird fed for at least 30 sec on high density seeds during each of the two parts of the experiment was considered, and its successful pecks during the first 30 sec of this bout were counted. We also counted all pecks during the whole feeding bout and then transformed it to pecks per 30 sec in order to test for potential differences in results between the two methods. When counting intake rate on low density seeds to compare between species we counted all successful pecks during the whole feeding bout and then calculated number of pecks per 30 sec.

Aggressive interactions were also recorded from videos. Aggressive interactions were defined as one bird successfully replacing the other from the feeding place. Species and trial number was noted for every aggressive interaction observed, and it was recorded whether replacing involved active fighting or pecking.

Data analyses

The total time each bird fed on low or high density seeds was calculated and the percentage time spent on low density seeds determined. Duration of feeding bouts was calculated as means for each individual. Total feeding times were corrected for the time filmed (different tapes differed in length by a few minutes) and calculated as time fed during 1.5 hr. Data were tested for significant deviation from normal distribution and equality of error variances over main effects. Data on feeding bout length were transformed using the natural logarithm to achieve normal distribution. Apart from bout frequency none of the data showed a significant deviation from homogeneity of error variances over main factors, however, some data differed significantly from normal distribution (percentage fed on low density seeds). Percentage of time spent feeding on low density seeds showed a Poisson distribution. It was therefore analysed using a general linear model (GLM) fitted for a Poisson distribution with treatment and species entered as factors and trial-number and time entered as random factors. Data were tested for differences between species and treatment by applying univariate GLMs with percentage time spent on low density seeds, intake rate and feeding bout length entered as independent variables, species and treatment as factors, trial number and time as random factors and the interaction of species and treatment included. For analyses of feeding bout length, only bouts on high density seeds were considered when running a GLM to test for the influence of treatment and species, because sample size on low density seeds for Rock Firefinches was not sufficient.

For analysis of intake rates on low density seeds from the treatment where birds were only given low density seeds, we calculated mean intake rate by counting all successful pecks during the first 30 sec of the first feeding bout, that was at least 30 sec long. This was then compared to the mean intake rate the focal bird had on high density seeds when feeding alone using a non parametric Wilcoxon signed rank test for two related samples.

Results

Field observations

Seasonal seed abundance

Mean percentage of grasses in crop differed significantly between the early dry (90.4 ± 4.6%) and the late dry season (16.8 ± 9.3%) (Mann Whitney U test, $Z_{14,14}$= -4.56, p<0.01). Mean number of seeds on the ground however, did not differ between early and late dry season ($Z_{26,13}$= -1.31, p=0.20; 39 ± 23.2 and 56.0 ± 36.5 respectively).

Food resources exploited

All bird species for which a sufficient sample size of feeding observations was achieved were found to mainly feed on small grass seeds (Table 1). During transects only Lavender Waxbills were seen utilising other food resources. They were also found to feed on pollen (n=4) and insects (flycatching termites, n=6) in addition to feeding on grass seeds (n=30). During sporadic observations they were also seen feeding on figs in a tree on three occasions. Lavender Waxbills used other food resources than grass seeds to a greater extent during the early dry than during the later dry season (Chi^2-test, Chi^2=4.86, df=1, p<0.05). Cinnamon-breasted Rock Buntings (n=19), Black-winged Bishops (n=11), Northern Red Bishop (n=17), Bronze Mannikins (n=47), Red-cheeked Cordon Bleus (n=29), Red-billed Firefinches (n=22) and Rock Firefinches (n=199) were only seen feeding on small grass seeds during transects. However, there were also two opportunistic observations of Red-cheeked Cordon Bleus flycatching for termites.

Microhabitat use and seasonal differences

When feeding on small grass seeds species could be divided into two main groups: ground - in which during transects species exclusively fed on seeds lying on the ground (Red-billed Firefinch, Rock Firefinch, Red-cheeked Cordon Bleu and Cinnamon-breasted Rock Bunting) and stem - in which species mainly fed on grass seeds from the grass ear (Northern Red Bishop, Black-winged Bishop, Bronze Mannikin and Lavender Waxbill). Of the stem group, all but Lavender Waxbills fed on seeds from the ear by perching on grass stems. Lavender Waxbills however, mainly perched on branches of bushes while feeding on the ear of a grass growing next to the bush (16 out of 24 observations while feeding on the grass ear), and during one instance one Lavender Waxbill fed on the ear of a grass while perched on the ground. Within the stem group, however, we also observed

Bronze Mannikins, Northern Red Bishops and Black-winged Bishops to exhibit seasonal differences: they almost exclusively fed from the ear during the early dry season but shifted to feed more on the ground during the late dry season. This seasonal difference was significant for all three species (Bronze Mannikins: $Chi^2=15.67$, df=1, $p<0.01$; Black-winged Bishop: $Chi^2=5.37$, df=1, $p<0.05$, Northern Red Bishop: $Chi^2=8.56$, df=1, $p<0.01$) (Table 1). Of Northern Red Bishops and Black-winged Bishops, however, only two observations each were obtained during the late dry season, which suggests that most individuals of these species had left the study area during that time. Within the ground group, one instance was witnessed where a Rock Firefinch fed on seeds from the ear while perched on a bush-branch and two instances where Red-cheeked Cordon Bleus perched on grass-stems until they bent down to the ground and then fed on the ear while holding it with one of their claws. All these sporadic observations occurred in August.

Species in the stem group, differed with respect to the distance from cover at which they fed (Kruskal Wallis test, $Chi^2=39.35$, df=2, $p<0.01$, Fig. 1a). Lavender Waxbills fed nearest to cover and differed significantly from all other species (Mann Whitney U test, from Bronze Mannikins: $Z_{24,35}= -5.15$, $p<0.01$ and from Northern Red Bishops: $Z_{24,15}= -4.93$, $p<0.01$). Northern Red Bishops fed furthest from cover and also differed significantly from Bronze Mannikins (Man Whitney U test, $Z_{15,35}= -3.32$, $p<0.01$).

Table 1. Feeding behaviour of granivorous savannah bird species at different seasons. Shown is the number of observations at which birds were seen feeding on different resources.

Season	**Species**	**grass seeds on the ground**	**grass seeds on the ear**	**pollen**	**insects**	**n total obser-vations**
late dry season March-May	Black-winged Bishop	2				2
	Northern Red Bishop	2				2
	Lavender Waxbill	4	9	3	6	22
	Bronze Mannikin	10	7			17
	Red-cheeked Cordon Bleu	22				22
	Red-billed Firefinch	16				16
	Rock Firefinch	112				112
	Cinnamon-breasted Rock Bunting	8				8
early of dry season Oct-Dec	Black-winged Bishop		9			9
	Northern Red Bishop		15			15
	Lavender Waxbill	2	15	1		18
	Bronze Mannikin	1	29			30
	Red-cheeked Cordon Bleu	7				7
	Red-billed Firefinch	6				6
	Rock Firefinch	87				87
	Cinnamon-breasted Rock Bunting	11				11

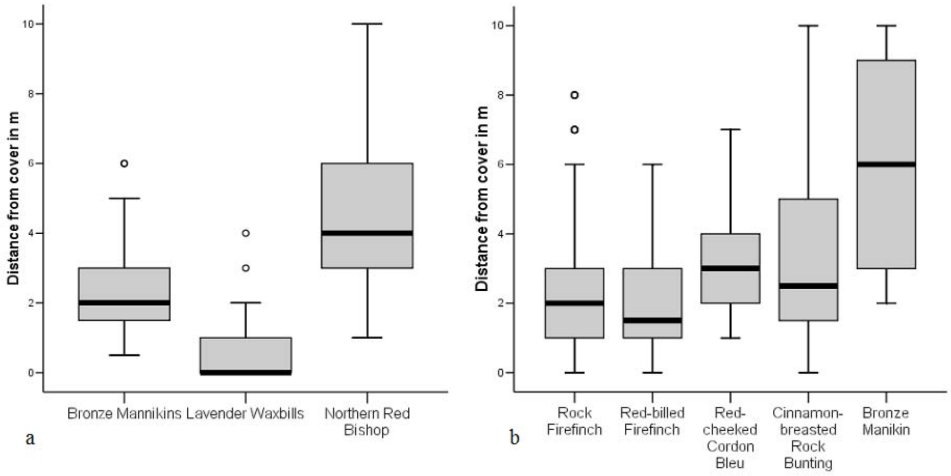

Fig. 1a-b. Distances from cover at which species fed while feeding on (a) seeds from the grass ear (stem group) and (b) seeds from the ground (ground group).

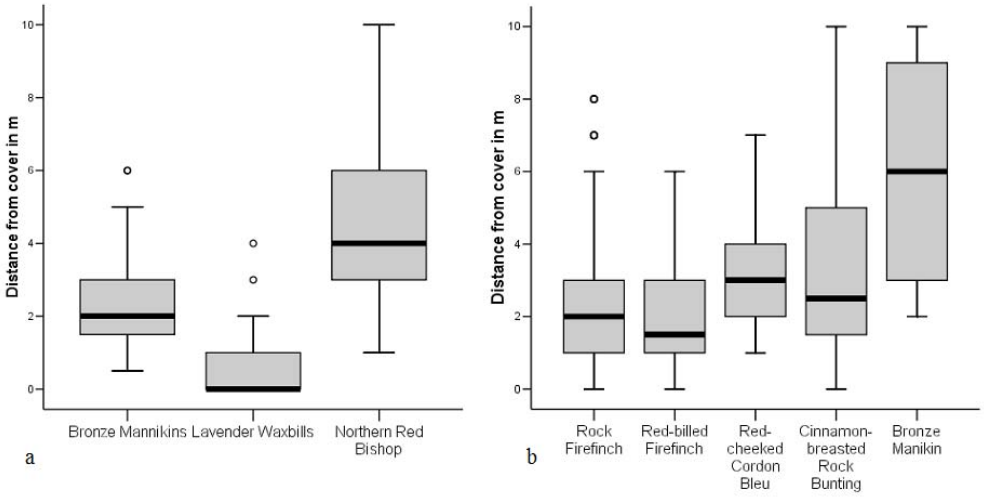

Fig. 1a-b. Distances from cover at which species fed (a) while feeding on seeds from the grass ear (stem group) and (b) while feeding on seeds from the ground (ground group).

Species within the ground group only partly differed significantly with respect to distance from cover. Red-billed Firefinches, Red-cheeked Cordon Bleus and Rock Firefinches all fed close to cover with no significant differences between them during neither season (Table 2, Fig. 1b). Cinnamon-breasted Rock Buntings fed further from cover than Rock Firefinches but only during the early dry season (Table 2). Bronze Mannikins however, fed further from cover and significantly differed from all other species apart from Cinnamon-breasted Rock Buntings during the late dry season, the only time when they were regularly observed to feed from the ground (Table 2, Fig. 1b). The only other microhabitat differences were found between Rock Firefinches and Red-billed Firefinches and Rock Firefinches and Red-cheeked Cordon Bleus during the late dry season (Table 2, Fig. 2) and between Rock Firefinches and Cinnamon-breasted Rock Buntings during the early dry season (Table 2). Rock Firefinches fed at locations with less bare ground and more vegetation <0.3 cm and vegetation >0.3 cm than Red-billed Firefinches and Red-cheeked Cordon Bleus. Red-billed Firefinches, Red-cheeked Cordon Bleus and Cinnamon-breasted Rock Buntings did not segregate on the basis of distance from cover or percentage of different vegetation of their feeding locations.

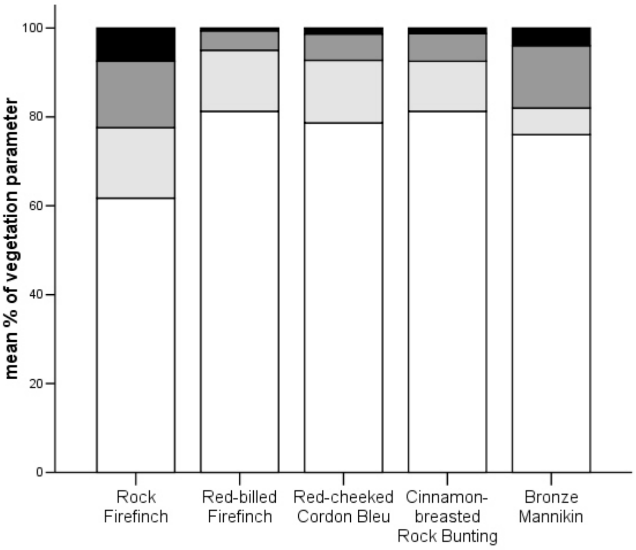

Fig. 2 Mean percentage of different vegetation variables at feeding locations of the different species. Colours represent the following habitat parameter: white = bare ground or rock, light grey = vegetation litter, dark grey = vegetation <0.03cm, black = vegetation >0.03cm.

There were seasonal differences in feeding locations of some ground species. Rock Firefinches fed at places further from cover (Mann Whitney U-test, $Z_{110,86}$= -2.54, $p<0.05$), a higher percentage of bare ground (M-W, $Z_{112,87}$= -6.29, $p<0.01$), less percentage litter (Mann Whitney U-test, $Z_{111,86}$= -4.70, $p<0.01$), less percentage vegetation <30cm (Mann Whitney U-test, $Z_{111,86}$= -4.04, $p<0.01$) and less percentage vegetation >30cm (Mann Whitney U-test, $Z_{111,86}$= -3.87, $p<0.01$) during the late dry season (all p values for vegetation parameters are Bonferroni corrected, k=4). Red-cheeked Cordon Bleus also fed at places further from cover (Mann Whitney U-test, $Z_{22,7}$=-2.13, $p<0.05$). No other seasonal differences were found between seasons in any other species where this could be tested (Mann Whitney U test, all $p>0.5$).

Table 2. Results of non parametric Mann-Whitney U test, testing for differences in microhabitat choice between species within the ground feeding group. Indicated are results that are significant after Bonferroni-correction (with K=4) has been applied to the four vegetation parameter tested. Abbreviations are: ROC = Rock Firefinch, REB = Red-billed Firefinch, REC = Red-cheeked Cordon Bleu, CIB = Cinnamon-breasted Rock Bunting, BM = Bronze Mannikin. For Bronze Mannikins data are only available for the late dry season as they did not often feed on the ground during the early dry season.

		late dry season					**early dry season**				
		distance from cover	% bare ground	% litter	% vegetation <0.3 cm	% vegetation <0.3 cm	distance from cover	% bare ground	% litter	% vegetation <0.3 cm	% vegetation <0.3 cm
ROC-REB	Z	-5.73	-3.06	-0.15	-3.39	-2.51	-0.17	-1.18	-0.09	-1.86	-1.12
	p	0.57	**0.002**	0.88	**0.001**	**0.012**	0.87	0.24	0.93	0.06	0.26
	n	110/16	112/16	111/16	111/16	111/16	86/6	87/6	86/5	86/5	86/5
ROC-REC	Z	-1.89	-3.28	-0.17	-3.25	-2.56	-0.12	-1.89	-0.91	-0.97	-1.99
	p	0.06	**0.001**	0.87	**0.001**	**0.01**	0.91	0.06	0.36	0.33	0.05
	n	110/22	112/22	111/22	111/22	111/22	86/7	87/7	86/7	86/7	86/7
ROC-CIB	Z	-0.81	-2.21	-0.70	-1.85	-1.50	-2.78	-4.18	-2.44	-1.73	-3.77
	p	0.42	0.03	0.48	0.07	0.13	**0.005**	**0.0001**	0.02	0.084	**0.0001**
	n	8/110	8/112	8/111	8/111	8/111	11/86	11/87	11/86	11/86	11/86
REB - REC	Z	-1.93	-0.13	-0.46	-0.67	-0.35	0.00	-0.22	-0.67	-0.84	-0.75
	p	0.06	0.92	0.72	0.59	0.87	1.0	0.84	0.53	0.43	0.64
	n	16/22	16/22	16/22	16/22	16/22	6/7	6/7	5/7	5/7	5/7
REB-CIB	Z	-1.07	-0.20	-0.96	-1.36	-0.51	-1.95	-1.58	-1.46	-0.60	-2.17
	p	0.32	0.88	0.42	0.26	0.83	0.06	0.12	0.18	0.58	0.22
	n	8/16	8/16	8/16	8/16	8/16	11/6	11/6	11/5	11/5	11/5
REC-CIB	Z	-0.22	-0.18	-0.66	-0.82	-0.23	-2.01	-1.38	-1.15	-0.47	-1.25
	p	0.84	0.87	0.57	0.48	0.91	0.06	0.18	0.29	0.66	0.66
	N	8/22	8/22	8/22	8/22	8/22	11/7	11/7	11/7	11/7	11/7

Table 2. continued

		late dry season				
		distance from cover	% bare ground	% litter	% vegetation <0.3 cm	% vegetation <0.3 cm
BM-ROC	Z	-3.74	-1.78	-2.24	-0.03	-0.96
	p	**0.001**	0.08	0.03	0.98	0.36
	n	10/110	10/112	10/111	10/111	10/111
BM - REB	Z	-3.35	-0.34	-2.66	-2.24	-1.25
	p	**0.001**	0.78	0.02	0.05	0.55
	n	10/16	10/16	10/16	10/16	10/16
BM - REC	Z	-2.57	-0.26	-2.36	-1.96	-0.92
	p	**0.01**	0.83	0.04	0.08	0.62
	n	10/22	10/22	10/22	10/22	10/22
BM - CIB	Z	-1.80	-0.41	-1.20	-1.46	-0.55
	p	0.08	0.70	0.27	0.17	0.76
	n	10/8	10/8	10/8	10/8	10/8

Dominance relationships

All species apart from Red-cheeked Cordon Bleus, for which this could not be tested due to low sample size, were found to be dominant over Red-billed Firefinches, which therefore ranked lowest in the dominance hierarchy. Rock Firefinches were also clearly dominant over Lavender Waxbills. The other species relationships remained unclear due to insignificant differences in interactions between them or due to low sample size (Table 3).

Table 3. Number of observed inter-specific aggressive interactions (replacements from feeding places). Broken lines indicate species pairs where less than 10 total observations were achieved. The first number in each case is the number of times the species in the row replaced the one in the column, the second number the number of times the species in the column replaced the species in the row.

	Bronze Manikin	**Red-cheeked Cordon Bleu**	**Lavender Waxbill**	**Red-billed Firefinch**
Rock Firefinch	13 - 16	10 - 6	90 - 27	27 - 3
Bronze Mannikin		------	24 - 18	17 - 1
Red-cheeked Cordon Bleu			5 - 10	------
Lavender Waxbill				17 - 3

Morphological characteristics

All species differed significantly from each other in bill-height (Mann-Whitney U test, all $p<0.01$). Bronze Mannikins were found to have a much greater bill-height than any other species and Red-billed Firefinches were found to have the lowest (Fig. 3a). Bronze Mannikins did not differ from Red-cheeked Cordon Bleus in bill-length but all other species pairs did (Mann-Whitney U test, all $p<0.01$). Rock Firefinches had the longest and Red-billed Firefinches the shortest bill (Fig. 3b).

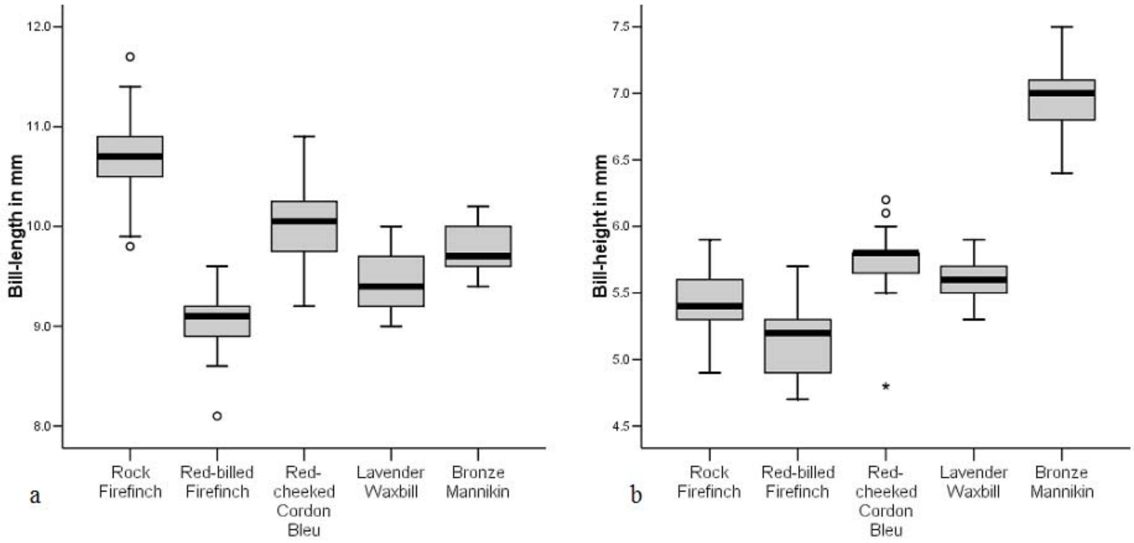

Fig. 3a-b. Bill-height (a) and bill-length (b) in mm of the different Estrildid species.

Group-size, -composition and flushing distances

Species differed significantly in the group size of flocks they formed (Kruskal-Wallis test: Chi^2=178.5, df=7, $p\leq0.01$). Cinnamon-breasted Rock Buntings, Rock Firefinches and Red-cheeked Cordon Bleus formed the smallest groups (1.4 ± 0.7m, n=19; 1.6 ±0.9m, n=199; 1.4 ± 0.5m, n=29 respectively), Lavender Waxbills formed intermediate groups (3.2 ± 2.1, n=41) and Bronze Mannikins, Black-winged Bishops and Northern Red Bishops formed the largest groups (9.7 ± 5.7m, n=47; 12.7 ± 11.8, n=11; 19.2 ± 18.4, n=17 respectively). The mean group size species formed correlated positively with the mean distance from cover at which species fed ($F_{1,6}=8.82$, $R^2=0.60$, $p<0.05$, Fig. 4). However, mean group size did not correlate with flushing distance ($F_{1,6}=0.01$, $R^2=0.002$, p=0.92). Within species no relationship between group size and distance from cover was found in any of the species (all $p \geq 0.1$).

Sex ratios of groups in species with sexual dimorphism was mainly 1:1. Out of 37 groups containing two individuals in Rock Firefinches in which sex could be determined 34 (92%) were made up of one male and one female, more than expected by chance (Chi^2 test, $Chi^2=12.16$, df=1, $p<0.01$). All 13 groups of Red-billed Firefinches and all ten groups of Red-cheeked Cordon Bleus containing two individuals had a sex ratio of 1:1 and this was also significantly different from chance (Chi^2 test, $Chi^2=5.54$, df=1, $p<0.05$ and $Chi^2 4.04$, df=1, $p<0.05$ respectively).

Mixed species flocking was observed in almost all species investigated (Table 4). Especially Red-billed Firefinches and Red-cheeked Cordon Bleus showed a high proportion of mixed species flocks, while in Rock Firefinches, Bronze Mannikins, Lavender Waxbills and Cinnamon-breasted Rock Buntings this was relatively low. Only Black-winged Weaver were not observed to show mixed-species flocking during transects, however, sample size for this species was relatively low and during opportunistic observations they were observed to mix with Northern Red Bishops.

Microhabitat changes in mixed species flock

When Rock Firefinches fed together with Red-cheeked Cordon Bleus their microhabitat preferences seemed to converge. Even though there was a significant difference in percentage bare ground at which these two species fed when in single species flocks, when feeding together these parameter did not significantly differ from either species feeding alone (Mann Whitney U test, $Z_{6,28}=-0.18$, $p>0.1$; compared to Red-cheeked Cordon Bleus alone and $Z_{6,28}=-1.34$, $p>0.1$; compared to Rock Firefinches alone) and was in between the values for both species alone. No other species pair could be tested due to low sample size.

Table 4. Mixed species flocking in the studied bird species. Shown are the percentage of all mixed flocks observed in this species containing another species as well as the % mixed flocks of all flocks observed for this species as well as the number of total observations. For Black-rumped Waxbills the number of observations of single species flocks are not known as they were not included in our study due to low encounter rate. Abbreviations are: ROC = Rock Firefinch, REB = Red-billed Firefinch, REC = Red-cheeked Cordon Bleu, CIB = Cinnamon-breasted Rock Bunting, LAV = Lavender Waxbill, BLR = Black-rumped Waxbill, BM = Bronze Mannikin, NRB = Northern Red Bishop, BWB = Black-winged Bishop.

	% with ROC	**% with REB**	**% with REC**	**% with CIB**	**% with LAV**	**% with BLR**	**% with BM**	**% with NRB**	**% with BWB**	**% mixed of total (n)**	**n total obser-vations**
ROC		50	56	6	6	6	0	0	0	8 (16)	215
REB	66		33	0	8	25	0	8	0	35 (12)	34
REC	75	33		0	0	0	0	8	0	29 (12)	41
CIB	1	0	0		0	0	0	0	0	5 (1)	20
LAV	100	100	0	0		100	0	0	0	2.5 (1)	40
BLR	20	60	0	0	20		30	0	0	(5)	
BM	0	0	0	0	0	40		60	0	3 (5)	53
NRB	0	0	25	0	0	0	75		0	19 (4)	21
BWB	0	0	0	0	0	0	0	0		0	11

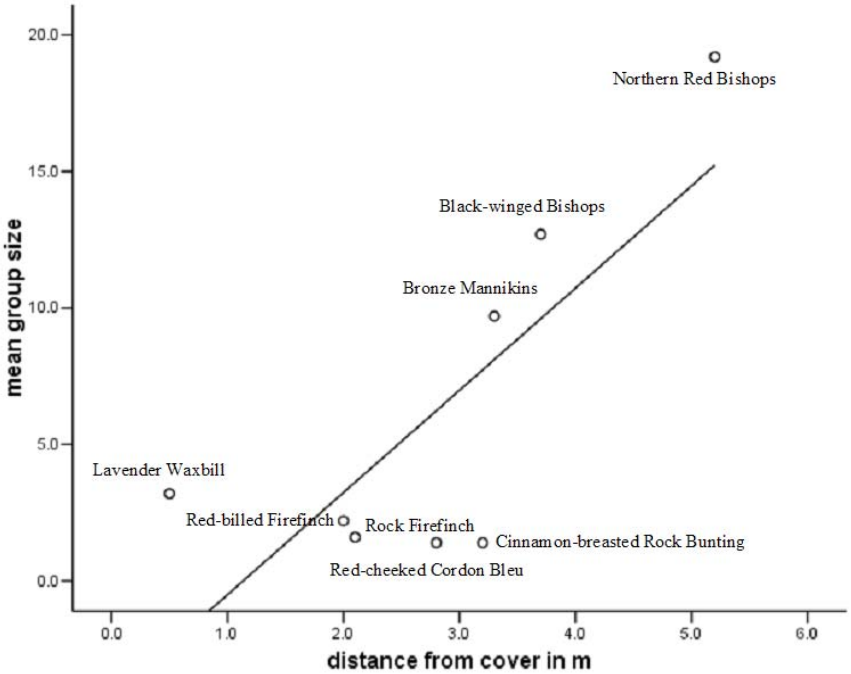

Fig. 4. Relationship between mean group size and mean distance from cover at which species fed.

Aviary experiment

Relative time spent on low density seeds

There was a highly significant influence of the interaction of species and treatment on the percentage of time a bird fed on low density seeds: Red-billed Firefinches fed significantly more on low density seeds when kept together with Rock Firefinches than when kept alone, while Rock Firefinches spent relatively little time feeding on low density seeds under both situations (Table 5, Fig. 5)

Feeding bout length

Treatment had no influence on feeding bout length on high density seeds. However, there was a significant difference between species, with Red-billed Firefinches having significantly shorter feeding bouts than Rock Firefinches (Table 6, Fig. 6).

Table 5. Results of GLM testing variables influencing % of time feeding on low density seeds.

Dependent variable	**% time feeding on low density seeds**			
	Type III Sum	df	F	p
Treatment	1809.38	1	3.74	0.07
Species	474.71	1	0.98	0.33
Trial number	4067.30	10	0.84	0.60
Time	2732.69	5	1.13	0.37
Treatment*Species	4213.26	1	8.70	<0.01
Intercept	5096.33	1	10.41	0.01
Overall sum of squares	12109.29			

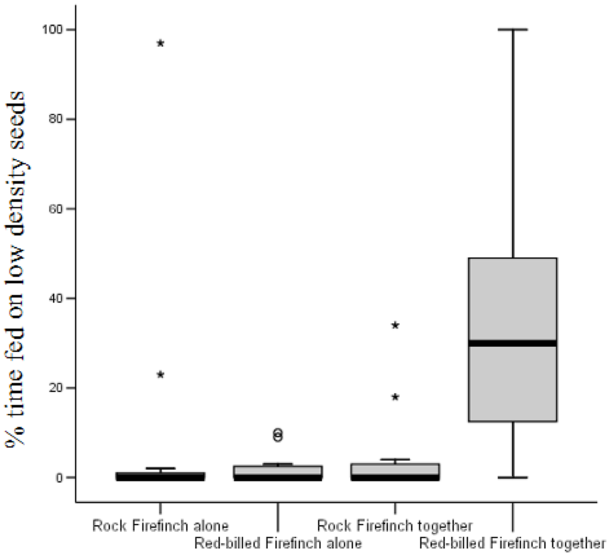

Fig. 5. Box plots showing the percentage of time Rock Firefinches and Red-billed Firefinches in the aviary spent feeding on low density seeds under the treatment when they were kept alone and together respectively.

Table 6. Results of GLM testing variables influencing length of feeding bouts on high density seeds.

Dependent variable	**Intake rate**			
	Type III Sum	df	F	P
Treatment	0.14	1	0.43	0.51
Species	14.09	1	44.35	<0.01
Trial number	11.55	10	3.63	<0.01
Intercept	620.43	1	627.07	<0.01
Overall sum of squares	82.93			

Treatment*Species interaction not significant ($F_{1,260}$=1.12, p=0.29)

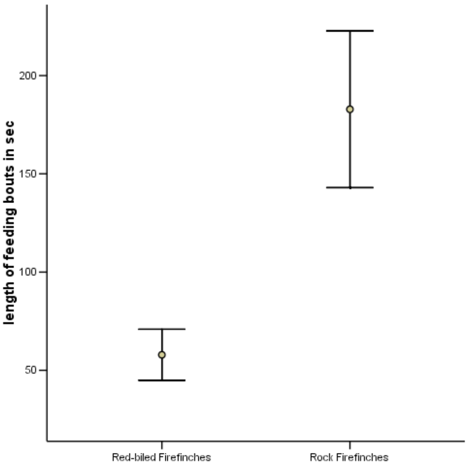

Fig. 6. Means and 95% confidence intervals for feeding bout length in seconds of the two species feeding on high density seeds.

Feeding bout frequency

Red-billed Firefinches significantly increased feeding bout frequency on low density seeds when kept with Rock Firefinches (Mann Whitney U test, n=11, Z=-2.69, p<0.01) while frequency on high density seeds did not change (n=11, Z=-0.5, p=0.96). For Rock Firefinches neither bout frequency on low (n=11, Z=-0-54, p=0.59) nor on high density seeds (n=11, Z=-0.88, p=0.38) changed between treatments. Red-billed Firefinches had significantly more feeding bouts on high density seeds than Rock Firefinches under both treatments, when kept alone (Mann Whitney U test, n=11, Z=-1.94, p≤0.05) and when kept together (Mann Whitney U test, n=11, Z=-2.09, p<0.05). Frequency on low density seeds only tended to significantly differ between the species when kept together, with Red-billed Firefinches having more feeding bouts on low density seeds than Rock Firefinches (n=11, Z=-1.80, p=0.07).

Intake rates

Intake rates on high density seeds were neither influenced by treatment nor by species. Rock Firefinches (37.1 ± 5.4 pecks / 30 sec) had similar intake rates to Red-billed Firefinches (37.7 ± 6.0 pecks / 30 sec). These results were the same whether intake rates for the first 30 sec (Table 7) or for the whole feeding bout corrected for bout length were considered. However, in the latter case, variation was much greater for both species (Rock Firefinches: 37.4 ± 6.5 pecks / 30 sec, Red-billed Firefinches: 36.3 ± 8.7 pecks / 30 sec).

Intake rates of Red-billed Firefinches on low density seeds were significantly lower than on high density seeds (Mann Whitney U test, n=7, Z=-2.20, p<0.05) and also tended to be lower in Rock Firefinches (Mann Whitney U test, n=6, Z=-2.20, p=0.059). Red-billed Firefinches had a significantly lower intake rate on low density seeds than Rock Firefinches (Mann Whitney U test, $Z_{7,6}$=-2.57, p<0.01).

Table 7. Results of GLM testing variables influencing intake rate on high density seeds.

Dependent variable	**Intake rate**			
	Type III Sum	df	F	P
Treatment	64.00	1	2.62	0.12
Species	2.78	1	0.11	0.74
Trial number	440.56	8	2.25	0.06
Treatment*Species	21.78	1	0.89	0.36
Intercept	440.56	1	913.85	0.00
Overall sum of squares	587.44			

Aggressive interactions

During filming a total of nine aggressive interactions occurred in eight of the ten species pairs tested. In all instances Rock Firefinches replaced Red-billed Firefinches from feeding places, the reverse was never observed. During all instances Red-billed Firefinches simply left when Rock Firefinches hopped onto feeding places. In one instance the Rock Firefinch perched in front of the feeding place, the Red-billed Firefinch stopped feeding and the birds stared at each other for three seconds until the Red-billed Firefinch moved away. There were no instances of birds pecking each other or escalated fighting.

Discussion

Field observations

Species-specific microhabitat choice and seasonal variation

From analyses of feeding patterns of granivorous birds in savannah habitat it appears that there were two groups specialised to feed on grass seeds in two quite different microhabitats: one which fed exclusively on seeds from the ground and the other which fed mainly on seeds from the grass ear. Only Lavender Waxbills were found to also use other food resources such as insects, pollen and figs to a great extent and this was more pronounced during the late dry season when seeds on the grass ear, from where they preferably took them, were rare and termites started to emerge with the first rains. Dostine (2001) also found the mostly granivorous Long-tailed finches (*Poephila acuticauda*) in Australia to feed on insects especially termites during the late dry season to a greater extent. It is likely that the other species also use alternative resources at particular times, and at least for Red-cheeked Cordon Bleus and Red-billed Firefinches this has been reported (Fry et al., 2004). However, such behaviour was seldom if ever observed in theses species during this study and we thus believe it to be much rarer than in Lavender Waxbills. Lavender Waxbills also showed high flexibility in where grass seeds were exploited as they utilised both microhabitats (grass seeds on the ground and on the ear) to a great extent. They thus probably represent a rather generalist species that changes its feeding behaviour according to what resources are abundant and were they occur.

Red-billed Firefinches, Rock Firefinches, Red-cheeked Cordon Bleus and Cinnamon-breasted Rock Buntings on the contrary exclusively fed on seeds from the ground while Bronze Mannikins, Black-winged Bishops and Northern Red Bishops mostly fed on seeds from the ear. However, towards the late dry season few grass seeds were still available on the grass ear as most had been depleted or fallen to the ground, and a shift in feeding behaviour occurred. Black-winged Bishops and Northern Red Bishop were only infrequently encountered and most individuals had probably left the study area. Northern Red Bishops were described as being partial migrants (Fry et al., 2004) and the same might apply to Black-winged Bishops, which are ecologically very similar. Possibly Northern Red Bishops and Black-winged Bishops pursue a partly nomadic life style as reported for many other savannah and desert bird species that rely on only temporarily available and / or unpredictable food resources (Davies, 1984; Dean, 1997). This nomadic life style possibly linked to the usage of grass seeds from the ear by the Weavers as compared to a more sedentary life style of the finches and their usage of seeds mainly from the ground might therefore enable coexistence of these two groups. The few Bishops that were still encountered during the late dry season fed on seeds from the ground. Bronze Mannikins were still frequently encountered during the late dry season but they too fed on the ground to a large extent now, a behaviour which for this species was not often seen during the early dry season. So while the Weaver species almost completely left the area during the late dry season when one microhabitat (seeds from the grass ear) disappeared the feeding microhabitat of Bronze Mannikins converged with that of the other ground feeding species. However, food might be partitioned on the basis of other parameters like distance from cover and vegetation composition, which we also investigated.

The three species feeding mostly on the grass-ear, for which differences could be tested, partly partitioned resources by using them at different distances from cover. Lavender Waxbills fed closest to cover, which was a result of them using a different feeding technique as they mostly perched on branches while feeding on the grass-ear, Bronze Mannikins fed further from cover and Northern Red Bishops fed at the greatest distances from cover. Within the ground group (ground feeding species) Bronze Mannikins fed at greater distances from cover than the other Estrildid finches but other species did not segregate on this basis and are thus unlikely to partition resources by using them at places of differing predation risks. These species all fed similarly close to cover compared to Bronze Mannikins; and Cinnamon-breasted Rock Buntings were found at distances intermediate between Bronze Mannikins and the other finches. Schluter (1988) also found that granivorous finch species in Kenya did not partition resources on the basis of distance to cover and concluded that rather than promoting habitat segregation predation risk confines the space in which species compete for food. Likewise the similarly close distance to cover at which ground-feeding species fed during this study provides evidence for some importance of predation risk, but predation risk only partly promoted habitat segregation only between Bronze Mannikins and the other ground feeding species.

Rock Firefinches, however, were found at places with a smaller percentage of bare ground and a higher percentage of vegetation than Red-cheeked Cordon Bleus and Red-billed Firefinches during the late dry season but at places of less bare ground and more vegetation than Cinnamon-breasted Rock Buntings during the early dry season. There was thus no clear direction in seasonal differences in species-specific microhabitat choice and our hypothesis that specialisation would be more pronounced during the late dry season could not be supported. Pulliam (1985) found sparrow species to converge in their diet when food became scarce and concluded that seed partitioning is unlikely to play a major role in the coexistence of these sparrow species. From this study it remains unclear if microhabitat segregation might be driven by competition and enable coexistence. However, seed density on the ground did not significantly differ between the early and the late dry season and food scarcity might occur later during the wet season (Chapter 2). Further negative results might be linked to low sample size and therefore results have to be treated carefully. Two species fed further from cover during the late dry season and this might be linked to seeds becoming scarcer at the favored places next to cover. The seasonal changes in vegetation parameters in feeding locations of Rock Firefinches however, possibly only reflect changes in available patches. Less vegetation exists during the late dry season, so the observation that Rock Firefinches fed at patches with more vegetation during the early dry season is probably simply due to more vegetation being present. Even though some inter-specific differences in microhabitat choice existed (Bronze Mannikins feeding further from cover and Rock Firefinches at places with less bare ground and more vegetation) similarities between species seemed to be more striking than the differences, and thus little support is given for competition to be very pronounced during our study period.

The change in vegetation parameters between the early and late dry season could influence detectability in that less vegetative ground cover during the late dry season makes it easier to observe birds feeding on the ground. However, changes in the vegetation affect detectability equally at different distances from cover and amount of ground vegetation such that differences in the distance from cover or extent of ground cover at which species fed cannot result from differences in detectability. It might however, lead to a higher percentage of birds observed feeding on the ground during the late dry season. In Lavender Waxbills the opposite was observed, as there was a higher percentage of individuals feeding in trees during the late dry season, such that these results are unlikely to be a result of differences in detectability. The lower percentage of Weavers, Bronze Mannikins and Lavender Waxbills feeding on the grass ear during the early dry season could potentially be a result of them being harder to observe on the ground during this time. However, a similar amount of individuals of the other species feeding on the ground during the early dry season despite less sampling effort and a higher number of Weavers, Bronze Mannikins and Lavender Waxbills feeding on the grass ear during the late dry season as compared to the early dry season point against vegetation parameters to be the cause for the observed seasonal differences.

Wiens (1989) found habitat segregation and species response to habitat variables in savannah habitat in North America not to be consistent between seasons and he also found inter-specific similarities in microhabitat choice to be more striking than the differences. He concluded that caution is needed when attaching great importance to apparent differences between species revealed during short-time studies. In our study area this is even more complicated by the large diversity of granivorous species present. Many more granivorous species including Black-rumped Waxbill (*Estrilda troglodytes*), Orange-cheeked Waxbill (*Estrilda melpoda*), Black-bellied Firefinch (*Lagonosticta rara*), Bar-breasted Firefinch (*Lagonosticta rufopicta*) and Little Weaver (*Ploceus luteolus*) were encountered during the study period but none of them frequently enough to enable analyses of microhabitat choice and comparison. Unfortunately we do not know, whether food limitation exists in the species investigated, and when we studied the seasonality of the birds’ feeding behaviour we found little evidence for its existence (Chapter 2). However, food partitioning might happen on a smaller scale than what we investigated and a longer-term study of the feeding behaviour of all these species covering several seasons would clearly be necessary to achieve a thorough assessment of microhabitat segregation within this granivorous bird community. However, as little quantitative information exist on the natural feeding behaviour of the species we studied, our data contribute valuable information on which further studies could be based.

Group formations and microhabitat choice

While there were differences in group sizes between species, which correlate with the mean distance from cover at which these species fed, no such correlation was found within species. Each species might be adapted to feeding at quite specific microhabitats with specific predation risks at which variability is not great enough to find differences in group formations. There seemed to be a trend that species generally feeding far from cover also formed larger groups. Within the ground group Bronze Mannikins fed furthest from cover and also formed the largest groups. This flocking behaviour might enable them to exploit the possibly riskier habitat to a greater extent as it has been shown that the speed of predator detection increases with group size (Kenward, 1978) and vigilance benefits (Caraco, 1979; Barnard, 1980; Bertram, 1980), predator confusion (Neill & Cullen, 1974) and a dilution effect (Hamilton, 1971; Calvert et al., 1979; Duncan & Vigne, 1979) might also apply. All three species that mainly fed on seeds from the grass ear also formed relatively large groups compared to the ground feeding species and this might be an adaptation to increased predation risk when feeding at relatively exposed locations up on the grasses.

However, the benefits from increased food resource detection by larger groups as demonstrated for Red-billed Queleas (*Quelea quelea*) by DeGroot (1980) and the semi-colonial breeding pattern of Bronze Mannikins (Fry et al., 2004) may be more important factors promoting the formation of large groups in the three species that mainly fed on seeds from the grass ear. Since seeds from the grass ear are a more fluctuating food resource than seeds from the ground, foraging in large groups would be beneficial to bird species specialising on this food resource due to enhanced food detection. Formation of larger groups by Bronze Mannikins promoted by the fluctuation of food in their preferred microhabitat and by the advantages of breeding in colonies might than enable them to exploit seeds further from cover than the other species when feeding on the ground. In contrast, the three species that exclusively fed on the more stable resource of seeds from the ground during both seasons form small groups of mainly just one or two birds. Most of these groups indeed consisted of one male and one female and thus probably represent pairs. This observation was consistent over both seasons so that it seems likely that these species form stable pair bonds, which are maintained outside the breeding season. Similar findings were reported by Hamed & Evans (1984) for Red-cheeked Cordon Bleus. Despite feeding close to cover, Lavender Waxbills formed groups of intermediate size. However, they fed on other resources to a great extent and this might impact on their flocking behaviour.

Even though most flocks encountered were single species flocks, the occurrence of several mixed-species flocks indicates that species readily aggregated. Several studies observed mixed-species flocking in various temperate birds (e.g. Schluter, 1982; Metcalfe, 1984; Monkkonen et al., 1996; Stutherland, 1996) and some were able to demonstrate some associated benefits via shared vigilance (Metcalfe, 1984; Beveridge & Deag, 1987) or increased food detection (Barnard & Stephens, 1983). The observation that Rock Firefinches and Red-cheeked Cordon Bleus met at intermediate microhabitats from where they were found when feeding alone suggests, that mixed species-flocking in this study was simply a result of species aggregating at an abundant food resource occurring in a microhabitat that overlaps with both species' minimum requirements, and that the costs associated with the exclusion of one species by another might not be outweighed by the benefits of defending a resource.

Species' dominance and microhabitat choice

We failed to find a clear relationship between a species' dominance and the predation risk of its feeding patch. Several explanations for the absence of this relationship are possible: predation risk was simply not strong enough to cause such an effect or assessment of variance in the degree of predation risk was to simplistic and should consider more variables than simply distance from cover, or alternatively, predation risk might be confounded by differing food profitability in patches, species might not be in immediate competition, or species are adapted to feeding at differing locations unrelated to their dominance. All species responded to disturbance by flying into cover (Chapter 3) and thus it seems reasonable to assume that predation risk increases with distance from cover. However, assessing predation risk on the basis of distance from cover alone might be too simplistic as a high abundance of predators attacking from cover (e.g. mammals or snakes) might change this assumption (Lima et al., 1987). A more rigorous approach to test this hypothesis (which might involve usage of a model predator) is needed to clarify this.

Importance of predation risk might also be outweighed by how profitable food patches are, so that only considering one variable at a time would not be sufficient (Lind & Cresswell, 2005). It should be easier for birds to find seeds at places with a higher amount of bare ground and one might assume that these are the locations at which more dominant bird species are found. Results from the aviary experiment clearly show that Rock Firefinches are dominant over Red-billed Firefinches and that they can exclude Red-billed Firefinches from the more profitable food patch. Red-billed Firefinches spent relatively more time feeding on low density seeds when kept together with Rock Firefinches, whereas Rock Firefinches did not change their feeding behaviour in the presence of Red-billed Firefinches. This was due to Red-billed Firefinches increasing bout frequency rather than bout length on low density seeds. Surprisingly in the field dominant Rock

Firefinches fed at the supposedly less favourable places with more vegetation cover than any of the other ground feeding species. Unfortunately we could not compare seed density nor intake rates at these different locations and are thus not able to conclude whether food rewards really differed between the microhabitats at which species fed, and it would be useful to further examine this.

Another possibility is that predation risk also depends on the amount of ground cover in a feeding patch. It is usually believed that less ground cover is advantageous as predators can be spotted earlier (Schluter, 1988; Whittingham et al., 2004) and intake rate in less vegetated patches is usually higher (Gluck, 1986; Whittingham et al., 2004), on the other hand, birds might be safer in dense vegetation as they themselves are also less likely to be detected by a predator (Gluck, 1986). For a species feeding on relatively small seeds where a high pecking frequency has to be maintained for food to be energetically rewarding (Gluck, 1986), it might actually be advantageous to feed in patches with much ground cover where birds might not have to worry so much about vigilance or can spent more time feeding. So Rock Firefinches might actually feed in the safer places. There clearly remain studies to be done to disentangle the ambiguous effects of ground cover and its consequences for predation risk and the birds’ patch choice.

In the aviary Red-billed Firefinches had shorter feeding bouts and a higher bout frequency than Rock Firefinchs under both treatments. They thus seem to have a different way of dealing with predation risk or are more vulnerable to predation such that they take flight more easily than Rock Firefinches. This could stem from them generally feeding in the more exposed patches where predation risk is higher than at patches with more ground vegetation at which Rock Firefinches were usually found to feed. It seems an interesting question to ask whether there might be a general behavioural difference between species feeding in exposed and those feeding in vegetated patches but a wider species variety would need to be considered to test this hypothesis.

However, the observation that Rock Firefinches fed in places with more ground cover but were the most frequently encountered species within our study area suggests, that they are well adapted to feeding at those places. Our study area consisted of quite bushy savannah habitat, and therefore few places with a high percentage of bare ground might be available so that species not well adapted to feeding at other places only find few suitable feeding locations. This might explain the lower encounter rate with these species and is supported by the observation that Red-billed Firefinches, Red-cheeked Cordon Bleus and Bronze Mannikins are frequently encountered in relatively open farmland and around houses (Fry et al., 2004), which is not so frequently observed in Rock Firefinches. Thus some species are probably well adapted to feeding at specific locations, which then feeds into their broader habitat choice. More studies linking micro- and macro-habitat selection are needed to confirm this. However, our results show that microhabitat choice is not necessarily easily predictable from dominance relationships and that several factors have to be taken into account to determine the cause of feeding patch choice.

Bill morphology and microhabitat choice

The differences in microhabitat use might relate to differences in species’ morphology such as bill shapes. In Galapagos finches bill shape was found to correspond to the size of seeds consumed. We did not measure seed size that finches selected but our observation that all studied Estrildid finches and Cinnamon-breasted Rock Bunting all readily fed on provided small acha seeds but not so much on the larger millet seeds and were all mostly observed to feed on the same grass species (even though we did not quantify this) led us to believe that food partitioning on the basis of grass species and seed size is of only little importance. Barshep (2005) also found RockFirefinches, Red-billed Firefinches and Lavender Waxbills to prefer acha seeds over millet seeds in our study area. Similarly Schluter (1988) found that seed size did not segregate finch species in Kenya and that microhabitat choice might be more important. Accordingly different bill shapes might rather relate to different microhabitat choices than to the size of seeds consumed. Rock Firefinches were found to have a longer bill than any of the other Estrildid finches and might thus be able to swipe away vegetation to pick up seeds underneath more efficiently than the other species. This might explain why only Rock Firefinches fed at places with a lower percentage of bare ground. Despite both species preferring high density seeds in the aviary and Rock Firefinches being able to exclude Red-billed Firefinches from the more profitable feeding patch, Rock Firefinches were more efficient in extracting seeds mixed with sand. This supports our suggestion that Rock Firefinches with a longer bill are well adapted to extracting buried seeds and might also be more efficient in obtaining seeds from beneath or between vegetation. The finding that Red-billed Firefinches fed at places with more bare ground is therefore probably indeed related to them not being able to use feeding patches with more vegetation cover and litter rather than Red-billed Firefinches excluding Rock Firefinches from the more profitable food patches. Accordingly more Red-billed Firefinches were encountered on open farmland with less vegetative cover than bush savannah and inselberg habitat (Barshep, 2005), while Rock Firefinches seem to avoid open farmland (Barshep, 2005; Wright & Jones, 2005, Chapter 6).

Bronze Mannikins were found to have the bills of greatest height, much more so than any of the other Estrildid species. This might be related to them feeding on grass seeds from the ear, which apart from Lavender Waxbills, none of the other species were observed to do. A high bill might facilitate a sweeping movement needed to sweep seeds from the grass ear while a longer, lower bill is adapted to a pecking and digging movement, needed to peck seed from the ground and separate them from sand and vegetation. However, our assumptions about the relation of bill shape and microhabitat use remain speculative due to low sample size, and further investigation considering a wider variety of species and further feeding experiments are needed.

Conclusions

Even though this work suffers from time limitation, it provides first insights in what factors might be important in enabling coexistence of granivorous bird species in tropical savannah habitat. Our hypothesis that microhabitat choice is more pronounced during the late dry season was not confirmed, but this could in part be due to small sample size or little difference in seed density on the ground between these to periods. However, species segregation in their feeding microhabitat was observed for some species and the disappearance of seeds from the grass ear at the late dry season might have lead to increased competition for seeds on the ground. Some species segregated in their feeding patch choice with respect to distance from cover, which might be linked to their flocking behaviour, and Rock Firefinches fed at places with less bare ground and more vegetation than other species, which might be due to them being more efficient in extracting seeds mixed with sand enabled by a longer bill. Further studies linking microhabitat choice with patch availability, macrohabitat choice and the species feeding efficiencies at the different places will enhance our understanding of how ecologically similar granivorous bird species can coexist in savannah habitat.

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Chapter 6: Breeding behaviour, home range extension and habitat shift in Rock Firefinches (*Lagonosticta sanguinodorsalis*) between the wet and dry season in central Nigeria

Abstract

Knowledge of a species' movement behaviour and habitat choice is a prerequisite for assessing its ecological requirements to plan successful conservation strategies. Little is known about these factors in the Rock Firefinch (*Lagonosticta sanguinodorsalis*), a recently discovered species, which is probably endemic to the Jos Plateau in central Nigeria. The Rock Firefinch has a negative association with farmland and relatively low adult survival rate, and so may be threatened by the high levels of human disturbance and habitat change there.

We investigated home range size, habitat use and breeding behaviour of the Rock Firefinch in Amurum forest reserve in central Nigeria during the wet and the dry season using radio-tracking. The reserve consists of mainly scrub savannah habitat interspersed with rocky inselbergs and strips of gallery forest and is surrounded by farmland. Birds showed a high degree of site fidelity. They mainly moved solitarily or in pairs but did not have exclusive territories. Home range size tended to be larger during the dry season due to long movements to water sources. Birds generally preferred inselberg habitat and avoided farmland. During the dry season they additionally utilised gallery forests where water was readily available, and as a result of having to cross scrub savannah to get to water, scrub savannah was also more used during the dry season. It is likely that the timing of breeding was limited due to water availability near nest sites.

Birds bred between the late rainy and the early dry season. Nest sites were associated with rocky boulders. Both sexes contributed to incubation. Daily egg survival rate calculated after the Mayfield method was 0.89 ± 0.03. Of all nests found 50% were depredated probably mostly by lizards. Two breeding attempts per year were recorded. Chick production may balance adult mortality such that the population is probably stable or slightly decreasing at present, but given the large uncertainty in our underlying assumptions, more data are needed to confirm this.

The Rock Firefinch’s association with isolated inselbergs, its nest site requirement and its need for fresh water sources during the dry season (which are often associated with gallery forest) not to far from inselberg habitat highlights potential future population effects of habitat loss. If water sources are far from suitable inselberg habitat, such that birds have to cross open habitat to access water, this could potentially decrease adult survival due to an increased risk of predation and increased rate of daily energy expenditure. We suggest that the presence of inselberg habitat in close proximity to water sources is the essential and limiting resource for this species. Water availability is especially likely to be one of the main factors limiting populations of small granivorous birds in subtropical regions.

Introduction

An animal’s movement pattern is linked to the abundance of essential resources and the animal’s ability to utilise them. Accordingly food abundance, availability and distribution have been described as one of the main factors influencing home range size and habitat use in a variety of animal species (Krebs & Davies, 1993; McIntyre & Wiens, 1999; DeVault et al., 2004; Eide et al., 2004; Prange et al., 2004; Wauters et al., 2005). Many granivorous bird species inhabiting desert or savannah habitats, where the occurrence of rain and associated seed availability is highly unpredictable and patchily distributed, were reported to show extensive nomadic movements (Davies, 1984; Dean, 1997), while under more predictable conditions more resident species occur (Dean, 1997). Subtropical savannah habitats in central Nigeria show a more predictable pattern in the occurrence of rain and food abundance, nevertheless drastic differences exist in these parameters between the dry and rainy season and an animal’s movement pattern and habitat use are expected to reflect this.

The scale at which an animal moves determines at what scale it interacts with its environment and has important consequences for conservation. Understanding the patterns, constraints and adaptability of a species’ movement behaviour is an important step towards understanding the dynamics of its ecological relationships (Gordon, 2000). The knowledge of a species’ movement behaviour is therefore a prerequisite for assessing a species’ habitat requirements and the scale of habitat connectivity necessary to ensure sufficient population connectivity. In a seasonal environment, where habitat requirements might change seasonally, it is important to consider movement and habitat choice during all seasons and investigate behavioural plasticity before effective conservation measures can be decided on.

The Rock Firefinch (*Lagonosticta sanguinodorsalis*) is a little known *Estrilid* species relatively recently discovered by Payne (1998). It is brood parasitised by the Jos Plateau Indigobird (*Vidua maryae*), whose song let to the Rock Firefinch’s discovery (Payne, 1998). The Rock Firefinch might be endemic to the Jos Plateau in central Nigeria, but a few observations have been reported off the Jos Plateau but in similar rocky habitat (Payne, 1998). Rock Firefinches were found to be associated with inselberg habitat and granite outcrops and to be negatively associated with more open farmland and scrub savannah (Wright & Jones, 2005). However, this study was carried out during the beginning of the wet season and differences during the dry season are likely. The causes of these habitat associations and individual movement patterns also remain unclear. No Rock Firefinch nests in the wild have been found prior to this study (Fry et al., 2004) and we know almost nothing about its breeding behaviour. Its restricted distribution and negative association with farmland makes the Rock Firefinch and its brood parasite, the Jos Plateau Indigobird, potentially vulnerable species to habitat loss and disturbance. This is especially true as the human population in Nigeria is growing rapidly and natural habitats shrink as farmland encroaches and activities such as grazing and the cutting of firewood increase. Only if the ecological requirements of a species are known will we be able to assess its conservation status and take conservation measures if necessary. It is essential therefore, that we gain more information on the habitat requirements, movement patterns and breeding biology of the Rock Firefinch to ensure its and the Jos Plateau Indigobird’s long term survival. While tropical birds in general have higher survival rates than their temperate counterparts, Rock Firefinches were found to have lower survival rates than other closely related species in similar habitats like the Red-billed Firefinch (McGregor, 2005), which raises the question whether the population is declining. We therefore need information on the species breeding behaviour and success before we can judge whether the relatively low survival rate of Rock Firefinches might be a reason for concern.

The Amurum forest reserve is located on the Jos Plateau in central Nigeria and consists of scrub savannah interspersed with inselbergs (elevations consisting of granite rocks vegetated with scrub and grass) and strips of gallery forest. This area is subject to a distinct dry and rainy season and seed abundance and water availability differ greatly between these. This might have implications for the birds habitat choice and movement patterns and consequently for its habitat requirements. During the dry season granite outcrops are often quite a distance from available water sources, while during the rainy season seed abundance declines markedly such that habitat requirements and / or movement patterns might change accordingly. The objectives of this paper are to (i) assess the spatial scale of individual Rock Firefinch movement, (ii) determine its habitat requirements, its causes and possible seasonal changes, (iii) provide the first information on nest site characteristics and breeding behaviour and (iv) gain an estimate of annual reproductive output and compare it to annual mortality to infer population trends.

Methods

Data collection

Study area

This study was carried out in Amurum Forest Reserve located on the Jos Plateau 15 km northeast of Jos city in central Nigeria (09.87°N 8.98°E). The reserve is about 300 ha in size. It comprises an area of mainly scrub savannah interspersed with patches of gallery forest, granite outcrops and inselbergs (elevations of granite rock rising from a relatively even landscape up to a height of ca 40 m within the reserve). The reserve is surrounded by extensively used and abandoned farmland and small villages. Within the reserve logging or hunting is prohibited and the cutting of grass is limited to the time after seed fall has taken place, while outside the reserve all these activities are widespread.

Bird trapping and handling

Birds were caught in mist nets at four different places within Amurum Forest reserve. Between four to eight nets were placed at each trapping site. Sites 1 - 3 were trapped regularly and an effort was made to trap a similar number of birds for radio tracking on each of these sites during each season. Site 4 was only trapped over four continuous days for logistical reasons but a Rock Firefinch female trapped there was also radio-tracked (locations of trapping sites can bee seen in Fig. 8). Nets were checked every 45 min during the morning and afternoon but at a more frequent interval during midday hours when temperature was high. Usually trapping occurred between 06:00 - 11:00 and 16:00 -

18:00 and only occasionally during midday. Birds were ringed with a uniquely numbered metal ring provided by SAFRING and a unique colour ring combination. Rock Firefinches were fitted with a radio-transmitter (Biotrack) weighing about 0.5 g, which was about 5% of a Rock Firefinch's body weight (10.5 ± 0.9, n=125). The transmitter was glued on to the feather-base on the birds' back after feathers were slightly trimmed. Birds were released directly after the glue had dried.

Radio-tracking

Radio-tracking began the day after capture. Birds were followed between 5 - 12 hours a day and located approximately once every hour with at least one hour between consequent fixes using a Mariner Receiver and a hand-held Yaggi antenna. They were located by triangulation and slowly homing in on the location where the bird was suspected to be located while trying not to flush the bird. After the bird had left, the location was determined with a Garmin GPS 12 and the coordinates and altitude recorded. In total we managed to radio-track 15 individuals (2 males and 13 females). One female was caught and tracked during the wet and again during the dry season. Due to a long time span between these two periods and the birds home range to have shifted slightly we treated these periods independently giving a total sample size of 16 (8 during the wet and 8 during the dry season).

Habitat mapping

To create habitat maps we discriminated between four different habitat categories. Inselbergs were characterised by rocky outcrops dominated by boulders with grasses and scrub growing between them, scrub savannah was characterised by long grasses (mostly >1 m) interspersed with scrub of several bushes and mainly occurred within the reserve, gallery forest consisted of many densely growing trees mostly higher than 2 - 3 m, growing along deep wet gullies and farmland was much more open land around the reserve with shorter grasses (due to grazing, cutting or burning) and less scrub. Part of this farmland was abandoned and part of it was still being used for growing various crops. Habitat was mapped by walking along the boundaries of inselbergs and gallery forest with a Garmin GPS 12 using its tracking function. Data were then downloaded to a computer to create a digital map using Arc View 3.1. Borders between scrub savannah and farmland were visually estimated from the top of inselbergs and drawn on top of the habitat map already showing inselbergs and gallery forest used as reference points.

Nest checks

If a Rock Firefinch nest was found we briefly checked how many eggs or chicks were present and left again as quickly as possible. Nests were then checked again between 4 - 8 days later unless we knew from radio-tracking that the bird was still incubating, in which case we only checked the nest again if we assumed chicks to have fledged or the nest to be depredated. This infrequent checking of nests was adopted in order to minimise disturbance and to minimise our effects on nest predation. In most cases nests were depredated some days after the first check (known from radio-tracking) such that it seems very unlikely that the checking of nests should have directly caused nest predation. When the nest was abandoned we measured the size of nests (length, height and entrance diameter) if it was still completely intact, recorded the material it was made from and took the following habitat parameters: general habitat of nest site (inselberg, scrub savannah or farmland, for detailed description see above) height above ground, feature the nest was attached to, nearest distance to rocky boulder (where a boulder was defined as at least 0.5x0.5x0.5 m), nearest distance to bush cover (where a bush was any shrub at least 1x1x1 m) and nearest distance to grass cover (where grass was at least 0.5 m high).

Data analyses

Movement

To test for site fidelity we used the site fidelity test option available in the Arc View extension Animal Movement. The movement path of the bird (i.e. the connection of the locations in chronological order) was compared with 100 random walks created by using the start point and distances from the birds' actual path and fitting random angles by using a Monte Carlo simulation (Hooge et al., 2000). The software then creates an R^2 value and a linearity value and tests if this is significantly different from that of random walks.

We calculated home ranges as 100% minimum convex polygon (MCP) home ranges, because we were interested in how the furthest movement a bird undertakes will be reflected in its use of space and how this differs between seasons. Home range size and diameter of home ranges were calculated using the software program Ranges 5. To test for saturation of home ranges we applied the Bootstrap-sampling technique (using 100 replicates for each fix with a starting sample of 5) offered in Animal Movement and then fitted a quadratic function to test if the area of MCP's levelled off during the period a bird was studied. General linear models (GLMs) were applied to test for seasonal differences in home range size and in diameter of home ranges. Number of locations was entered as a covariate and season as a fixed factor.

Overlap of MCP home ranges was calculated using Ranges 5. We only considered overlaps between individuals tracked at the same site during the same season and calculated for each individual the average of all overlaps this bird had with others. Overall average overlap was then calculated as the mean overlap values of all individuals.

Centres of activity were calculated as arithmetic and harmonic means using the basic statistic function in Animal Movement. The distance of these to the nearest border of gallery forest was then measured using the measurement tool in Arc View. Values were compared between seasons using independent samples t tests.

Habitat selection

Habitat selection was tested on a landscape level following the suggestions of White & Garrott (1990). We calculated the proportion of each habitat within home ranges (use) and the proportion of each habitat within a larger area (availability), which we defined as follows. As we could not assume that the whole study area was available to all birds and birds tracked came from four different locations, we had to adopt a more complicated procedure to define habitat availability. We defined available habitat as the area within a circle around the centre of the trapping site just containing the outermost point where a resident bird (caught at that site) had been located. Thus we created four circles around the four trapping locations. Birds were assigned to the circle around the trapping site where they were caught (Fig. 1). However, birds 3 and 8 were not included in this as bird 3 left the study area after trapping and was found to be resident in a place 2500 m away from the trapping site one week after trapping, and bird 8 had an unusually large home range as compared to the other birds and did not show significant site fidelity. Bird 8 was treated just like the other birds but separately as it moved over a much larger scale and we could not assume the space available to this bird to also be available to the others. For bird 3 we defined availability as the area within a circle just containing the trapping location and the outermost location of this bird, assuming that the area from the trapping spot to the furthest point the bird flew was available to this bird. Habitat maps were digitised and analysed using Arc View GIS Version 3.1.

We tested for divergence from random habitat use using compositional analyses as described by Aebischer & Robertson (1993) due to potential problems with using dependent proportions in the analysis. We calculated the log ratios for all habitat types and then used multivariate GLMs to test whether habitat use differed from random and whether there were seasonal differences in the habitat preference relative to each other.

To test for seasonal differences in the extent to which different habitats were used we divided the proportion of each habitat used by the proportion available and compared these values between the seasons using a non parametric Kruskal-Wallis test for several independent samples.

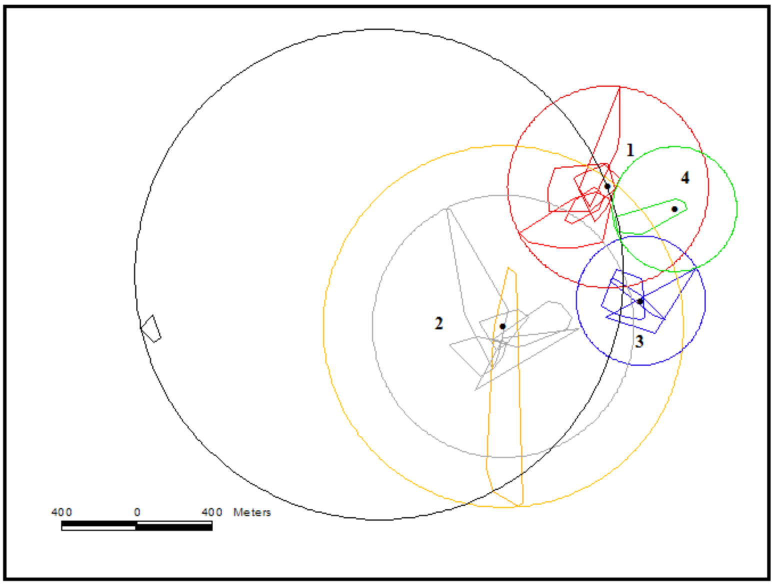


Fig. 1. Shown are all 100% MCP home ranges of Rock Firefinches and the area defined as available for the birds to illustrate methods of calculating habitat availability and use. Colour of MCPs corresponds to colour of the circle which defines availability for these birds. Black dots represent trapping sites and numbers correspond to the nearest trapping site. Availability was defined as the area within a circle around the trapping location just containing the outermost location of a bird caught there. Birds no 3 and 12 were treated in a different manner due to them showing movement behaviour much different from that of others (for more details see methods).

Nest survival

We calculated nest survival rates following Mayfield (Mayfield in Johnson, 1979) with confidence intervals following Johnson (1979). If we did not know when a nest was depredated or when chicks hatched the period between nest checks was divided by two and the date of predation or hatching was assumed to be in the middle of that period. However, sometimes we knew from radio-tracking that a bird was incubating up to a point until the radio was lost or the bird was no longer tracked. Such days were then counted as nest still active with eggs, and the period following it until the nest was known to be depredated or chicks hatched was divided by two. Nests that only contained indigobird chicks but initially had more eggs were also counted as having failed.

Incubation periods

When we recorded time intervals during which males and females were incubating, we counted each 15 min period during which the bird was known to constantly be present (i.e. if an incubation period lasted from 06:10 - 06:55 the following periods were counted: 6:15, 6:30). Fifteen-minute periods are shown with their start time (i.e. 6:15 indicates the period between 6:15 - 06:30). Single fixes were counted as a 15 min incubation period. To compare the incubation behaviour of males with females we then calculated the proportion that each individual was present during each period and then calculated a mean for the two sexes over these values. Note however, that sample sizes are not equal for each time period because some individuals were not tracked during each time interval.

Results

Trapping

Between 12/02/04 - 07/12/05 149 new Rock Firefinches were trapped and ringed at four different trapping sites. Out of these 127 were adult birds, 9 subadults and 13 juveniles. Out of the 127 adult birds 62 were females and 65 were males, giving a sex ratio of roughly 1:1. During the trapping period for this study (19/08/2005 - 07/12/2005) 23 new adult Rock Firefinches and 17 adult Rock Firefinches ringed during previous trapping periods, 3 subadults and 2 juveniles were caught. Of the 40 adult birds caught, 16 were females and 24 were males. We trapped 27 birds at site 1, eight birds at site 2 and ten birds at site 3. One bird was trapped at site 4, which was not regularly used. We recaptured seven of these 45 birds (15.6%) during this study period, details of which are given in Table 1. As can be seen from Table 1, only one bird was captured at a different site while all other recaptures occurred at the same site from where they were first caught.

Table 1. Recaptures of Rock Firefinches at the three trapping sites between 19.08.05-07.12.05.

Ring no	Age	Sex	Trapping site	Date	Days since last capture
AM27716	adult	F	1	11/09/05	
			2	21/11/05	40
AM27981	adult	F	1	04/12/05	
			1	07/12/05	3
AM28009	adult	F	1	19/08/05	
			1	04/10/05	55
			1	07/11/05	34
AM28080	adult	M	3	11/10/05	
			3	02/11/05	22
AM28097	adult	M	2	01/11/05	
			2	28/11/05	27
AM47819	subadult	M	1	15/11/05	
			1	23/11/05	8
AM47820	adult	M	1	16/11/05	
			1	02/11/05	16
			1	07/11/05	5

Movement patterns

We were able to radio-track a total of 15 birds (2 males and 13 females). One female was trapped and radio tracked twice, first during the wet and again during the dry season. Due to the home range having shifted and two months between the tracking periods we treated these movements separately (bird no. 1 and 10). A total of 621 locations were obtained over a period of 102 days of radio tracking with 36.5 ± 16.9 locations per individual.

The movement paths of 15 out of 16 birds were significantly more constrained than 100 randomly created paths (all $p<0.05$), so all these birds showed higher site fidelity than randomly expected (Fig. 2). Only the movement path of bird no 12 did not differ from randomness ($p=0.45$). This bird also had the largest MCP home range. However, it made two breeding attempts in the study area such that it seems unlikely that it did not stay within a restricted area.

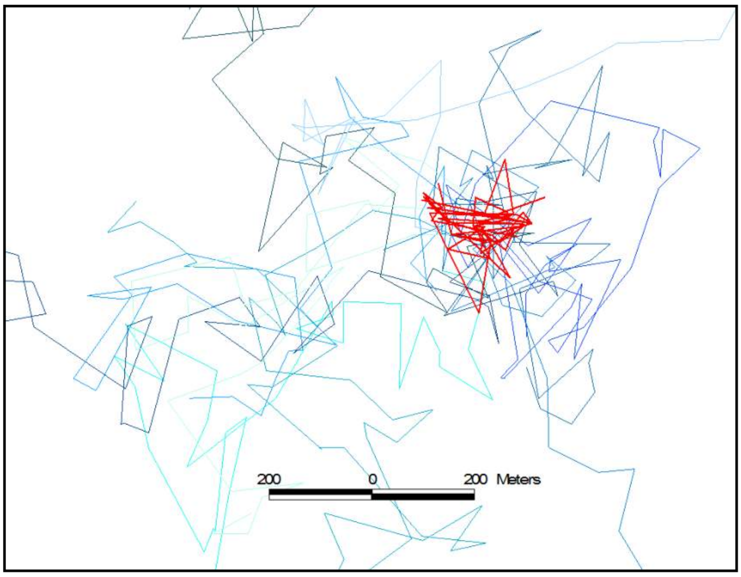


Fig. 2. Movement path of Rock Firefinch no. 1 (red lines) compared to ten random movement paths (blue lines with different shades for different paths). The movement path of the bird is significantly less dispersed that the random paths so the bird shows high site fidelity.

Home range size, calculated as 100% MCP area, levelled off between 20 - 30 location as shown by a Bootstrap sampling procedure. Saturation of MCP home range size was not achieved for five individuals (3, 7, 8, 13, 14). As exclusion of these animals would have severely compromised sample size we instead statistically controlled for variation in the number of fixes when testing for the influence of season on MCP home range size. Information on radio-tracked birds is summarised in Table 2. Home ranges tended to be larger during the dry (7.34 ± 4.78 ha, n=8) than during the wet season (3.56 ± 2.04 ha, n=8; Table 3a, Fig. 3, 6), and the diameter of these MCP home ranges was significantly greater during the dry (470 ± 278 m, n=8) than during the wet season (329 ± 125 m, n=8; Table 3b, Fig. 4, 5). When we removed bird 12 from this analysis, the differences between the size and diameter of MCP home ranges became weaker but the tendency remained ($F_{1,14}$=2.80, p=0.12 and $F_{1,14}$=4.15, p=0.06 respectively).

Table 2. Summary of movement patterns of Rock Firefinches radio-tracked. Note that birds 1 and 10 are identical.

ID	**Sex**	**Trapping site**	**Period tracked**	**Season**	**No of fixes**	**MCP in ha**	**Diameter of MCP in m**
1	F	1	20/08 - 09/09	wet	63	3.94	302
2	F	1	21/08 - 27/08	wet	41	7.28	395
3	F	1	31/08 - 06/09	wet	39	0.76	142
4	F	2	10/09 - 16/09	wet	51	2.98	249
5	F	2	12/09 - 28/09	wet	25	3.67	304
6	F	3	01/10 - 06/10	wet	40	4.17	294
7	F	3	11/10 - 12/10	wet	9	1.09	355
8	F	1	12/10 - 14/10	wet	17	5.03	645
9	M	2	02/11 - 11/11	dry	69	5.10	633
10 (1)	F	1	09/11 - 16/11	dry	38	9.07	506
11	F	2	22/11 - 23/11	dry	20	5.17	438
12	F	2	10/11 - 21/11	dry	46	16.81	1269
13	F	2	10/11 - 15/11	dry	25	10.68	875
14	F	3	16/11 - 17/11	dry	11	5.27	540
15	F	4	29/11 - 06/12	dry	46	3.91	390
16	M	1	19/10 - 27/10	dry	42	2.01	243

Average overlap of 100% MCP home ranges only considering overlap between birds tracked at the same site during the same season was 28.8 ± 26.9% (n=12). Average overlap of 50% MCP home ranges was 8.2 ± 27.2% (n=12). However, eight individuals had no overlap with others, two only very slight overlap (<0.2%) and the two birds tracked at site 3 during the wet season had 3.8 and 94.4% overlap resulting in a relatively high mean with a wide standard deviation.

There was no significant difference in 50% MCP home ranges between seasons ($F_{1,13}$=0.52, p=0.48, controlled for number of fixes). Mean 50% MCP home range was 1.0 ha (n=16). There was also no statistical difference in the mean distance of the arithmetic mean or harmonic mean to gallery forest (t-test, t=1.14, df=14, p=0.27 and t=0.73, df=14, p=0.47 respectively). However, bird 1 was tracked during both seasons and appeared to have shifted its home range closer to the gallery forest. The distance between the nearest border of the gallery forest and the centre of activity calculated as the arithmetic mean decreased from 139 to 0 m during the dry season and the same was true for the distance of the harmonic mean to the gallery forest (139 to 2 m).

Table 3 a-b. Results of GLM testing the influence of season (dry and wet) on a) the size of MCP home ranges (in ha) and b) diameter of MCP home ranges (in m) of Rock Firefinches.

a) Dependent variable				
	Type III Sum of Squares	df	F	p
Corrected Model	58.40	2	2.02	0.15
Number of locations	1.29	1	0.09	0.67
Season	56.24	1	3.89	0.06
Intercept	65.98	1	4.56	0.01
Error	188.21	13		
Corrected Total	246.61	15		

b) Dependent variable				
	Type III Sum of Squares	df	F	p
Corrected Model	320238.23	2	2.49	0.12
Number of locations	1860.17	1	0.03	0.87
Season	319915.14	1	4.97	<0.05
Intercept	688086.27	1	10.69	<0.01
Error	188.21	13		
Corrected Total	246.61	15		

When birds flew to the gallery forest they left the inselberg habitat via an almost straight line and very fast such that we often had difficulties in keeping up with them. They then stayed in the gallery forest for about 30 min until they slowly made their way back to the inselberg. These trips usually occurred between late morning and early afternoon when temperatures were highest and birds had probably already foraged some time.

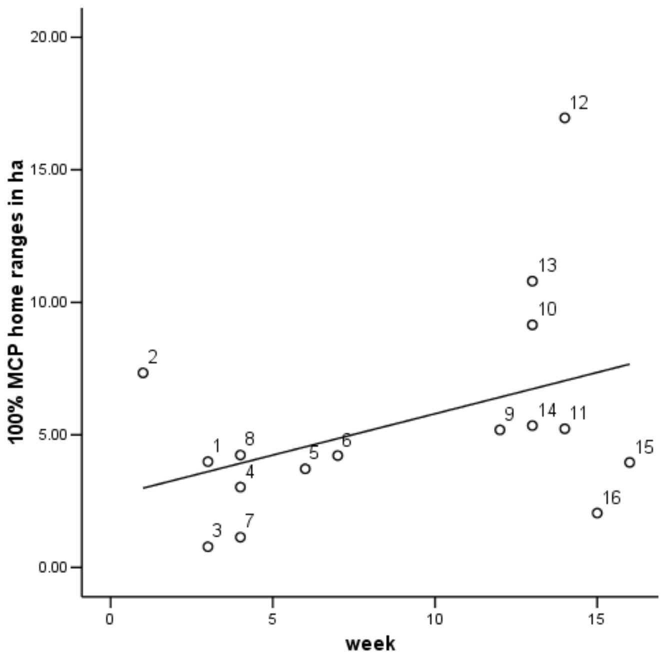


Fig. 3. Size of MCP home ranges (in ha) of Rock Firefinches plotted by progressive week of tracking. Points are labelled with the ID number of the bird. Week 1 – 7 fall into the wet season, weeks12 – 16 into the dry season.

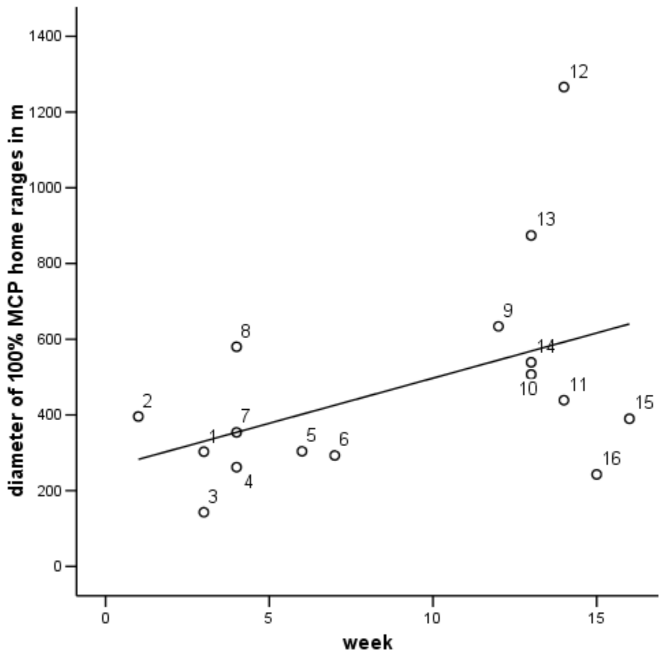


Fig. 4. Diameter (in m) of MCP home ranges of Rock Firefinches plotted by progressive week of tracking. Points are labelled with the ID number of the bird. Week 1 – 7 fall into the wet season, weeks12 – 16 into the dry season.

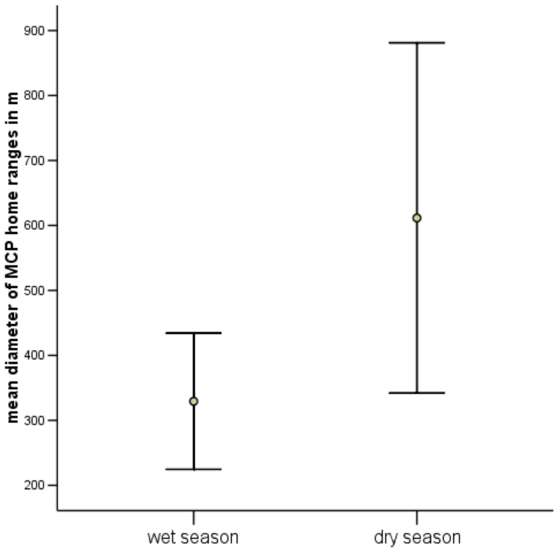


Fig. 5. Error bars showing the mean and 95% confidence limits of the diameter (in m) of MCP home ranges of Rock Firefinches during the wet and the dry season.

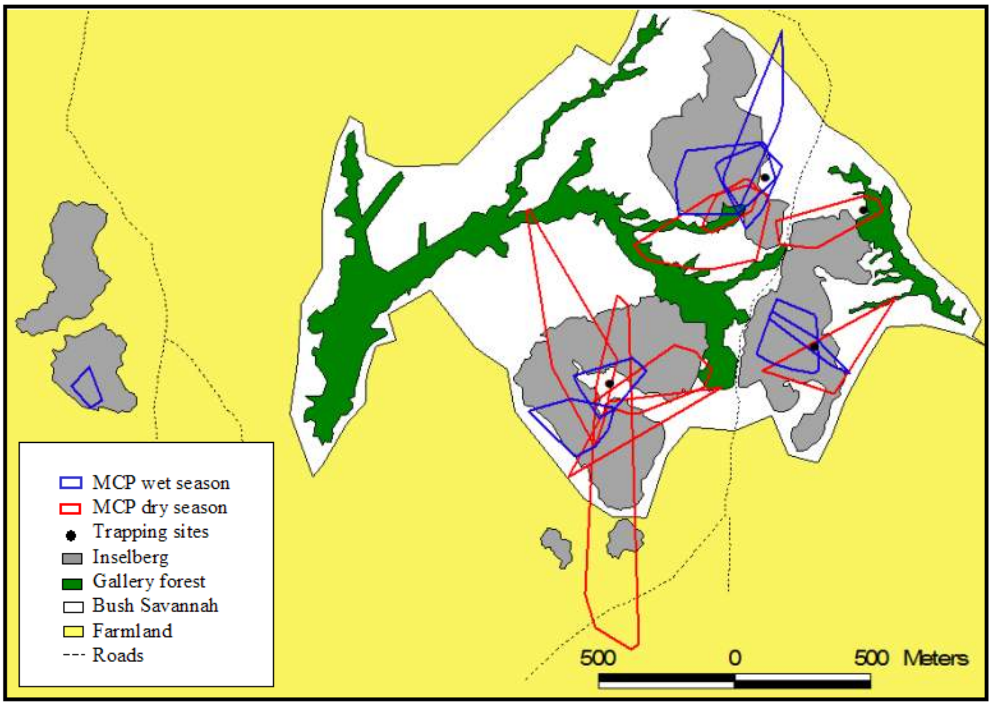


Fig. 6. Map of the study area and 100% MCP home ranges of Rock Firefinches during the dry and the wet season.

Habitat selection

When testing for divergence from random habitat use using compositional analysis, habitat selection was non random during both seasons (wet: Wilk’s Lamda=0.05, $F_{3,5}$=30.14, p<0.01; dry: Wilk’s Lamda=0.05, $F_{3,5}$=30.30, p<0.01). There was no seasonal difference in habitat selection relative to each other (Wilk’s Lamda=0.69, $F_{3,12}$=1.84, p=0.19). Habitat ranking was inselberg > scrub savannah > gallery forest > farmland during both seasons. However, as indicated by the following analysis the extent to which each habitat was used differed between the seasons. Scrub savannah was selected during the dry season (Chi^2=5.30, df=1, p<0.05), there was a slight tendency for gallery forest to be used to a higher degree during the dry season (Chi^2=2.83, df=1, p=0.09) but selection of inselberg habitat did not differ between seasons (Chi^2=0.54, df=1, p=0.46), and the usage of farmland did also not differ seasonally (Chi^2=0.01, df=1, p=0.93; Table 4, Fig. 6, 7).

Table 4. The % of each habitat type available to a bird (calculated as the area within a circle around the trapping location trajecting the outermost point of the MCP home range of the outermost resident bird) and % of each habitat type within MCP home ranges of birds. Abbreviations for habitat types are: I = inselberg, G = gallery forest, S = scrub savannah, F = farmland.

Bird ID	Sea-son	% Availability				% Use (habitat within MCP home range)				% Availability / % Use			
		I	G	S	F	I	G	S	F	I	G	S	F
1	1	32	11	42	15	78	3	20	0	2.41	0.25	0.47	0.00
2	1	32	11	42	15	90	3	7	0	2.78	0.29	0.18	0.00
3	1	11	7	19	63	100	0	0	0	8.94	0.00	0.00	0.00
4	1	24	9	33	34	48	0	52	0	1.99	0.00	1.58	0.00
5	1	24	9	33	34	89	0	11	0	3.66	0.00	0.34	0.00
6	1	43	5	36	15	100	0	0	0	2.31	0.00	0.00	0.00
7	1	43	5	36	15	95	0	5	0	2.19	0.00	0.14	0.00
8	1	32	11	42	15	52	0	43	5	1.62	0.00	1.02	0.35
9	2	24	9	33	34	63	0	36	0	2.60	0.03	1.11	0.00
10	2	32	11	42	15	29	18	54	0	0.89	1.59	1.28	0.00
11	2	61	1	33	5	67	4	29	0	2.77	0.42	0.88	0.00
12	2	20	9	29	42	48	0	18	34	2.36	0.00	0.63	0.81
13	2	24	9	33	34	53	1	46	0	2.19	0.13	1.40	0.00
14	2	43	5	36	15	57	0	43	0	1.31	0.08	1.19	0.00
15	2	19	11	42	28	53	10	37	0	2.85	0.88	0.89	0.00
16	2	32	11	42	15	68	31	1	0	2.10	2.81	0.03	0.00

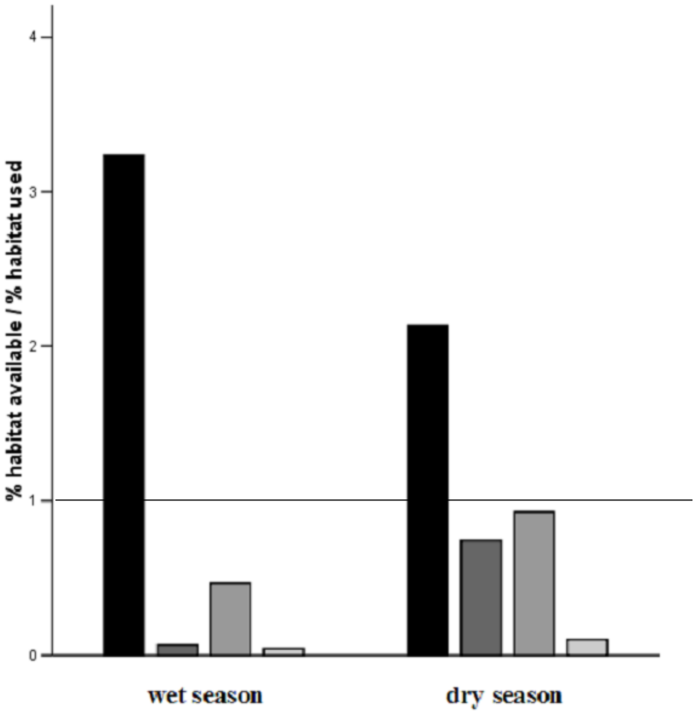


Fig. 7. The proportion of available habitat used during the wet and the dry season (bar colours: black = inselberg, dark grey = gallery forest, grey = scrub savannah, light grey = farmland).

One bird was caught at site 1 and located there several times on the day of release but not found again the day after. One week later we located it on a small inselberg where it had an active nest 2.5 km away from the place of capture. Between the reserve and this inselberg lie extensive areas of abundant and used farmland, which this bird must have crossed.

Nests, nest sites and breeding success

Fourteen nests of Rock Firefinches were found on the Jos Plateau in central Nigeria between September and November 2005. Four nests were found when adult birds were flushed from the nest and ten were found via radio-tracking of two adult males and six adult females (two females making two breeding attempts). Information on the nest site characteristics is summarised in Table 5. The majority of nests (79%) were located on inselbergs within a bushy savannah habitat with many rocks and boulders. Nests were relatively round grass nests about 9 cm in diameter with an approximately 5 cm wide round entrance. They were woven from rough grasses on the outside and finer grasses on the inside. Thirteen nests (93%) also contained feathers as lining. Six nests were hidden in small tufts of grasses near the ground (n=2) or on rocks (n=4) all in close proximity of big boulders providing shelter, four were woven into longer grasses 0.3 - 0.7 m above the ground but in all cases also in close proximity to boulders (<0.05 m distance), while four were located above ground in dense bushes (1 Lantana bush, two unknown bush species and one nest in dense lianas and rank plants hanging down from a tree near a big boulder). The three nests located on farmland and in the garden were all located in bushes and in one case was still built in close proximity to a granite outcrop.

When found, nests contained two (n=2), three (n=3), four (n=3) or five (n=4) eggs. Seven nests were depredated within eight days of finding the nest, most probably still during the egg stage. In five cases no remains or signs were found and we believe lizards or snakes to have predated the eggs. In one case three eggs were gone, one egg was broken and one egg remained and so we believe rodents to have predated the eggs. In another case the nest was not accessible but the female (bird 13) was radio-tracked incubating until she left the nest in the morning when the male entered. About three hours later she went back to the nest when the male was flying around the nest calling. She briefly inspected the nest after which both birds left the nest site and never returned to it. We thus believe that this nest was probably also depredated. Two nests were abandoned during the egg stage for unknown reasons. In five nests chicks hatched and probably fledged. Of these, two were parasitised by Indigobirds (probably Jos Plateau Indigobirds). In one nest only one Indigobird chick hatched despite three eggs initially being present and in the other nest three Indigobird chicks and one Rock Firefinch chick hatched and probably fledged despite five eggs being initially present. The Rock Firefinch chick was less developed than the Indigobird chick as apparent from weight and wing growth. In three cases nests were not depredated or parasitised: in two nests four Rock Firefinch chicks hatched (one had initially four eggs, the other nest was found when it already contained chicks) and in one nest three Rock Firefinch chicks hatched and probably fledged (4 eggs initially present). This gives a nest predation rate of 64% (n=14), a parasitism rate by

Table 5. Summary of nest parameters of Rock Firefinches

Nest No	Date found	No eggs	Discovered by	Habitat	Height above ground	Fate	Note
1	01.09.05	2	bird flushed	farmland, bush	0.7	predated (reptile?)	
2	10.09.05	5	radio-tracking	inselberg, grass between boulders	0.7	parasitised, 1 ROCFF, 3 IB fledged	
3	15.09.05	5	bird flushed	inselberg, ground between boulders	0	predated (reptile?)	
4	15.09.05	5	radio-tracking	inselberg, in grass-tuffs in gap of rock	5	predated (reptile?)	
5	16.09.05	5	bird flushed	inselberg, grass between boulders	0.3	predated (rodents?)	
6	04.10.05	2	bird flushed	garden, bush	0.4	abandoned	
7	05.10.05	3	radio-tracking	inselberg, ground between boulders	0	parasitised, 1 IB fledged	
8	06.10.05	2	radio-tracking	inselberg, in grass-tuffs in gap of rock	2	predated (reptile?)	
9	11.10.05	4 chicks	radio-tracking	inselberg, in bush between boulders	1.1	4 ROCFF fledged	
10	19.10.05	4	radio-tracking	inselberg, in grass-tuffs in gap of rock	2.3	4 ROCFF fledged	
11	03.11.05	4	radio-tracking	inselberg, grass between boulders	0.5	3 ROCFF fledged	
12	12.11.05	3	radio-tracking	inselberg, grass between boulders	0.5	abandoned	
13	10.11.05	?	radio-tracking	inselberg, in grass-tuffs in gap of rock	3	predated?	from birds behaviour, nest not accessible
14	14.11.05	3	radio-tracking	farmland, bush between boulders	1.7	predated (reptile?)	

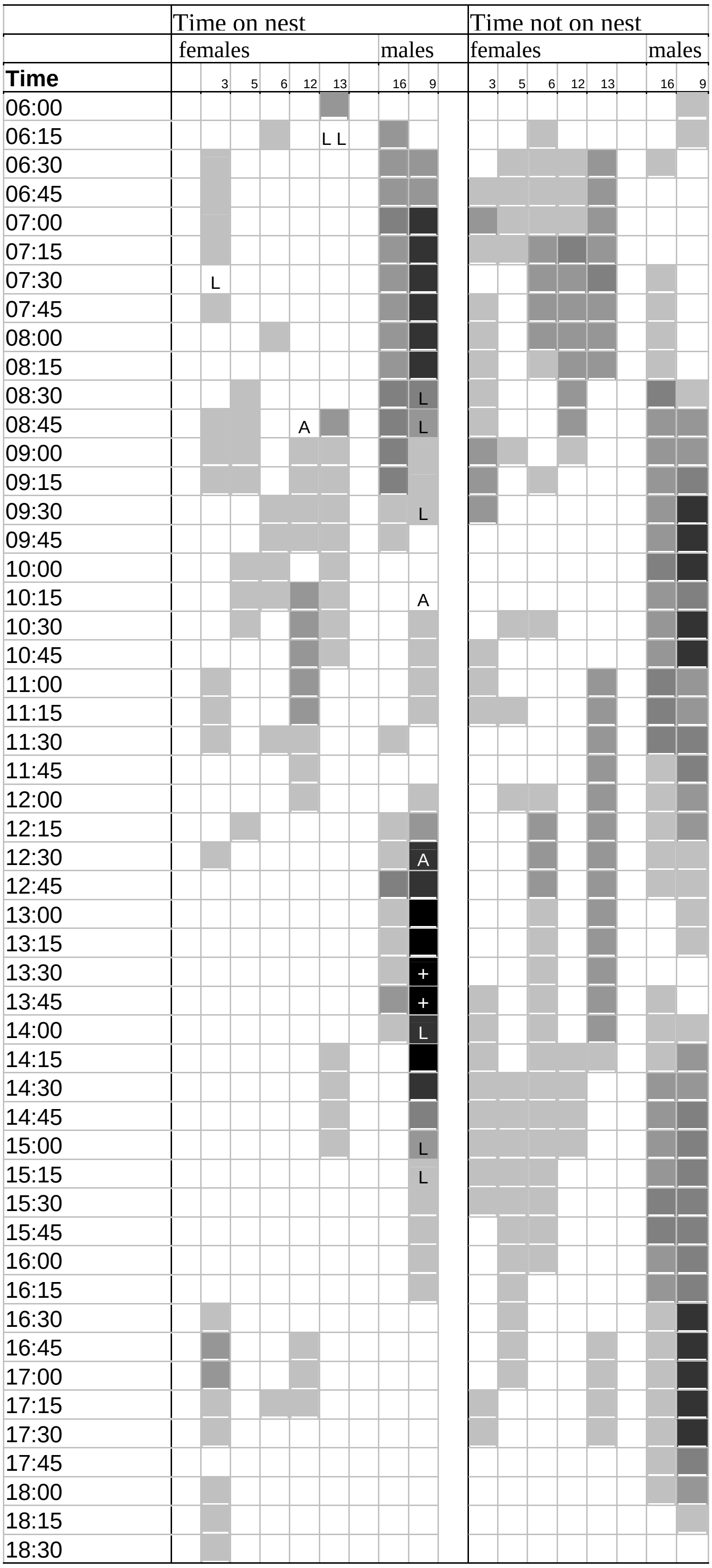
Indigobirds of 40% (n=5) and 31% of nests produced Rock Firefinch chicks (n=14). Clutch size of Rock Firefinches is hard to establish because it is unclear how many Indigobird eggs were contained within the Rock Firefinch clutches. However, they seem to be able to lay clutches of at least 4 eggs as indicated by four Rock Firefinch chicks in two nests.

Nest survival rate as calculated after the Mayfield method (Mayfield in Johnson, 1979) gave a daily survival rate of 0.89 ± 0.03 during the egg stage (91.5 days of exposure, 4 of 14 nests survived) and a survival rate of 1.0 during the chick stage (37.5 days of exposure, 4 of 4 nests survived). Assuming 14 days until hatching (which is the time until hatching in the closely related Black-bellied Firefinch (Fry et al., 2004) and which also seems to be reasonable for Rock Firefinches judged by our data), this gives a total nest survival rate of 0.20 (0.12 - 0.31). The two birds whose nests failed and which we were able to track long enough to witness a second breeding attempt both did so. It is therefore reasonable to assume that Rock Firefinches are able to at least make a second breeding attempt should the first one fail. Therefore the chance of a pair to successfully reproduce would be 0.36 (0.24 – 0.52). With an average of 3 chicks per successful nest (n=4) this gives an average of 1.08 (0.72 - 1.56) chicks per breeding pair per year. Given a survival rate of 0.65 (McGregor, 2005) in Rock Firefinches, and assuming that juvenile survival is the same than adult survival, 0.70 (0.47 - 1.01) birds per pair reach sexual maturity, approximately 35% (23.5 - 50.0%) of the reproductively active population will be replaced each year based on our productivity and nest survival data. This is lower than the approximate annual loss of 45% of adult Rock Firefinches, which have an estimated survival rate of 0.65 (McGregor, 2005).

Incubation behaviour

Males and females were both observed to incubate. We obtained radio-tracking data of two males and five females while they had an active nest with eggs and were thus able to gather data on their incubation behaviour. Data suggest that females probably attended the nest during the night until the male took over in the early morning between about 06:30 - 08:30 freeing the female to forage. The female then seemed to attend the nest during the late morning between 08:30 - 11:30 until the male again incubated until the early afternoon. Nest attendance seemed to generally be lower during the afternoon and nests were probably unattended for some time during the afternoon until the female started incubating again during the late afternoon and probably stayed on the nest during the night (Fig. 8, 9). Note that always only one sex of each nest was radio-tracked, so each individual belonged to a different nest. The percentage of times that a male was on the nest in relation to total nest attendance at the different times of the day differed from an equal distribution (Chi² test, $Chi^2=80.80$, $df=23$, $p<0.05$). In four radio-tracked individuals, where the nest could be observed relatively easily without disturbance (due to an elevation nearby), we observed several occasions when one sex took over incubation from the other. While one bird sat on the nest, the other one approached the nest calling, until the incubating bird left. The other bird was then seen to enter the nest. The occurrences of these observations are indicated in Fig. 8. In one instance we checked the nest after the tracked bird left and no other bird approached, and it was found unattended. This instance was during the afternoon when tracking data also show that neither males nor females show high nest attendance (Fig. 8, 9).

Fig. 8 (next page). Time periods when radio-tracked birds were known to be attending the nest or known not to be attending the nest. Different individual birds are shown in different columns, sex is given in the second row, ID codes are given in the third row. Colour shades show sample sizes for each individual during that time period (5 shades from light to dark representing sample sizes 1 - 5 and black with a white cross representing 6; for further details see methods). Occasions when the bird took over incubation from the non tracked birds and when the non tracked bird took over from the observed are indicated by A and L respectively (for further details see results). (For Fig. 8 see next page).



	Time on nest										Time not on nest							
	females						males			females						males	
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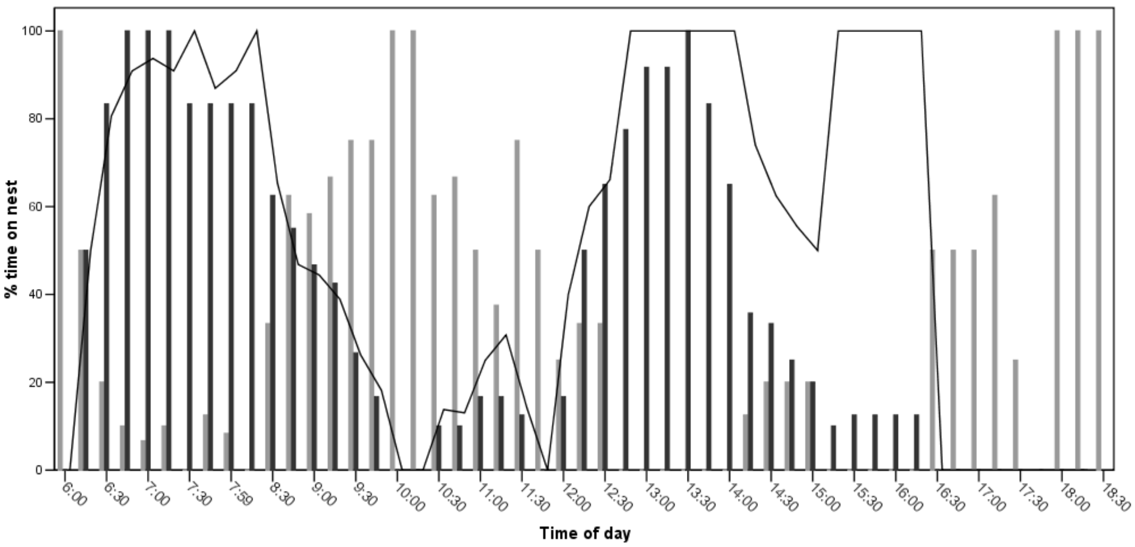

Fig. 9. The percentage of 15 min periods that females (light bars) and males (dark bars) spent on the nest incubating in relation to the total number of all 15 min period radio-tracked. Data are pooled over individuals (5 females and 2 males). The line indicates the proportion of each 15 min period that a male incubated in relation to the number of time period either sex incubated.

Discussion

Site fidelity

Rock Firefinches in this study showed a high degree of site fidelity as evident from radio-tracking and from locations of recaptures. The relatively low recapture rate was probably due to birds becoming net shy as many more individuals were re-sighted (pers. obs.). Only one bird that was fitted with a radio could not be found again, but whether this was due to it leaving the study site or the radio having failed was not clear. Only one of the 16 birds tracked left the study area and became resident at a site with similar habitat 2.5 km further away. Therefore, Rock Firefinches do not respond to changes in the availability of food and water by moving to different areas like many nomadic birds in desert as well as savannah habitat do, where the occurrence of rain and food is less predictable (Davies, 1984; Dean, 1997). Rather they pursued a resident strategy by gaining advantage of detailed knowledge of a restricted area, probably enabling them to locate remaining food resources that are harder to find (Sinclair, 1884). Granivorous species that showed a more nomadic behaviour within our study site and moved in large groups like Northern Red Bishops (*Euplectes franciscanus*) and Black-winged Bishops (*Euplectes hordeaceu*) all fed mainly on seeds from the grass-ear (Chapter 5). This microhabitat is only available during a short period of time. Rock Firefinches on the contrary are specialised to feed on grass seeds from the ground, which is probably a more stable food supply as seeds remain on the ground a long time after seed fall has taken place (Chapter 2). In addition, Rock Firefinches have a relatively long and narrow bill, which probably enables them to separate seeds from vegetation litter and sand more efficiently than other species with shorter bills (Chapter 5). They are thus probably able to use the remaining food resources within the study area more efficiently than other species can, enabling them to stay in the area throughout the year.

Movement behaviour and habitat choice

Rock Firefinches clearly preferred inselberg habitat, which has also been found by Wright & Jones (2005). Barshep (2005) also found Rock Firefinches to be more abundant in inselberg habitat and bush savannah than in farmland. One reason emerging from this study might be nest site requirements. Most nests were found within inselberg habitat next to or between boulders despite birds also using other habitats to some extent. Rocky boulders might provide shelter from predators as nests are well hidden from view. Rock shelter may further serve as shade from sun exposure and high temperatures. Nests sites indeed appeared to be cooler than their surroundings, but temperature measurements are lacking and would be desirable. However, Rock Firefinches also preferred inselberg habitat outside the breeding season (Wright & Jones, 2005), suggesting, that inselbergs might be selected for reasons other than nesting. Adult birds might also benefit from the shade that rocks provide and this might enable them to also feed during high temperatures. Further, seeds blown away from savannah habitat might accumulate between rocks and be available there for longer than in other habitats, but this remains to be investigated. Rock Firefinches were indeed often flushed from between rocks and appeared to have been feeding on seeds aggregated there. During transects Rock Firefinches were also found to only feed close to cover (Chapter 5) and this might highlight their need for safe feeding places. Rock shelter could also provide this.

During the dry season Rock Firefinches used scrub savannah to a greater extent than during the wet season and this was a consequence of them having to move through these habitats to get to water sources. There was only a tendency for gallery forest to be present within home ranges to a larger extent during the dry season but seven out of eight birds had gallery forest within their home range during the dry season, while only two out of eight birds' home ranges contained gallery forest during the wet season. This was a result of water still being available in the gallery forest, while water sources on inselbergs and in savannah habitat had dried out. Gallery forest grows along deep wet gullies in the reserve with many of them bearing water throughout the year. Only a very small area of gallery forest was contained within home ranges as birds always flew to the same spot to get water, and because of this the seasonal difference was probably only apparent as a tendency. Gallery forest might therefore be quite important in preserving water for granivorous birds such as the Rock Firefinch, which seems to depend on fresh water for digestion.

While some granivores appear relatively independent of water sources (e.g. the Zebra Finch (*Poephila guttata*) and the Silverbill Finch (*Lonchura malabarcia*)), most rely on it, even though metabolic adjustments are likely to exist in most dry habitat species (Macmillen, 1990; Macmillen & Baudinette, 1993; MacMillen & Hinds, 1998). Ward (1978) also noted that Red-billed Quelea (*Quelea quelea*) had to wet their crop content during the midday heat to aid digestion. All but one Rock Firefinch tracked during the dry season used gallery forest (the other one used a water source in the village) and birds were indeed sometimes observed to fly up from water when we approached them. The straight line with which birds flew to the gallery forest, the time of the day when these trips occurred and the short time they stayed there, further supports the assumption that these trips served to get water. Male no. 9 for example often left the nest in the morning, then foraged for some time before finally flying to the gallery forest. Other observers at the study site have noted that Rock Firefinches in the dry season tend to move to the gallery forest during the midday heat and to stay there for some hours until the afternoon (unpublished data). They seemed to be resting in the trees and not be active. It is possible therefore, that, as the dry season continues, temperatures become hotter and Rock Firefinches no longer have to return to their nests or provide food for their chicks, they also use the forest as a cool resting place.

Use of gallery forest as a source of water and possibly shelter highlights the Rock Firefinch's need not only for inselberg habitat but also for forest habitat. It further highlights the seasonal differences in their requirements and points out that a species' habitat choice has to be investigated during all seasons before basing conservation considerations on results from habitat studies. It might also be important that these two habitats occur in close proximity. Larger home ranges during the dry season were a result of birds having to wander between inselberg and gallery forest habitat. While doing so, they had to cross bush savannah habitat, which was otherwise not extensively used. Besides raising energy expenditure, flying through this more open habitat probably increases predation risk, and this would be even more pronounced if they had to cross more open farmland, which was otherwise generally avoided. It is possible also, that birds inhabiting more isolated inselbergs during the wet seasons (like bird 3) cannot do so during the dry season and Wright’s & Jones’ (2005) finding, that Rock Firefinch abundance was also high at granite outcrops outside the reserve and therefore away from gallery forest during the wet season, might no longer hold during the dry season. It seems likely that these birds leave to go to areas where better conditions prevail. We were indeed under the impression that Rock Firefinch density within the reserve increased during the dry season despite few observations of juvenile birds so that this increase would not be due merely to reproductive output but also invasion. Investigating Rock Firefinch abundance, movement and survival during the wet and dry season in areas further from gallery forest and comparing it to that within the reserve promises to shed more light on these assumptions.

Water availability may determine much of the natural history of Rock Firefinches as it might limit time available and timing for breeding. Since Rock Firefinches bred in inselberg habitat, the need to be at the nest site to provide shade to eggs and chicks during the midday heat might conflict with the need to regularly fly to gallery forest to get water. Also provisioning of chicks with fresh water might become increasingly difficult as the dry season continues, temperatures rise and the need for fresh water also increases. This might explain why breeding only occurs between the late wet and the very early dry season.

While home ranges tended to be larger during the dry season there might also be a tendency for home ranges to be closer to gallery forest. We did not find a seasonal difference in the distance of arithmetic or harmonic means from gallery forest, however, one bird, which was tracked during both seasons (bird 1) shifted its home range closer to the gallery forest during the dry season. It might be the case that dominant birds are able to inhabit areas in closer proximity to gallery forest while subdominant ones are pressed to areas further away and this could also be an interesting point to investigate further.

However, Rock Firefinches did not seem to behave territorially. Home ranges of Rock Firefinches overlapped greatly and seemed to be too large to be defended. Large overlapping home ranges do not rule out that defended territories exist. Radio-tracked male nightingales, for example, were found to use a larger spatial scale than that of their defended singing territories because they made forays into neighbouring territories (Naguib, 1997). From radio tracking data alone one might therefore falsely conclude that no defended territories exist. However, several sightings of other Rock Firefinch individuals within the home range of radio-tracked birds (also in close proximity to the nest site), the lack of any territorial disputes observed during radio-tracking and only one opportunistic observation of two males chasing each other, do not support territoriality as a major character of home ranges in Rock Firefinches. Brown (1964) pointed out that a food resource ought to be limited and efficiently defendable for territoriality to occur and more recent work has shown that inter-individual aggression increases with the spatial and temporal clumping of food resources (Grant & Guha, 1993; Robb & Grant, 1998; Goldberg et al., 2001). As grass seeds are widely dispersed it is possibly not efficient for Rock Firefinches to defend territories for the purpose of securing food resources. Most cases of well studied feeding territories in passerines stem from insectivorous and nectivorous species (e.g. Stenger, 1958; Gill & Wolf, 1975; Carpenter & Macmillen, 1976; Carpenter et al., 1983; Smith & Shugart, 1987; Marshall & Cooper, 2004) where food resources are more likely to occur clumped, and so territoriality in granivorous birds is likely to be less common.

Territories may also be defended as a means to attract and secure a mate (Brown, 1964). However, if an even sex ratio exists, birds are monogamous and form stable pair bonds this might not be necessary. Rock Firefinches were found to have an even sex ratio and radio-tracked birds as well as birds during transects in different seasons (Chapter 5) were mostly seen in pairs (unless during radio-tracking birds had an active nest and incubated). It is therefore likely that they form stable pair bonds and rather than defending a territory for reproductive purposes, the male might guard the female from competitors by following her around. Direct mate guarding might generally be more efficient than defending a territory for that purpose alone (Brown, 1964). Stable pair bonds might arise from the need for both parents to share the care for nests and young and experienced pairs being more efficient as recently demonstrated for oystercatchers (van de Pol et al., 2006).

Incubation behaviour

Rock Firefinch parents shared incubation and probably also the feeding of chicks, which was also reported for the closely related Black-bellied Firefinch (Fry et al., 2004). However, only females were observed to develop a visible brood patch (pers. obs.). This might be due to the female attending the nest during the night, which seemed to be the case judged by our radio-tracking data. Cooler overnight temperatures probably require better heat transfer to the eggs and by developing a brood patch the female is able to do this. During the day males incubate several hours, and indeed there seemed to be a routine procedure in what times of the day the two sexes incubate. During the midday hours it might in fact be necessary to actually shade eggs from too much sun exposure (which might also account for the closed nest shapes), for which an incubation patch might not be necessary. During the afternoon, when temperatures are moderate, nests are probably often unattended.

The sharing of breeding activities might also be necessary for both birds to be able to gain enough food without the nest being unattended over long time periods. It might be further favoured by high nest predation in that it enables the female to quickly produce a new clutch should the first one fail, because renesting ability has been shown to be of high importance under such situations (Roper, 2005).

Breeding success

We found a relatively high nest predation rate and most predation events occurred during the egg stage rather than during the chick stage. This is in line with the assumption that most predators are small reptiles such as lizards, which might find it more difficult to devour a chick than an egg. Placing nests between rocky boulders, while hiding the nest from avian predators, might actually cause a high nest predation rate by reptiles because lizards in the study area were usually associated with rocks. Our results support previously assumed high nest predation rates in tropical birds (Martin, 1996; Roper, 2005). Ropers’ (2005) estimate of a nest survival rate of 0.91 per day in the tropical Western Slaty Antshrike (*Thamnophilus atrinucha*) is close to our estimate of 0.89 per day for Rock Firefinches during the egg stage, however in the Rock Firefinches other causes than only nest predation contributed to low breeding output. The average of 35-70% nesting success in north temperate birds (Martin, 1996) seems to be well above the 31% of nests succeeding in this study.

From our simple calculations of breeding output it appears that Rock Firefinch populations ought to be stable or only slightly decreasing, but these results have to be treated with caution. We assumed two breeding attempts per pair per year, 14 days for incubation, an average of 3 chicks per clutch and juvenile survival to be the same than adult survival. Slight changes in these assumptions will result in drastic differences in population trends. We calculated an annual breeding output of 0.36 mature birds per year per pair. Only a few juvenile birds were seen in the field such that this figure does not seem unrealistic. However, we also found a chick survival rate of 1.0, which seems to be overoptimistic and is unfortunately based on a sample size of only 4 nests. Most likely there are also more than two breeding attempts per year as found in other tropical bird species (Roper, 2005), which would increase reproductive output. Therefore, we urgently need more data on nest, chick and juvenile survival and number of breeding attempts before firm conclusions about breeding output and population trends can be drawn. However, in the absence of any other knowledge on Rock Firefinch breeding performance, we believe our data provide valuable information despite being based on a low sample size and several assumptions.

Further work will be constrained by the difficulty in finding nests. Despite extensive searches only four nests were found by flushing birds, the majority was found by radio-tracking, and this therefore seems to be a more promising technique. There might also be a bias for nests found by flushing birds to be more conspicuous and indeed all nests found visually were depredated while this happened to only 30% of those found by radio-tracking. For this reason, finding nests by radio-tracking appears more promising to yield representative results.

Two nests were found to be parasitised by Indigobirds. In one nest three indogobird chicks and one Rock Firefinch chick resulted from initially five eggs. Indigobirds were further developed than the Rock Firefinch chick and it is likely that Indigobird chicks take less time to develop such that they can out compete Rock Firefinch chicks. This strategy seems sensible given that the parasites' egg might be added some time after the host eggs have been laid and is well documented in other Indigobird species (Davies, 2000). More knowledge on Rock Firefinch breeding success will also provide information on those of its host, which might even be of more conservation concern due to its undoubtedly smaller population size and dependence on Rock Firefinches as a host. Clearly more studies are needed.

Conclusions

We found that Rock Firefinches showed different habitat requirements during the wet and the dry season due to water being no longer available within preferred inselberg habitat during the dry season. While inselberg habitat was used for breeding where almost all nests were located between boulders, birds additionally utilised wet gullies within gallery forest when water sources elsewhere had dried out. Close proximity of these water sources to inselberg habitat might be necessary for Rock Firefinches to inhabit inselbergs during the dry season. Distances between inselberg habitat and water sources may further be an important determinant of Rock Firefinch survival as predation risk might increase when birds have to cross open, otherwise non preferred habitat to access water sources. The necessity to fly long distances to water sources and a greater water demand during the dry season might further limit time available for breeding. Most likely water availability also limits time available for breeding in other granivorous bird species and little consideration has been given to this so far. It would be an interesting experiment to investigate whether provisioning of artificial water sources in inselberg habitat during the dry season would cause birds to stop these trips to the gallery forest and could prolong breeding activities.

Daily egg survival rate calculated after the Mayfield method was 0.89 ± 0.03 and of all nests found 50% were depredated probably mostly by lizards and additional nests were parasitised or abandoned. Nest predation therefore probably plays a major role in determining life history traits of Rock Firefinches and might be one factor promoting the formation of stable pair bonds via enhanced renesting ability. Assuming two breeding attempts per year, a mean clutch size of three Rock Firefinch eggs, an incubation period of 14 days, a nestling survival rate of 1.0 (all these assumptions based on our preliminary findings) and juvenile mortality to be the same than adult mortality we calculated an annual 35% of the reproductively active population being replaced. This is below the estimated 45% of annual mortality and thus the Rock Firefinch population might be slightly decreasing at present. However, due to the large uncertainty of our assumptions and low sample size of nests found more studies are urgently needed to evaluate these assumptions. The protection of inselberg habitat and nearby habitats providing water and possibly shade during the dry season like gallery forest might be essential for the Rock Firefinches' and therefore also the Jos Plateau Indigobirds' long term survival.

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Chapter 7: Concluding discussion

Seasonality of starvation risk

As found in other regions of Africa (a woodland savannah in Zimbabwe (Linzey & Washok, 2000) and a semi-arid desert in South Africa (Kerley, 1991)), birds in savannah habitat in central Nigeria contributed the major part to small seed consumption in our study area. This was also found by Kelt (2004) in semi-arid Chile, but contrasts findings for deserts in North and South America, where birds were found to be of little importance and the majority of seeds was consumed by rodents and also ants (Morton, 1985). Rodents were of little importance in this study (however, they might feed on larger seeds mainly), and consumption by ants was only noticeable during the dry season, when they still consumed much less then birds. Avian granivores in our study area are thus probably mainly faced with competition for seed resources by other con- or hetero-specifics within the same guild rather than having to compete with mammals or insects to a great extent. It seems interesting to further investigate whether this is a general pattern in African savannah environments and whether it contrasts those in desert regions.

Seasonal differences in foraging patterns, as typically observed in temperate passerines, were largely absent from the foraging behaviour of tropical granivores Estrildid finches inhabiting savannah habitat in central Nigeria. In temperate system such differences in foraging behaviour reflect marked seasonal changes in the risk of starvation. During winter when energy demands are raised due to increased thermoregulation and when less food is available, temperate birds carry more fat reserves (e.g. Rogers, 1987; Haftorn, 1989; Haftorn, 1992; Cresswell, 1998; Macleod et al., 2005a), feed earlier during the day (Macleod et al., 2005a) and show more risk taking behaviour (Hilton et al., 1999; Yasue et al., 2003). All this reflects that during these times the risk of starvation becomes relatively more important to these birds compared to the risk of predation. Tropical granivores in this study carried slightly more mass during the early wet season when grass seeds (which these birds mainly fed on) on the ground declined, and this might indicate an increased risk of starvation. However, in the late wet season when see density on the ground was still low, mass decreased again, and the reason for this remains unclear. Many other granivorous species left the study area during this time, which might have relaxed competition for those that remained. It is also possible that alternative food resources such as insects, berries or young, green grass seeds become abundant, and this remains to be investigated further. However, mass gain, timing of feeding and risk taking behaviour did not vary in a consistent manner between seasons, and so we did not find strong evidence that these parameters followed a seasonal pattern reflecting changes in starvation risk. We believe that, while food abundance might be of some importance, other important factors, which have different implications for different aspects of the birds' feeding behaviour, might override the importance of food abundance. Such factors might include changes in the abundance of parasites and pathogens, water availability, availability of other food resources and the abundance of different bird species throughout the year.

Timing of moult and breeding

Breeding activities started during the late wet season, when seeds on the ground were still relatively scarce. They lasted into the early dry season, where they overlapped with the beginning of moult. Moult then continued during all of the dry season and was usually finished by the start of the rainy season. The overlap of moult and breeding, while less common in temperate birds, is often observed in tropical birds (Foster, 1974; Foster, 1975; Moreno, 2004), and it was speculated that this could stem from an increased demand on the immune system due to a high abundance of pathogens in tropical regions requiring a longer period for moulting and leading to an overlap with breeding (Moreno, 2004). Why, however, did breeding not last longer into the dry season, when seed abundance was still high? One possibility is that birds time their breeding so that food abundance is highest when offspring becomes independent so as to facilitate post-breeding activities such as moult (Young, 1994). However, seed abundance during our study was still high several months after breeding had finished and it seems unlikely that it would have restricted timing of breeding. Russel et al. (2004) noted that the availability of space might be limiting for young tropical birds due to generally high population densities and that this might lead to extended parental care and to young birds staying within their parents territories for a longer period. If this was so, high food abundance might be more important during these times than during chick feeding. However, we did not find Rock Firefinches (*Lagonosticta sanguinodorsalis*) to be territorial and believe it to be unlikely in the other species investigated. Abundance of grass seeds therefore seems unlikely to explain the timing of breeding in the Estrildid finches we investigated. Grant & Grant (1980) and Schluter (1984) noted that rather than the availability of seeds it is the availability of invertebrates that determined the timing of breeding in some otherwise mainly granovorous finches, as they rely on a diet high in protein to raise their chicks.

Breeding might thus be timed so that insect abundance is still high when chicks have to be fed but seed abundance is high by the time young birds fledge. However, while Payne (1980) found Red-billed Firefinches (*Lagonosticta senegala*) to supplement their diet with insects when feeding chicks, at least 90% of the crop content of chicks consisted of seeds, and he concluded that seasonal changes in insect abundance should have little influence on the annual cycle of this species. We cannot rule out that insect abundance influences timing of breeding in the Estrildid finches we investigated, however, we also found the crops of Rock Firefinch chicks to be filled with seed only, and we never observed adult Rock Firefinches to catch insects.

Another factor we found that could also be of importance in determining the timing of breeding is the availability of water. Rock Firefinches had to move long distances between their breeding habitat and water sources during the dry season, and this might conflict with the need of nest attendance causing breeding to cease when water sources dry out in their breeding habitat.

The importance of predation and competition in shaping the feeding behaviour of tropical granivores

If adult birds are subject to a high predation risk, they should be expected to behaviourally respond in several parameters of their feeding behaviour to differences in predation risk. We did not find strong evidence that birds responded in their feeding behaviour to changes in predation risk, although most species feeding in small groups preferred patches next to cover, while those usually feeding in large groups readily fed further from cover. This shows that they do perceive a difference in predation risk with respect to different distances from cover as also found in several temperate granivores (Lima, 1990; Lima, 1993). However, neither intake rate nor timing of feeding varied with distance from cover and therefore predation risk might not be as important in tropical granivores as it is in temperate ones. Intake rate increased with group size but rather than this reflecting risk dilution (Hamilton, 1971; Calvert et al., 1979; Duncan & Vigne, 1979) or shared vigilance (Caraco, 1979; Barnard, 1980; Bertram, 1980) we believe it to be a consequence of scramble competition (Elgar, 1989; Roberts, 1995; Beauchamp, 2003) because intake rate did not increase faster with group size next to cover as compared to away from cover. This would be expected if this effect was an outcome of risk dilution (Bohlin & Johnsson, 2004).

While we found no evidence for a marked seasonal variation in the risk of starvation, this does not rule out that competition is of importance in shaping foraging behaviour. If populations constantly stay close to carrying capacity they may constantly compete for food despite low mortality (Dobzhansky, 1950). However, results were ambiguous such that more detailed studies are needed to confirm our assumptions.

Microhabitat choice and coexistence

We expected bird species to differ in their behavioural responses (intake rate and timing of feeding) to predation risk leading to differences in microhabitat choice, which might then facilitate coexistence of similar species feeding on the same food resources. Species did not show marked responses in intake rate or timing of feeding to distance from cover, and accordingly most species were observed to feed close to cover when feeding on seeds from the ground with no significant differences between them. Schluter (1988) also found that granivorous finch species in Kenya did not partition resources on the basis of distance to cover and concluded that rather than promoting habitat segregation, predation risk confines the space in which species compete for food. The only difference found between species in this study was that Bronze Mannikins (*Lonchura cucullatus*) fed further from cover and also formed larger groups and that Rock Firefinches fed at places with more vegetation cover than other species, which is probably related to them having a longer bill and being able to extract seeds from vegetation, litter and sand more efficiently than other species. Unlike several studies on temperate passerines (Suhonen et al., 1993; Krams, 1996; Carrascal & Alonso, 2006) we also did not find microhabitat choice to depend on a species' dominance. Differences in microhabitat choice were thus probably linked to morphological differences. The differences in flocking behaviour we detected were probably not a consequence of predation risk: flocking behaviour in Bronze Mannikins probably results from colonial breeding and enhanced food detection (Degroot, 1980). Overall, it seems unlikely that the evolution of different anti-predator behaviour in the species we investigated would have led to differences in microhabitat choice and thus food partitioning. While some inter-specific differences existed, it remains unclear if these are an outcome of competition for resources acting on bird populations or of other factors.

Some species were highly specialised to feed on grass seeds mainly from the ground, while other species were more flexible. Rock Firefinches, Red-billed Firefinches and Red-cheeked Cordon Bleus (*Uraeginthus bengalus*) mainly fed on seeds from the ground, while Bronze Mannikins and Lavender Waxbills (*Estrilda caerulescens*) were observed to additionally utilise seeds from the grass ear. This might give them some flexibility such that they can already utilise fresh seeds from the ear, when little food remains on the ground and switch to seeds on the ground once seed-fall is complete. It remains interesting to investigate if these two species have traded off their efficiency in locating and handling grass seeds on the ground. Lavender Waxbills also utilised alternative food resources such as insects, pollen and figs to a great extent, again giving them more flexibility in their food requirements and they might be a truly generalist species. However, while grass seeds are abundant in savannah habitat, pollen and figs might be more abundant in gallery forest, and Lavender Waxbills might thus be expected to show habitat switching between seasons depending on what resources are most abundant. Sporadic observations indeed confirmed that they are more abundant in the gallery forest during the wet season and in savannah habitat during the dry season. It would be interesting therefore to investigate their habitat preferences and movement behaviour between seasons in more detail and compare it to species that are more specialised on grass seeds from the ground like Rock Firefinches.

It might also be expected that species feeding in larger groups might move more extensively than those usually occurring in small groups like Rock Firefinches and Red-cheeked Cordon Bleus, as birds in larger groups probably rely on richer food patches if all individuals are to gain sufficient food at the same patch. Again this might lead to more extensive movements during times when food becomes scarce, while Rock Firefinches for example can stay within a smaller area, that they know well. Lavender Waxbills and Bronze Mannikins might thus be “cream skimmers” taking resources from where they are most abundant, resulting in larger movements, and this also poses interesting questions for future research.

The disappearance of seeds from the grass ear during the late dry season resulted in Bronze Mannikins also feeding on seeds from the ground and this might lead to increased competition. However, as Bronze Mannikins fed further from cover this might be avoided. We did not find strong evidence that bird species diverged in their microhabitat choice during the late dry season as would be expected if microhabitat segregation acts so as to decrease inter-specific competition as found by Smith (1978) and Feinsinger (1985).

However, our results are based on small sample sizes for all species apart from Rock Firefinches and future studies concentrating on a greater variety of species would be useful.

A case study: foraging, habitat choice, reproduction and population trends in the Rock Firefinch

Rock Firefinches, which were recently discovered by Payne (1998), are probably endemic to central Nigeria and are of potential conservation concern due to rapid loss of habitat in a country such as Nigeria, where the human population is growing rapidly. Our study helps to shed light on a few basic issues like the habitat requirements, movement and breeding behaviour of the Rock Firefinch, which, in the absence of much previous knowledge about this species, provides valuable information for their conservation.

Rock Firefinches were found to show high site fidelity in contrast to many other tropical granivorous bird species (Davies, 1984; Dean, 1997). This might be enabled by the Rock Firefinches’ specialisation on grass seeds from the ground, which are a relatively stable food resource compared to seeds from the grass ear. Rock Firefinches moved mainly singly or in pairs and might therefore not rely on food rich patches like birds moving in large flocks. By gaining familiarity with the area they might be able to find enough food resources even when seed abundance declines.

Rock Firefinches mainly selected inselberg habitat as earlier found by Wright and Jones (2005), and most nests were located between boulders within this habitat either on the ground or woven between grasses. However, during the dry season, when water sources within inselberg habitat had dried out, Rock Firefinches had to move to water sources in the gallery forest, and as a consequence they had to cross scrub savannah habitat, which was otherwise avoided. It is possible that they face increasing predation risk the longer these movements through open habitat have to be. This highlights the Rock Firefinches dependence on external water and emphasizes the importance of conserving inselberg habitat in proximity to water sources for the Rock Firefinches’ long-term survival.

Another important factor likely to limit breeding output of Rock Firefinches and maybe also shaping their life history traits seemed to be nest predation, which was relatively high. We found a nest survival rate during the egg stage of 0.89 ± 0.03 calculated after the

Mayfield analysis (Mayfield cited in Johnson, 1979). Nest failure was mainly due to predation probably mainly by lizards. Nest predation might therefore impact on Rock Firefinch eggs and small chicks but probably does not pose a threat on large chicks or adults. This therefore represents a situation where nest predation should compromise reproductive effort but does not compromise adult survival. This is a situation different from that highlighted by Bennett & Owens (2002) and Martin (2004), where high nest predation should result in high fecundity due to decreased adult survival. Instead birds should only invest so much in one nesting attempt that they are able to quickly re-nest should the first clutch fail. Male and female Rock Firefinches shared incubation according to a relatively fixed time schedule and it is possible that this increases re-nesting ability as the female might be able to store more resources and allocate them to the production of new eggs more quickly. However, with a clutch size of 3-4 eggs, Rock Firefinches have a fairly large clutch compared to the usual two eggs reported for most tropical bird species (Skutch, 1985). However, they fall well within the range of most Estrildid finches, in which most species lay clutches between 3-6 eggs (Fry et al., 2004). As this group consist of only tropical species it is surprising, that little consideration has been given to this family when discussing life history traits of tropical birds. This purely tropical family apparently does not match the tropical paradigm of small clutch size, and it would be interesting to discover the causes for this. However, high nest predation might have been of importance in shaping Rock Firefinches' life history traits in that it might have promoted a high re-nesting ability, which might be facilitated by both parents sharing nest attendance and the raising of chicks.

Avian life History Traits in Tropical Environments

During our study we found no indication that the feeding behaviour of Estrildid finches in central Nigeria showed any marked seasonal variation as found in temperate passerines, and we therefore believe that there is no marked seasonal change in the risk of starvation. This was despite seasonal changes in the abundance of grass seeds, which these species mainly fed on. Breeding also did not coincide with highest seed abundance. It seems unlikely therefore, that seed abundance plays a major role in determining the life history traits of these birds and other factors might be more important. Birds might feed on alternative resources during times of low seed abundance, such that they do not encounter food shortage. This seemed to be the case for Lavender Waxbills but remains unlikely to be true for the other Estrildid species under investigation. If however, some species feed on alternative resources during seed shortage and some species leave the area (as Northern Red Bishops (*Euplectes franciscanus*) probably did), competition for remaining seeds might be relaxed for those species still feeding on seeds during such times.

The lack of a seasonal change in starvation risk does not rule out the importance of competition for food. If there is no seasonal variation in the risk of starvation, populations may stay close to carrying capacity throughout the year, and food availability might limit breeding output while it does not impact on the condition of adult birds (Ashmole, 1963). Furthermore in temperate regions seasonal variation in starvation risk does not only result from changes in food abundance alone but is mainly due to increased and unpredictable energy expenditure during periods of low temperature and higher thermoregulatory demands. Even if food abundance stays high, starvation risk might still increase during winter due to the unpredictability of energy expenditure and an apparent trade-off between starvation and predation. High starvation risk results in increased predation risk, and it might only be because of this important trade-off that a marked seasonal change in feeding patterns occurs. Changes in food abundance alone without being accompanied by unpredictability and high predation risk might not cause marked changes in foraging behaviour. We did not find strong evidence for a seasonal change in starvation risk, or adult birds to be strongly influenced by food availability, and this could partly be the cause for the relatively higher survival rates found in these birds compared to temperate counterparts (McGregor et al., in press). However, we could not rule out that food availability is of importance in the tropical bird populations under investigation.

Another possibility is that population growth is limited by a factor other than food supply, and one such factor could be predation. However, we did not find birds to show marked responses in their feeding behaviour to changes in the risk of predation apart from some species preferring to feed in the safer places, and we did not witness a single predatory attack on passerines despite hundreds of hours of observations on feeding places. It seems unlikely therefore that predation on adult birds is a main environmental constraint. But why should this be so different from temperate regions? One possibility is the higher diversity and probably also density of passerines observed in Nigeria as compared to temperate regions, spreading the risk of predation over a much higher number of individuals. This implies however, that there is no proportional increase in the number of predators because their populations are limited by something other than food supply. This also assumes that predation risk depends on per capita mortality rate, where it seems more likely that it is perceived predation risk and predator density that drives anti-predation behaviour (see Lima, 1986; Gosler et al., 1995; Macleod et al., 2005b). Even if the majority of avian predators eat mainly lizards or large insects, even occasional depredation on small birds should maintain selection for anti-predation behaviour: an individual that does not pay attention to predation risk is likely to be very vulnerable in a population of prey where the rest are paying attention. All this remains speculative as we know little about the relative abundances of the different guilds in tropical regions and are unable to compare it to temperate systems. More studies investigating trophic interactions in the tropics are clearly needed to shed light on these important issues. Nevertheless it seems likely to us that our results from a tropical system demonstrate what we know from some temperate systems: that in the absence of starvation risk, then predation risk is negligible (e.g. Yasue et al., 2003; Quinn & Cresswell, 2004). Predation risk in tropical systems may therefore be relatively unimportant because there is little starvation risk.

If neither food density nor predation on adult birds limits population growth of passerines within our study system (which we could not prove beyond reasonable doubt), what other factor could be of importance? One indication comes from studying reproduction in the Rock Firefinch, where we found a high rate of nest predation and water availability to be of importance. While the availability of water might prevent Rock Firefinches from extending their breeding season into the late dry season and the occurrence of heavy rains prevent breeding during the peak rainy season, nest predation might limit breeding output during this relatively short time available for breeding. Nest predation has often been assumed to be an important factor in shaping avian life history traits in the tropics (Skutch, 1994; Roper, 2005), but some also doubted that nest predation rates in the tropics really are higher than in temperate regions (Martin, 1996). However, does nest predation necessarily have to be higher in the tropics to limit populations or influence life history traits? With the relative unimportance of starvation and predation risk of adult birds, population fluctuations might be less pronounced and nest predation might still be the factor keeping populations below carrying capacity even if the relative rates are no different from temperate systems. Accordingly if starvation risk and adult depredation is less important, the same rates of nest predation might become relatively more important in shaping life history traits.

However, if nest predation is the main factor limiting population growth and also shaping life history traits, we should find clutch size to be relatively low so as to enable higher re-nesting ability (Martin, 1996). However, Estrildid finches in general do not seem to have the typical clutch size of two eggs observed in other tropical passerines (Skutch, 1985). If food is not in limited supply and sexes spread reproductive effort between them, females might still be able to produce a new clutch relatively quickly, and only if food density interacts with nest predation would it markedly influence clutch size (Martin, 1996). Indeed, if as we have been arguing, starvation risk (and consequently predation risk) is very low, then high rates of feeding may be possible at little cost: re-nesting ability in the tropics may then be a completely different proposition in the sense that it is not as limiting as in temperate areas.

The often proposed correlation of high adult survival and decreased fecundity (Martin, 1995; Bennett & Owens, 2002; Martin, 2004) could not really be tested during this study. Rock Firefinches had relatively high survival rates compared to temperate counterparts (McGregor et al. in press) but their rate of fecundity remains largely unknown. Almost all radio-tracked Rock Firefinches were found to make at least one breeding attempt, and in those two individuals that could be tracked long enough to witness a second breeding attempt, it also occurred. However, we were unable to follow individuals long enough to assess their total breeding output or observe the extent of post-fledging care and thus are unable to go beyond speculations. All in all, apart from having relatively high survival rates Rock Firefinches might not be all that different in their life history traits from temperate birds, as they have a similar clutch size and also a relatively short breeding season. However, more studies on the breeding behaviour of the Estrildid finches are needed to disentangle the relative importance of environmental constraints on their life history traits.

Another factor that might be of relatively more importance in shaping avian life histories in the tropics, as pointed out by Moreno (2004), might be higher demands on the immune systems due to a higher density of pathogens and parasites than in temperate systems. This could lead to an extended period of moult, which than might also limit the time available for breeding, unless it widely overlapped with moult. All four Estrildid species under investigation showed a relatively long period of moult, but an extensive overlap with breeding could only be confirmed for Red-billed Firefinches. Studies investigating the extent and importance of parasite load and disease in tropical passerines promise to be an interesting area for future research.

Conclusions

We found little evidence for a seasonal variation in the risk of starvation in tropical granivorous bird species in savannah habitat in central Nigeria. Predation also seems to be of minor importance. Despite birds mainly choosing the safer places next to cover, intake rate did not vary with distance from cover and Rock Firefinches also did not change their daily feeding pattern or feeding length under the higher risk situation. It might be inferred from these behavioural patterns that high adult survival of these birds is probably a consequence of a lower risk of starvation due to reduced seasonality but also of decreased risk of predation on adult birds. The results fit into the general framework that there is a trade-off between starvation and predation risk, and in the absence of starvation risk, predation risk will be relatively unimportant.

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Appendix

Fig. 1. Aviary used during experiments in captivity.

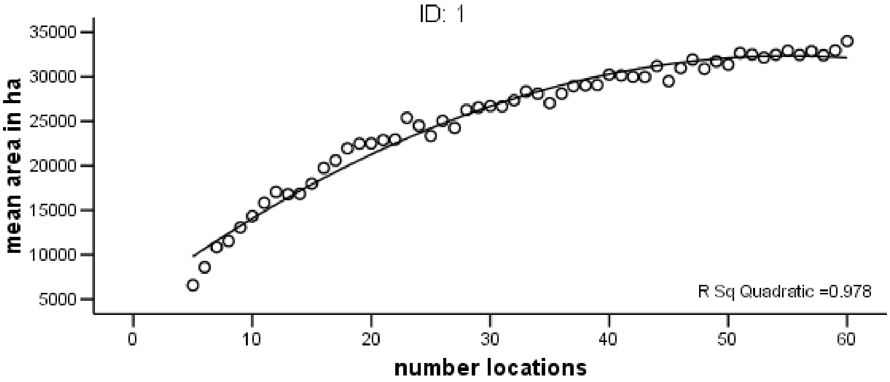
Fig. 2. The study area. Inselberg habitat can be seen in the foreground and bush savannah in the background.

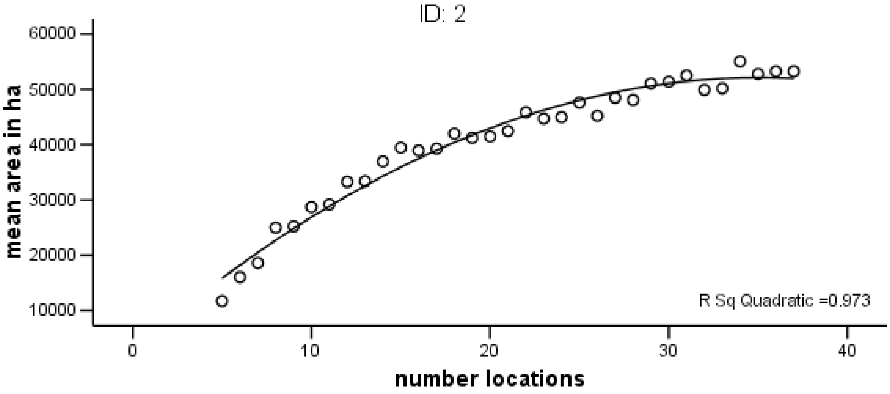
Fig. 3. Male Rock Firefinch.

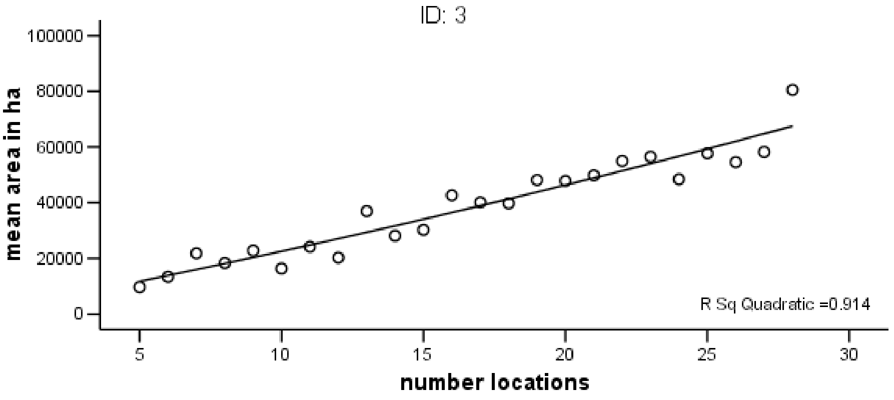
Fig. 4. Rock Firefinch chicks. The chick on the bottom left has its crop completely filled with seeds.

Fig. 5a-b. Nest sites of Rock Firefinches. For a close up of the nest from 5b) see Fig. 6.

Fig. 6. Nest of a Rock Firefinch.



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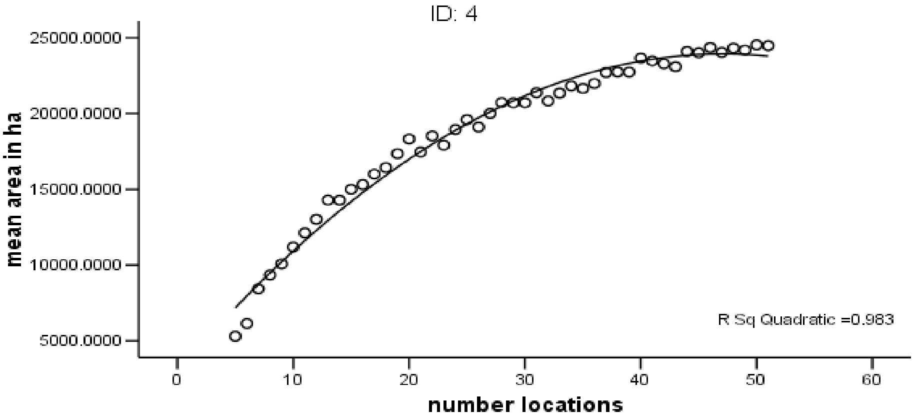
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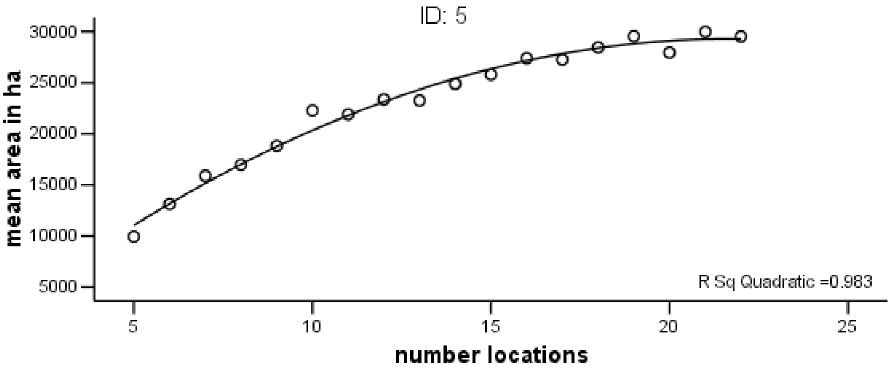
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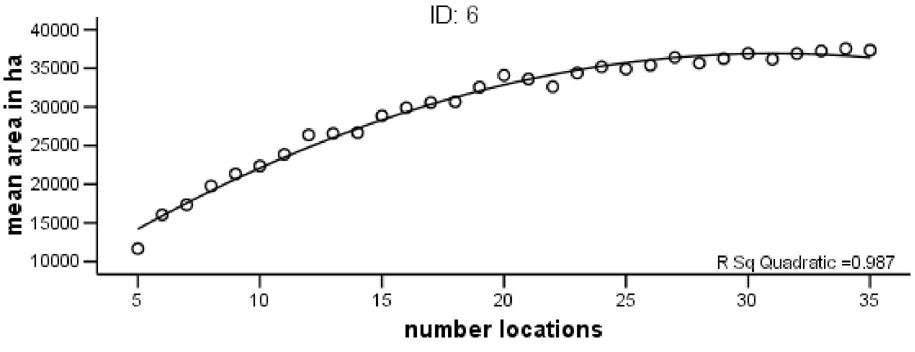
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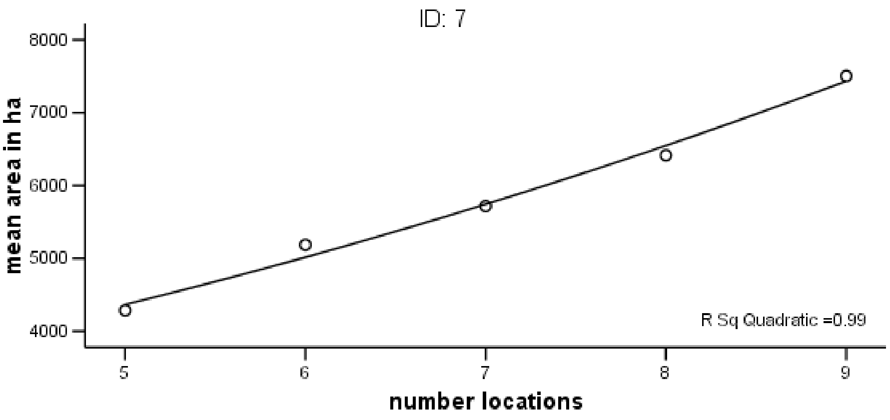
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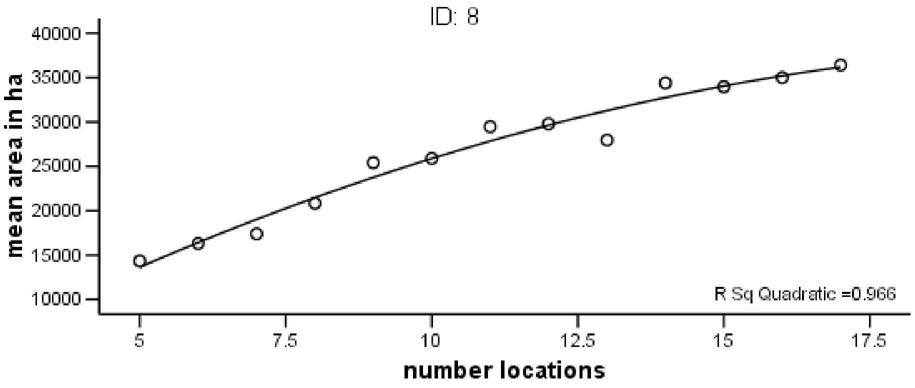
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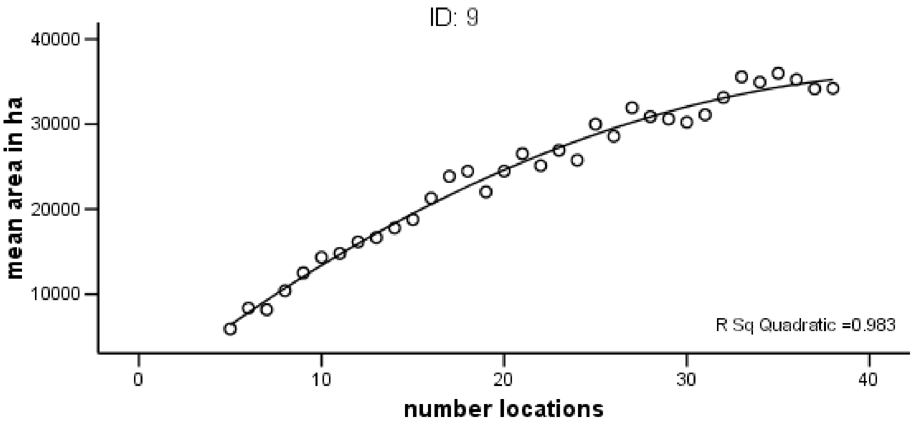
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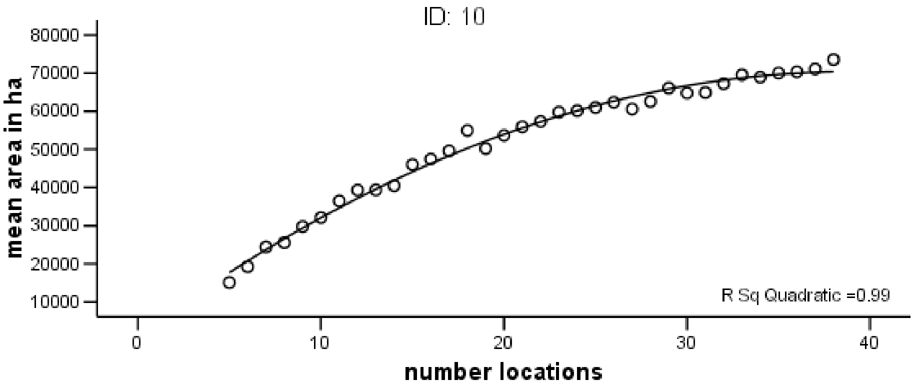
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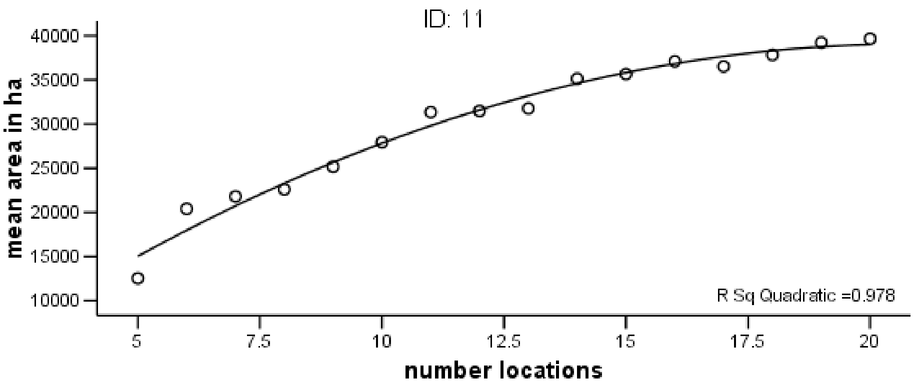
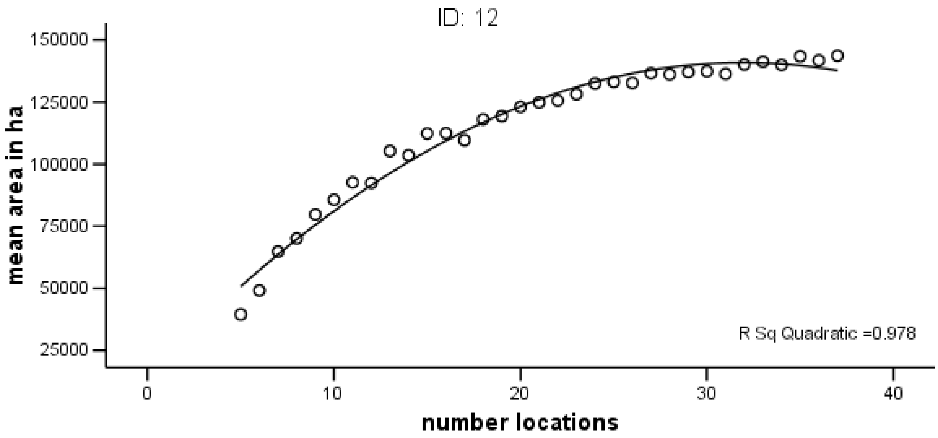
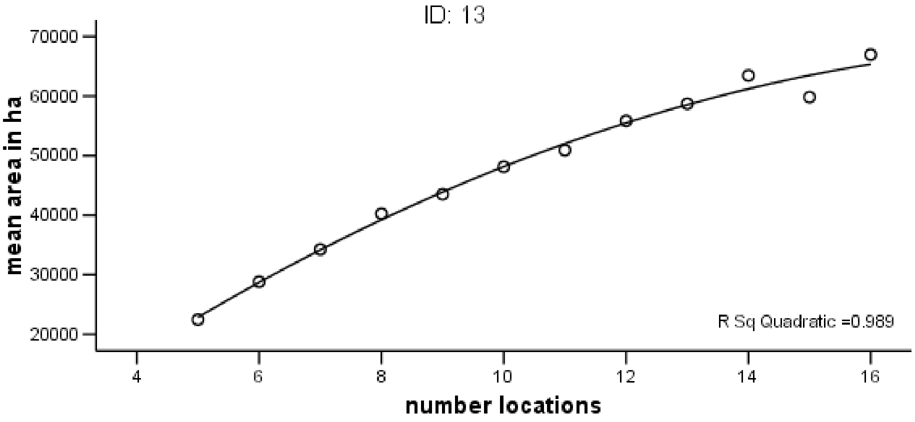
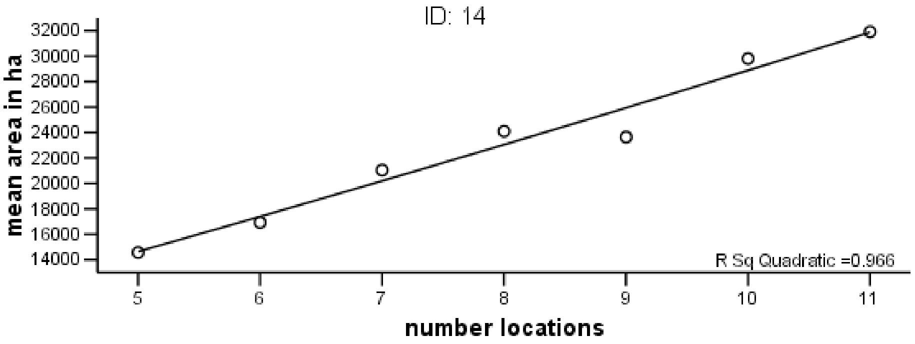
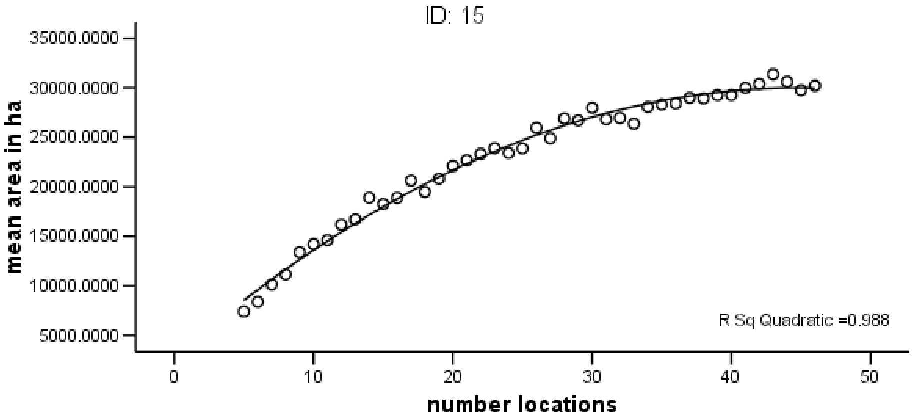
20000
10000
R Sq Quadratic =0.99
0
10
20
30
40
number locations


ID: 11
mean area in ha
40000
35000
30000
25000
20000
15000
10000
R Sq Quadratic =0.978
5
7.5
10
12.5
15
17.5
20
number locations


ID: 12
mean area in ha
150000
125000
100000
75000
50000
25000
R Sq Quadratic =0.978
0
10
20
30
40
number locations


ID: 13
mean area in ha
70000
60000
50000
40000
30000
20000
R Sq Quadratic =0.989
4
6
8
10
12
14
16
number locations


ID: 14
mean area in ha
32000
30000
28000
26000
24000
22000
20000
18000
16000
14000
R Sq Quadratic =0.966
5
6
7
8
9
10
11
number locations



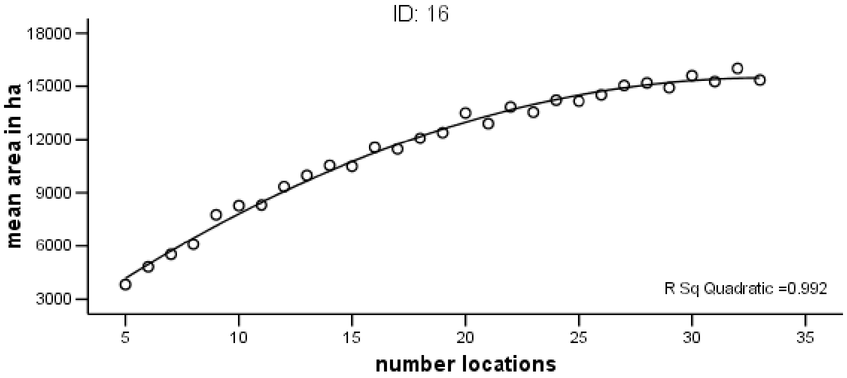


Fig. 7. Area of 100% MCP home ranges of al Rock Firefinches radio-tracked (ID 1-16) calculated following a bootstrap sample procedure plotted my number of locations.

Table 1 a-d. GLM results testing for seasonal variation in fat score in Rock Firefinches (a), Lavender Waxbills (b), Red-billed Firefinches (c) and Red-cheeked Cordon Bleus (d). ID was specified as a random factor. As the interaction of sex*season was never significant in the initial model, the model was rerun without the interaction term included. Values for sex, season and time of day are from the model without the interaction term included.

a.	**Fat score of Rock Firefinches**			
	B	df	F	p
sex		1, 141	12.13	<0.01
season		3, 198	10.85	<0.01
time of day	0.05	1, 240	27.48	<0.01
sex*season		3, 208	2.01	0.11

b.	**Fat score of Lavender Waxbills**			
	B	df	F	p
season		3, 301	3.33	<0.05
time of day	0.05	1, 304	36.56	<0.01

c.	**Fat score of Red-billed Firefinches**			
	B	df	F	p
sex		1, 179	0.16	0.69
season		3, 219	4.47	<0.05
time of day	0.06	1, 224	22.26	<0.01
sex*season		3, 210	0.38	0.77

d.	**Fat score of Red-cheeked Cordon Bleus**			
	B	df	F	p
sex		1, 126	2.15	0.15
season		3, 159	2.06	0.11
time of day		1, 156	1.85	0.18
sex*season		3, 151	1.79	0.15

Table 2 a-d. GLM results testing for seasonal variation in pectoral muscle in Rock Firefinches (a), Lavender Waxbills (b), Red-billed Firefinches (c) and Red-cheeked Cordon Bleus (d). ID was specified as a random factor. As the interaction of sex*season was never significant in the initial model, the model was rerun without the interaction term included. Values for sex, season and time of day are from the model without the interaction term included.

a.	**Pectoral muscle score of Rock Firefinches**			
	B	df	F	p
sex		1, 190	0.93	0.34
season		3, 242	3.22	<0.05
time of day	0.01	1, 203	10.06	<0.01
sex*season		3, 246	0.78	0.51

b.	**Pectoral muscle score of Lavender Waxbills**			
	B	df	F	p
season		3, 300	3.94	<0.01
time of day		1, 291	2.05	0.15

c.	**Pectoral muscle score of Red-billed Firefinches**			
	B	df	F	p
sex		1, 202	1.76	0.19
season		3, 226	12.90	<0.01
time of day		1, 198	2.13	0.15
sex*season		3, 223	0.26	0.85

d.	**Pectoral muscle score of Red-cheeked Cordon Bleus**			
	B	df	F	p
sex		1,120	0.06	0.80
season		3, 157	2.35	0.08
time of day		1, 134	0.07	0.79
sex*season		3, 150	0.85	0.47

Table 3 a-d. GLM results testing for seasonal variation in the amount of crop content in Rock Firefinches (a), Lavender Waxbills (b), Red-billed Firefinches (c) and Red-cheeked Cordon Bleus (d). ID was specified as a random factor. As the interaction of sex*season was never significant in the initial model, the model was rerun without the interaction term included. Values for sex, season and time of day are from the model without the interaction term included.

a.	**Crop score of Rock Firefinches**			
	B	df	F	p
sex		1,80.5	0.59	0.45
season		3, 145	2.37	0.07
time of day	0.05	1, 147	5.49	<0.05
sex*season		3,137	2.36	0.07

b.	**Crop score of Lavender Waxbills**			
	B	df	F	p
season		3, 171	11.88	<0.01
time of day	0.12	1, 181	26.48	<0.01

c.	**Crop score of Red-billed Firefinches**			
	B	df	F	p
sex		1, 67.9	0.1	<0.75
season		3, 68	3.18	<0.05
time of day	0.43	1, 3	6563.6	<0.01
sex*season		3, 68	1.41	0.25

d.	**Crop score of Red-cheeked Cordon Bleus**			
	B	df	F	p
sex		1,42.7	0.06	0.81
season		3, 41.9	1.29	0.29
time of day	0.12	1, 15.4	25.03	<0.01
sex*season		3, 50.5	0.79	0.50

Table 4. Summary of observed occasions when birds took over the nest from each other for incubation or when birds were observed to leave the nest and the nest was checked afterwards.

ID and sex of tracked bird	**Date**	**Time**	**Sex taking over**	**Comments**
3 F	03/09/05	7:42	M	M approaching, calling, F leaves nest, M enters
11 M	03/11/05	15:20	F	F approaching, calling, M leaves nest, F enters
11 M	05/11/05	08:32	F	F approaching, calling, M leaves nest, F enters
11 M	05/11/05	10:20	M	M approaching, when F already hopping around nest calling, F then flying off when M enters nest
11 M	07/11/05	13:58	F	F approaching, calling, M leaves nest, F entered
11 M	08/11/05	08:53	F	F approached calling, M leaves nest
11 M	10/11/05	09:35	F	M leaves nest, F flushed from nest afterwards (nest checked)
11 M	10/11/05	15:09	F	F approaching, calling, M leaves, F enters
11 M	11/11/05	12:55	M	M approaching, calling, F leaves, M enters
11 M	11/11/05	16:32	none	M leaves nest, no other bird around, nest without bird afterwards (nest checked)
12 F	11/11/05	9:00	F	F approaches calling, M leaves, F enters
13 F	12/11/05	6:28	M	M approaches calling, F leaves nest
13 F	15/11/05	06:14	M	M approaching, F leaves nest, M enters