



Diurnal foraging routines in a tropical bird, the rock finch *Lagonosticta sanguinodorsalis*: how important is predation risk?

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An animal's foraging decisions are the outcome of the relative importance of the risk of starvation and predation. 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 show a unimodal foraging pattern with foraging concentrated at the end of the day under conditions of predictable food resources and high predation risk. 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 lib* and the risk of predation was varied by providing food either adjacent to, or 5 m away from cover. Rock firefinches showed a bimodal foraging pattern regardless of the risk of predation at which they fed. The results suggest that predation is relatively unimportant in shaping their daily feeding pattern despite mass gain during the day being similar to temperate birds. Foraging patterns closely follow diurnal temperature variation and this is suggested to be the main determinant of the observed bimodal pattern.

An animal's foraging decisions are an outcome of the relative importance of the risk of starvation and predation (Lima and Dill 1990, Brodin 2001, Lind and Cresswell 2005). In birds, individuals regulate their fat reserves, and so their body mass to minimise starvation or predation risk. But 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 1986, McNamara and Houston 1990, Houston and McNamara 1993, Witter and Cuthill 1993) and/or longer exposure to predators as birds must feed for longer to maintain higher reserves (Lima, 1987). Theoretically, therefore, increased starvation risk should lead to foraging early during the day and increased predation risk to foraging later in the day (Houston et al. 1993, McNamara et al. 1994). This "small bird in winter" paradigm has been developed theoretically to account for mass and foraging routine variation in temperate birds, where predation risk and starvation risk are known to be high, and there is much evidence to support it (Pravosudov et al. 1997, Brodin 2007).

In tropical birds starvation risk may be low because of higher temperatures and reduced seasonality (Rogers and Heath-Coss 2003), and perception of predation risk may be different because tropical birds on average have higher survival rates (Jullien and Clobert 2000, Peach et al. 2001, McGregor et al. 2007), and the range and density of predators may be higher (Thiollay 1999). This suggests that diurnal foraging patterns in small tropical birds may be different from temperate birds, but there have been few empirical studies (Strong and Sherry 2000, Taylor and Paul

2006). Other factors, such as temperature, that may influence availability of prey or the energetics of foraging, may then be more important in determining diurnal foraging patterns (Poulsen 1996, Lindsell 2001, Fernandez et al. 2002). In this paper we test experimentally whether variation in predation risk under conditions of predictable foraging, in a small tropical granivore, results in foraging patterns consistent with those expected from temperate bird species.

Although the exact pattern of diurnal foraging varies dependent on the absolute values and relative strengths of starvation and predation risk (Brodin 2007) some general patterns are predicted for temperate environments. Foraging or mass gain has been shown to occur late in the day under good or predictable foraging conditions (Olsson et al. 2000, Macleod et al. 2005a), becoming more bimodal as foraging conditions become more unpredictable, such as during the winter (Lees 1948, Aschoff 1966, Morton 1967), and finally becoming concentrated early in the day under very unpredictable conditions (Cresswell 1998, Macleod et al. 2005a). As predation risk increases, foraging and mass gain have also been shown to occur later in the day (van der Veen and Sivars 2000, Macleod et al. 2005b), or birds may compensate through minimising time exposed to foraging risk, or by varying their choice of foraging areas (Brodin 2001, Lind and Cresswell 2005). But, in general, assuming low starvation risk and some degree of predation risk operate in tropical areas, tropical birds should forage later in the day, becoming later as the perceived risk of predation increases.

In this study we explore the degree to which the diurnal foraging patterns that occur in a tropical granivorous finch, the rock firefinch *Lagonosticta sanguinodorsalis* are influenced by predation risk. Preliminary observations suggested that the finches had a bimodal foraging pattern with peaks in the morning and afternoon, and that the finches foraged close to cover into which they retreated in the presence of raptors. We kept finches in an aviary with *ad lib* food to remove starvation risk, and varied perceived predation risk by providing the only food either next to or 5 m away from cover. Theoretically, under predictable and good foraging conditions, foraging should occur mostly late in the day, and this should become more pronounced as predation risk increases. We also measured daily mass variation in wild rock firefinches to test the degree to which daily mass gain might affect mass-dependent predation risk.

Methods

Bird trapping and handling

Rock firefinches were caught in mist nets, aged, sexed and ringed within Amurum Forest reserve on the Jos Plateau in central Nigeria (9.87°N, 8.98°E) March-May 2005. We measured body weight to the nearest 0.1 g using a Pesola spring balance and wing length (Svensson 1992). Thirty-four individual males were caught and when birds were caught more than once, only their first weight measurement was used.

Experimental set-up

Ten male and female pairs of rock firefinches were placed in the aviary one to two d prior experiments started between 23 March – 12 May 2005 giving a sample size of ten males. Only males were fitted with a PIT-tag (Francis Scientific Instruments, UK) glued onto a plastic colour-ring around its leg (Macleod et al. 2005b), because only one PIT-tag can be detected by the antenna at a time and pairs feed mostly together. PIT-tags weighed less than 0.1 g and no adverse effects were noted. Food was presented within the antenna's detection distance (30 cm in diameter). This antenna was placed on the feeding table and attached to a data-logger, which took a reading every 1/16 of a s during daylight h. Birds were placed in pairs of males and females because in the field they were mainly observed to feed in pairs without aggression (pers. obs.). The tables were used entirely for feeding (from 56 h of video recording of experimental birds, unpublished data). Rock firefinches in Amurum were found to breed between Sept. and Nov. (Brandt and Cresswell 2008) so our manipulation did not interrupt breeding.

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. The aviary was located in a cleared area approximately 10m from the corner of a house, with bare areas on either side of the aviary extending at least 30m on either side of the long axis of the aviary. A bush was positioned in one end of the aviary to serve as cover. Food and water were provided *ad lib*. 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 the second this table was moved to a distance of 5 m from cover. The starting order of the two parts of the experiment was alternated for consecutive pairs. All birds were kept in the large aviary for a maximum of four days and then released in a healthy state at the place of capture with PIT-tags removed. Different individual birds were used in separate trials. No license was needed to carry out this work, as there is no formal legislation regarding the capture, treatment and experimentation on wild birds in Nigeria. We however, applied the same criteria to our experimental design as if the experiment had taken place in the UK.

Weather data

Weather data were collected by a Davis Vantage Pro2 weather station within the study area between 15 April – 11 May 2005. The period of gathering weather data does not entirely coincide with the time of the aviary experiment 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 (pers. obs.).

Data analyses

Daily feeding patterns of male rock firefinches were obtained from PIT-tag data. Data were analysed by pooling all readings per s 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 constructed a model including feeding time (number of seconds fed per hour) as the dependent variable, time of day and distance from cover as fixed factors and bird-ID as a random factor. Two further models were constructed including time of day squared, and time of day squared and time of day cubed, to test for non-linear effects of time of day on feeding time. We assessed the best model by comparing AIC values. We then tested for a difference in the interaction of distance from cover with time of day and time of day squared (this model was found to be the best – see below) in the best model to test if the function of feeding time with time of day differed between the two treatments. Analyses were carried out using generalised linear mixed models: procedure GLIMMIX in GLIM for SAS v.9 (SAS), with a Poisson distribution (feeding time was approximately Poisson distributed and the model accounted for over dispersion). To further analyse the shape of the daily feeding pattern we ran the curve estimation function in SPSS 11 (SPSS) 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).

We investigated daily mass changes from all wild male birds caught using a GLM with weight as dependent variable and hour of the day as a covariate, including wing length as a covariate to control for variation in body size and month as a 3 way factor (March, April, May) to control for any confounding seasonal effects.

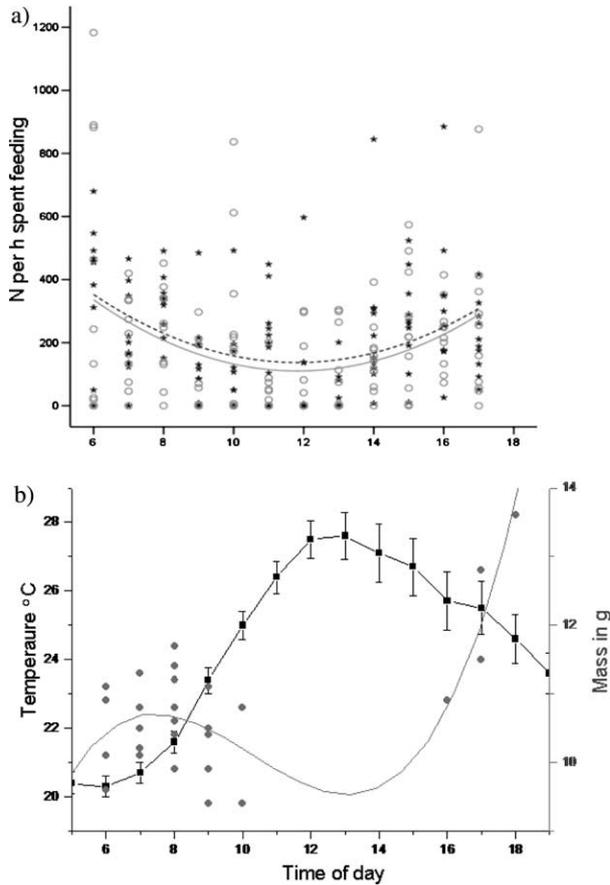


Figure 1. a-b. In: a) the number of seconds male rock firefinches spent feeding per h with food provided next to cover (represented by stars and broken black line) and 5 m away from cover (represented by open grey circles and grey solid line) with quadratic fitting lines. In: b) the daily temperature curve is shown as average temperatures for each hour (\pm SE) between 14 April – 12 May 2005 (black error bars denoting standard error), and the weight of male rock firefinches for each hour with a cubic fitting line (grey dots and grey line; $R^2=0.5$, $F=16.2$, $P<0.01$). Numbers on the x-axis represent the starting h for feeding times (i.e., 6 = 06:00–07:00).

Results

Distance to cover did not affect a strong bimodal foraging pattern (Fig. 1a,b). The best model included time of day ($F_{1,183}=16.7$, $P<0.001$) and time of day squared ($F_{1,183}=15.0$, $P<0.001$), showing significant peaks in feeding time in the early morning and the late afternoon, but no significant effect of distance from cover ($F_{1,183}=0.03$, $P=0.86$) while controlling for bird ID ($F_{9,183}=3.9$, $P<0.001$). The interaction between distance to cover and time of day ($F_{1,181}=0.2$, $P=0.66$), or the interaction between distance to cover and time of day² ($F_{1,181}=0.2$, $P=0.67$) were not significant when added to this model (AIC = 450.4). Mass of wild birds increased significantly during the day (13.3% increase in average mass of 10.8 ± 0.15 g, $n=34$, over 12 h, $F_{1,28}=9.1$, $P<0.01$, $B=0.12 \pm 0.039$, controlling for month ($F_{2,28}=3.4$, $P=0.047$) and wing length ($F_{1,28}=1.0$, $P=0.34$; Fig. 1b). Temperatures rose from 20°C at 06:00 to 27°C between 12:00–14:00 and

then declined to 24.5°C at 18:00 with an overnight minimum of about 20°C at 06:00 (Fig. 1b).

Discussion

Our data did not support the hypotheses that rock firefinches delayed feeding towards later in the day when presented with food away from cover. Theoretically if foraging is dependable (we provided ad libitum food), but subject to interruptions (i.e. from predators) then a bimodal foraging pattern can arise (McNamara and Houston 1994, McNamara et al. 1994). However, the bimodal foraging pattern we observed was not sensitive to predation risk even though wild rock firefinches showed a similar increase in diurnal mass to temperate species (e.g. Cresswell 1998, Macleod et al. 2005b, Polo et al. 2007), that should lead to mass-dependent predation costs (Witter and Cuthill 1993). Although overnight temperatures for rock firefinches at our study site were between 20 and 22°C this would possibly still result in use of significant energy reserves overnight when foraging is not possible. This is suggested by the lower critical temperature (T_{LC} , temperature below which an animal must increase its metabolism to offset heat loss) of 28°C in the smaller black-rumped waxbill *Estrilda troglodytes* (Lasiewski et al 1964 in MacMillen 1990) and of 33°C in the silverbill *Lonchura malabarica* (Willoughby 1969 in MacMillen 1990), both of which occur in the same habitat and feed on similar food resources. The costs and benefits for energy reserves in rock firefinches are perhaps not radically different to those of temperate bird species, and therefore the assumptions that underpin the “small bird in winter” paradigm (e.g. Brodin 2007), and therefore the predictions of it, apply. Our results then suggest that predation risk may not be a major factor responsible for the pattern of diurnal foraging in tropical rock firefinches.

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 perceived risk. This could for example be because the aviary was covered with a roof creating a degree of cover for both tables, or because distance from cover of the tables was not sufficiently different. However, despite not altering intake rate with distance from cover, rock firefinches were observed to feed relatively close to cover in the field and they preferred artificial feeding patches in the field next to cover over those 3 m away from cover (unpubl. data). They also responded to the appearance of a predator by flying into cover (pers. obs.) and in the aviary they also fled into the bush upon our approach.

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 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. Diurnal temperature variation may affect diurnal feeding patterns through the need for birds to conserve water (MacMillen 1990). In the zebra finch *Poephila guttata* respiratory water loss exceeds

metabolic water production so that birds rely on external water sources somewhere around 22°C (MacMillen 1990). Under field conditions some rock firefinches had to fly over 0.5 km to get water during the dry season (Brandt and Cresswell 2008), so gaining water is expensive. Even though physiological adaptations to heat and water shortage have been found in small bird species (Weathers 1997, Tieleman and Williams 1999), most 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.

Digestive constraints may also have given rise to the bimodal foraging 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 and Houston (1994) stated that digestive constraints may cause feeding to be spread more evenly through the day. Rock Firefinches during this study spent overall only about 10 % of their time feeding, which is relatively low and means that they were easily able to quickly meet their food requirements. The *ad lib* supply of food 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. 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.

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