

Nest predation versus resources in a Neotropical passerine: constraints of the food limitation hypothesis

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Food limitation is one explanation for differences in life-history traits, such as clutch size or nestling mortality, between tropical and temperate birds. Also predation has been considered one of the major factors shaping life-histories. We found mixed support for the food-limitation hypothesis when we experimentally manipulated food abundance and evaluated subsequent effects on breeding and behavioural parameters of the Blue-black Grassquit (*Volatinia jacarina*). Food-provisioned males increased territorial disputes and received more female visits, and a higher proportion of supplemented pairs produced more eggs and had faster growth rates in their broods compared to non-provisioned pairs. However, egg laying was delayed in the fed group. Unexpectedly, predation in the food-provisioned group was twice that of the control group. We presume that nest detection by predators increased due to higher nest attentiveness in food-provisioned nests. Food availability constitutes a proximate mechanism resulting in changes in behaviours and breeding parameters, but nest predation may be the prevailing selective pressure.



1. Introduction

Quality and quantity of food shape avian life-histories (Martin 1987) and have been considered critical elements limiting reproduction (Lack 1954). Studies have often suggested a positive correlation between food supply and fitness (Boutin 1990, Przybylo *et al.* 2001, Searcy *et al.* 2004). Food availability can influence laying date (Smith *et al.* 1980), clutch size (Soler & Soler 1996), offspring growth rate (Blancher & Robertson 1987), interval between breeding attempts (Arcese & Smith 1988), predation rate (Dewey & Kennedy 2001), nest attentiveness during incubation (Chal-

foun & Martin 2007) and occurrence of extra-pair young (Westneat 1994, Václav *et al.* 2003). Additionally, food resources may influence aggressive behaviour (Pierottu 1981), display rate (Tamm 1985), and migration patterns (Fransson 1998). In a few manipulation studies, however, increased food had no detectable effect on offspring growth rate (Lepczyk & Karasov 2000, Masmemin *et al.* 2002) or on clutch size (Yom-Tov 1974).

Food availability may also have a negative association with territory size (Adams 2001), although exceptions to this pattern have also been found (Arvidsson *et al.* 1997, Brown & Long 2006). Birds may respond to increased food by

modifying their display rate and style (Boutin 1990) because when food is abundant, more time may be allocated to other activities, such as singing and displaying (Searcy 1979). Reduction in territory size may also be associated with higher food availability due to an increased intrusion rate (Ewald & Rohwer 1982).

Variation in life-history traits of birds in general, and more specifically the contrast between tropical and temperate birds, has been debated but still remain largely unresolved (Martin 1996, Ricklefs 2000, Ferretti *et al.* 2005). The connection between food supply and reproduction in temperate birds has been reasonably established, and extra food generally leads to higher fitness (Svensson & Nilsson 1995). The food limitation hypothesis (Lack 1947, reviewed in Martin 1987) suggests that tropical birds are limited in food availability, and predicts that energetically restricted parents will delay clutch initiation, produce smaller clutches, and have decreased nestling growth and survival. Food has been frequently suggested as a limiting factor for tropical birds and could explain life-history contrasts with temperate species (Lack 1947, Klomp 1970, Murray 1985). A comparison between a tropical and a temperate guild of insectivorous birds showed that the foraging attack rate of tropical species is 4–6 times lower than that of temperate counterparts (Thiollay 1988), which suggests that food may be a constraint for reproductive output (e.g., clutch size) at least for insectivorous birds. Following the same line, a study on the American Redstart (*Setophaga ruticilla*) in both temperate and tropical regions demonstrated that, despite the fact that the species uses similar foraging techniques in both regions, individuals have lower foraging attack rates and higher foraging movements in the tropics, suggesting a lower abundance of prey availability in that region (Lovette & Holmes 1995). However, experiments using food supplementation that would allow comparisons to temperate birds are rare for tropical regions, precluding broad interpretations of latitudinal patterns concerning the link between food and reproduction.

Despite the great emphasis on the effects of food limitation, several studies suggest that nest predation may be a more important selective force than food limitation in determining life-history traits of birds (Martin 1995, Owens & Bennett

1995, reviewed in Martin 2004). This may be especially true for tropical birds: both early and more recent studies suggest that tropical birds lose 80% or more of their nests due to predation, in contrast to about 40–60% for temperate-zone species (reviewed in Stutchbury & Morton 2001). Skutch (1949) suggested that greater nest visitation by parents could lead to a higher rate of nest predation. Thus, there may well be an interaction between food abundance and nest predation, if higher resource abundance leads to more frequent feeding trips to the nest by parents. Alternatively, higher predation risk incurred by parents in areas with high density of predators may reduce nest-feeding rates even when resources are abundant (Eggers *et al.* 2008). Recent studies have confirmed this pattern, revealing that parents are flexible in their reproductive strategies, being able to modify their behaviour in relation to predation risk (Eggers *et al.* 2005; Fontaine & Martin 2006). Despite the many hypotheses, few empirical studies have documented food limitation and its effects upon breeding or provided detailed data for nest predation rates of tropical species (Stutchbury & Morton 2001).

To study the effects of food resources on multiple life-history traits of a Neotropical passerine, we manipulated food abundance, by provisioning seed, on breeding territories of the Blue-black Grassquit (*Volatinia jacarina*). We predicted that, similar to their temperate counterparts and in accordance with the food-limitation hypothesis, food-provisioned pairs would exhibit earlier laying dates, produce larger clutches, and have accelerated nestling growth and higher survival due to increased parental investment in feeding. Apart from the predictions of this hypothesis, we also expected that food provisioning would generate more intensive territorial defence, more successful attraction of females, decreased territory sizes, and higher nest predation because of changes in parental behaviour.

2. Material and methods

2.1. Study species and general field procedures

The Blue-black Grassquit is a small, primarily granivorous bird with an extensive distribution

throughout Latin America (Sick 1997). The species breeds in central Brazil during the rainy season, i.e., from mid-November to April, with peak nest initiation from February to March. Although socially monogamous (Almeida & Macedo 2001), the species has a very high rate of extra-pair fertilization (Carvalho *et al.* 2006). Both males and females build nests and care for offspring (Almeida & Macedo 2001), but our and Marcondes-Machado's (1988) observations suggest that females perform more direct parental care than do males. Parents feed nestlings with seeds (we have observed seeds through the transparent skin over the oesophagus and crop of nestlings several times), insects and other small invertebrates (Alderton 1963). Daily nest mortality for Blue-black Grassquits varies seasonally, but as for many tropical grassland species, nest mortality is very high; for example, a previous study found 95.3% overall nest failure (Carvalho *et al.* 2007).

We conducted the study within the Campus of the University of Brasilia (15°46' S, 47°52' W) in central Brazil from November 2005 to March 2006. The study area was a disturbed tropical savannah consisting mainly of grasses and shrubs with sparse trees. Human-induced changes in the vegetation of the area have resulted mostly from more frequent fires and increasing fragmentation due to the urbanization process, but there is no source of supplementary water or food for animals. On the other hand, Blue-black Grassquits are known to be found almost exclusively on modified areas composed of open habitats with high abundance of grasses.

Therefore, the study area should not have influenced differentially the reproduction of the population under study in comparison to other populations. Similarly, the nest-predator community in the study area is not expected to differ from more natural areas, because the main predators in Brazilian savanna, such as Anis and Jays, are commonly found in both types of habitat. We mist-netted and marked birds at least two months before the beginning of the experiment with unique combinations of coloured plastic rings, weighed them, and measured the length of their right tarsus and wing, tail and beak (0.05 mm precision). The blue-black plumage and the white underwing patch may represent secondary sexual traits important for intra-sexual competition and/or mate choice, and

were evaluated as likely cues of male quality. The percentage of breeding plumage cover for the entire body was estimated visually. To determine the size of the white underwing patch relative to the wing, we gently flattened the wing against an overlaid acetate sheet and traced the outline of patch and wing, and calculated areas of both using ImageJ software (U.S. National Institutes of Health).

2.2. Food-provisioning experiment

Of birds captured at the site, only 25 males established territories and successfully reproduced in the study area, and we randomly assigned these males to either the experimental food-provisioned group (fed) or to the control group (non-fed). All territories of monitored individuals were at least 30 m apart (nearest edge). For both groups we placed a feeder on the ground in the approximate centre of the territory. The feeder consisted of a 20-cm diameter dish covered by a roof to minimize conspicuousness to birds flying overhead. Food (200 g) consisted of equal parts of yellow, green, and red millet (*Panicum miliaceum*), canary seed (*Phalaris canariensis*), barnyard millet (*Echinochloa* sp.), and niger seed (*Guizotia abyssinica*), and was provided to the fed group three times weekly for the duration of breeding (see below). The non-fed group was treated similarly, although without the food. Supplementation started when males established their territories and lasted until the end of the breeding season, a period of roughly two to three months depending on the tenure of each breeding pair in its territory. In all cases the supplementary food was available for a minimum of one week before a clutch was initiated, but usually for at least 15 days. All feeders of the fed group were found by territory owners, and only the territorial pair was ever seen accessing the resources. We never observed other bird species or any other animals eating the seeds during observation periods described below.

To estimate natural food availability within territories, we determined the proportion of seeding grasses relative to total grasses at the end of the reproductive season (defined as the moment after the last nestling fledged). We counted all grass stalks and recorded those with seeds or vestiges of pro-

duction within five 1-m² quadrats, one in the centre of the territory and the other four at distances of one meter in the cardinal directions. For each territory we averaged the counts from the five quadrants as a measure of food availability.

2.3. Male behaviour and territoriality

We conducted behavioural observations from 06:00 to 11:00 hours (BRT) for the 25 males with territories in the area throughout the breeding season, of which 12 were in the fed group and 13 in the non-fed group. Time constraints did not allow the behaviour of females to be monitored simultaneously. We conducted an initial 20-min observation bout of all focal males before the manipulation, and two additional rounds of focal animal samplings of 20 min, two and three weeks after food provisioning started. We recorded display rate (leaps/min), territorial disputes (chases and physical contacts), and the number of other male and female intrusions in the territory. Additionally, we monitored nests to register the visitation rate of the territorial male to the nest throughout the whole nesting cycle (incubation and nestling feeding).

To demarcate territorial boundaries we tagged perches used by displaying males and places where we observed territorial disputes. Territories were measured before and two weeks after the food or empty feeder was in place for each breeding pair. Due to the small territory size of the Grassquits (13.0 to 72.5m², Almeida & Macedo 2001) and ease of observing displaying individuals, we are confident that the samples truly represent the territory size of the studied individuals. Territorial size was calculated by the minimum polygon convex (MPC) method, by joining the outermost points of the territory to form a polygon from which the area was calculated (Odum & Kuenzler 1955).

2.4. Reproduction and nestling growth

We found nests by searching the vegetation and using behavioural cues of adults, and these were monitored every 2–3 days. Laying date was defined as the day the first egg was laid. We weighed

chicks and measured their right tarsus on alternate days after hatching until they fledged. Nestlings fledged on average 11–12 days after hatching. To avoid premature fledging, we stopped measuring nestlings on the 9th day. Nests were considered successful if at least one chick fledged, and depredated if all eggs or nestlings disappeared (typical of avian predation) or if the nest was destroyed or disappeared (typical of mammalian predation).

2.5. Statistical analyses

All tests are two-tailed, and data are reported as means \pm SE. We tested all distributions for normality with Shapiro-Wilk W test, and used non-parametric tests when data were non-normally distributed. There were no significant differences in morphology between males assigned to the two treatment groups: Student's t test showed $t < 0.5$ and $p > 0.60$ for tarsus, tail, bill length, underwing patch size and proportion relative to wing, and Mann-Whitney U test had $U > 53.0$ and $p > 0.15$ for weight, wing length, and breeding plumage coverage. The amounts of seeding grass in the territories of fed and non-fed birds were similar (Student's t test: $t_{23} = 0.865$, $p = 0.396$). Thus, the majority of food variability in terms of seeds was due to experimental manipulation. We used a t test to compare chick growth rate (body weight and tarsus) on fed and non-fed territories. We calculated growth rate for each chick (g or mm/day) and then used the mean growth rate of each brood in the analyses. We used t tests also to compare nestling morphometry at fledging (i.e., 8–9 days) between the two groups.

We used the nest-survival module in MARK (White & Burnham 1999, Rotella 2004) to compare nest-survival models and to obtain estimates of daily survival rate (DSR) as a function of continuous, categorical and time-varying factors (Dinsmore *et al.* 2002). We evaluated the relationship between DSR and the potentially influencing factors based on a priori hypotheses, and used a hierarchical modelling procedure (Dinsmore & Dinsmore 2007). Following Dinsmore *et al.* (2002) we did not standardize individual covariates. We assessed the models using Akaike's information criterion for small sample sizes (AIC_c)

Table 1. Behavioural comparison of male Blue-black Grassquits between fed and non-fed treatment groups before and after food supplementation (Wilcoxon test).

| Variable | Fed | | | | Non-fed | | | |
|-------------------------------|---------------|--------------|-------|----------|--------------|--------------|-------|----------|
| | Before | After | Z | <i>p</i> | Before | After | Z | <i>p</i> |
| Territorial disputes | 0.83 ± 0.32 | 1.54 ± 0.42 | -1.97 | 0.05 | 0.92 ± 0.26 | 1.57 ± 0.31 | -1.75 | 0.08 |
| Male intrusions | 1.41 ± 0.51 | 1.41 ± 0.31 | -0.52 | 0.61 | 1.69 ± 0.41 | 1.50 ± 0.41 | -0.54 | 0.59 |
| Display rate (leaps/20min) | 39.41 ± 11.87 | 25.33 ± 8.00 | -0.89 | 0.37 | 30.92 ± 9.45 | 20.65 ± 7.28 | -0.94 | 0.35 |
| Female intrusion rate | 0.75 ± 0.18 | 1.30 ± 0.17 | -2.36 | 0.02 | 1.07 ± 0.31 | 1.07 ± 0.20 | -0.12 | 0.91 |

and sorted by AIC_c , the difference between the AIC_c value for a given model and the top model (Burnham & Anderson 2002). We identified the most appropriate time-varying factor by fitting models with constant, linear, and quadratic time trends. Subsequently, we investigated how the DSR varied with nest age using a covariate with the age of the nest on the first day of the nesting season. We predicted that nests would become more vulnerable as they aged, because parental activity increases during the nestling stage, generating possible cues for predators. Finally, we investigated the best model by searching for the food-supplementation treatment effect, and obtained estimates by model averaging when the best model carried less than 90% AIC_c weight (Burnham & Anderson 2002).

We compared the absolute territory sizes of fed and non-fed groups (after square root transformation) with *t* test, and used Wilcoxon matched-pairs signed-ranks test to assess possible changes in behavioural parameters and territory size before and after supplementation for fed and non-fed groups. We compared clutch size between the two groups using a one-tailed exact permutation test. Except for the permutation test, we performed all statistical analyses using SPSS 13.0 (SPSS 13.0 2004, Chicago, Illinois, USA).

3. Results

Significant behavioural changes were found only for the fed birds before and after supplementation (Table 1). Fed males increased the frequency of territorial disputes despite not suffering any increase in the rate of other male intrusions. After

food provisioning, they did not change their display rates but attracted a higher number of females. For the non-fed males, no differences were found for any behaviour exhibited before and after manipulation, including frequency of territorial disputes, display rate, female intrusion rate and intrusion rate of other males.

Before manipulation, there was no significant difference in the size of territories between fed and non-fed males ($t_{23} = 0.83$, $p = 0.41$). Territory size increased significantly after the manipulation, but only for non-fed males (Fig. 1). Fed birds maintained their territory size after the manipulation, but there was no significant difference in the area

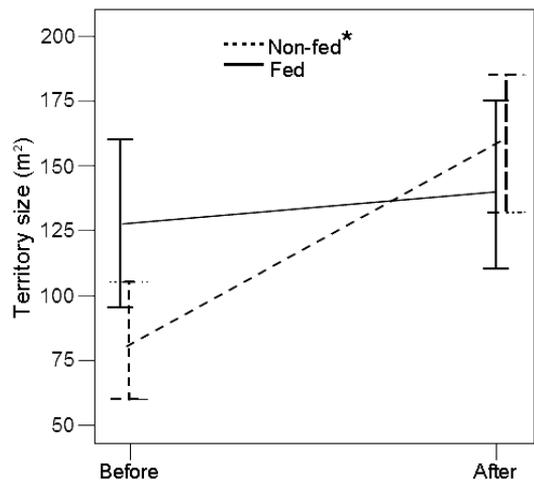


Fig. 1. Territory size (m^2) for the fed and non-fed groups of the Blue-black Grassquit before and after food supplementation. After food provisioning, non-fed males had a significant increase in territory size ($Z = -3.0$, $p = 0.003$) while no significant changes in size occurred for fed males ($Z = -0.6$, $P = 0.58$).

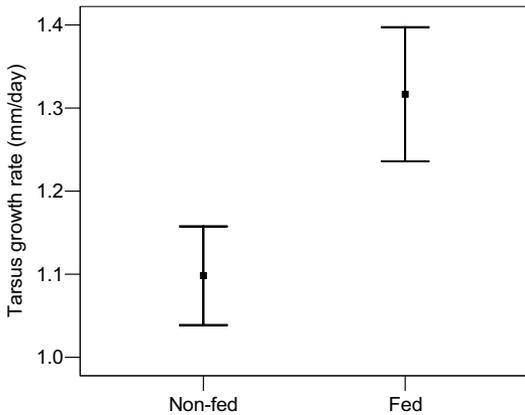


Fig. 2. Comparison of tarsus growth rate (mm/day) of the nestlings of Blue-black Grassquit between the fed and non-fed groups.

of fed and non-fed territories ($t_{23} = 0.4, p = 0.70$). Although there were modifications in territory boundaries, none of the territorial males left the territory after the manipulation.

Twenty-five nests were found, ten of which belonged to fed males and 15 to non-fed males, but only 24 nests were included in the analyses because one nest was not visited by the territorial male during the study. Individuals in the non-fed group initiated laying an average of four days earlier than did the fed group, but the fed group produced larger clutches (2.85 ± 0.14 eggs versus 2.40 ± 0.16 ; one-tailed exact permutation test, $p = 0.04$). In the non-fed group, four of the ten nests (40%) had three-egg clutches, while in the group of fed pairs six of seven (86%) had three-egg clutches. There was no significant difference in male nest visitation rate between groups (Mann-Whitney U test; $U = 76.0, n_1 = 12, n_2 = 13, p = 0.90$). Chicks from the fed group had significantly faster tarsus growth than had chicks from the non-fed group ($t_{14} = -2.2, p = 0.04$; Fig. 2), but treatment did not significantly affect body-mass growth rate ($t_{14} = -0.9, p = 0.38$). However, when chicks approached fledging (i.e., 8–9 days) there were no significant differences between the two groups in mass ($t_{12} = -0.6, p = 0.56$) or tarsi ($t_{12} = -0.5, p = 0.66$).

None of the nestlings died from starvation or any cause other than predation. Chicks of the non-fed group had a daily survival rate of 0.989 ± 0.007 , while chicks of the fed group had a lower

Table 2. Summary of model selection for daily survival rates of the nests of Blue-black Grassquits using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) with associated AIC_c , AIC weights (w_i), and the number of parameters of each model given by K .

| Model | K | AIC_c | AIC_c | w_i |
|-------------------------------|-----|---------|---------|-------|
| $S_{(treatment)}$ | 2 | 60.49 | 0.00 | 0.314 |
| $S_{(.)}^a$ | 1 | 61.45 | 0.96 | 0.193 |
| $S_{(nest\ age + treatment)}$ | 3 | 62.28 | 1.79 | 0.128 |
| $S_{(T + treatment)}$ | 3 | 62.35 | 1.85 | 0.123 |
| $S_{(.)}^b$ | 2 | 62.83 | 2.33 | 0.097 |
| $S_{(T)}$ | 2 | 63.24 | 2.75 | 0.079 |
| $S_{(nest\ age)}$ | 2 | 63.67 | 3.18 | 0.063 |
| $S_{(TT)}^c$ | 3 | 63.67 | 3.18 | 0.063 |

- a) Constant daily survival
b) Linear time trend
c) Quadratic time trend

survival probability with a daily survival rate of 0.957 ± 0.018 . Evidence for treatment effects on nest survival was found (Table 2). The evidence ratio indicated that the model in Table 2 was 1.62 times more likely to be the best one than the constant model, although the parameter estimate for the treatment effect based on model averaging suggested no statistical difference ($\beta = -0.768, 95\% \text{ CI} = -1.981 \text{ to } 0.446$). The models that included nest age had weak support (Table 2), suggesting that nest vulnerability was not enhanced with age.

4. Discussion

Our results do not generally conform to the predictions of the food-limitation hypothesis, especially as they apply to tropical passerines. However, a conservative evaluation of the results suggests that fed pairs produced larger clutches with faster-growing chicks, and that males of this group exhibited more agonistic behaviour, indicating that food does generate some constraints and modify behaviour. Notwithstanding these results, we suggest that nest predation may have more important implications for the evolution of life-history traits of tropical birds than does food.

Some expectations concerning behavioural responses associated with food abundance were met. For example, Blue-black Grassquit males supplemented with food intensified territory defence

through physical disputes, although there was no increase in intrusion rate of other males. Aggression may have occurred as a consequence of increased food availability, because time saved during foraging could be allocated to territory defence. Our results are consistent with other studies that associate male aggression with territory resource level (Pierotti 1981, Arvidsson *et al.* 1997). Food supplementation also generated increased visitation by females that may have been seeking extra-pair copulations from males exhibiting higher rates of aggression (passive choice) or searching for direct access to the food.

There was no reduction of territory size in the fed group, which was surprising given the inverse relation found in several supplementation studies (Boutin 1990, Adams 2001). In the experiment, non-fed territories almost doubled in size between the two field assessments. In some cases, an increase in food abundance can attract a greater number of intruders (Ewald & Rohwer 1982), generating a defensive cost to territory owners. Although the rate of defence by food-provisioned males increased, the pressure of male intrusion was probably not the main factor restricting the increase of territory size, as there was no difference in intrusion rate of neighbouring males after supplementation. The natural pattern for these birds may thus be to increase territory size through the breeding season due to declining seed resources, as verified for the non-fed group. Thus, food provisioning may have reduced the benefits of enlarging territories.

The food-limitation hypothesis has been supported in several studies with temperate birds, wherein supplemented birds have exhibited earlier clutch initiation than non-supplemented individuals (Yom-Tov 1974, Blancher & Robertson 1987; but see Hoi-Leitner *et al.* 1999). Clutch initiation ranged from 1.8 days earlier in Jackdaws (*Corvus monedula*; Soler & Soler 1996) to 25 days earlier in Song Sparrows (*Melospiza melodia*; Smith *et al.* 1980). In a stark contrast to the food-limitation hypothesis, however, we found that clutch initiation in the fed Blue-black Grassquits presented a delay of four days when compared to the non-fed group. One explanation for this incongruity is that the delay may be related to the larger investment in clutches made by females in the supplemented group. In our study area, clutch size varied from

one to three eggs, but pairs from the fed group had two times higher frequency of three-egg clutches than had pairs from the non-fed group. Similar increases in clutch size have been observed in food-provisioning studies with other species (Blancher & Robertson 1987, Arcese & Smith 1988) and may represent an alternative reproductive strategy to early clutch initiation.

A typical expectation is that increased food abundance should intensify parental feeding of chicks for at least two reasons: (1) there is more food available to invest directly in the nestlings; and/or (2) parents themselves have better access to food, which improves their condition and decreases the time they have to spend foraging for self-maintenance, leading to more intensive parental care. In the case of the Blue-black Grassquit, because chicks are fed a mixed diet composed of seeds and insects, we would expect greater food abundance to enhance parental investment directly and indirectly. Intensified parental feeding can increase chick growth rate and/or final size at fledging, as verified for supplemented territories in some cases (Lozano & Lemon 1995). However, others have not found such a direct link between food and chick parameters (Yom-Tov 1974, Lepczyk & Karasov 2000). In our study the supplemental food for the Blue-black Grassquits did not lead to increased male visitation to the nest. It is reasonable to assume that chicks have a fixed requirement for food and hence do not benefit from additional food over a particular threshold. Alternatively, increased food supply could make it unnecessary that both parents work as intensely to feed the nestlings, and may have shifted the burden of feeding toward the female. Although males did not increase nest visitation, the growth rate of chicks was higher in the fed group, but the size of fledgings did not differ between the fed and non-fed groups. The difference in nestling growth rate may be due to increased maternal care, which was not directly evaluated in our study.

Our study showed that the survival probability in the fed group was half of that found for the non-fed group when comparing survival for the whole nestling period. Skutch (1949) hypothesized that nest predation increases with parental activity, peaking during the nestling period when parents most frequently visit the nest (Simons & Martin 1990, Eberhard & Ewald 1994, Martin *et al.* 2000,

Muchai & du Plessis 2005). Despite that, and the fact that we indeed observed an effect of the treatment on nestlings' condition, we did not find any effect of nest age on predation probability. There is little consensus about the effects of high food availability on nest predation: some studies have found a reduction in nest predation due to increased antipredatory behaviour (Soler & Soler 1996, Rastogi *et al.* 2006), whereas others have reported either no or an increased effect of supplementation on rate of nest predation (Ewald & Rohwer 1982, Arcese & Smith 1988). Studies conducted on nest predation in the tropics indicate that predation, at least during incubation, occurs during daytime hours, implying the role of snakes and predatory birds (Robinson *et al.* 2005, Libsch 2008). In our study area, we observed predation by Guira Cuckoos (*Guira guira*), Smooth-billed Anis (*Crotophaga ani*) and Curl-crested Jays (*Cyanocorax cristatellus*). Parental visitations and the nestlings' begging calls may be important cues used by such daytime predators, but different cues should be relevant in areas with nocturnal predators. Further experimental studies, using resource manipulation and camera monitoring of nests to detect and identify predators would expand the meagre information available concerning the effects of food resources and predators upon the evolution of life-history traits of tropical birds.

A possible source of error of this and many other studies that have evaluated the influence of food availability on nest survival is that juvenile mortality was not accounted for. Recent studies have revealed that the juvenile survival of the Neotropical Spotted Antbird (*Hylophylax naevioides*) is lower in larger than in smaller broods (Styrsky *et al.* 2005) due to differences in extended parental investment (reviewed in Russell 2000). Disparities in juvenile survival could be an important source of variation influencing the evolution of life-history traits in the tropics.

In conclusion, we showed mixed support for a relationship between food availability and several behavioural and reproduction measures using an experimental manipulation of food abundance. Food supplementation resulted in an increase in aggressive behaviour by territory owners and greater intrusion of females, but apparently did not alter territory size. Compared to non-fed females, females in supplemented territories did not ad-

vance their laying date, but laid larger clutches more often, and chicks of fed pairs grew faster. Chicks of the non-fed group did not die from starvation, and they fledged in the same condition as chicks from the fed group, leading us to conclude that Blue-black Grassquits under natural conditions in this tropical region are not food-limited. On the other hand, chicks from the supplemented group were more likely to die from predation, suggesting an association between parental activity and the likelihood of predators to detect the nest. The importance of food limitation in explaining differences in life-history traits between temperate and tropical birds may be negligible relative to nest predation. Our results suggest that the action of predators as a selective pressure is of greater importance in shaping life-history traits of tropical birds than has usually been considered in the literature.

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Pesäsaalistus ja resurssit neotrooppisella sirkkusella: ravinnon rajoittavuushypoteesin rajoituksia

Ravinnon rajoittavuus on yksi selitys elinkierto-
muuttujien, kuten pesyekoon ja pesäpoikaskuol-
leisuuden, eroihin trooppisilla ja temperaattisilla
linnuilla. Myös saalistusta pidetään yhtenä tär-
keimmistä elinkiertomuuttujia määräävistä teki-
jöstä. Löysimme varsin vaihtelevaa tukea ravin-
non rajoittavuushypoteesille, kun kokeellisesti
säätelimme ravinnon määrää ja tutkimme sen vai-
kutusta pesintä- ja käyttäytymisparametreihin sa-

mettisirkkusella (*Volatinia jacarina*). Verrattuna lisäravintoa saamattomiin koiraisiin, lisäravintoa saaneet koiraat lisäsivät reviiriikistoihin osallistumistaan ja useammat naaraat vierailivat niiden reiviirillä. Lisäravintoa saaneet parit taas tuottivat enemmän munia ja nopeampikasvuisia poikasia kuin lisäravintoa saamattomat parit. Muninnan aloitus kuitenkin viivästyti ruokituilla pareilla.

Yllättäen lisäruokitut linnut joutuivat kaksi kertaa lisäravintoa saamattomia useammin saalis-tetuiksi. Oletamme, että petojen kyky havaita pesä kasvoi lisäravintoa saaneilla pareilla, koska ne viettivät enemmän aikaa pesän tuntumassa. Ravinnon saatavuus on mekanismi, joka johtaa käyttäytymisen ja pesimäparametrien muutoksiin, mutta pesäsaalistus luultavasti on vallitseva evolutiivinen valintatekijä.

References

- Adams, E.S. 2001: Approaches to the study of territory size and shape. — *Annual Review of Ecology and Systematics* 32: 277–303.
- Alderton, C.C. 1963: The breeding behavior of the blue-black grassquit. — *Condor* 65: 154–162.
- Almeida, J.B. & Macedo, R.H. 2001: Lek-like mating system of the monogamous blue-black grassquit. — *Auk* 118: 404–411.
- Arceese, P. & Smith, J.N.M. 1988: Effects of population density and supplemental food on reproduction in song sparrows. — *Journal of Animal Ecology* 57: 119–136.
- Arvidsson, B., Askenmo, C. & Neergaard, R. 1997: Food supply for settling male rock pipits affects territory size. — *Animal Behaviour* 54: 67–72.
- Blancher, P.J. & Robertson, R.J. 1987: Effect of food supply on the breeding biology of western kingbirds. — *Ecology* 68: 723–732.
- Boutin, S. 1990: Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. — *Canadian Journal of Zoology* 68: 203–220.
- Brown, D.R. & Long, J.A. 2006: Experimental fruit removal does not affect territory structure of wintering hermit thrushes. — *Journal of Field Ornithology* 77: 404–408.
- Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. — Springer-Verlag, New York.
- Carvalho, C.B., Macedo, R.H. & Graves, J. 2006: Breeding strategies of a socially monogamous neotropical passerine: extra-pair fertilizations, behavior and morphology. — *Condor* 108: 579–590.
- Carvalho, C.B., Macedo, R.H. & Graves, J. 2007: Reproduction of blue-black grassquits in central Brazil. — *Brazilian Journal of Biology* 67: 275–281.
- Chalfoun, A.D. & Martin, T.E. 2007: Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. — *Animal Behaviour* 73: 579–585.
- Dewey, S.R. & Kennedy, P.L. 2001: Effects of supplemental food on parental care strategies and juvenile survival of northern goshawks. — *Auk* 118: 352–365.
- Dinsmore, S.J. & Dinsmore, J.J. 2007: Modeling avian nest survival in program MARK. — *Studies in Avian Biology* 34: 73–83.
- Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002: Advanced techniques for modeling avian nest survival. — *Ecology* 83: 3476–3488.
- Eberhard, J.R. & Ewald, P.W. 1994: Food availability, intrusion pressure and territory size: an experimental study of Anna's hummingbirds (*Calypte anna*). — *Behavioral Ecology and Sociobiology* 34: 11–18.
- Eggers, S., Griesser, M. & Ekman, J. 2005: Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*). — *Behavioral Ecology* 16: 309–315.
- Eggers, S., Griesser, M. & Ekman, J. 2008: Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. — *Behavioral Ecology* 19: 1056–1062.
- Ewald, P.W. & Rohwer, S. 1982: Effects of supplemental feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds *Agelaius phoeniceus*. — *Journal of Animal Ecology* 51: 429–450.
- Ferretti, V., Llambías, P.E. & Martin, T.E. 2005: Life-history variation of a neotropical thrush challenges food limitation theory. — *Proceedings of the Royal Society of London, B* 272: 769–773.
- Fontaine, J. J. & Martin, T. E. 2008: Parent birds assess nest predation risk and adjust their reproductive strategies. — *Ecology Letters* 9: 428–434.
- Fransson, T. 1998: A feeding experiment on migratory fuelling in whitethroats, *Sylvia communis*. — *Animal Behaviour* 55: 153–162.
- Hoi-Leitner, M., Hoi, H., Romero-Pujante, M. & Valera, F. 1999: Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the 'constrained female hypothesis'. — *Proceedings of the Royal Society of London Ser. B* 266: 1021–1026.
- Klomp, H. 1970: The determination of clutch-size in birds – a review. — *Ardea* 58: 1–124.
- Lack, D. 1947: The significance of clutch-size. — *Ibis* 89: 302–352.
- Lack, D. 1954: The natural regulation of animal numbers — Clarendon Press, Oxford.
- Lepczyk, C.A. & Karasov, W.H. 2000: Effect of ephemeral food restriction on growth of House Sparrows. — *Auk* 117: 164–174.
- Libsch, M.M., Batista, C., Buehler, D., Ochoa, I., Brawn, J. & Ricklefs, R.E. 2008: Nest predation in a Neotropi-

- cal forest occurs during daytime. — *Condor* 110: 166–170.
- Lovette, I.J. & Holmes, R.T. 1995: Foraging behavior of American redstarts in breeding and wintering habitats: implications for relative food availability. — *Condor* 97: 782–791.
- Lozano, G.A. & Lemon, R.E. 1995: Food abundance and parental care in yellow warblers (*Dendroica petechia*). — *Behavioral Ecology and Sociobiology* 37: 45–50.
- Marcondes-Machado, L.O. 1988. Comportamento reprodutivo de *Volatinia jacarina* (Linnaeus, 1766) em cativado (Passeres, Emberizidae). — *Revista Brasileira de Zoologia* 4: 319–330. (In Spanish)
- Martin, T.E. 1987: Food as a limit on breeding birds: a life-history perspective. — *Annual Review of Ecology and Systematics*. 18: 453–487.
- Martin, T.E. 1996: Life history evolution in tropical and south temperate birds: what do we really know? — *Journal of Avian Biology* 27: 263–272.
- Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. 2000: Parental care and clutch sizes in North and South American birds. — *Science* 287: 1482–1485.
- Massemin, S., Korpimäki, E., Pöyri, V. & Zorn, T. 2002: Influence of hatching order on growth rate and resting metabolism of kestrel nestlings. — *Journal of Avian Biology* 33: 235–244.
- Muchai, M. & du Plessis, M. 2005: Nest predation of grassland bird species increases with parental activity at the nest. — *Journal of Avian Biology* 36: 110–116.
- Murray, B.G. Jr. 1985: Evolution of clutch size in tropical species of birds. — *Ornithological Monographs* 36: 505–519.
- Odum, E.P., Kuenzler, E.J. 1955: Measurement of territory size and home range size in birds. — *Auk* 72: 128–137.
- Pierottu, R. 1981: Male and female parental roles in the western gull under different environmental conditions. — *Auk* 98: 532–549.
- Przybylo, R., Wiggins, D.A. & Merilä, J. 2001: Breeding success in blue tits: good territories or good parents? — *Journal of Avian Biology* 32: 214–218.
- Rastogi, A.D., Zanette, L. & Clinchy, M. 2006: Food availability affects diurnal nest predation and adult anti-predator behaviour in song sparrows, *Melospiza melodia*. — *Animal Behaviour* 72: 933–940.
- Ricklefs, R.E. 2000: Lack, Skutch, and Moreau: The early development of life-history thinking. — *Condor* 102: 3–8.
- Robinson, W.D., Rompre, G., Robinson, T.R. 2005: Videography of Panama bird nests shows snakes are principal predators. — *Ornitología Neotropical* 16: 187–195.
- Rotella, J.J., Dinsmore, S.J. & Shaffer, T.L. 2004: Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. — *Animal Biodiversity and Conservation* 27: 187–205.
- Russell, E.M. 2000: Avian life histories: is extended parental care the Southern secret? — *Emu* 100: 377–399.
- Searcy, W.A. 1979: Sexual selection and body size in male red-winged blackbirds. — *Evolution* 33: 649–661.
- Searcy, W.A., Peters, S. & Nowicki, S. 2004: Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. — *Journal of Avian Biology* 35: 269–279.
- Sick, H. 1997: Ornitologia Brasileira. — Ed. Nova Fronteira S. A., Rio de Janeiro, Brazil. (In Spanish)
- Simons, A.F. & Martin, T.E. 1990: Food limitation of avian reproduction: an experiment with the cactus wren. — *Ecology* 71: 869–876.
- Skutch, A.F. 1949: Do tropical birds rear as many young as they can nourish? — *Ibis* 91: 430–455.
- Smith, J.N., Montgomerie, R.D., Taitt, M.J. & Yom-Tov, Y. 1980: A winter feeding experiment on an island song sparrow population. — *Oecologia* 47: 164–170.
- Soler, M. & Soler, J.J. 1996: Effects of experimental food provisioning on reproduction in the jackdaw *Corvus monedula*, a semi-colonial species. — *Ibis* 138: 377–383.
- Stutchbury, B.J. & Morton, E.S. 2001: Behavioral ecology of tropical birds. — Academic Press, San Diego.
- Styrsky, J.N., Brawn, J.D. & Robinson, S.K. 2005: Juvenile mortality increases with clutch size in a Neotropical bird. — *Ecology* 86: 3238–3244.
- Svensson, E. & Nilsson, J.A. 1995: Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). — *Ecology* 76: 1804–1812.
- Tamm, S. 1985: Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. — *Behavioral Ecology and Sociobiology* 16: 203–207.
- Thiollay, J.M. 1988: Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. — *Oikos* 53: 17–30.
- Václav, R., Hoi, H. & Blomqvist, D. 2003: Food supplementation affects extrapair paternity in house sparrows (*Passer domesticus*). — *Behavioral Ecology* 14: 730–735.
- Westneat, D.F. 1994: To guard or to forage: conflicting demands affect the paternity of male red-winged blackbirds. — *American Naturalist* 144: 434–454.
- White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. — *Bird Study* 46: 120–138.
- Yom-Tov, Y. 1974: The effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L.). — *Journal of Animal Ecology* 43: 479–49.