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Experimental food supplementation increases reproductive effort in an antbird in subtropical Brazilian Atlantic Forest fragments

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Food limitation may interact with nest predation and influence nesting patterns, such as breeding season length and renesting intervals. If so, reproductive effort should change with food availability. Thus, when food is limited, birds should have fewer attempts and shorter seasons than when food is not limiting. Here we experimentally test that increased food availability results in increased reproductive effort in a fragmented landscape in the Variable Antshrike (Thamnophilus caerulescens) in southern Brazil. We followed nesting pairs in five natural fragments (4, 23, 24, 112, 214 ha) in which food was supplemented for half of those pairs, beginning with the first nest. Nest success in the largest (214 ha) fragment was 59%, compared to 5% in the 112 ha fragment and no nest was successful in the smallest (24 ha) fragment. Birds were seen, but evidence of nesting was never found in the two smallest fragments. Pairs with supplemented food were more likely to increase clutch size from two to three eggs, tended to renest sooner (20 d on average) than control pairs. Also, fragment size interacted with breeding and pairs in the largest fragment had greater daily nest survival rates, and so nests tended to last longer, and so these pairs had fewer nesting attempts than those in the 112 ha fragment while more than those in the smallest fragment with nesting (24 ha). Clearly, pairs increased their reproductive effort when food was supplemented in comparison to control pairs and fragment size seems to influence both predation risk and food abundance.
Experimental food supplementation increases reproductive effort in an antbird in subtropical Brazilian Atlantic Forest fragments

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ABSTRACT. Food limitation may interact with nest predation and influence nesting patterns, such as breeding season length and renesting intervals. If so, reproductive effort should change with food availability. Thus, when food is limited, birds should have fewer attempts and shorter seasons than when food is not limiting. Here we experimentally test that increased food availability results in increased reproductive effort in a fragmented landscape in the Variable Antshrike (Thamnophilus caerulescens) in southern Brazil. We followed nesting pairs in five natural fragments (4, 23, 24, 112, 214 ha) in which food was supplemented for half of those pairs, beginning with the first nest. Nest success in the largest (214 ha) fragment was 59%, compared to 5% in the 112 ha fragment and no nest was successful in the smallest (24 ha) fragment. Birds were seen, but evidence of nesting was never found in the two smallest fragments. Pairs with supplemented food were more likely to increase clutch size from two to three eggs, tended to renest sooner (20 d on average) than control pairs. Also, fragment size interacted with breeding and pairs in the largest fragment had greater daily nest survival rates, and so nests tended to last longer, and so these pairs had fewer nesting attempts than those in the 112 ha fragment while more than those in the smallest fragment with nesting (24 ha). Clearly, pairs increased their reproductive effort when food was supplemented in comparison to control pairs and fragment size seems to influence both predation risk and food abundance.

Key words. Experimental food supplementation, breeding season length, renesting intervals, nest predation, forest fragments, Variable Antshrike.
Nest predation is the greatest cause of nesting failure among open nesting passerine birds and is likely to have influenced avian life-history evolution (Nice 1957, Skutch 1949, 1985, Ricklefs 1969, 2000a, b, Roper et al. 2010). Food is also important and can limit reproduction in birds (Ricklefs 1968, 2010, Martin 1987) and may interact with predation, thereby causing complex (behavioral and life history) responses to predation risk. For example, the seasonal decline in clutch size in North American passerine birds may be due to reduced food availability with each nesting attempt (Martin 1987, Milonoff 1991, Bauchau and Seinen 1997, Castro et al. 2003). Where breeding seasons are long, nest predation rates are high and birds are “income breeders,” food availability may limit annual reproductive success because of its influence on both the number of nesting attempts and individual nest success (Soler and Soler 1996, Davis et al. 2005, Ricklefs 2010, Roper 2005, Stephens et al. 2014). Lower food abundance can result in fewer renesting attempts following predation (Rolland et al. 1998, Roper et al. 2010, Zanette et al. 2011) and more food may increase nesting success since both young and parents may be well-fed by fewer trips to the nest, thereby reducing the potential effect of visitation rate on predation risk (Holmes et al. 1992, Kuituken and Makinen 1993, Soler and Soler 1996, Martin et al. 2011). Experimentally increased food abundance may, therefore, reduce the incubation period, increase growth rates and permit second nesting attempts in species that usually have only one successful nest per year (Martin 1987, Davis and Graham 1991, Meijer and Drent 1999, Castro et al. 2003).

2006), declining food abundance may still influence the likelihood of repeated nesting attempts following predation due to a reproductive cost or decreased survival (Ruiz-Gutiérrez et al. 2008). Thus, annual reproductive success is expected to decline due to any inverse relationship between both predation risk and food abundance with fragment size. When predation rates are high renesting is even more important for annual reproductive success (Roper 2005, Roper et al. 2010). Therefore, a consequence of high predation rates, renesting rates may decline and brood reduction may occur more often in smaller fragments due to reduced food abundance (Suarez et al. 1997, Huhta et al. 1998, Zanette and Jenkins 2000, Barding and Nelson, 2008, Hinam and St.Clair 2008).

Here, we examine nesting success and experimentally manipulate food abundance in a fragmented landscape to test for the importance of food abundance in a subtropical understory-nesting bird, the Variable Antshrike (*Thamnophilus caerulescens*) in southern Brazil. We predict that food supplementation will result in increased reproductive effort, which may be manifest as increased number of nesting attempts, reduced intervals between nesting attempts, greater nesting success and combinations thereof.

**METHODS**

*Study Area.*---Nesting in the Variable Antshrike was studied in a region of natural forest fragments separated by open grassland and savanna, Vila Velha State Park (25.25°S, 50.08°W, ~1000 m above sea level) in Paraná, southern Brazil (Figs. 1, 2). The entire park comprises 3,122 ha and the forest fragments are typical of the mixed Atlantic Forests of Brazil, dominated by *Araucaria angustifolia*. Natural fragments range in size from 1 – 450 ha and are separated from each other by a minimum of 50 m. We selected five fragments (with > 100 m separation from each other, and from other fragments) with areas of 4, 23, 24, 112 and 214
ha to include the approximate range of local fragment size and maintain the > 100 m distance
between fragments.

Study Species.---Nesting in the Variable Antshrike *Thamnophilus caerulescens* (Vieillot 1816)
(Passeriformes: Family Thamnophilidae) was monitored in the 2000 to 2002 breeding
seasons that begin in October and end in January of the subsequent year. The antshrike is a
sexually dimorphic, insectivorous, understory bird. As in other members of the family, it is
territorial, monogamous (as far as is known), and nests in the forest understory, building an
open-cup nest in horizontal forks of shrubs and saplings usually less than 3 m above the
ground, as is typical of the genus (Oniki 1975, Ridgely and Tudor 1994, Roper 2000, 2005).
Variable Antshrikes lay clutches of two or three eggs (see below) and both parents contribute
in all aspects of reproduction, including nest construction, incubation, feeding nestlings and
post-fledging care (Oniki and Willis 1999, Zimmer and Isler 2003). Details of the breeding
season, such as start and end of the breeding season, number of clutches per year, variation in
clutch size, are all unknown or very poorly know, and will be reported here for the first time.

We captured Variable Antshrikes using mist-nets and banded each with a unique com-
bination of colored leg bands and a metal band provided by CEMAVE (the Brazilian govern-
mental agency that oversees bird studies). Because we wished to know annual reproductive
success, we followed banded pairs to find nests (each year attempting to capture more pairs).
Song playbacks to attract birds to the nets were sparingly used when pairs were difficult to
find. Nests were checked every 2 -3 days until they either fledged (success, when one or more
young fledged) or failed (when no young fledged). Predation was assumed to be the cause of
failure when eggs or nestlings disappeared prior to the fledging date and adults were not seen
with young birds away from the nests.
Experimental food supplementation.---To test the importance of food on nesting success about half of the pairs found in each fragment were randomly chosen to receive supplemental food. In these territories, food (mealworms, Tenebrionidae) was placed in a small dish (~10 cm in diameter, used for placing food in small, domestic cages, about the same diameter as a nest; Zimmer and Isler 2003) attached to a branch within 5m of the first active nest found for each pair. We did not attempt to quantify how much food we gave, but placed ~10 mealworms in each dish each day, until fledging or nest failure. If a nest failed and when a new nest of that same pair was found, the dish was moved closer to the new nest and food was again made available. We visually confirmed that all pairs with supplemented food took the offered mealworm larvae. Assignment of experimental treatments were constant (each pair was used for only one treatment) throughout the study. Because food supplementation began with the first nest attempt found for pairs in the supplementation treatments, we did not compare date of first nest among treatments (see below).

Reproductive effort---Effort was measured in four main ways: the number of nesting attempts, length of the renesting interval, breeding season length and nesting success (and their possible interactions). Because our study area is fragmented, we also tested for interactions with fragment size (area) as a covariable with interaction terms when sample sizes allowed. Four potential outcomes of the experiment were possible with respect to the above measurements of effort: 1) effort is independent of food treatment and fragment size, 2) effort increases with supplemented food but is independent of fragment size, 3) effort is independent of food treatment but dependent on fragment size and 4) effort increases with both supplemented food and fragment size. If fragment size was unimportant, then the test simply compares effort between food treatments.
We tested these possibilities with nesting success using the program MARK (version 6.0). MARK permits the estimation of daily survival rate that may be compared (using $\Delta AIC_c$ to select the best model) among groups (White and Burnham, 1999, Dinsmore et al. 2002). The other variables are continuous, and so we compared renesting intervals, number of renesting attempts, among food treatments and fragments of different size and their possible interactions using analysis of variance (ANOVA) or analysis of covariance (ANCOVA) when appropriate. Only the intervals following failed nesting attempts were used in this analysis because the interval after success involves an extended period of post-fledging care. We compared clutch size among treatments (both fragment size and food supplementation) using log-likelihood ratio test ($G$).

Finally, while we predict that annual productivity will reflect effort, it is harder to predict because it is the complex interaction between predation rate and number of nesting attempts (Roper et al. 2010). Once a nest is successful, parents must then spend some amount of time in parental care of fledglings. Also, if the number of successes are limited, even in relatively poor conditions, pairs, by renesting, may finally beat the odds and successfully nest (Roper 2005). Thus, to examine how annual productivity might change with food abundance and the correlated variables (renesting intervals, breeding season length) we simulated the annual breeding cycle (see Roper et al. 2010) using the parameters found in this study (daily nest survival rates, renesting intervals and clutch size by fragment size), and generated 100 replicates of 30 pairs under each combination of conditions. We compared annual productivity under the combinations of conditions using multivariate analysis of variance (MANOVA).

Under the assumption that the parameters measured and estimated in this study reflect actual field conditions, this simulation allows generating larger samples that are then comparable (Roper et al. 2010).
RESULTS

During preliminary censuses prior to beginning of this experiment, we found antshrikes in all fragments. However, while capturing and marking birds, we never captured (nor saw) antshrikes in the smallest fragment (4 ha), even though observations suggest that their territory size can be much smaller (~1 ha, J. Roper, pers. observ.). Nine females were captured in the larger of the two small fragments (23 ha), but never again seen again in the fragment in which they were captured. Four of them were later found and followed in the 112 ha fragment where they remained in the same territory for the duration of this study.

Nests (a total of 103) were only found in use in the 24, 112 and 214 ha fragments, and so food supplementation was only possible in those fragments. A total of three pairs were followed in the 24 ha fragment, and eight pairs each in the 112 and 214 ha fragments. Once pairs were marked and followed, most pairs remained together for the duration of this study. When an individual disappeared, it was replaced by a previously unbanded bird and no “divorce” or mate-switching was ever observed.

Timing of Breeding --- We describe the second two years because during the first year we spent time early in the season capturing birds and may have missed some nests. During the next two years of this study the breeding season began on 26 Oct 2001 (first egg laid the following day) and 9 Oct 2002 (with the first of two eggs) and ended on 26 Jan 2002 (last nest found with 2 eggs) 9 Jan 2003 (found with two eggs, 92 days). Breeding season length varied by fragment size. Pairs in the 112 ha fragment had the longest season length (91 d in 2001, 89 d in 2002), followed by pairs in the 214 ha (77 d in 2001, 82 d in 2002) and 24 ha (42 d in 2001, 48 d in 2002).
Reproductive effort and success.---Nesting success (as daily nest survival rate) was lowest in the 11 nests (all of which failed) in 2000 (0.836 day$^{-1}$, SE = 0.045). We do not include those nests in analysis because it being the first year of study, when we were also actively capturing birds, we cannot be certain that our activities did not affect success, and sample size was small. In subsequent years, the field season began with banded birds, so we captured less often, thereby reducing our potential influence on nesting. Thus, in 2001 (0.911 day$^{-1}$, SE = 0.014, N = 41) and 2002 (0.935 day$^{-1}$, SE = 0.011, N = 51), daily survival rates were similar.

None of the seven nests was successful in the small (24 ha) forest fragment. Five of 63 nests (8%) were successful in the 112 ha fragment and 17 of 29 nests (59%) were successful in the 214 ha fragment (Table 1). Daily survival rate (DSR) was consequently greatest in the large fragment (0.97 day$^{-1}$, SE = 0.01), which was greater than that of the other two fragments (in which DSR was similar: 105 ha = 0.88 day$^{-1}$, SE = 0.01, 24 ha = 0.85 day$^{-1}$, SE = 0.05, P < 0.05). The large differences in daily survival rate among the fragments dominates the relationship between food abundance and nesting success and the model with only forest fragment size as a predictor variable and the model including supplemented food and fragment size were similar (other models had ΔAICc > 10, likelihood ratio test, $\chi^2 = 5.0$, SE = 3.0, P > 0.05, Table 2, Fig. 3).

The combined effect of food supplementation and forest fragment size (with no interaction) explained 37% of the variance in number of nesting attempts per pair per year, with 26% explained by supplementation and 11% by fragment size ($F_{3,35} = 8.58$, $R^2 = 0.37$, P < 0.001). With supplemented food, the number of nesting attempts increased to an average of 2.17 nests year$^{-1}$ (SE = 0.47) as compared to 1.3 nests (SE = 0.13) in controls ($F_{3,38} = 8.5$, $r^2 = 0.37$, p < 0.05). The 112 ha fragment had the greatest number of attempts pair$^{-1}$ year$^{-1}$ (least squares mean = 3.2, SE = 0.2, maximum = 5) followed by the 214 ha fragment (1.95, SE = 0.24, max = 3) and 24 ha fragment (mean = 1.75, SE = 0.45, max = 2, P < 0.05).
Variable Antshrikes may renest after both failed and successful nests. In all years, pairs varied from no renesting attempts (3 pairs, one both years), one renesting (N = 16), two (N = 9), three (N = 5), and four (N = 4), for a total of 65 renesting attempts. Overall, renesting occurred from 3 – 54 days after failure (median = 15 days) and 11 – 45 days after success (median = 26 days, Table 1). Renesting interval was independent of year (ANOVA, $F_{2,52} < 1$, $P > 0.5$) and so we combined years in the following analysis. Renesting interval after unsuccessful nests was influenced by both, food supplementation and fragment size with no interaction (ANCOVA, adjusted $R^2 = 0.87$, $F_{3,47} = 110.7$, $P < 0.001$, Table 1, Fig. 4). Of the variance explained by the full model (87%), 65% was due to the addition of food and the remaining 12% was explained by fragment size. In control territories, renesting interval was shorter by 7.8 d in the large (214 ha, 28 d) versus the small (24 ha, 35 d) fragment which was similar to the 112 ha (34 d) fragments. In food supplemented territories, renesting in the large fragment and medium fragment (15 and 12 d respectively) were similar, and less than that in the small fragment (22 days, Table 1).

Clutch size varied between 2 – 3 eggs, and 23 of the 25 three-egg clutches followed food supplementation. Only 2-egg clutches were found in the smallest fragment ($n = 7$ clutches), 2 ($n = 51$) and 3 ($n = 16, 24\%$) egg clutches in the 112 ha fragment and 2 ($n = 20$) and 3 egg ($n = 9, 31\%$) clutches in the 214 ha fragment. Due to limited sample size, we could not test an additional effect of fragment size on clutch size.

As predicted, the probability of renesting increased in food supplemented pairs, with an interaction with fragment size ($F_{5,174} = 29.0$, $R^2 = 0.44$, $P < 0.0001$). In the full model, 21% of the 44% of the variance was explained by food supplementation, 18% by fragment size, and the remaining 5% by the interaction. In the simulations, up to five attempts were possible (Fig. 5) and annual productivity was always greatest with supplemented food (Fig. 6, Table 3). Also, multiple successful nests within a year were only likely to occur in the food...
supplemented scenarios (Table 3), and the four pairs that had two successful nests in 2002 all
received supplemented food. Total failure to reproduce was likely to occur in a large
proportion of the control pairs and occurred in 5 (2001) and 4 (2002) control pairs, and 3
(both years) fed pairs.

DISCUSSION

Three clear trends demonstrate that food abundance can influence reproductive effort and, as
a consequence, annual reproductive success. When food was added, 1) pairs renested after
shorter intervals, 2) pairs increased their number of nesting attempts per year, and 3) females
laid larger clutches. Further, preliminary evidence suggests that fragment size also matters
even though an ideal fragmentation study should include replicates of fragments. Breeding
began sooner and ended later in larger fragments, nesting success was greatest in the largest
fragment, all nests failed in the smallest fragment, and all nest failure was due to predation.

Food supplementation reduced renesting intervals and so with added food, more rapid
renesting, and consequently more nesting attempts summed to greater annual success (Roper
2005, Roper et al. 2010). Combining breeding season length with renesting intervals, we can
see that ~38 days in the 24 ha (small) fragment with 19 – 37 day renesting intervals, a max-
imum of two attempts can fit into a season. Indeed, only two attempts at most were initiated
by pairs in that small fragment. With food supplementation in larger fragments, the combined
benefits of increased clutch size, longer breeding season and more rapid renesting result in as
many as five attempts (in the 112 ha fragment) and much greater potential reproductive suc-
cess (in the 214 ha fragment). Thus, in the simulation, annual productivity may vary from 1.5
(control) to 3.1 (fed) fledglings pair\(^{-1}\) yr\(^{-1}\), with \(\leq 30\%\) of the population being unsuccessful in
the 214 ha fragment, in comparison with annual productivity always less than 1 fledgling
pair\(^{-1}\) yr\(^{-1}\) and > 90% unsuccessful in the 24 ha fragment and > 75% unsuccessful in the 112 ha fragment (Table 3).

Food abundance also influenced clutch size as has long been suggested (Lack 1947, 1948, 1949, Ricklefs 1968, 1980, 2000, 2010) and here, all but two of the 25 3-egg clutches (8%) followed food supplementation. Also, 3-egg clutches were only found in the two larger fragments. However, elsewhere at the same latitude, Variable Antshrikes often lay 3-egg clutches and at least one has been found with 4 eggs (J. J. Roper, pers. obs.). Thus, the more common 2-egg clutch in this study may reflect local food limitation and therefore emphasizes the greater importance of food and predation for nesting success.

The association between supplemental food and increased clutch size in the large fragments suggests complex associations between forest fragment size, food abundance and reproductive effort (Donovan et al. 1995, Robinson et al. 1995, Burke and Nol 1998, Vergara and Simonetti, 2004, Lloyd et al. 2006, Tielemann et al. 2008). In some experimental studies, supplemental food resulted in no change in clutch size, which was then attributed to inflexibility in the genetic determination of clutch size (Meijer and Drent 1999, Bourgault et al. 2009). In our study, the impact of additional food was clear because supplementation began with the first nest attempt, and the increase in clutch size usually occurred after that first attempt when food was added. This result was different than the expected for the Variable Antshrike because other species of *Thamnophilus* usually have a fixed clutch size of two (Oniki 1975, Skutch 1985, Roper and Goldstein 1997, Oniki and Willis 1999, Roper 2005, Roper et al. 2010).

The decreased nest predation rate in the largest fragment may be the result of several interactions (Sinclair et al. 2005, Cain et al. 2006, Vergara and Hahn 2009). Greater food abundance may have allowed less activity at nests (Skutch 1949, 1985) and greater nest attentiveness (Chalfoun and Martin 2007). Greater distances to the edge in the large fragment
may have reduced the likelihood of predators from the matrix between fragments from reaching the nests (Gates and Gysel 1978, Duca et al. 2001, Sinclair et al. 2005), although these fragments are natural and it is not clear whether the matrix has more or fewer predators than the forest itself. Alternatively, greater habitat heterogeneity within the larger fragments may reduce predator efficiency at finding nests makes the formation of a “search image” by the predator less probable (Martin and Roper 1988).

Here, with this food supplementation experiment in a tropical understory bird, we demonstrate a clear increase in reproductive effort with increased food availability. Evidence suggests that food abundance interacts with forest fragment size, even in natural forest fragments, resulting in reduced fecundity, reduced time in which to breed, and consequent loss of population viability, especially when predation risk is greater in the smaller fragments (Por- neluzi and Faaborg, 1999). The combined effect of renesting faster, renesting more often and a longer breeding season results in the likelihood of nearly 100% of successful nesting every year. Thus, reproductive effort can increase with even a small addition of food in a fragmented forested landscape in southern Brazil, which suggests that annual reproduction may also vary widely among years, if food abundance also varies.

ACKNOWLEDGMENTS

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ICMBio/CEMAVE provided license for banding. All methods followed standards of ethics under Brazilian law.

LITERATURE CITED


Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.


Table 1. Comparison among the reproductive parameters, forest fragment size and supplemental food treatment.

<table>
<thead>
<tr>
<th>Fragment size (ha)</th>
<th>Food Treatment</th>
<th>Pairs (N)</th>
<th>Nesting attempts (N)</th>
<th>Successes (N)</th>
<th>Nest DSR$^1$ (SE)</th>
<th>Renesting interval days$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td>Control</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>0.85 (0.05)</td>
<td>35 – 38 (3)</td>
</tr>
<tr>
<td>24</td>
<td>Fed</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td></td>
<td>23 (1)</td>
</tr>
<tr>
<td>112</td>
<td>Control</td>
<td>4</td>
<td>27</td>
<td>2</td>
<td>0.88 (0.02)</td>
<td>25 – 44 (26)</td>
</tr>
<tr>
<td>112</td>
<td>Fed</td>
<td>4</td>
<td>40</td>
<td>3</td>
<td></td>
<td>3 – 18 (40)</td>
</tr>
<tr>
<td>214</td>
<td>Control</td>
<td>3</td>
<td>10</td>
<td>4</td>
<td>0.97 (0.01)</td>
<td>23 – 54 (9)</td>
</tr>
<tr>
<td>214</td>
<td>Fed</td>
<td>5</td>
<td>19</td>
<td>13</td>
<td></td>
<td>14 – 45 (3)</td>
</tr>
</tbody>
</table>

$^1$DSR was similar for control and fed treatments, but was greater in the large fragments (P < 0.05). $^2$Minimum and maximum intervals in days, number of nests in parentheses is different from the total number of nesting attempts because only intervals after failed nests are included.
Table 2. Model comparison of the interactions between nesting success, fragment size and experimental food supplementation (Fig. 3). Fragment size had the lowest AICc value at 415.4.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAICc</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragment Size</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Fragment Size + Food</td>
<td>2.2</td>
<td>6</td>
</tr>
<tr>
<td>Food</td>
<td>27.4</td>
<td>2</td>
</tr>
<tr>
<td>Constant</td>
<td>30.1</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 3. Data-based simulation (1000 runs) results showing parameters used in the simulation (daily survival rate – DSR, clutch size – CS, breeding season length – BSL, renesting interval after failure and success). Consequences are the average number of nests pair\(^{-1}\) (Attempts) to achieve the resulting Productivity (average number of offspring pair\(^{-1}\)), and the percentage of successful nests over all nesting attempts (Rate) and the probability of a second successful nest during the season (> 1 success). See Figures 5 and 6.

<table>
<thead>
<tr>
<th>Fragment (DSR)</th>
<th>Food</th>
<th>CS</th>
<th>BSL</th>
<th>Renest(^1)</th>
<th>Attempts</th>
<th>Productivity (SD)</th>
<th>Success Rate</th>
<th>&gt; 1 success</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Failure</td>
<td>Success</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small (0.85)</td>
<td>Control</td>
<td>2</td>
<td>3(^2) 45</td>
<td>37</td>
<td>48</td>
<td>1.816</td>
<td>0.074 (0.378)</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>Added</td>
<td>2</td>
<td>3(^2) 23</td>
<td>34</td>
<td>45</td>
<td>2.837</td>
<td>0.348 (0.779)</td>
<td>17.0 0.004</td>
</tr>
<tr>
<td>Medium (0.88)</td>
<td>Control</td>
<td>2</td>
<td>3(^3) 90</td>
<td>34</td>
<td>45</td>
<td>2.837</td>
<td>0.348 (0.779)</td>
<td>13.4 0.004</td>
</tr>
<tr>
<td></td>
<td>Added</td>
<td>2</td>
<td>3(^3) 14</td>
<td>25</td>
<td>34</td>
<td>4.732</td>
<td>0.516 (0.916)</td>
<td>24.9 0.009</td>
</tr>
<tr>
<td>Large (0.97)</td>
<td>Control</td>
<td>2</td>
<td>3(^3) 80</td>
<td>53</td>
<td>64</td>
<td>1.516</td>
<td>1.458 (0.889)</td>
<td>72.9 0</td>
</tr>
<tr>
<td></td>
<td>Added</td>
<td>2</td>
<td>3(^3) 26</td>
<td>37</td>
<td>52</td>
<td>2.195</td>
<td>2.144 (1.260)</td>
<td>83.5 0.237</td>
</tr>
</tbody>
</table>

\(^1\)Because failed nests are the most common, we calculated renesting interval after failure for each treatment. For renesting interval after success, we estimated the average renesting interval after success and failure over all nesting attempts and added the difference (11 days) to renesting intervals after failure as the estimate of renesting interval after success. We added a cost to 3-egg clutches as two additional days in the nesting cycle, because egg laying occurs every other day. \(^2\)While there were no 3-egg clutches in the small fragment, we simulated the possibility as described here.
Figure Legends

Figure 1. The location of Vilha Velha State Park where this study took place, in southern Brazil.

Figure 2. Schematic map of the study area indicating the forest fragments included in this study.

Figure 3. Comparisons of daily nest survival rates (mean with 95% confidence interval) in three fragment sizes with ambient and supplemented food. The large fragment has the greatest survival rates and the apparent trend follows that predicted (see text for details).

Figure 4. Comparisons of renesting intervals among food treatments and forest fragment sizes (least squares means and 95% confidence intervals). Birds renest more quickly with added food, and renesting in 24 ha fragments is delayed in comparison with 214 ha fragments, and 112 ha had the smallest variance due to the greater number of renesting attempts.

Figure 5. The number of nesting attempts expected based on simulations of the consequences of supplemented food based on the nesting data in Table 3. Only birds with supplemented food can attempt more than three nests each breeding season.

Figure 6. Annual productivity (fecundity) based on 100 replicates of 30 pairs and the breeding parameters described in this study (Table 3), compared between fragment sizes and experimental food treatments. The increase in the largest fragment is a consequence of both, reduced predation rates and food treatments. Note that the increased clutch size came at a cost of reduced time in which to breed, so while three-egg clutches produced more, the increase was not simply additive.
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