Experimental food supplementation increases reproductive effort in the Variable Antshrike in subtropical Brazil

James J Roper Corresp., [1, 2] , **André M. X. Lima** [1] , **Angélica M. K. Uejima** [2, 3]

[1] Programa de Pós Graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

[2] Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

[3] Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Vitória de Santo Antão, Pernambuco, Brazil

Corresponding Author: James J Roper
Email address: jjroper@gmail.com

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James J. Roper[1,2], André M. X. Lima[1] and Angelica M. K. Uejima[2, 3]

[1]Programa de Pós-Graduação em Ecologia e Conservação

Universidade Federal do Paraná

Curitiba, Paraná, Brazil

[2]Departamento de Zoologia

Universidade Federal do Paraná

Curitiba, Paraná, Brazil

[3]Centro Acadêmico de Vitória

Universidade Federal de Pernambuco

Vitória de Santo Antão

Pernambuco, Brazil

Corresponding author: James J. Roper, , Telephone 55 41 36730409, e-mail: jjroper@gmail.com

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 a naturally fragmented habitat and experimentally supplemented food for half of those pairs. Birds were seen, but evidence of nesting was never found in two small fragments, even though these fragments were larger than individual territories. Pairs with supplemented food were more likely to increase clutch size from two to three eggs and tended to renest sooner (20 d on average) than control pairs. Also, fragment size was associated with breeding patterns, although fragment replicates were unavailable. Nest duration, nest success and breeding season length were all greater, while renesting intervals were shorter, in the largest fragments. Simulations showed that only the largest fragments were able to have a net production of young. Food availability clearly influenced reproductive effort and as a consequence, because of the interaction with predation risk, forest fragments of varying sizes will have complex reproductive dynamics.

Introduction

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, Derbyshire et al. 2015) 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). Thus, experimentally increased food abundance may reduce the incubation period (if it is flexible and not genetically constrained), and reduce nest predation (because of fewer trips to and from the nest), increase growth rates and permit additional 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, Roper et al. 2010).

Food abundance may interact synergistically with fragment size, predation risk and other causes of nest failure (Gates and Gysel 1978, Donovan et al. 1995, 1997, Burke and Nol, 1998, Batáry and Báldi 2004, Huhta et al. 1998, 2004, Abensperg-Traun et al., 2000, but see Tewksbury *et al*. 1998). However, even though both predation risk and food abundance may be independently influenced by fragment size (Askins, 1995, Melo and Marini 1997, Weinberg and

Roth 1998, Stratford and Stouffer 2001, Fort and Otter 2004, Tewksbury et al. 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).

The landscape of fear concept (Bleicher 2017) may be applicable in fragmented landscapes if the probability of nest predation is associated with fragment size. Thus, we may expect complex interactions and responses to both food abundance and nest predation in birds that are found in fragmented landscapes (Zanette et al., 2011). How those interactions are manifest in nature remain to be studied because of their complexity.

Here, we examine nesting success and experimentally manipulate food abundance in a fragmented landscape to test for the importance of food abundance and predation risk and their interactions in a subtropical understory-nesting bird, the Variable Antshrike (*Thamnophilus caerulescens*, Vieillot, 1816) in southern Brazil. The Variable Antshrike was chosen because the genus *Thamnophilus* has been studied in the tropics and so its breeding biology may be compared with other species in the genus (Roper and Goldstein 1997, Roper 2003, 2005; Tarwater 2008, Roper et al. 2010, Tarwater and Brawn 2010). Also, it is a relatively common, yet poorly studied species of the Atlantic Forest southeastern South America (Oniki and Willis 1999). Finally, visits to the study area always found antshrikes in the visited forest fragments. 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 (Ruffino et al. 2014).

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 (25.25ºS, 50.08ºW, ~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. Due to time constraints, it was not feasible to include more fragments in this study, hence we will emphasize the analysis of food supplementation.

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 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 combination of colored leg bands and a metal band provided by CEMAVE (the Brazilian governmental 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. All methods and animal manipulation followed standards of ethics under Brazilian law.

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 feeding cage birds, about the same diameter as a nest; Zimmer and Isler 2003, Londoño et al. 2008) 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, food supplementation was not important in first nest initiation (see below). Also, because the food dish was small and inconspicuous, we assumed that the presence of a dish itself was unimportant, therefore we did not put empty dishes in the control territories.

120 *Reproductive effort*--- Effort was measured in four main ways: the number of nesting attempts,
121 length of the renesting interval, breeding season length and nesting success. Because our study
122 area is fragmented, we also tested for interactions with fragment size (area) as a covariate with
123 interaction terms when sample sizes allowed. Four potential outcomes of the experiment were
124 possible with respect to effort: 1) effort is independent of food treatment and fragment size, 2)
125 effort increases with supplemented food but is independent of fragment size, 3) effort is
126 independent of food treatment but dependent on fragment size and 4) effort increases with both
127 supplemented food and fragment size.

128 We tested these possibilities with nesting success using the program MARK (version 6.0).
129 MARK permits the estimation of daily survival rate that may be compared (using ΔAICc to select
130 the best model) among groups (White and Burnham, 1999, Dinsmore et al. 2002). We compared
131 renesting intervals, number of renesting attempts, among food treatments and fragments of
132 different size and their possible interactions using analysis of variance (ANOVA) or analysis of
133 covariance (ANCOVA) when appropriate. Only the intervals following failed nesting attempts
134 were used in this analysis because the interval after success involves an extended period of post-
135 fledging care. We compared clutch size among treatments (both fragment size and food
136 supplementation) using log-likelihood ratio test (G).

137 Finally, while we predict that annual productivity will reflect effort, it is harder to predict
138 because it is the complex interaction between predation rate and number of nesting attempts
139 (Roper et al. 2010). Once a nest is successful, parents must then spend some amount of time in
140 parental care of fledglings. Also, if the number of successes are limited, even in relatively poor
141 conditions, pairs, by renesting, may finally beat the odds and successfully nest (Roper 2005).
142 Thus, to examine how annual productivity might change with food abundance and the correlated
143 variables (renesting intervals, breeding season length) we simulated the annual breeding cycle
144 (see Roper et al. 2010) using the parameters found in this study (daily nest survival rates,
145 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 antshrikes nor found evidence of nesting in the smallest fragment (4 ha), even though observations suggest that their territory size can be much smaller (~1 ha, J. Roper, pers. Observ.). We state this for two reasons: 1) we attempted replicates of small fragments, 2) to demonstrate that small fragments may be unsuitable, perhaps for reasons we will describe here. 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 67 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: 112 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 $\Delta AICc > 10$, likelihood ratio test, $\chi^2 = 5.0$, SE = 3.0, $P > 0.05$, Table 2, Fig. 2A).

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,

197 SE = 0.2, maximum = 5) followed by the 214 ha fragment (1.95, SE = 0.24, max = 3) and 24 ha
198 fragment (mean = 1.75, SE = 0.45, max = 2, $P < 0.05$).

199 Variable Antshrikes may renest after both failed and successful nests. In all years, pairs
200 varied from no renesting attempts (3 pairs, one both years), one renesting (N = 16), two (N = 9),
201 three (N = 5), and four (N = 4), for a total of 65 renesting attempts. Overall, renesting occurred
202 from 3 – 54 days after failure (median = 15 days) and 11 – 45 days after success (median = 26
203 days, Table 1). We do not have data that indicate whether the renesting after success was
204 influenced by post-fledging mortality or dispersal.

205 Renesting interval was independent of year (ANOVA, $F_{2,52} < 1$, $P > 0.5$) and so we
206 combined years in the following analysis. Renesting interval after unsuccessful nests was
207 influenced by both, food supplementation and fragment size with no interaction (ANCOVA,
208 adjusted $R^2 = 0.87$, $F_{3, 47} = 110.7$, $P < 0.001$, Table 1, Fig. 2B). Of the variance explained by the
209 full model (87%), 65% was due to the addition of food and the remaining 12% was explained by
210 fragment size. In control territories, renesting interval was shorter by 7.8 d in the large (214 ha,
211 28 d) versus the small (24 ha, 35 d) fragment which was similar to the 112 ha (34 d) fragments. In
212 food supplemented territories, renesting in the large fragment and medium fragment (15 and 12 d
213 respectively) were similar, and less than that in the small fragment (22 days, Table 1).

214 Clutch size varied between 2 – 3 eggs, and 23 of the 25 three-egg clutches followed food
215 supplementation. Only 2-egg clutches were found in the smallest fragment ($n = 7$ clutches), 2 (n
216 = 51) and 3 ($n = 16$, 24%) egg clutches in the 112 ha fragment and 2 ($n = 20$) and 3 egg ($n = 9$,
217 31%) clutches in the 214 ha fragment. Due to limited sample size, we could not test an additional
218 effect of fragment size on clutch size.

219 As predicted, the probability of renesting increased in food supplemented pairs, with an
220 interaction with fragment size ($F_{5, 174} = 29.0$, $R^2 = 0.44$, $P < 0.0001$). In the full model, 21% of the
221 44% of the variance was explained by food supplementation, 18% by fragment size, and the
222 remaining 5% by the interaction. In the simulations, up to five attempts were possible (Fig. 3) and

223 annual productivity was always greatest with supplemented food (Table 3, Fig. 4). Also, multiple
224 successful nests within a year were only likely to occur in the food supplemented scenarios
225 (Table 3), and the four pairs that had two successful nests in 2002 all received supplemented
226 food. Failure to reproduce in a give breeding season was likely to occur in a large proportion of
227 the control pairs and occurred in 5 (2001) and 4 (2002) control pairs, and 3 (both years) fed pairs.
228

229 DISCUSSION

230 In this first experimental test of food supplementation as an influence of parental nesting effort in
231 neotropical birds, three trends clearly demonstrate that food abundance can influence effort and,
232 as a consequence, annual reproductive success. When food was added, 1) pairs renested after
233 shorter intervals, 2) pairs increased their number of nesting attempts per year, and 3) females laid
234 larger clutches. Further, preliminary evidence suggests that fragment size also matters even
235 though an ideal fragmentation study should include replicates of fragments (unavailable in this
236 study area). Breeding began sooner and ended later in larger fragments, nesting success was
237 greatest in the largest fragment, all nests failed in the smallest fragment, and all nest failure was
238 due to predation. Also, we emphasize that two smaller fragments (in which we previously found
239 singing birds) had no nesting attempts and during this study, birds were not consistently found in
240 these fragments, thus indicating that small fragments are problematic.

241 Food supplementation reduced renesting intervals and so with added food, more rapid
242 renesting, and consequently more nesting attempts summed to greater annual success (Roper
243 2005, Roper et al. 2010, Ruffino 2014). Food availability may also interact with other variables
244 (self-maintenance, time incubating, etc.) during nesting (Londoño et al. 2008), but we did not
245 measure behavior *per se*, and so we cannot comment on exactly how food influenced nesting
246 aside from nesting intervals. Timing of breeding as a response to food abundance is clearly
247 important and can explain a decline in clutch size over time (Murphy 1986). Also, high expected
248 predation can reduce reproductive effort (Zanette et al., 2003, Zanette et al., 2011). However, in

249 birds with potentially long breeding seasons and high predation risk, perhaps the best strategy is
250 repeated nesting attempts (Roper 2005). If so, then food abundance is especially likely to be
251 important to allow repeated investment in eggs. Combining breeding season length with renesting
252 intervals, we can see that ~38 days in the 24 ha (small) fragment with 19 – 37 day renesting
253 intervals, a maximum of two attempts can fit into a season. Indeed, only two attempts at most
254 were initiated by pairs in that small fragment. With food supplementation in larger fragments, the
255 combined benefits of increased clutch size, longer breeding season and more rapid renesting
256 result in as many as five attempts (in the 112 ha fragment) and much greater potential
257 reproductive success (in the 214 ha fragment). Thus, in the simulation, annual productivity may
258 vary from1.5 (control) to 3.1 (fed) fledglings $pair^{-1}$ yr^{-1}, with ≤ 30% of the population being
259 unsuccessful in the 214 ha fragment, in comparison with annual productivity always less than 1
260 fledgling $pair^{-1}$ yr^{-1} and > 90% unsuccessful in the 24 ha fragment and > 75% unsuccessful in the
261 112 ha fragment (Table 3). In our simulation, when food was supplemented in the large fragment,
262 all "populations" of 30 birds had an average predicted fecundity ≥ 1, and widely variable over the
263 range of 1 to 4, and the food supplmented treatments having the greatest values (> 2.5). In stark
264 contrast, in both smaller fragments, average predicted fecundity was always less than 1,
265 regardless of supplemented food (even though when food is supplemented, success still increases,
266 Fig. 4). The irregular curves in Figure 4, rather than smooth lines, are due to the complex
267 interaction between the number of days a nest survives, renesting intervals and breeding season
268 length. For example, when nest success is greater, nests that fail last longer on average than at
269 lower success rates, thereby reducing future opportunities to renest. This leads us to conclude that
270 high predation rates can overwhelm the effects of food abundance.

271 Food abundance also influenced clutch size as has long been suggested (Lack 1947, 1948,
272 1949, Ricklefs 1968, 1980, 2000, 2010) and here, all but two of the 25 3-egg clutches (8%)
273 followed food supplementation. Also, 3-egg clutches were only found in the two largest
274 fragments. Elsewhere at the same latitude, Variable Antshrikes can lay 3-egg clutches and at least

one has been found with four eggs (J. J. Roper, pers. obs.). Thus, the more common 2-egg clutch in this study may reflect local food limitation and also emphasizes the importance of the synergy between 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 expected for the Variable Antshrike because other species of *Thamnophilus* 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).

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, Zanette et al. 2011). Greater food abundance may have allowed reduced 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 by impeding the development of a “search image” by the predator (Martin and Roper 1988). Perhaps simply increasing food abundance generates the perception that predation risk is lower, thereby allowing the increased clutch size (Zanette et al. 2011). Also, greater nest predation risk in smaller fragments may have created a different

landscape-of-fear which contributed to a shorter breeding season length and fewer attempts than the larger fragment (Zanette et al. 2011 , Bleicher 2017).

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 (Porneluzi 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

We would like to thank the several field assistants that helped monitor nests and endured the long walks between forest fragments. Thanks to Vila Velha State Park for their help both in allowing the study in the park as well as providing housing and additional help. We thank anonymous reviewers for their constructive suggestions.

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

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

[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.

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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.

Model	ΔAICc	Parameters
Fragment Size	0	3
Fragment Size + Food	2.2	6
Food	27.4	2
Constant	30.1	1

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Table 3. Data-based simulation (100 runs of 30 simulated pairs) results with values used in the simulation (daily survival rate – DSR, clutch size – CS, breeding season length – BSL, renesting interval after failure and success), average number of nests pair^{-1} (Attempts) to achieve the resulting Productivity (average number of offspring pair^{-1}), and the percentage of successful nests (Rate) and the probability of a second successful nest during the season (> 1 success). See figure 4.

Fragment (DSR)	Food	CS	BSL	Renest[1]		Attempts	Productivity (SD)	Success Rate	
				Failure	Success			Rate	> 1 success
Small (0.85)	Control	2	45	37	48	1.816	0.074 (0.378)	3.7	0
		3		39	50	1.614	0.126 (0.602)	4.2	
	Added	2		23	34	2.138	0.094 (0.423)	4.7	
		3		25	37	2.088	0.150 (0.654)	5.0	
Medium (0.88)	Control	2	90	34	45	2.837	0.348 (0.779)	17.0	0.004
		3		36	47	2.754	0.414 (1.069)	13.4	0.004
	Added	2		14	25	4.732	0.516 (0.916)	24.9	0.009
		3		16	27	4.400	0.642 (1.309)	20.3	0.011
Large (0.97)	Control	2	80	53	64	1.516	1.458 (0.889)	72.9	0
		3		55	66	1.484	2.244 (1.303)	74.8	0
	Added	2		26	37	2.195	2.144 (1.260)	83.5	0.237
		3		28	39	2.162	3.114 (1.960)	80.5	0.233

[1]Failed nests are the most common so we calculated renesting interval after failure for each treatment. Renesting interval after success was the average of all observed renesting intervals plus 11 days. We added a cost to 3-egg clutches as two additional days in the nesting cycle, because egg laying occurs every other day.

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Figure Legends

Figure 1. A) Location of Vilha Velha State Park where this study took place, in southern Brazil. B) Schematic map of the study area indicating the forest fragments included in this study.

Figure 2. Comparisons of the response to food treatments (control and added food) of A) daily nest survival rates (mean, with 95% confidence interval) and B) renesting intervals in days. Both are compared by forest fragment sizes to illustrate interactions.

Figure 3. Distributions of 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 4. Average annual productivity (fecundity) based on a simulated 30 pairs (a field population) and the breeding parameters described in this study (Table 3), compared between fragment sizes and experimental food treatments (A – 214 ha. fragment, B – 112 ha fragment, C – 24 ha fragment). Increase fecundity 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. The average productivity in both smaller fragments was less than one offspring per pair per year, and many “populations” (50% in the smallest fragment) were never successful.

522 Figure 1.

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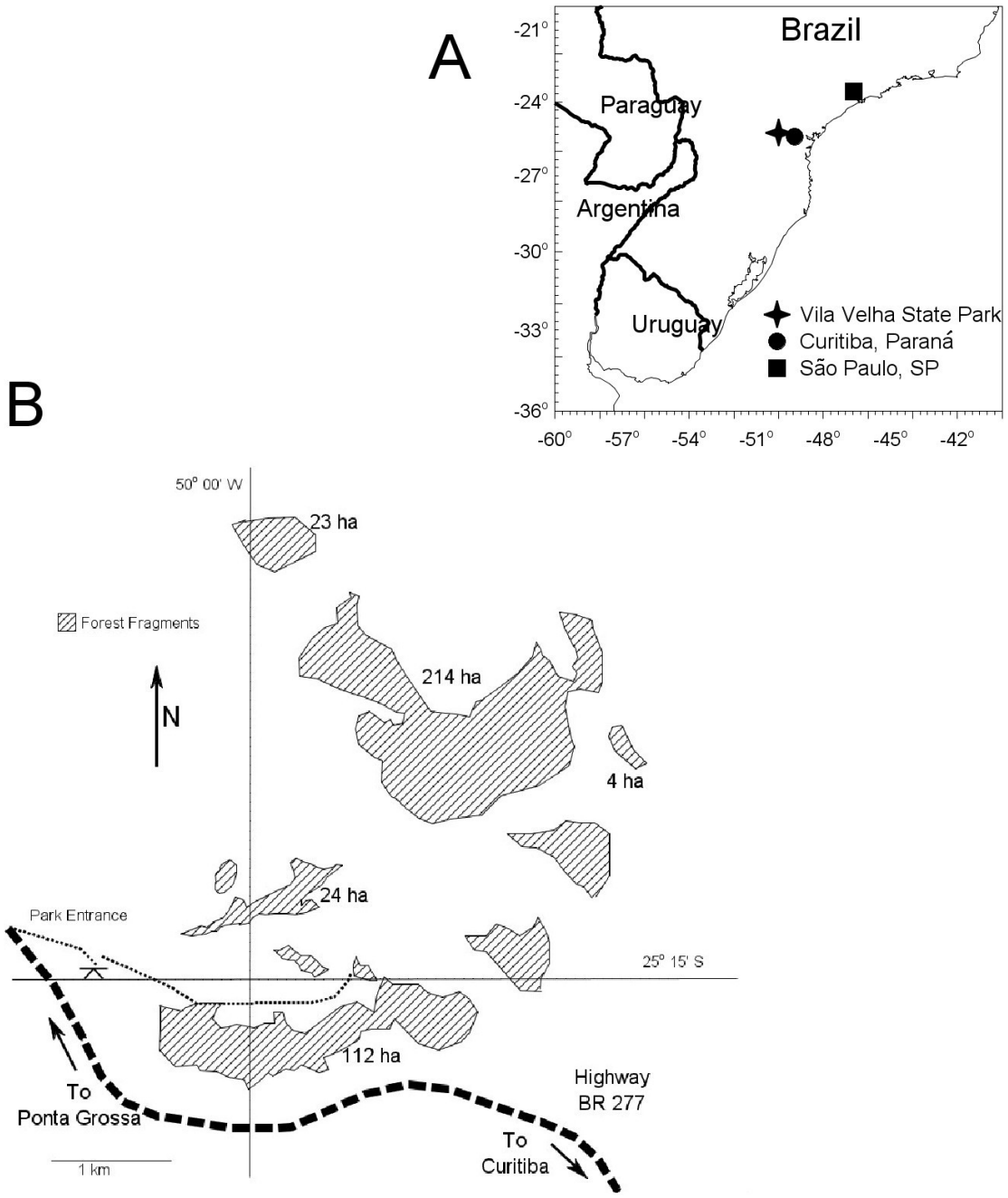

524 Figure 2.

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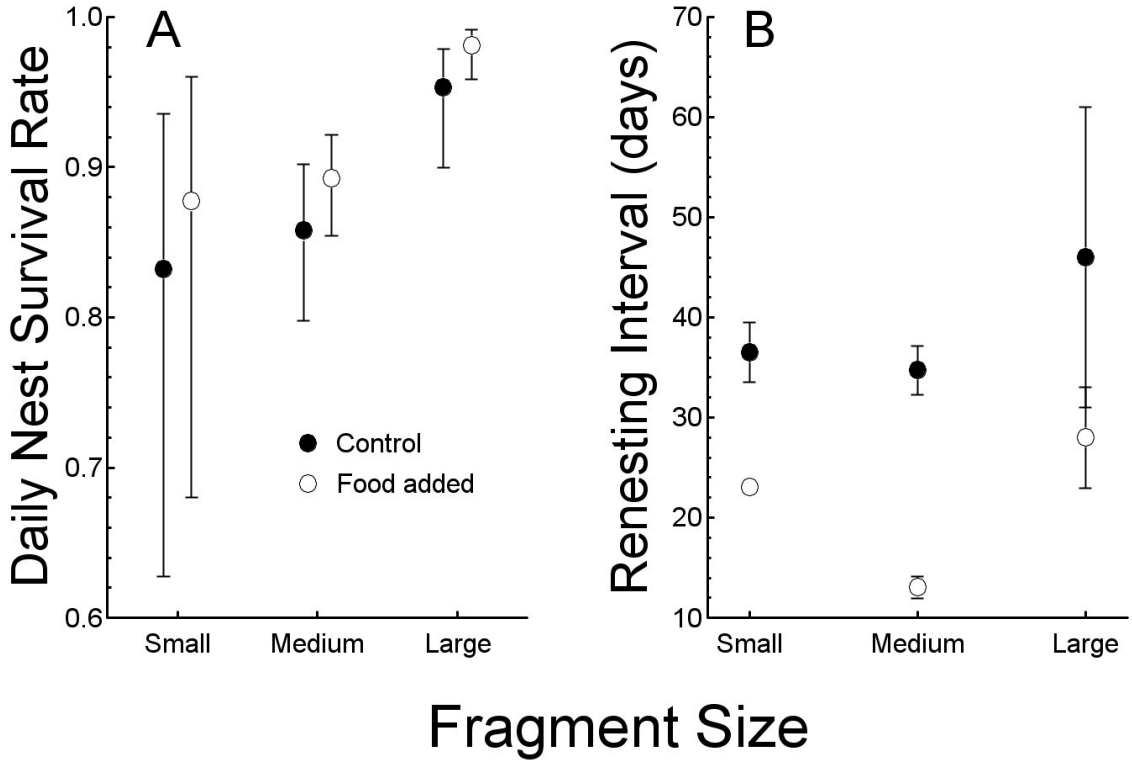

527 Figure 3.

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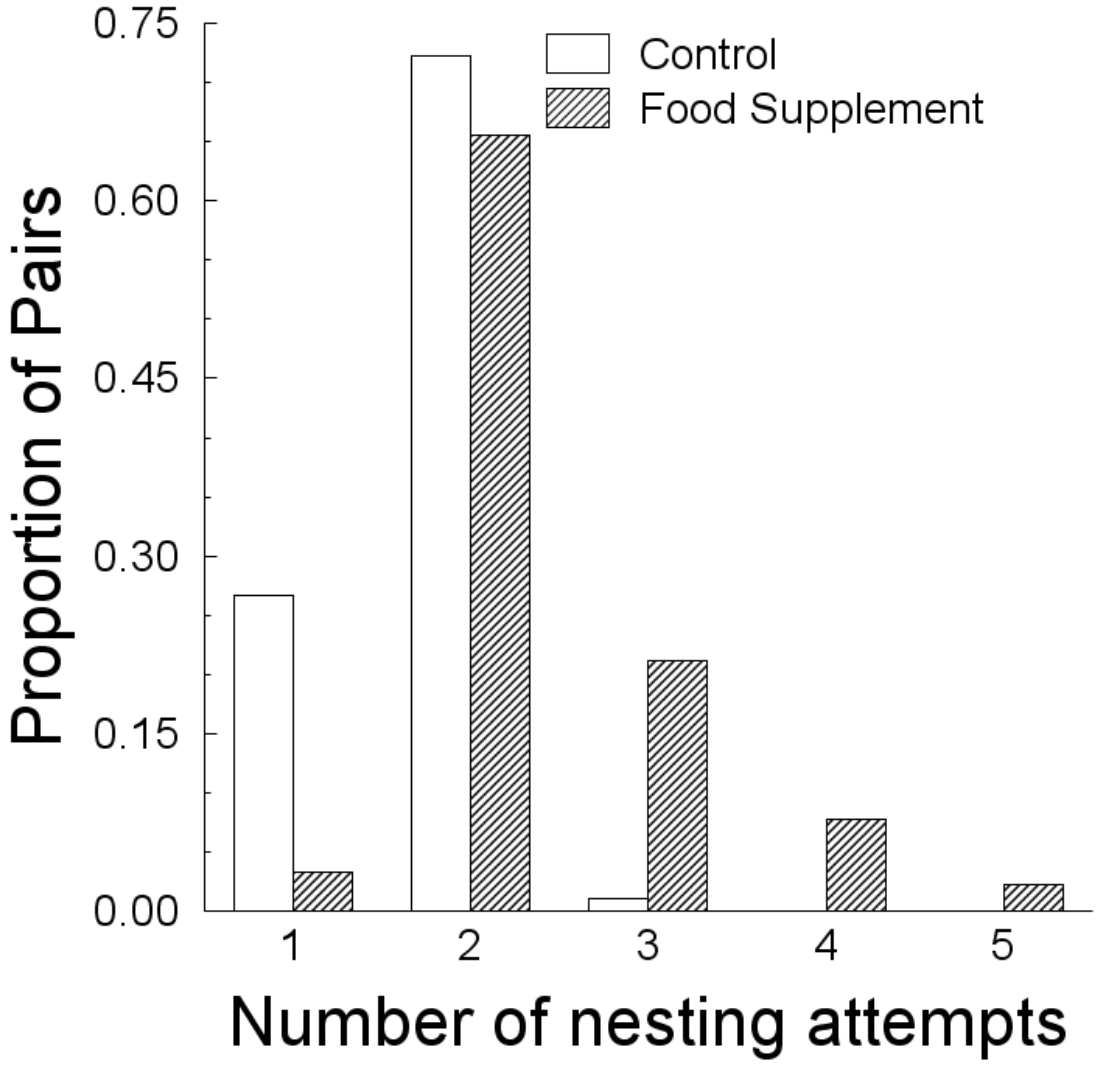
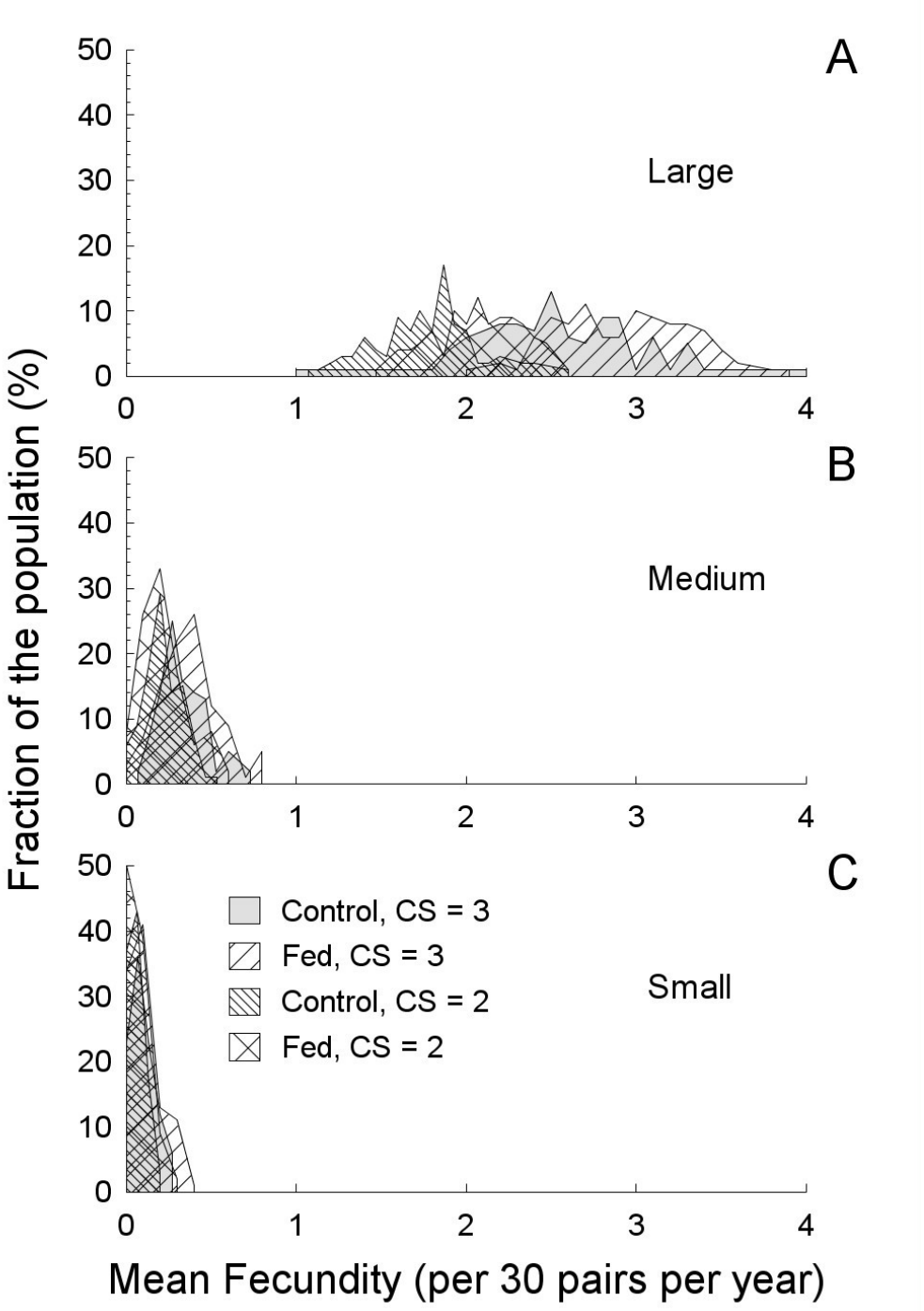


529 Figure 4.

530