WHOSE NEST IS BEST: THE ALLOMETRY OF HABITAT CREATION BY NEST-BUILDING BIRDS AND IMPLICATIONS FOR SECONDARY NESTER CONSERVATION

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Abstract. An important consequence of ecosystem engineering is habitat creation, which allows for an ecosystem to support higher biodiversity. Allometry (how body size influences behavior) can reveal the driving forces behind ecosystem engineering. Bird nests are one example of how allometry may determine the degree to which a species creates habitat in its ecosystem. There are two modes of nest use: primary nesting species build their own and secondary species choose from those already constructed by another. A nest's size relative to the engineer's directly determines breeding success because if too big or too small the safety of the clutch is compromised. Therefore it is necessary to have a strategy when either building or choosing the best sized nest. By comparing body size to nest volume of over 300 bird species globally, it was possible to discern these strategies and which species, nest types, and body sizes create the most habitat using allometric analysis. Both primary and secondary species prefer nests slightly larger than their body size dictates, secondaries even more so. These strategies in concert with the trend of lower abundance with increasing body size point towards larger primary nesting species being more important to biodiversity via their habitat creation. This relationship was also tested using an extinction simulation model which predicts that secondary species suffer the most from extinctions of larger primary species than other body masses. This interpretation of interspecies relationship should be used for focusing conservation efforts effectively to preserve and foster biodiversity.

INTRODUCTION

Ecosystem engineers are organisms that either directly or indirectly modify their abiotic environment through their behavior (Jones 1994). This includes many well-known species such as beavers, termites and even humans. Nearly all organisms exhibit some degree engineering, but arguably the most important consequence of this behavior is habitat creation. A key ecosystem engineer is a species whose engineering modulates or facilitates a resource, such as habitat, that is used by another species (Robles 2013). Habitat is a limiting resource for many organisms because the optimal quality and quantity of habitat is essential for survival; an organism's habitat partially controls whether it breeds successfully, evades predation and obtains food and nutrients. Because engineering creates habitat, the engineers are responsible for the survival of many other species, allowing for a higher degree of biodiversity in an ecosystem (Tilman 2006).

One example of key ecosystem engineering is bird nests. Nearly every known bird species uses a specific physical structure to incubate their eggs and raise their young. Breeding success is integral to the survival of a species (Negro and Hiraoldo 1993). A decline in population and/or genetic variation that can result from breeding failure raises extinction risk, and nestlings are the most vulnerable to predation and the elements. A nest's ability to properly protect young is therefore crucial to sustain a species (Windsor 2013). There is a great variety of shapes and sizes in which bird nests are constructed, although within a species there is little variation. Bird species have individually developed unique nest building strategies to best suit their breeding requirements.

Not all birds build their own nests, however. Rather than constructing their own nests from raw materials, these secondary nesting birds choose one from those already built and abandoned by other species. In this way, primary nesters are key ecosystem engineers that create breeding habitat for other species. Because of this reliance, habitat can be a limiting factor for secondary nesters as they must compete for the use of the available nests in their ecosystem (Robles 2012). Just as the primary species on which they rely, these birds had to develop a strategy for how to choose the best nest to use. A nest's preferred quality is determined by its engineer (Windsor 2013). Certain engineering species provide nests that are preferred by some species more than others due to the nest's ability to accommodate that species' breeding requirements (Robles 2014). Secondary nesters therefore have strategies to choose the best nest. The flexibility of that strategy determines how well that species will respond to stochasticity and human disturbance (Aitken 2008). Being a generalist nester reduces the amount of time and energy spent to find the best nest but the opportunity to find the best nest is sacrificed, and as a result breeding success is compromised. A specialist will likely eventually choose the perfectly sized nest but there is a greater risk of devastation if the specific engineers responsible are lost (Aitken 2008).

Strategies regarding nest construction and choice are extremely important to species survival and ecosystem biodiversity; therefore there must be some evolutionary strategies being employed or else birds would be choosing any size or shaped nest they find. Although this relationship has been studied from several different angles, very little research has been conducted on how body size could be a driver for these nesting strategies. Allometry is the study of how physical body size of part or the whole of an organism manifests in its intrinsic life history traits (Wu 2003). Body size has been shown to be a powerful influence on many aspects of survival, from metabolism to reproductive output to predator-prey interactions (Strayer 1991). In regards to bird nests, a nest's size compared to its user's size is extremely important. If the nest is too small to fit the clutch then the reproductive output is reduced. If too large then the clutch is exposed to the elements and predators.

We therefore predict that body size is a strong determinant as the strategy for building and choosing the best nest. Understanding these strategies is integral for more effective and sophisticated secondary nester conservation efforts. First, to determine if nest choice and construction are dictated allometrically, we compared body size to the nest size and population abundances of 332 primary and 42 secondary species across North America, Europe and Asia to discern whether body size drives nesting strategies. Second, we compared how these two strategies differ from one another and how that indicates which primary species are more important engineers through their habitat creation. Lastly, by simulating various calculated extinction events, we observed how secondary species would respond to loss of breeding habitat through the extinction of primary species.

METHODS

Data on the species used were compiled from a variety of sources including field guides, online databases and scientific literature, the majority of which came from the Peterson Field Guide series, Cornell Lab of Ornithology and Bird Life International. We included nest shape, average nest dimensions, global population estimates, geographic range estimates, average body mass, average egg size, average clutch size, and any known secondary nesting affiliations. Nest type was divided into 4 categories (cup, shallow, cavity/burrow, orb) based on fundamental shape in order to accurately calculate nest volume and for comparison across nest shape. A separate dataset of secondary nesters included the same data types in addition to average used-nest dimensions and their respective primary species.

Nesting Strategies

The logarithmic transformation of average nest volume (cm^3) was plotted against that of average body mass (g) for each primary nester regardless of nest type. The model 2 regression analysis conducted using

R statistical software produced a line of best fit. The parameters of this line reflect the allometric relationship between the two variables (elaborated later on). This analysis was also conducted on each of the nest types separately. Because of the extraordinary result for cavity nests, those of that category were overlaid on the plot of all primary species for visual comparison.

The secondary nesters were compared to the primary strategy by plotting each species in the same manner as the primary species but with the primary line of best fit to represent the construction strategy. This regression line represents the nest volume that a secondary species would build if it were a primary nester. Any discrepancy represents a difference in nesting strategies based on body mass.

In order to disprove the possibility that secondary birds are choosing nests simply based on what sizes are more abundant rather than on an evolutionary strategy, we compared the body mass frequencies of the two types of nester by dividing them into 4 body size categories. This reveals both which nest sizes are most abundant and the difference in size distribution between primary and secondary species.

Extinction simulation

This component of the analysis modeled different scenarios to illustrate how secondary nesting species respond to the extinction of primary species based on their body mass. In order to determine which extinction simulation scenario would be most realistic, we confirmed that the relationship between body size and population density is significantly negative. Therefore the most realistic scenario is the extinction of species of larger body mass, being more prone to isolation and disturbance.

For this simulation, we removed primary species in increments of 10, 20, 30, and 50% from a hypothetical ecosystem inhabited by all species in the database in three different scenarios: removing the smallest mass, a random assortment, and then the largest mass species. All species were placed in categories based on their nest volume; predicted nest choice was based on nest volume alone, not location or shape, in order to isolate the body-nest size relationship. The width of these categories was determined using a primary-secondary matrix. The average range of nest volumes used by secondary species resulting from this matrix loosely represents the amount of flexibility these species exhibit when choosing nests. During these trials, if a nest volume category was reduced to 0 primary species, then all secondary species in that category were considered extinct because without any nests available in their generalized size-range of use, they cannot breed successfully. The random assortment scenario was conducted by averaging the results from 10 duplicate trials for each percentage bracket removed.

RESULTS

Nesting Strategies

The allometric nest construction strategy trend across all primary nesters is represented by the regression line of Figure1 (Slope: 1.1287, CI 97.5% :1.05 -1.21, $p<0.001$, $R=0.60$, $N=323$). The notable parameter here is the slope which is significantly greater than the predicted value of 1 even at the 97.5% confidence intervals. The same analysis produced similar regression slopes in three of the specific nest types Cups, Shallow, and Orb with values significantly greater than 1 (Table 1, Figures 2-4). The slope for Cavity nests is greater than the rest and also has a much greater y intercept value (Figure 5), and when overlaid on the all-primaries graph consist of the vast majority of species found significantly higher than the overall regression line (Figure 6).

When comparing the regression line of primary nest construction with secondary species, 60% species lay significantly higher (Figure 7). Those below the primary regression line are all Shallow nest users with the exception of one (*C. brunneicapillus*). If the secondary species points lay along the primary regression line then the allometric nesting strategies for constructing and choosing are equivalent. Figure 7 shows that most secondary species lay above the line, signifying a relatively larger nest used than constructed for the same body mass.

The first body mass frequency histogram depicts the difference in body mass distribution among species (Figure 8a). There are many more small sized (8-60 grams) primary species than very small (1-8 g), medium (60-175 g), large (175-2050 g) or very large (2050-10200 g) species with over 60% in that category. Secondary species however exhibit a right shift; although they are most common the small category there are relatively many more medium and large secondaries than primaries. When incorporating species abundances, this relationship is also depicted (Figure 8b). This second histogram also represents the abundance distribution of different nest sizes. There are many more small sized nests than larger because there are many more small birds creating small nests. The disparity between primary and secondary abundance is greatest in the large body mass category, with a difference of 35%.

Extinction Simulation

By plotting population density versus body mass, the negative trend reflects the commonly accepted theory that population density decreases with increasing body mass (Figure 9). With low population density, the risk of extinction increases. This result was then used to designate the most realistic scenario in the extinction simulation as being the removal of the larger primary species.

In the scenario in which the smallest primary species were removed, there were no extinctions in the secondary species populations even with half of the primaries removed (Figure 10a). The same result came from the random removal of primary species (Figure 10b). These are the unrealistic scenarios used for comparison. The removal of the largest primary species in contrast caused a significant decrease in secondaries (Figure 10c). As primaries steadily decreased so too did secondaries. Therefore, the extinctions of the largest species had the most impact on the secondary species' survival.

DISCUSSION

Nest Strategies

When conducting allometric analysis, the parameters of the regression line reflect the relationship between the logarithmic transformation of body size and another intrinsic factor. Because nest volume is in three dimensions, the anticipated slope of the regression line is 1, meaning that body size is directly influencing nest size. The slope of the regression line for all primary species is significantly greater than 1 (CI 97.5% : 1.05 -1.21, $p<0.001$, $R=0.60$, $N=323$). This means that birds are constructing nests larger than their body size dictates. One explanation for this is that they are anticipating for the size of their clutch and eventual size of their growing chicks.

The specific nest types follow similar trends except for Cavities which exhibit a steeper slope and higher intercept (Table 1). Cavity excavating birds engineer much more volume than the other nest type species do. This is partially due to the geometric nature of the cavity. More volume is required since the structure must include any open space as opposed to a cup for example that does not encapsulate the clutch.

The vast majority of primary-secondary nester research has been conducted on cavity nesting birds and cavity nest webs or CNWs (Robles 2014). There are many more observed secondary cavity species than the other nest types but little insight exists investigating why this may be besides nest longevity. Allometry can offer an explanation based on the following conclusions: 1) secondary species tend to choose nests much larger than their body size dictates 2) cavity building species build the largest nests compared to their body size 3) smaller species are more abundant. Therefore, there are more cavity nesting species making nests that can support more secondary species.

The difference between nest construction and nest choice strategies is apparent when overlaying the data. 60% of the secondary species lay above the primary regression line, indicating that secondary nesters tend to choose nests larger than they would have if they made their own (Figure 7). This makes logical sense because as it is highly unlikely to find a perfectly sized nest and highly limiting to clutch size to choose one too small, birds would settle for larger nests. Therefore, secondary species rely more heavily on birds with a larger body mass than themselves. As a result, larger primary species are supporting relatively more secondary species than smaller ones do.

In order to confirm that secondary species are not simply choosing larger nests because they are more abundant in their ecosystems, we observed body mass frequencies of both types (Figure 8b). This reveals several points: first, that smaller primary species are more abundant. This implies that there are more small nests constructed. Secondly, the distribution of secondary species exhibits a right shift with a higher frequency of larger species than that of primaries. These two observations in concert illustrate secondaries' heavy reliance on larger primary species for habitat creation and breeding success. There are more small nests and yet secondary species compete over the less frequency larger ones. These trends are prevalent when comparing the distribution of both the number of species and number of individuals.

Extinction simulation

Because larger species have lower population densities and therefore high risks for extinction, the most realistic extinction events involve the removal of the largest species (Figure 9). In order to create a baseline for comparison, the first 2 scenarios included the removal of the smallest species and a random assortment. In both of these cases, as primary species were removed, there were no observed extinctions in the secondary species population (Figure10a & 10b). Even with half of the primary species extinct, all of the secondary species were able to still find adequately sized nests to use.

When removing the largest primary species however, there was a significant decrease in secondary species (Figure 10c). Without the larger species there were no properly sized nests for many secondary species to use, and therefore they could not persist. This result further points to larger primary species having the most responsibility for sustaining secondary species.

CONCLUSION

Nearly all subsets of this analysis support larger primary species as being the most integral and keystone to biodiversity via their ecosystem engineering. Interactions such as the secondary use of constructed nests are one of many examples of how the biosphere supports itself in its wide variety and nearly limitless evolution. As ecosystems shift more drastically due to the changing global climate it is becoming more and more imperative to better monitor and understand how biota are responding and will respond. Breeding success is one of the most pivotal factors that determine a species' persistence, and through understanding the driving factors of nesting behavior it is possible to focus conservation efforts on those key species that add the most to biodiversity.

Because the larger primary nesting species have been shown to support relatively more secondary species they merit the most attention and protection. Most of the focus regarding the secondary-nesting web has been on cavities and with good reason. They however only represent a small percentage of species involved in this complex system. Further research is required in order to confirm the evidence found here.

LITERATURE CITED

Aitken, K E.H., and K. Martin. 2008. Resource selection plasticity and community responses to experimental reduction of a critical resource. Ecology **89:**971-980.

Jimenez-Franco, M.V., J.E. Martinez, and J.F. Calvo. 2014. Lifespan analyses of forest raptor nests: patterns of creation, persistence and reuse. PloS One **9:**10.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69:**373-386.

Negro, J.J., and F. Hiraldo. 1993. Nest-site selection and breeding success in the lesser kestrel *(Falco-naumanni)*. Bird Study **40:**115-119.

Norris, A.R., and K. Martin. 2010. The perils of plasticity: dual resource pulses increase facilitation but destabilize populations of small-bodied cavity-nesters. Oikos **119:**1126-1135.

Robles, H., C. Ciudad, and E. Matthysen. 2012. Responses to experimental reduction and increase of cavities by a secondary cavity-nesting bird community in cavity-rich Pyrenean oak forests. Forest Ecology and Management **277:**46-53.

Robles, H., and K. Martin. 2013. Resource quantity and quality determine the inter-specific associations between ecosystem engineers and resource users in a cavity-nest web. Plos One **8:**12.

Strayer, D. L. 1991. Perspectives on the size and structure of lacustrine zoobenthos, its causes, and its consequences. Journal of the North American Benthological Society **10:**210-221.

Tilman, D., P.B. Reich, and J.M.H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature **441:**629-632.

Windsor, R.L., J.L. Fegely, and D.R. Ardia. 2013. The effects of nest size and insulation on thermal properties of tree swallow nests. Journal of Avian Biology **44:**305-310.

Wu, R., C.-X. Ma, X.-Y. Lou, and G. Casella. 2003. Molecular dissection of allometry, ontogeny, and plasticity: a genomic view of developmental biology. BioScience **53:**1041-1047.

APPENDIX

TABLE 1. Regression line values for primary species.

Nest Type	N	Slope	Lower 97.5% CI	Upper 97.5% CI	P value	R^2
All Primary	323	1.1287	1.052904	1.209853	1.12E-65	0.599075
Cup	218	1.094	1.017294	1.176472	2.72E-59	0.705725
Shallow	57	0.959	0.826194	1.113143	9.63E-16	0.693477
Cavity	28	1.2822	1.005703	1.634793	4.71E-07	0.629696
Orb	13	1.9473	1.197775	3.165836	0.947295	0.420155

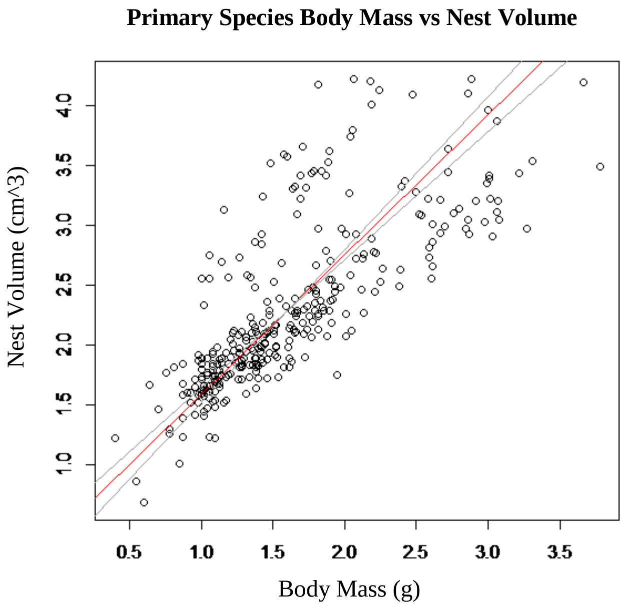

FIGURE 1. Logarithmic comparison of average species body mass and average species nest volume for all primary species.

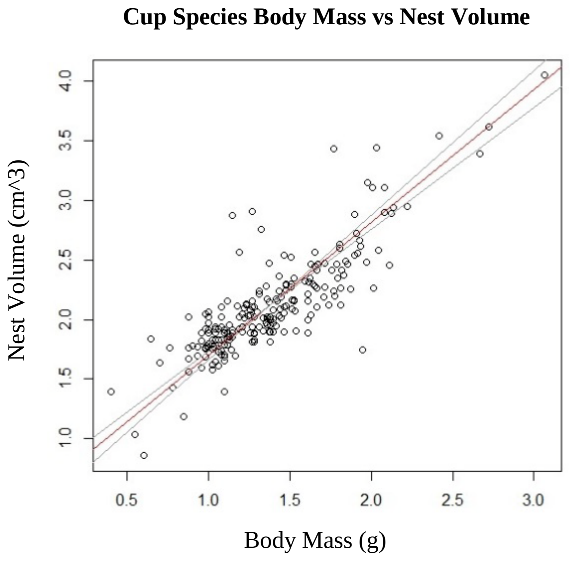

FIGURE 2. Logarithmic comparison of average species body mass and average species nest volume for all cup building species.

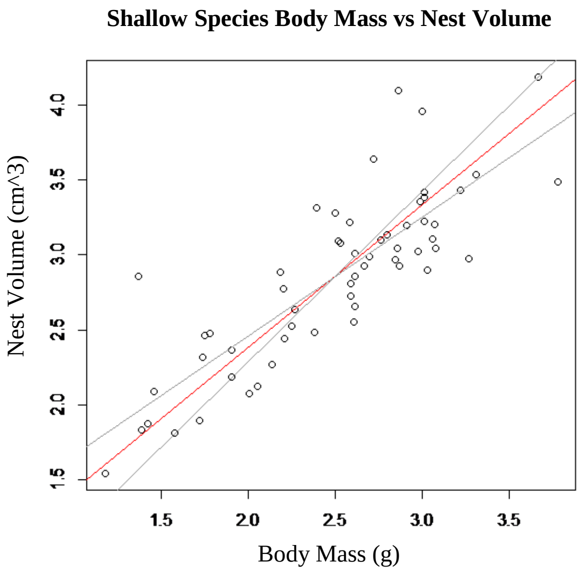

FIGURE 3. Logarithmic comparison of average species body mass and average species nest volume for all cup building species.

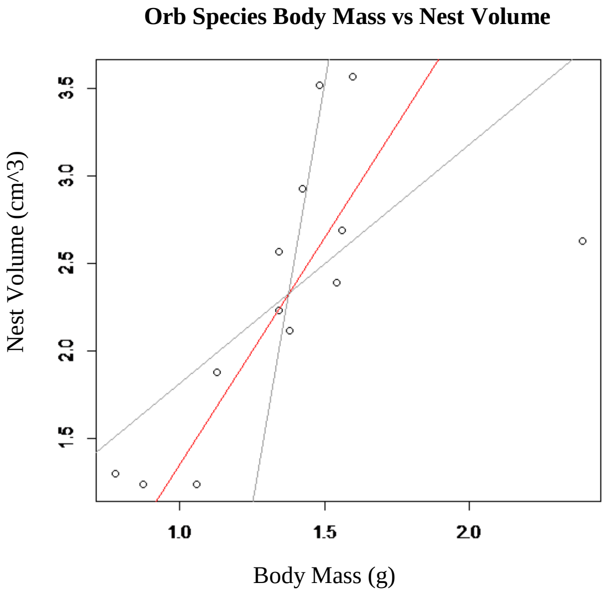

FIGURE 4. Logarithmic comparison of average species body mass and average species nest volume for all orb building species.

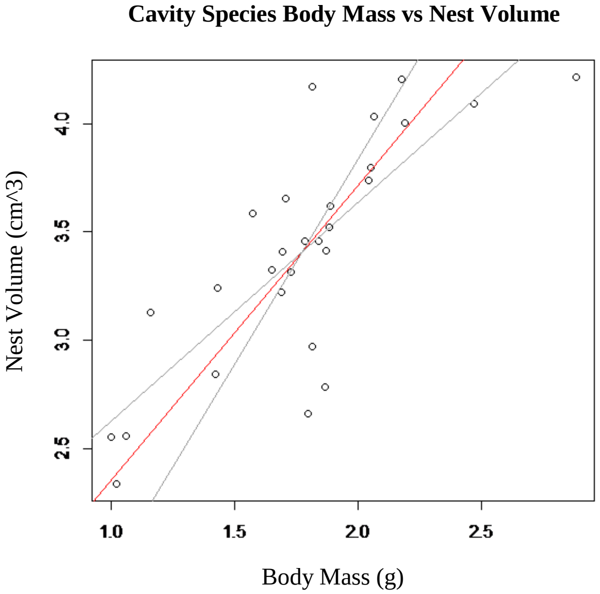

FIGURE 5. Logarithmic comparison of average species body mass and average species nest volume for all cavity building species.

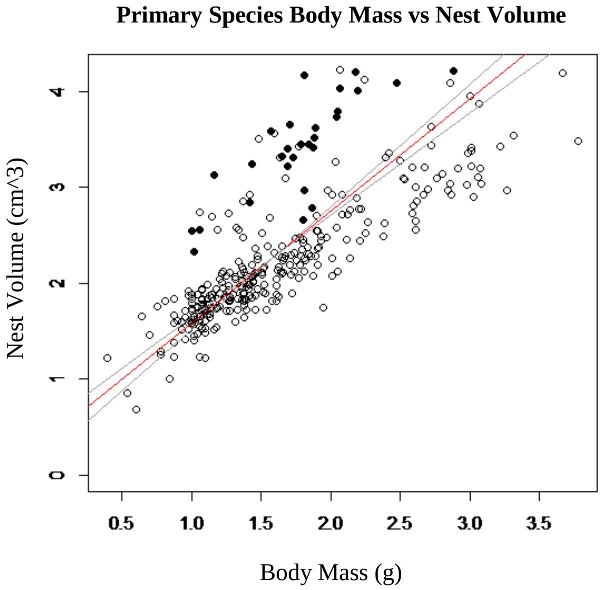

FIGURE 6. Logarithmic comparison of average species body mass and average species nest volume for all primary species with cavity nesters in black.

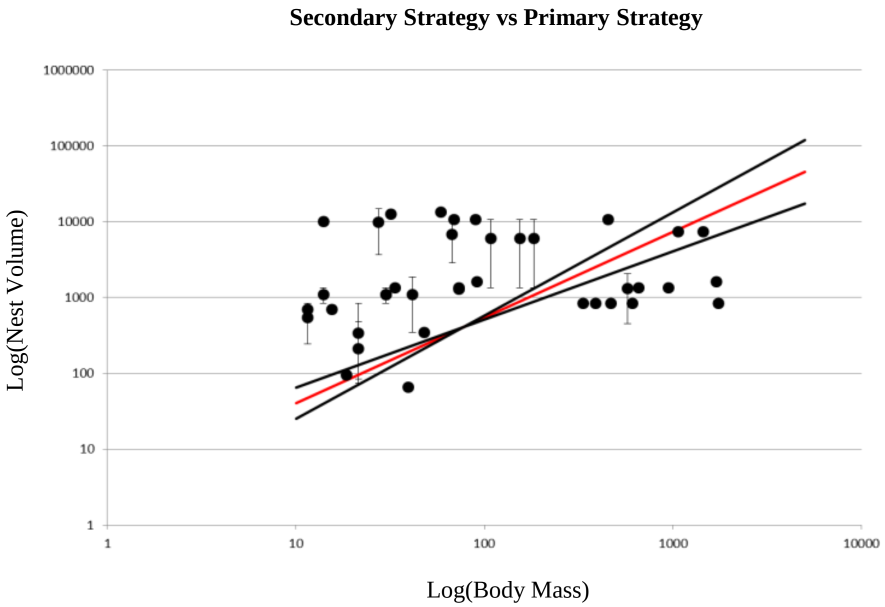

FIGURE 7. Secondary species in relation to primary construction nest strategy.

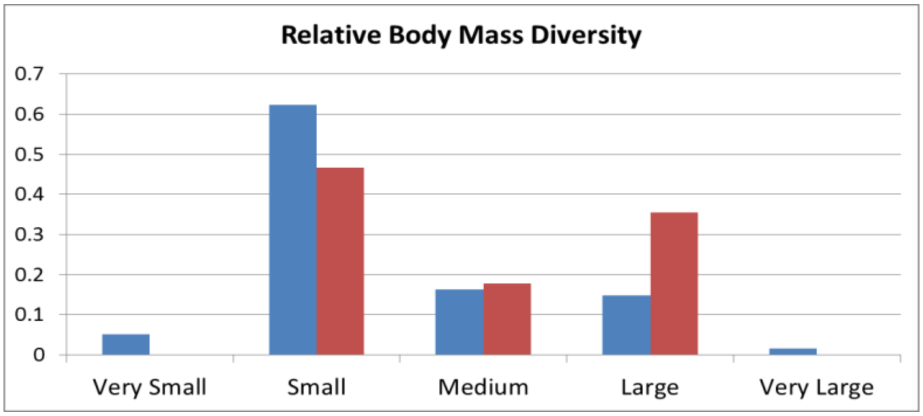

FIGURE 8A. Relative Body mass frequencies of primary and secondary species.

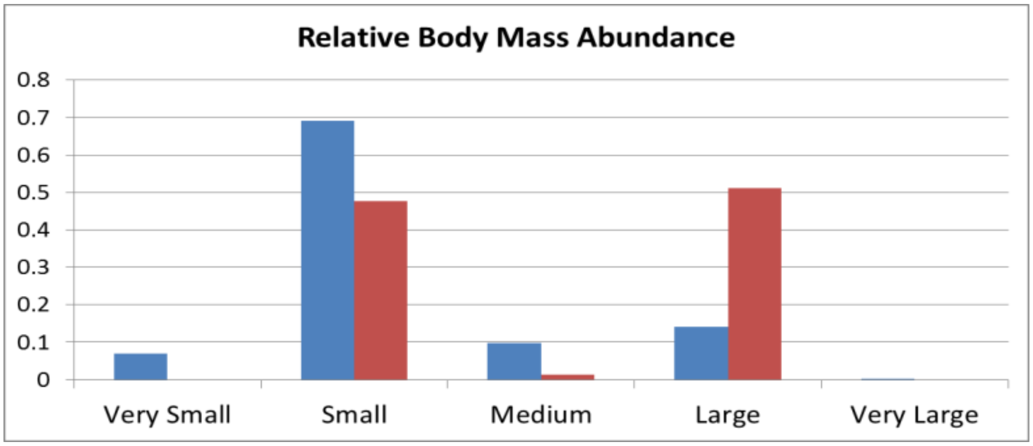

FIGURE 8B. Relative Body mass frequencies by abundance of primary and secondary species.

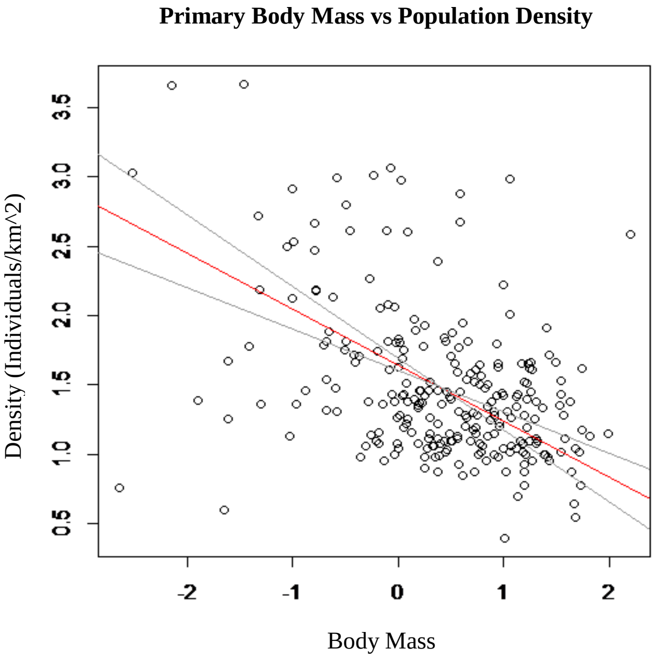

FIGURE 9. Logarithmic comparison of average species body mass to estimated population density.

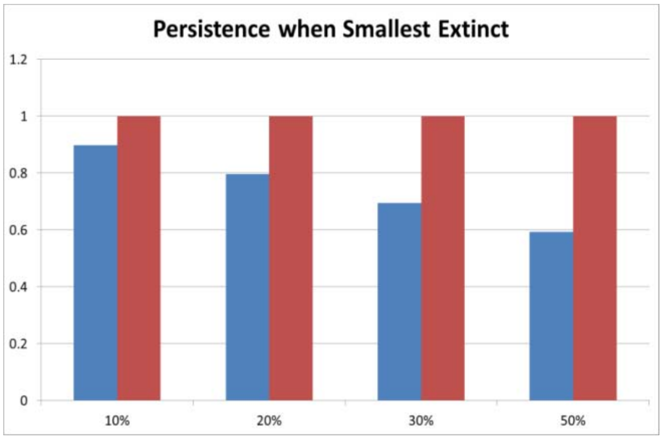

FIGURE 10A. Secondary species response to extinction of the smallest primary species.

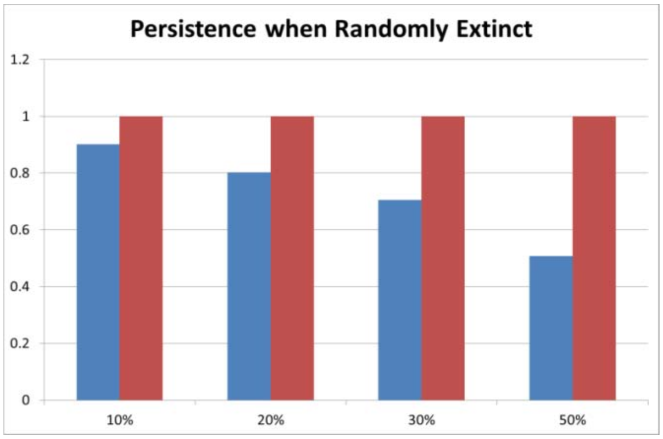

FIGURE 10B. Secondary species response to extinction of a random selection of primary species.

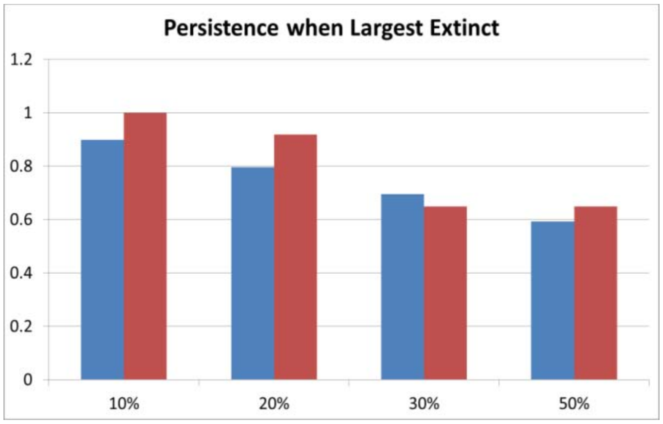

FIGURE 10C. Secondary species response to extinction of the largest primary species.