Island diameter and distance effects on tropical mammal populations

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Abstract

The theory of island biogeography generally holds that species richness is impacted by both the size of an island and its distance from a larger source population. The following research put this theory to the test by observing how different island sizes and distances of tropical islands in a virtual environment affected the total population of 10 non-volant mammal species. Findings concluded that larger islands hold more mammal species than smaller islands, while islands farther away from a given mainland exhibit less mammal species than islands closer to the mainland, thus confirming the Target Effect and colonization rates. Both findings stress the importance of single large reserves in preserving mammal biodiversity, particularly as it relates to non-volant species.

Introduction

Islands have historically provided researchers from natural science fields with what Whittaker and Fernández-Palacios (2007) describe as replicable and simplified model systems. Put more specifically, islands as quantifiably discrete entities that are both numerous, varied, and not by strict definition, ecosystems always or necessarily bounded by water, are ideal systems that have consequently allowed the isolating of definitive factors and processes to examine spatial and temporal effects (Whittaker and Fernández-Palacios, 2007). Thus has the interdisciplinary field of island biogeography enabled a better understanding of the distribution and diversification of species through observations of islands as living laboratories (Fernández-Mazuecos & Vargas, 2011). Such knowledge can consequently be applied to theoretical frameworks and real-world challenges. Island biogeography may be of an especially heuristic value at a time when the loss of Earth's biota is accelerating by way of anthropogenically-caused species extinctions (Ceballos et al., 2017). This, according to Ceballos et al. (2017), is particularly true for vertebrate species.

Accordingly, the following research questions were posed under which four variables in both time and space—island diameter, island distance, immigration, and species population dynamic—aided in answering:

1) How does the diameter of a tropical island affect the total mammal population size of 10 mammal species?

2) How does the distance of a tropical island from the mainland affect the total mammal population size of 10 mammal species?

Concluding such questions, and after an in-depth review of the literature, it was hypothesized that as the diameter of a tropical island increases, so too would the total population of mammals on that island increase. Furthermore, it was hypothesized that as the distance of a tropical island from the mainland increases, then that island will exhibit a lower total mammal population than islands closer to the mainland.

The following experiment utilized an online virtual island biogeography laboratory, known as GoLabz, Island Biogeography New® by Thomas C. Jones (Jones, 2020) to test these variables. Here, the focus was on mammal species existing in the tropics due to higher rates of species biodiversity resulting from a closer proximity to Earth's equator (Brown, 2014). The experiment revealed that islands larger in diameter contained greater numbers of mammal species than islands with smaller diameters, thus giving credence to MacArthur and Wilson's (1967) Target Effect, whereby larger islands serve as larger targets leading to higher immigration rates. Furthermore, the experiment revealed that islands with greater distances from the mainland contained significantly less mammal species than islands closer to the mainland. This underscored Simberloff & Wilson's (1969) proposal that islands closer to their source populations hold a larger number of organisms, while islands farther away from the mainland have less.

These results may well lead to a better understanding of mammal biodiversity patterns resulting from the study of island size and distance effects on species richness, thus adding to the cumulative knowledge of the island biogeography field within applied scientific disciplines. Furthermore, such findings may be particularly applied to conservation biology measures, which will be touched upon further in the discussion section of this report.

Literature Review

While biogeography, an older and equally integrative field, addresses the distribution of biodiversity across Earth and its oceans through various processes, the theory of island biogeography was developed in the 1960s by ecologists Robert H. MacArthur and Edward O. Wilson (MacArthur & Wilson, 1963; MacArthur & Wilson, 1967; Jenkins & Ricklefs, 2011). Both observed that not only did islands make more manageable study sites—being more condensed than mainland ecosystems—but that relationships exist between species abundance and the isolation and size of their inhabited areas (MacArthur & Wilson, 1967; Powledge, 2003).

The island biogeography theory describes how the number, or richness, of species found on islands reflects a balance, or equilibrium, between the rates upon which new species will colonize them, and the rate at which species populations on them go extinct (MacArthur & Wilson, 1967). The theory, in short, describes island and mainland distribution unevenness of species (MacArthur &

Wilson, 1967).

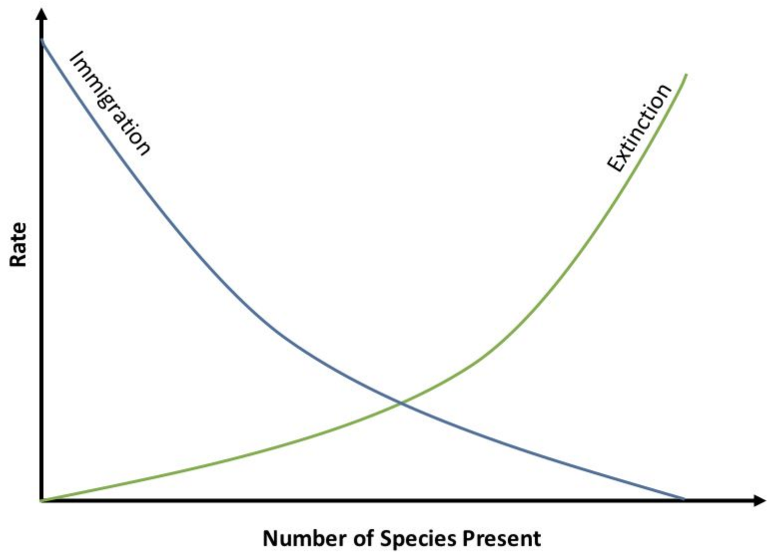


Image 1. Above graph showcasing the equilibrium model of island biogeography—new species immigration rate and resident species extinction rate compared with current resident island species. The intersection denotes species number equilibrium. Graph courtesy of Marcus Lapeyrolerie.

MacArthur and Wilson's (1967) theory of island biogeography assumes the number of species reflects dynamic equilibrium between immigration and extinction rates, that rates of immigration are determined by an island's size and its distance from the mainland, and both immigration and extinction rates are random in that species will have equal opportunities for immigration or extinction outcomes. Calow (1998) states that MacArthur and Wilson discovered a consistent relationship between the area of islands on Earth and the number of species found therein. This was also later tested and confirmed by Daniel Simberloff and Wilson through a zoogeographical experiment involving four mangrove islands located off the Florida coast (Simberloff & Wilson, 1969; Calow, 1998).

By inventorying insects and additional arthropods, both observed that closer islands held the largest species number, while more distant ones had fewer faunistic numbers (Simberloff & Wilson, 1969; Calow, 1998). Additionally, clearing island biota via methyl bromide fumigation and recording recolonization rates confirmed the Dynamic Equilibrium Theory, or total species numbers remaining consistent in spite of species composition flux (MacArthur & Wilson, 1967; Wilson & Simerloff, 1969). Since equilibrium exists between mainland colonization and species extinction on islands, immigration is then the function on an island's distance from a mainland, while extinction is the function of an island's area (Thomas & Goudie, 2016).

Following MacArthur, Wilson, and Simberloff's discoveries, additional experiments have shown basic relationships described by the island biogeography theory, observing both the size of "islands" (insular communities not necessarily surrounded by water) in relation to biodiversity and the size and fluctuations of populations in learning more about species extinction rates (Calow, 1998). Lovejoy and Oren (1981), for example, developed a Minimal Critical Size of Ecosystems Project, observing tropical rainforest patches between 1 and 1000 hectares. Following ten years, a rapid reduction in species diversity in smaller rainforest patches compared with larger ones was noted (Lovejoy & Oren, 1981; Calow, 1998). Essentially, the smaller an island, the less species supported. Or, as MacArthur and Wilson's (1967) theory predicted, island species richness increases as island area increases, suggesting habitat size impacts biodiversity.

Yet island biogeography theory has had its critics. Though Schafer (1990), for example, agrees that a correlation exists between species number and island size, he argues that additional relationships have not been effectively tested to establish it as incontrovertible. Concerning size specifically, it has been found that islands consisting of small areas still contain ranges of habitats, thus supporting wider ranges of species than previously thought (Calow, 1998).

Despite criticisms, however, island biogeography continues informing applied science, such as biodiversity loss in the Anthropocene and efforts to counter it. As Mueller-Dombois (2001) notes, the Dynamic Equilibrium Theory remains of biogeographical and ecological interest since understanding such processes will make way for an improved island biogeography theory.

Concerning variables that can impact the distribution and diversification of species on spatial and temporal bases, one primary factor is island size. As mentioned, MacArthur and Wilson discovered that the size of an island may affect the number of species found there. In short, the larger the island, the larger number of species observed (MacArthur & Wilson, 1967). A recent study by Ortiz-Lozada et al. (2020) confirms that smaller patches of rainforests acting as island models in southeastern Mexico are not as likely to host as many mammal species than larger rainforest patches, thereby informing biodiversity conservation for mammal taxa in tropical ecosystems.

The study involved a quantitative assessment of islands referred to as either protected natural areas (PNA) under threat of isolation due to heavy anthropogenic activities, or a newer system of protection in the form of privately protected areas (PPAs). Despite a high recording of 32 mammal species in a 100 hectare PPA known as the The Area for the Protection and Development of Ceratozamia, which is normal for a rainforest considering proximity to the equator, a comparison of two larger PPAs and one PNA found greater species richness, including a complete absence (and likely extinction) of large mammals of the Artiodactyla, Carnivora, and Perissodactyla Orders in the smaller PPA (Brown, 2014; Ortiz-Lozada et al., 2020).

The Ortiz-Lozada et al. study not only showcases greater mammal species richness in larger rainforest patches, but also validates what is known as the Target Effect, whereby the size of an island influences the rate of species immigration, with larger islands acting as greater targets having higher immigration rates (MacArthur & Wilson, 1967). The findings of Ortiz-Lozada et al. concerning island size and species richness coalesces with island isolation and species immigration, the latter specifically referring to an island's distance from a mainland and concomitant source population.

Stracey and Pimm (2009) put the island biogeography theory to the test by examining the visitation rates of bird taxa to British islands in order to explain decreased richness in species on both distant and smaller islands. Their study consisted of compiling datasets of bird species visiting the British islands and dividing them into five exclusive categories based on breeding grounds and migratory status (Stracey & Pimm, 2009). For species groups on each island, Stracey and Pimm were able to calculate the average number that visited annually, followed by regressing their average species number against area and distance of islands from the mainland, then comparing the average species number visiting each island with the average species number breeding on each island (Stracy & Primm, 2009).

Results showed that the average number of birds decreased as island distance from the mainland increased. Moreover, and despite no relationship between visiting species and island distance of non-European and European vagrant species, the relationship between the number of visiting species and island area remained significant in that as the area of an island increased, so too did the number of species visiting (Stracey & Primm, 2009). All told, their study confirmed MacArthur and Wilson's supposition that both island distance and island area act as determining factors for rates of species immigration, not to mention the positive correlation between the increasing area of an island and greater species richness.

Materials and Methods

To test the above-mentioned hypotheses, the following study utilized an online virtual laboratory exclusively designed for island biogeography experimentation. GoLabz, Island Biogeography New® by Thomas C. Jones (2020) includes information on MacArthur and Wilson's Island Biogeography Equilibrium, and the ability to apply virtual experimentation through the manipulation of a combination of variables for two islands with one mainland and a discrete selection of source population organisms. This includes island size in diameter (Km2), distance of the island from the mainland (Km) and concomitant source populations of different zoological taxa, habitat type (tropical, subtropical, temperate, tundra, desert), and types of species (arthropods, birds, mammals, reptiles) (Jones, 2020). For each taxon (e.g. mammals), 10 unnamed species are represented, each of which is color coded: red, orange, yellow, light green, green, light blue, blue, navy blue, purple, and pink.

The study made use of four different variables in a virtual simulation designed to test their effects on species richness, which in this case, is the total number of mammal species of two tropical islands, located off the coast of the mainland. While the two islands were used for observation in the experiment, the four variables were island diameter, island distance, immigration, and 10 species of non-volant mammals. Of those four variables, island diameter and island distance were manipulated in two experiments to determine the effects on non-volant mammal species richness. This was demonstrated by utilizing different island size parameters and different island distance parameters from the mainland.

The first experiment involved seven runs to observe tropical island diameter effects on mammal richness, measured by the total population of mammal species. Both the experimental and control island were given a set distance of 50Km from the mainland. Island 1 was experimental, while Island 2 was used as a control, with a set diameter measurement of 160Km2. Island 1 was issued diameter measurements in the following ascending order of Km2: 64, 96, 128, 160, 192, 224, 256. It should be noted that 64 and 256 were the diameter limitations. Each run was executed at 2X speed to observe mammal migration and number of island inhabitants, and was stopped once a tipping point was reached, otherwise known as a state of equilibrium where diameter changes no longer impacts mammal populations. Numbers of individual species—ranging from species 1 to species 10—were individually recorded, along with an aggregate of the total population at the end of each run. Graphs were then created based on the total population of mammal species recorded following the conclusion of each run.

The second experiment involved six runs to observe tropical island distance effects on mammal richness, measured again by the total population of mammals concluding each run. Both islands were given a set diameter of 256Km2. Island 1 was experimental, while Island 2 was used as a control with a set distance measurement of 210Km, which is the middle distance between the closest and farthest possible position from the source population. Island 1, meanwhile, was issued distance measurements in the following order in kilometers, from closest to the mainland to the maximum allowable distance away in consistent increments of 80 additional kilometers: 10, 90, 170, 250, 330, 410. Each run was executed at 2X speed to observe mammal migration and number of island inhabitants, and was also stopped once a tipping point was reached, otherwise known as a state of equilibrium where diameter changes no longer impacts mammal populations. Numbers of individual species—ranging from species 1 to species 10—were individually recorded, along with an aggregate of the total mammal population concluding each run. Graphs were then created based on the total mammal population recorded at the end of each run.

Results

Figure 1. Tropical Island Diameter Effects on Mammals Bar Graph

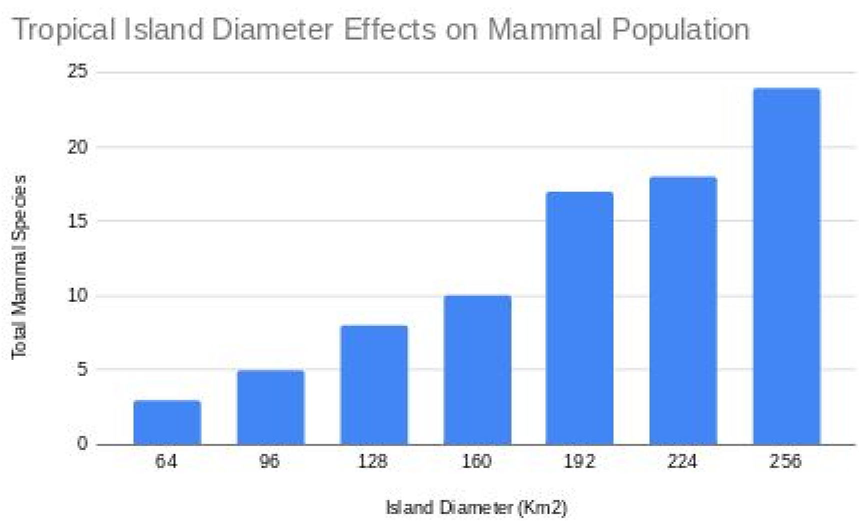


Figure 2. Tropical Island Diameter Effects on Mammals Line Graph

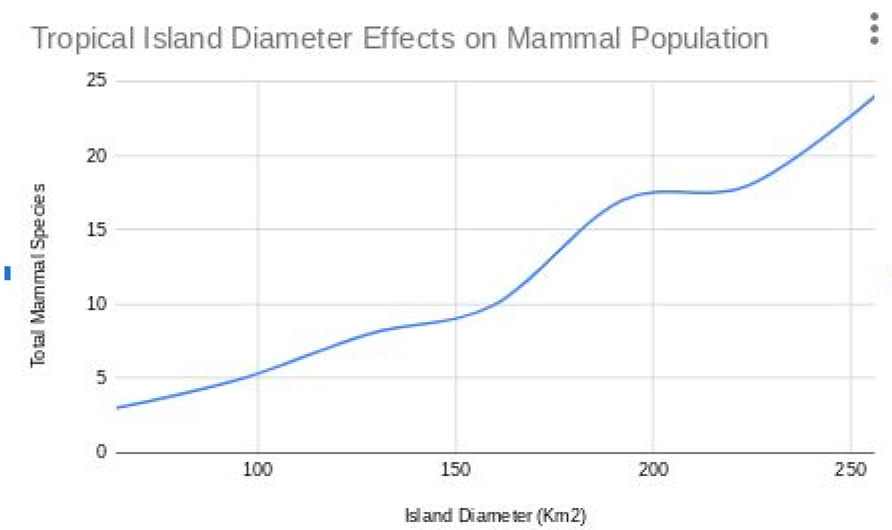


Figure 3. Tropical Island Distance Effects on Mammals Bar Graph

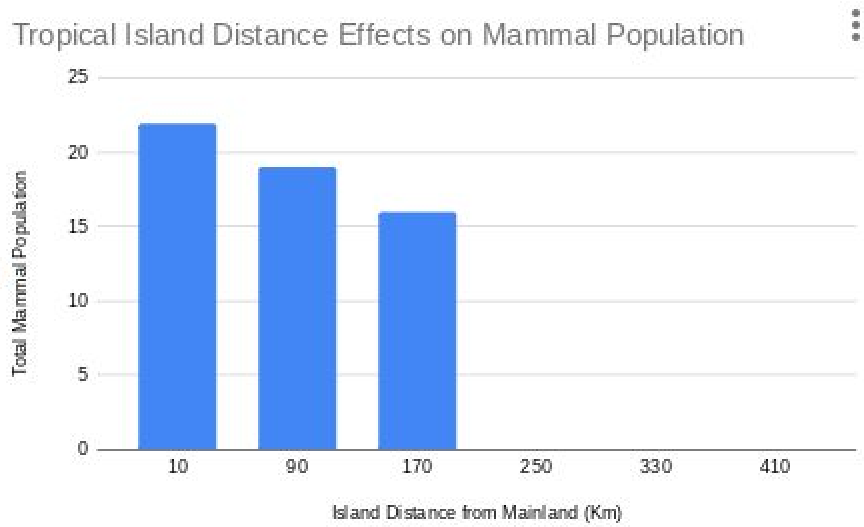
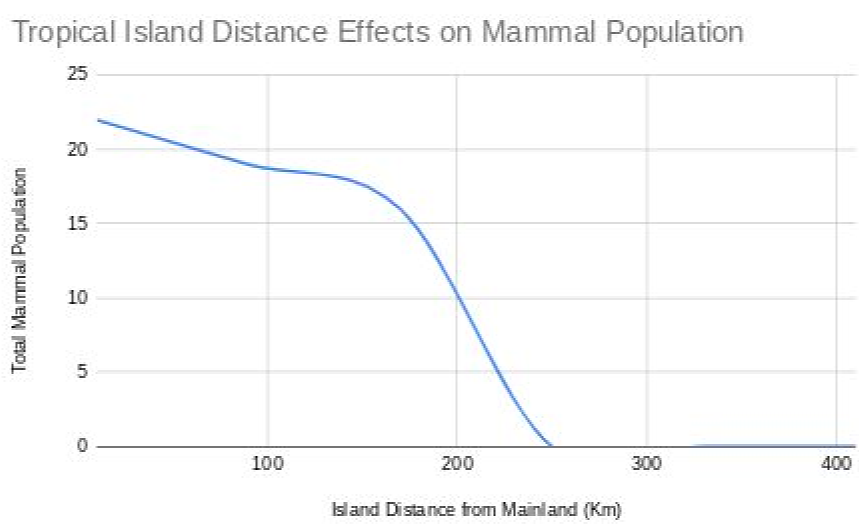


Figure 4. Tropical Island Distance Effects on Mammals Line Graph



Results from the first experiment show an increase in total mammal population as the size of the experimental island's diameter grew. Total mammal population between the first and second run rose by 66.7%. Total mammal population between the second and third run increased by 60%. Total mammal population between the third and fourth run increased by 25%. Total mammal population between the fourth and fifth run grew by 70%. Total mammal population between the fifth and sixth run saw an increase of 5.88%. Total mammal population between the sixth and seventh run rose by 41.2%.

Island distance from the mainland showed a drastic reduction in total mammal population as distance of the experimental island from the source population increased. There was a decrease of -13.64% between the first and second run, followed by a -15.8% reduction between the second and third run. The population then relaxed to an equilibrium of 0 after the fourth run, remaining at 0 through the fifth and sixth runs, representing a -100% reduction.

Discussion

Recordings show a positive correlation between an increasing island size and an increasing number of mammal species, thus confirming the first alternative hypothesis. It was found that as diameter increased, so too did the total population of mammals on Island 1 (see Figure 1 and Figure 2). Note, for example, that the percentage difference recorded between the experimental (3 species/64Km2) and control island (9 species/160Km2) on the first run was 200%, largely accounting for the extreme differences in diameters. However, as the diameter of Island 1 trended closer to the diameter of Island 2, eventually matching it, the current number of species on both islands became more consistent. For instance, the third run, with an island diameter of 128Km2 for Island 1, yielded a total number of 8 mammal species, while the fourth run, with the diameter of Island 1 matching Island 2 at 160Km2, produced a current number of mammal species at 10, an increase of 25%. Note that although the percentage increase in species number is smaller due to increasing similarity of island diameter between Island 1 and Island 2 during run one through run four, the current number of species on Island 1 still increased, eventually surpassing the number of species on Island 2.

Of note, however is the slight decrease in the average number of species, particularly on Island 1 between the second run (96Km2/4 species) and third run (128Km2/3.2 species), representing a -20% reduction in the average number of species recorded at the end of both runs (see diameter table in appendix section). This was also true for Island 1, between the fifth run (192Km2/6.9 species) and sixth run (294Km2/6.5 species), representing a -5.8% reduction in the average number of different mammal species at the end of each run. Finally, with Island 1 producing an average of 6.7 mammal species during the seventh and last run with the largest diameter (256Km2), it remained lower than the average number of species recorded at the end of the sixth run (6.9), thus representing a -2.9% reduction in the average number of species. However, there still remained an overall increase of 148% in the average number of species between the first run of Island 1 and the final run of Island 1. It is possible that these slight percentage reductions in the average number of species between runs on Island 1 are stochastic in nature. This raises additional questions regarding the impact(s) of environmental stochasticity on the average number of different mammal species that would need further exploration, possibly in a real-world scenario. Furthermore, this may potentially be attributed to one mammal species taking over a niche, thus increasing competition.

Island distance recordings strongly indicate a correlation between an increase in tropical island distance from the mainland and a reduction in mammal species, thereby supporting the alternative hypothesis. For the current number of mammal species (see Figure 3, and Figure 4 above), there was a noticeable relaxation to an equilibrium of 0 mammal species for Island 1 at the end of the fourth run, when the distance from the source population was set at 250Km, a distance of 40Km past the control island. As an example, the total number of species on Island 1 at the end of the first (10Km), second (90Km) and third run was 22, 19, and 16 species respectively. However, the current number of species dropped to 0 by the end of the fourth run and remained at 0 following the fifth and sixth runs, representing a -100% decrease between the initial value recorded at the end of the first run and the final value recorded at the end of the sixth and final run. This may be an indicator of non-volant mammals as a zoological taxa and their inability to successfully reach islands that are farther away from source populations. This is confirmed by Lawler's (1986) observation that the species numbers of terrestrial mammals found on islands are the result of an historical legacy consisting of low immigrtion rates to oceanic islands.

Regarding the average number of species recorded, there was only one increase noted as distance from the mainland increased. While the end of the second run recorded an average of 5.6 different mammal species, the end of the third run recorded an average of 6.2, an increase of 10.71% between the initial and final value. This could also be attributed to a spatiotemporal fluctuation, such as a dominant mammal species taking control of a niche as a direct result of interspecific competition.

Conclusion

Despite environmental stochasticity, applying virtual ecological modeling revealed how the diameter of tropical islands affected mammal species, as well as the impact based on distance of tropical islands from the mainland/source population. Given that mammal species richness is thought to be negatively impacted by islands both smaller in size and farther away in distance from an assumed source population, these findings underscore the importance of the establishment of additional single large reserves to preserve mammal species biodiversity. It must be stressed, however, that when considering the single large or several small (SLOSS) reserve debate, specific species protection plans must be carefully evaluated on a case-by-case basis to determine the course of action deemed best for implementation (Tjørve, 2010). While such individual cases do not necessarily preclude large reserves, applying island size and isolation to virtual mammal populations provides a baseline template by which researchers can emphasize the need for large protected areas and necessary migratory corridors. This will ensure adequate species gene flow and offset high rates of extinction, thus sustaining an ecological matrix of which mammals as indicators of ecosystem health remain an integral part.

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Appendices

Tropical Island Diameter Effects on Mammal Populations Table 1: Experimental & Control Island Recording

Mammal Species	**ISL1: 64**	**ISL2: 160**	**ISL1: 96**	**ISL2: 160**	**ISL1: 128**	**ISL2: 160**	**ISL1: 160**	**ISL2: 160**	**ISL1: 192**	**ISL2: 160**	**ISL1: 224**	**ISL2: 160**	**ISL1: 256**	**ISL2: 160**
Species 1	0	1	0	1	1	0	1	0	2	1	2	2	3	2
Species 2	0	0	0	1	1	3	1	1	2	4	3	1	2	1

Species 3	1	2	0	1	0	1	1	1	1	2	1	1	1	0
Species 4	0	1	1	2	1	2	1	1	2	0	1	0	3	0
Species 5	0	2	2	0	2	1	3	1	1	1	3	3	1	1
Species 6	1	1	1	0	1	2	2	1	1	2	3	1	5	0
Species 7	0	1	0	3	0	1	0	2	2	0	1	2	2	1
Species 8	0	1	0	0	0	2	0	1	0	1	1	1	2	0
Species 9	0	2	0	1	2	0	0	0	2	0	0	0	5	0
Species 10	1	1	1	0	0	2	1	0	4	1	3	3	0	2
Island Total	3	12	5	9	8	14	10	8	17	12	18	14	24	7

Tropical Island Diameter Effects on Mammal Populations Table 2: Experimental & Control Island Additional Data

Mammal Species	**ISL1: 64**	**ISL2: 160**	**ISL1: 96**	**ISL2: 160**	**ISL1: 128**	**ISL2: 160**	**ISL1: 160**	**ISL2: 160**	**ISL1: 192**	**ISL2: 160**	**ISL1: 224**	**ISL2: 160**	**ISL1: 256**	**ISL2: 160**
Current # Species	3	9	4	6	6	8	7	7	9	7	9	8	9	5
Average # Species	2.7	4.5	4	5.8	3.2	5.4	5	5.4	6.9	4.6	6.5	5	6.7	4.4
Time Used	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
Distance	50	50	50	50	50	50	50	50	50	50	50	50	50	50

Tropical Island Distance Effects on Mammal Populations Table 1: Experimental & Control Island Recording

Mammal Species	**ISL1: 10**	**ISL2: 210**	**ISL1: 90**	**ISL2: 210**	**ISL1: 170**	**ISL2: 210**	**ISL1: 250**	**ISL2: 210**	**ISL1: 330**	**ISL2: 210**	**ISL1: 410**	**ISL2: 210**
Species 1	4	1	2	0	2	0	0	0	0	1	0	0
Species 2	3	1	4	0	1	2	0	1	0	0	0	0
Species 3	1	0	0	0	3	0	0	0	0	0	0	0
Species 4	2	0	2	0	2	0	0	1	0	1	0	0

Species 5	2	0	3	0	0	0	0	0	0	0	0	0
Species 6	3	0	1	1	2	0	0	1	0	0	0	0
Species 7	3	1	3	0	2	1	0	0	0	0	0	1
Species 8	3	0	1	0	2	1	0	2	0	1	0	0
Species 9	0	0	2	0	0	0	0	1	0	1	0	0
Species 10	1	0	1	0	2	0	0	0	0	0	0	0
Island Total	22	3	19	1	16	4	0	6	0	0	0	0

Tropical Island Distance Effects on Mammal Populations Table 2: Experimental & Control Island Additional Data

Mammal Species	**ISL1: 10**	**ISL2: 210**	**ISL1: 90**	**ISL2: 210**	**ISL1: 170**	**ISL2: 210**	**ISL1: 250**	**ISL2: 210**	**ISL1: 330**	**ISL2: 210**	**ISL1: 410**	**ISL2: 210**
Current # Species	9	3	9	1	8	3	0	5	0	4	0	1
Average # Species	5.8	2.3	5.6	0.7	6.2	1.8	0	1.9	0	2.3	0	0.2
Time Used	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
Diameter	256	256	256	256	256	256	256	256	256	256	256	256