The Effects of Isolation on Endemic Cozumel Island Rodents: A Test of the Island Rule

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The Effects of Isolation on Endemic Cozumel Island Rodents:

A Test of the Island Rule

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ABSTRACT

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Island isolation can cause changes in body size, cranial characteristics, and genetic variation in mammals. We use geometric morphometrics to test skull and mandible shape and size change across three species of endemic Cozumel Island rodents in order to test the “island rule” of larger size in isolated rodents. We also sequenced the D-Loop and cytochrome b region of the mitochondrial genome and tested for differences in genetic variation between island and mainland groups, as well as population structure and gene flow in order to assess the effect of island isolation on these three rodents. We found that the three species of rodents showed varying degrees of size and shape differences from island to mainland with some species varying considerably and others not at all. The genetic results were similar with some species exhibiting potential founder effects, while others showed little differentiation between the island and mainland. We conclude that evolution on islands is highly conditional on the history, community composition, and biology of the colonizing species.

Keywords: island rule, geometric morphometrics, Cozumel, Reithrodontomys spectabilis, Reithrodontomys gracilis, Oryzomys couesi, Peromyscus leucopus
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INTRODUCTION

Island mammals typically exhibit shifts in body size as well as differences in cranial, skeletal and dental characteristics compared to their mainland counterparts. These morphological changes are variously referred to as the “island rule”, “island effect” or “island syndrome” which is manifested by evolution of larger size in smaller mammals and shifts to dwarfism in larger mammals (Gompper, Petrites & Lyman, 2006; Van Valen, 1973).

Lomolino (2005) assessed the generality of the island rule by comparing means of species body size of selected insular mammals to their nearest mainland counterpart. He found that the majority of changes were consistent with the island rule, in which there was a graded trend toward gigantism in smaller species and dwarfism in larger species. Lomolino (2005) hypothesized that this trend is a result of selection to converge on an optimal body size for a given species for a certain ecological strategy. He further suggested that mainland populations do not reach this optimum due to interspecific challenges and temporal and spatial variation in environmental characteristics (Case, 1978; Grant, 1965; Lomolino, 1985). Other possibilities for body size shifts on islands include ecological release, resource limitation, and immigrant selection.

Studies showing the generality of the island rule (Bromham & Cardillo, 2007; Gompper et al., 2006; Krystufek, Tvrkovic, Paunovic & Ozkan, 2009; White & Searle, 2007) have been criticized on the basis of inadequate size indices (Meiri, Dayan & Simberloff, 2006), distantly related island mainland pairs, exceedingly large islands, and phylogenetically non-independent data (Meiri, Cooper & Purvis, 2008). In response to these criticisms, Meiri et al. (2008) conducted a study comparing island and mainland conspecifics, using islands less than 50,000 km². Their analyses also favored indices based on body mass rather than other
measurements, and used only adult specimens of known sex. Meiri et al. (2008) found that evolution on islands is highly conditional on history, community composition, and biology of the colonizing species. Certain clades favor insular dwarfism (artiodactyls, heteromyids, and some carnivores) or insular gigantism (murid rodents) while others (e.g. shrews, squirrels and bats) exhibited no such tendencies. Hence, it is unclear if the island rule applies broadly across all taxonomic groups.

In addition to body size, other factors, such as body shape and genetic variation, are likely to be influenced by island isolation. Island populations have been shown to have lower levels of genetic diversity than their mainland counterparts (Frankham, 1997). According to Kilpatrick (1981) a major cause of this loss of diversity in rodents is the result of a founder event. Island evolution is likely to be more complicated than just a change in body size. To determine the effect of island isolation on not only body size, but also body shape and genetic variation, an island/mainland system of several replicated rodent species would be preferable in order to compare changes across different groups in the same system.

Cozumel Island is located approximately 18 km off the Caribbean coast of the Mexican state of Quintana Roo and is separated from the mainland by a 914 m deep channel. The island is about 36 km long and 15 km wide with an area of approximately 540 km$^2$. It has a subtropical climate with seasonal rainfall, high humidity, and nearly constant warm temperatures. The island is often impacted by hurricanes and tropical storms. The formation of Cozumel Island apparently occurred when high blocks on the Yucatán Peninsula became isolated carbonate banks at least during the late Quaternary (0.5-1 million years). Analysis of the exposed limestone on the island suggests that there have been two periods of submergence and two periods of exposure during the late Pleistocene, with the last submergence occurring about 125,000 B.P. (Spaw, 1978).
Currently, Cozumel Island has 31 endemic animal taxa including three rodents: *Reithrodontomys spectabilis* (Cozumel Harvest Mouse), *Oryzomys couesi cozumelae* (Cozumel Coues’ Rice Rat), and *Peromyscus leucopus cozumelae* (Cozumel White-footed Mouse) (Fuentes-Montemayor, Cuarón, Vazquez-Dominguez, Benitez-Malvido, Valenzuela-Galvan & Andresen, 2009).

*Reithrodontomys spectabilis* is one of the largest species in the genus, and was allied with *R. mexicanus* and *R. gracilis* of the *R. mexicanus* species group when it was first described by Jones and Lawlor (1965). Due to the great morphological differences in size between *R. gracilis* and *R. spectabilis*, Jones and Lawlor (1965) hypothesized that the two have been separated for a relatively long time, perhaps since the late Pleistocene. More recently, *R. spectabilis* and *R. gracilis* were found to be sister taxa and not closely related to *R. mexicanus* based on allozyme and mitochondrial cytochrome *b* (*Cytb*) sequence data (Arellano, Gonzalez-Cozatl & Rogers, 2005; Arellano, Rogers & Cervantes, 2003). Interestingly, *R. gracilis* was rendered paraphyletic or formed an unresolved node with *R. spectabilis* samples based on *Cytb* sequence data.

*Oryzomys couesi cozumelae* (Merriam, 1901) was originally regarded as a species-level taxon, but later was relegated to subspecific rank as *O. couesi cozumelae* (Jones & Lawlor, 1965). It differs from mainland populations currently regarded as *O. c. couesi* by overall larger external size. The cranial differences between these two forms are considered minor (Engstrom, Schmidt, Morales & Dowler, 1989). It was also demonstrated that *O. c. cozumelae* exhibits high genetic and allelic diversity which is in contrast with what is expected from island animal populations (Vega, Vazquez-Dominguez, Mejia-Puente & Cuarón, 2007).

*Peromyscus leucopus cozumelae* (Merriam, 1901) was originally described as a species but later was regarded as a subspecies of *P. leucopus* by Osgood (1909). In 1984 it was the most common small mammal found on the island (Engstrom et al., 1989). However it has not been
captured since 2001 (Fuentes-Montemayor et al., 2009). It differs from its mainland counterpart (\textit{P. l. casteneus}) by overall larger external and cranial size, as well as heavier teeth (Jones & Lawlor, 1965).

These three endemic Cozumel Island rodents each exhibit a general size increase when compared to their mainland counterparts and generally adhere to the island rule; however, only \textit{Reithrodontomys spectabilis} is regarded as specifically distinct. This likely is due to the greater morphological differences between \textit{R. spectabilis} and \textit{R. gracilis} compared to observed morphological differences in \textit{Oryzomys couesi} and \textit{Peromyscus leucopus} island/mainland populations.

Recently, researchers have used geometric morphometrics to detect and quantify differences in size and shape (Barciova & Macholan, 2006; Nagorsen & Cardini, 2009; Nunes, Piorski & De Araoujo, 2008; Rohlf & Marcus, 1993). This tool allows researchers to detect morphological differences that previously were difficult to measure and compare. Morphometrics itself is the study of shape variation and its covariation with other variables (Adams, Rohlf & Slice, 2004; Bookstein, 1991; Dryden & Mardia, 1998). Investigators have used this technique to compare interspecific changes in skulls (Cardini, 2003; Corti, Aguilera & Capanna, 2001; McNulty, 2004). In addition, researchers have used geometric morphometrics to compare and contrast island populations from mainland populations (Nagorsen & Cardini, 2009; White & Searle, 2008).

Here, we use geometric morphometrics to compare skull and mandible shape and size of the three island rodents to their mainland counterparts in order to explore the “influence” of island isolations on these three rodent pairs. Should the island rule apply broadly, one could predict that all three rodents would change in skull size. Therefore, we predict that all three
rodent species will have larger skulls compared to those on the mainland. However, it is unknown whether we should expect identical shape changes across all three pairs of taxa. In addition, because populations of endemic rodents are isolated on Cozumel Island we predict that these populations will have experienced a loss of genetic diversity, genetic bottlenecks, and higher inbreeding, or a combination of all these when compared to their mainland counterparts. To test this prediction, we sequenced two parts of the mitochondrial genome (cytochrome b and the D-loop or control region), and compared diversity measurements. We are also interested in determining how population genetic structuring differs between island and mainland rodents and we predict island populations should also have a more structured population and reduced or no gene flow with adjacent populations on the Yucatan Peninsula. Unlike other island studies, this study will be able to quantify the “island effect” in skull/mandible shape, size, and genetic variation across three pairs of differing species isolated on the same island, which will help identify any common differences that may come from the island.

MATERIALS AND METHODS

Geometric Morphometrics

Skulls and mandibles of *R. gracilis*, *R. spectabilis*, *O. couesi*, and *P. leucopus* from the Yucatan Peninsula and Cozumel Island were obtained through Angelo State University and the University of Kansas (Appendix 1). A total of 322 specimens were analyzed. This included 106 *O. couesi* (46 island samples, 60 mainland samples), 120 *P. leucopus* (96 island samples, and 24 mainland samples), and 96 *Reithrodontomys* (31 island samples, 61 mainland samples (Figure 1, Figure 2, Figure 3). Individuals included in all analyses were adults, evidenced by completely fused skulls and fully erupted teeth.
We captured images of the mandible and dorsal and ventral views of the skull using a Nikon D50 Digital SLR camera with a 60 mm f/2.8D AS Micro-Nikkor lens at a resolution of 3008 x 2000 pixels. Landmarks were collected using the TPSdig software (Rohlf, 2008) and were determined to be homologous across the three genera of rodents examined. Thirteen landmarks were chosen for the dorsal view of the skull (Table 1 and Figure 4a). Landmarks 11 and 9 were designated semilandmarks because we were only interested in the variability in the breadth of these landmarks. For the ventral view of the skull, 19 landmarks were chosen with points 13 and 14 designated as semilandmarks (Table 2 and Figure 4b). Due to the bilateral symmetry of skulls, only half of the skull was landmarked. This limited any redundant information. Twelve landmarks were chosen for the mandible (Table 3 and Figure 4c). Landmarks were chosen to highlight potential functional areas of the skull/mandible that could be most easily influenced by environmental factors (i.e. toothrow) (Cardini, 2003; Klingenberg, Leamy & Cheverud, 2004).

The shape of an object is the variation that remains after the object has been moved, rotated, enlarged, or reduced (Bookstein, 1998). TPSrelw (Rohlf, 2008) was used to dismiss any non-shape variation by using Generalized Procrustes Analysis (GPA) for superimposition. The slide method was set to chord min- $d^2$ and a consensus view was obtained.

Relative warps were then calculated from a principal components analysis to allow multidimensional information to be more easily viewed. For the dorsal view, 22 relative warps were retrieved and the first 15 were used in the analysis. Of these, the first two warps contained 66.56% of the informative shape change. For the ventral view, 34 relative warps were retrieved and the first 15 were used in the analysis, with the first two describing 56.14% of the shape
change. For the mandible, 20 relative warps were obtained and the first 12 were used in the analysis with the first two describing 61.97% of the shape change.

Shape variation was analyzed with a multivariate mixed model using proc MIXED in SAS (2008). Because relative warps are orthogonal and ordered, they can be treated as repeated measures with the use of an index variable. The identifying order number of the relative warps was treated as an index variable and included in the mixed model analysis. This was done according following Hassell, et al. (2012), and Wesner, et al. (2011). Main effects included island/mainland, male/female, and species. All interactions among main effects were included in the analysis. The interaction between main effects and the index variable provides the most direct test of our hypothesis because the index variable tests for differences in shape on each of the relative warps independently (Wesner et al., 2011). In addition to the statistical assay on shape change, and in order to view size only variation, a paired t test was performed on the centroid sizes from each species pair in order to assess any size difference between island/mainland pairs.

**Molecular Analyses**

DNA sequences of the mitochondrial cytochrome b (cyt-b) and the D-loop were used to assess the amount of genetic variation present both between and among island/mainland counterparts. Mitochondrial DNA (mtDNA) has been the genetic marker most often used in comparing within and among population variation in mammals (Searle, Jamieson, Gunduz, Stevens, Jones, Gemmill & King, 2009). When compared to nuclear genes, there is evidence that mtDNA acts as a good marker for a first colonization event (Searle et al., 2009). Moreover due to its maternal inheritance, high mutation, rate, single-copy orthologous genes, and lack of
recombination this gene is appropriate for evolutionary studies focusing within or among correlated species (Larizza, Pesole, Reyes, Sbisa & Saccone, 2002) such that it has become the marker of choice for many systematists (Bradley & Baker, 2001). The D-Loop region, located between the genes tRNA$^{\text{Phe}}$ and tRNA$^{\text{Pro}}$, is the main non-coding region in mtDNA (Fernandez-Silva, Enriquez & Montoya, 2003), and exhibits high within-species variability (Forster, Gunduz, Nunes, Gabriel, Ramalhinho, Mathias, Britton-Davidian & Searle, 2009). The D-loop region is especially well suited for this study due to its high variability even among members of the same species and subspecies (Larizza et al., 2002; Searle et al., 2009). As a result, species-specific evolution is evident in this region (Pesole, Gissi, De Chirico & Saccone, 1999).

Tissues were obtained by loan from Angelo State University and the Royal Ontario Museum (Appendix 1). Sequence data were obtained from 290 individuals, including 38 samples of *Reithrodontomys spectabilis*, 48 samples of *Reithrodontomys gracilis*, 126 samples of *Oryzomys couesi* (25 from the island, 101 from the mainland), and 72 samples of *Peromyscus leucopus* (68 from the island, 4 from the mainland). All mainland samples of *R. gracilis* and *O. couesi* were restricted to the greater Yucatan Peninsula. Because of the lack of Yucatan Peninsular samples for *Peromyscus leucopus* we included six more samples from outlying regions in Mexico (see Figure 1, Figure 2, Figure 3).

Whole genomic DNA from each individual was extracted from tissue either frozen or preserved in 95% ethanol using the Qiagen DNeasy™ Tissue Kit (Cat. No. 69504), and the Qiagen QIAamp™ DNA Micro Kit (Cat. No. 56304). PCR was used to amplify the entire cyt b gene (1143 bp) using primers MVZ-05-M (5’ - CTT GAT ATG AAA AAC CAT CGT TG – 3’) with MVZ-14-M (5’ - CTT GAT ATG AAA AAC CAT CGT TG – 3’) (Smith & Patton, 1993). Internal primers included MVZ 16 (5’-TAG GAA RTA TCA YTC TGG TTT RAT – 3’), MVZ
45 (5’-GTH ATA GCH ACA GCA TTY ATA GG-3’) (Smith & Patton, 1993), CB40 (5’ - GCT TTG GGT GCT GGT GGT GG – 3’) (Hanson & Bradley, 2008), and F1 (5’ - TGA GGA CAR ATA TCH TTY TGR GG – 3’) (Whiting, Bauer & Sites, 2003). The mtDNA control region for *Reithrodontomys* (873 bp) and *Peromyscus* (933 bp) was amplified using the primers LGL283mod (5’ – TAC NCT GGT CTT GTA AAC C – 3’) (modified from (Bickham, Patton & Loughlin, 1996), and H21 (5’ – GCA TTT TCA GTG CTT TGC TT – 3’) (Yasuda, Vogel, Tsuchiya, Han, Lin & Suzuki, 2005). When the primers above were used for the samples of *Oryzomys couesi*, the PCR product yielded bright bands, but the sequences returned were double peaked, possibly due to the presence of a pseudogene. Therefore primers designed specifically for this study were used to amplify the control region of *Oryzomys couesi* (652 bp): OCF (5’ – GCT TTG GGT GCT GGT GGT GG – 3’) and OCR (5’ – GCC TTG ACG GCT ATG GTG AG – 3’) and produced single peaks when sequenced. The PCR protocol for the control region primers LGL283mod and H21 included an initial denaturation at 94°C (5 min), 35 cycles with denaturation at 93°C (30 sec), annealing 51°C (1 min), extension at 72°C (1 min 30 sec), and a final extension cycle of 72°C (7 min). The PCR protocol for primers OCF and OCR included an initial denaturation at 93.5°C (1 min), 35 cycles with denaturation at 93.5°C (40 sec), annealing 58°C (40 sec), extension at 72°C (2 min 40 sec), and a final extension cycle of 72°C (2 min).

The resulting polymerase chain reaction products were purified using a Millipore Multiscreen™ 96-Well Filtration System (Cat. NO. MANU03050). Sequencing was performed using the Applied Biosystems Big Dye v.3.1 Dye Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems, Foster City, CA). Excess dye terminator was removed using Millipore Multiscreen™ Filter Plates for High Throughput Separations (Cat. NO. MAHVN4510). Sequences were determined using the Perkin-Elmer ABI Prism 377 housed at
Brigham Young University. Sequences were then edited manually using the original chromatograph data in the program Geneious (http://www.geneious.com/; Bradley, Edwards, Carroll & Kilpatrick, 2004) version 5.6.5. The resulting sequences were aligned with the MAFFT v. 1.3 software (Katoh, Misawa, Kuma & Miyata, 2002). The aligned sequences were further examined using Mesquite v. 2.73 (Maddison & Maddison, 2010).

*Population Genetic Analyses*

We predicted island populations would possess lower levels of population diversity than mainland populations. To test this prediction we calculated nucleotide diversity $\pi$ (Tajima, 1993), $\theta (\pi)$ (Tajima, 1983), and $\theta (S)$ (Watterson, 1975) using Arlequin v. 3.5.1.2 (Excoffier et al., 2005). Input files for Arlequin were created using Dnasp v. 5 (Librado & Rozas, 2009). Due to the likelihood of sampling error, standard deviations for all diversity measurements were calculated in Arlequin (Excoffier et al., 2005). The standard deviation of nucleotide diversity $\pi$ was calculated according to Tajima (1993), Watterson’s estimate ($\theta (S)$) as per Tajima (1989) and $\theta (\pi)$ by Nei (1987).

To assess the degree of genetic variation among mainland and island populations, F statistics were calculated using a hierarchical analysis of molecular variance (AMOVA) as implemented in Arlequin (Excoffier et al., 2005). Corresponding probabilities were inferred with 10 000 permutations. We also calculated the genealogical sorting index (gsi) of Cummings et al. (2008). This analysis measures the degree of exclusive ancestry on labeled groups of a rooted tree. This is done using a statistical method to estimate the accumulated genetic ancestry of a group in one or more trees, with the null hypothesis being that labeled groups form a single group of mixed genealogical ancestry. Gsi enables one to test the hypothesis of significant
genealogical divergence at a given locus before monophyly is achieved, and thus allows us to see the amount of genealogical divergence between Cozumel island populations and mainland populations. If the two populations have been separated for a long period of time, the divergence between them should be high. The relative degree of ancestry is measured on a scale from 0 to 1, where 1 indicates complete monophyly. A maximum likelihood tree was computed using PhyML 3.0 web based software (Guindon, Dufayard, Lefort, Anisimova, Hordijk & Gascuel, 2010). The substitution model parameters were: HKY85 model, empirical equilibrium frequencies, estimated transition/transversion ratio, fixed proportion of invariable sites, and estimated gamma shape parameter.

If the Cozumel island populations were separated from the mainland by a single vicariant event with no subsequent dispersal from mainland source populations to the island, gene flow should have ceased at that time. We estimated \( M = m/\mu \) (migration per generation) with the program IMa2 (Hey & Nielsen, 2007) which implements a Markov chain Monte Carlo coalescent approach. IMa2 was chosen due to the fact that the divergence between island and mainland could have occurred relatively recently. IMa2 is known to deal well with recently diverged populations and the analysis is robust even faced with violations of the IM model (Strasburg & Rieseberg, 2010). To obtain demographic rates for mutation rate scaled parameters, a 7.5-12% per million year substitution rate for cyt-b was used (Arbogast, Browne & Weigl, 2001). The substitution for the control region was 5.56e-8 ± 2.02e-8/year (Goios, Pereira, Bogue, Macaulay & Amorim, 2007). For IMa2 analyses, the generation time was set to 1 year, the inheritance scalar to 0.25, and the HKY model of evolution was selected. Preliminary runs were used to determine the starting values of prior distribution. For each analysis, two final runs were conducted with different random seeds, setting prior values to \( m = 2, t = 100.88 \), and \( q = 300 \). A
geometric heating scheme was adopted using 20 chains for 50000 steps after a burn in of 1000 steps. Independent runs produced similar posterior distributions with effective sampling sizes >100 indicated that the parameters had reached stationary distribution.

RESULTS

Geometric Morphometrics

According to the paired t-test, *Reithrodontomys spectabilis* was significantly larger in size than *R. gracilis* in all three skull views. *Peromyscus* exhibited a significant size difference in only in the dorsal view of the skull, while *Oryzomys* did not differ significantly in size in any view (Table 7).

In views of both the skull and the mandible, shape varied significantly by taxon and by island/mainland location with significant interaction between the two (Table 4, Table 5, Table 6). Sex was not a significant effect within species across island/mainland. Therefore, sexes were pooled in subsequent analyses.

*Reithrodontomys spectabilis* is significantly different from *R. gracilis* in the dorsal view of the skull on both relative warps from island to mainland indicating dramatic changes in skull shape. *Oryzomys* differs significantly only along RW1. Island and mainland *Peromyscus* is not significantly different in either warp (Figure 5A). The main shape change in the skull is across RW1, with a shift in the zygomatic arch from point of curvature to point of greatest breadth. With RW2, of which only *Reithrodontomys* differed significantly, there is a slight shift forward in the nasal region.

In the ventral view of the skull, *Oryzomys* differed significantly in RW2, while *Reithrodontomys* and *Peromyscus* differed significantly in only RW1 (Figure 5B). Both island
Reithrodontomys and Peromyscus moved in the same spatial direction along RW1 compared to mainland samples. The response was similar in the dorsal view of the skull. The shape change among all three rodent skulls in RW1 can be described as a compression of the central area of the skull from mainland to island. On RW2, the toothrow on the mainland samples is more expanded than those on the island.

There were also taxon specific differences between RW1 and RW2 for the mandible. Reithrodontomys was significantly different in both RW1 and RW2, Peromyscus differed significantly in RW1, and Oryzomys was not significantly different in either relative warp. Peromyscus and Reithrodontomys moved in the same spatial direction from mainland to island (up and left) while Oryzomys moved down and left (Figure 5C). The change from mainland to island on RW1 was characterized by an elongation of the coronoid process and larger breadth of the posterior portion of the mandible. With RW2, from mainland to island, the coronoid process is shifted up and back, while the curvature of the ramus is moved toward the anterior portion of the mandible.

Molecular Analyses

In all diversity measurements, island populations of Peromyscus leucopus and Reithrodontomys exhibited significantly less diversity than their mainland counterparts. There were no significant differences between island and mainland populations of Oryzomys for cyt-b θ (π), and cyt-b nucleotide diversity π (Table 8).

The results of the pairwise Fst and gsi analysis indicate both Reithrodontomys and Oryzomys have less genetic structure on the island compared to the mainland (Table 9). This is in contrast to Peromyscus leucopus which has a higher Fst value, indicating a more structured
island population. Gsi values for all island populations were higher than their mainland counterparts. *P. l. cozumelae* had an estimated gsi of 1 indicating complete monophyly. *Reithrodontomys spectabilis* had a gsi of 0.9092, indicating strong support for island monophyly. *O. c. cozumelae* had the lowest gsi estimate (0.636).

IMa2 analysis under the isolation with migration coalescence model produced well resolved marginal posterior probability distributions of all parameters. The three genera showed varying amounts of gene flow between island and mainland (Table 10). Both *Peromyscus* and *Reithrodontomys* had larger gene flow estimates going from the island to the mainland, while gene flow estimates from the mainland to the island were higher for *Oryzomys*. However, when 95% confidence intervals were included, the difference between island and mainland gene flow estimates was not significant. Likewise, 95% confidence intervals indicate there are no significant differences in gene flow estimates among the three genera.

**DISCUSSION**

*Geometric Morphometrics*

The island rule predicts that small sized mammals evolve larger sizes when isolated on an island. However, whether or not this may also affect skull and mandibular shape has not been evaluated. *Reithrodontomys spectabilis* exhibited the most dramatic shape change across all three views of the skull and mandible when compared to *R. gracilis*. The shape of the skull and mandible of *R. spectabilis* is significantly different in all three views in at least one relative warp. Both *Peromyscus* and *Oryzomys* have also experienced some shape change from mainland to island, however, both have instances wherein they have not significantly changed in shape. For example, *Oryzomys* differs from island to mainland in the skull but not mandibular shape, while
*Peromyscus* differs from island to mainland in the ventral view of the skull and in the shape of the mandible.

Shape change in the skulls and mandibles of isolated island rodents is a pattern that has been observed by other researchers. For example Nagorsen et al. (2003), found that marmot mandibles from Vancouver Island, British Columbia, Canada, had dramatically changed shape in a relatively short amount of time. These findings support those of Millien (2006), in which it is found that insular mammals undergo more rapid evolutionary changes in linear measurements when compared to mainland populations.

There was a difference in the direction and magnitude of the shape change within *Oryzomys* when compared with the other two rodents. In all three views, both *Peromyscus* and *Reithrodontomys* displayed a similar shift in direction and magnitude between mainland and island populations. For example, in the dorsal view, both *Reithrodontomys* and *Peromyscus* moved to the upper right quadrant with the greatest change in RW2, although the shape change in *Peromyscus* is not significant. In contrast, *Oryzomys* shifted center right with the greatest change in RW1. In the ventral view with *Reithrodontomys* and *Peromyscus* moved center right with the greatest change in RW1, while *Oryzomys* shifted lower center with the greatest change in RW2. A similar pattern is evident for the mandible in that *Reithrodontomys* and *Peromyscus* exhibited similar shape changes relative to *Oryzomys*.

Size differences between island and mainland forms seem to be linked with amount of change in the shape. The size change is significantly different for *Reithrodontomys*, marginally different for *Peromyscus* and not evident for *Oryzomys*. This follows the shape change in that island *Reithrodontomys* have changed in size the most, island *Peromyscus* are
only slightly larger, and there are no significant differences between island and mainland

*Oryzomys*.

In addition, it is interesting that *Reithrodontomys*, although more distinct in shape and size, shares a similar pattern of change with *Peromyscus* and not *Oryzomys*. *Reithrodontomys spectabilis* usually does not occur in the same habitat as *P. l. cozumelae* and, in fact, is more often found with *O. c. cozumelae* (Engstrom et al., 1989; Jones & Lawlor, 1965). However both *Reithrodontomys* and *Peromyscus* are more ecologically similar in terms of diet when compared to *Oryzomys* which could lead to the covarying shape change. This similar direction of change in size and shape may also be due to phylogenetic constraint because *Reithrodontomys* and *Peromyscus* share a more recent common ancestor (both are in the subfamily Neotominae) relative to *Oryzomys*, which is in the subfamily Sigmodontinae.

*Molecular Analyses*

Insular rodent populations often exhibit unique genetic signatures. It has been found that these isolated rodent populations generally exhibit lower levels of genetic diversity (Frankham, 1997). Often this relatively low level of genetic diversity is attributed to a founder event, population bottleneck, severely reduced level of gene flow, or a combination of these factors (Kilpatrick, 1981). For example, Abdelkrim, et al. (2005) observed that ship rats exhibited lower levels of genetic diversity on the Guadeloupe Archipelago and even lower levels on islands surrounding the main island of Guadeloupe. Our study found that two of the three Cozumel Island rodents exhibited lower levels of genetic diversity than their mainland counterparts.

*Oryzomys couesi* was not significantly lower in genetic diversity as estimated by two out of the six diversity measurements. An earlier study using five microsatellite loci found that
Oryzomys couesi from the island did not have lower levels of genetic diversity (Vega et al., 2007). This could indicate that O. couesi cozumelae has a unique evolutionary history when compared to Reithrodontomys spectabilis or Peromyscus leucopus cozumelae. However, despite this exception, generally these rodents have undergone a reduction in genetic diversity presumably due to their insular nature.

In addition to their low levels of genetic diversity, the three rodents follow another island pattern in having a distinct population structure. The Fst results from Arlequin show an Fst value significantly different from zero for all three pairs of species. This is in support of other findings, for example, Peromyscus keeni was found to exhibit higher levels genetic distinction when isolated in the Alexander archipelagos (Lucid & Cook, 2004).

The gsi results also support a highly structured island population. All three island species exhibited higher gsi values, indicating island populations more genetically homogeneous when compared to their mainland counterpart populations. The high gsi value estimated for P. l. cozumelae indicates that this form is monophyletic compared to the mainland populations. However, this result may reflect the inclusion of P. leucopus samples from outside the Yucatan Peninsula. R. spectabilis also displays a very high gsi which supports island monophyly. O. c. cozumelae did have a higher gsi than O. couesi from the mainland, but was much lower when compared to P. l. cozumelae and R. spectabilis. This indicates that O. c. cozumelae is in an earlier stage of lineage sorting compared to P. l. cozumelae and R. spectabilis.

Because Cozumel Island is 18 km off the coast and is separated from the mainland by a 914 m deep channel, it is expected that the island fauna have reduced or no gene flow with the mainland. The gene flow results from this analysis are inconclusive. The exact amount of gene flow may be difficult to recover due to a recent divergence event. Because gene flow varies from
low to high amounts (e.g. for *Oryzomys*, lowest mainland to island measurement at 0.0, and highest measurement at 0.7410), this indicates that a potential recent divergence is causing the divergence and gene flow measurement to become entangled (Runemark, Hey, Hansson & Svensson, 2012). There may not have been enough time for gene flow to shape divergence.

**CONCLUSIONS**

*Reithrodontomys spectabilis*, *Oryzomys couesi cozumelae*, and *Peromyscus leucopus cozumelae*, have likely been separated from the Yucatan Peninsula only recently, at the longest 125,000 YBP (Spaw, 1977). Despite this relatively recent split, all three island forms have undergone changes in both size and shape of the skull and mandible and show changes in genetic structuring consistent with founder events and reduction in gene flow. *R. spectabilis* is more distinct, both genetically and morphologically, when compared to its mainland sister taxon *R. gracilis*. There is significant shape change throughout the skull and a well as a significant change in size. Genetically, *R. spectabilis* is much lower in diversity than *R. gracilis*. When *R. spectabilis* and *R. gracilis* are included in a phylogenetic analysis of *cyt-b* sequence data which included all *Reithrodontomys* species from Middle America, *R. gracilis* was rendered paraphyletic or formed an unresolved node with samples of *R. spectabilis* (Arellano et al., 2005). This means that, despite its morphological distinctness, *R. spectabilis* has not yet achieved monophyly with respect to *R. gracilis* for a relatively fast evolving gene. The gsi analyses supports this finding but also illustrates that there is a significant genealogical divergence between *R. spectabilis* and *R. gracilis* despite the fact that *R. spectabilis* is not yet monophyletic with respect to *R. gracilis*. This supports the hypothesis that *R. spectabilis* is a recent derivative
of *R. gracilis*. Overall, *R. spectabilis* follows the “island rule” predictions: larger size, and less genetic diversity.

The morphological evidence presented herein supports the recognition of *Reithrodontomys spectabilis* as a distinct species on the basis of differences in both size and shape of the skull and lower mandible. This larger size and change in shape could be due to a longer separation from the mainland population. It is not surprising that a size and shape change has occurred as small mammals have been known to change in shape and size in a very short amount of time (Nagorsen & Cardini, 2009; Pergams & Lacy, 2008; Pergams & Lawler, 2009; Smith & Patton, 1988).

*Peromyscus leucopus cozumelae* also follows “island rule” expectations in that *P. l. cozumelae* exhibits lower genetic diversity and high genetic structure than *P. leucopus* from the mainland. There is an increase in size from island to mainland, but only in certain areas of the skull and mandible and not of the same magnitude as *R. spectabilis*. The fact that *P. leucopus* follows a similar shape trajectory as *Reithrodontomys* is intriguing as it is likely due to shared ecology or phylogenetic constraint between the two island forms (Engstrom et al., 1989).

*Oryzomys couesi cozumelae* seems to be the least distinct relative to its mainland counterpart and when compared with *R. spectabilis* and *P. l. cozumelae*. It experienced shape change from mainland to island, but not in the same direction or magnitude as the other two genera as there is no significant difference in size between island and mainland *O. couesi* samples. It also does not unequivocally follow the lower genetic diversity expected from island populations. This includes genetic assays from other research on microsatellites (Fuentes-Montemayor et al., 2009). *O. c. cozumelae* does not appear to conform to the “island rule.”
The varying responses of these three rodents may likely be due to length of divergence. Perhaps *R. spectabilis* is derived from *R. gracilis* that colonized Cozumel Island prior to the appearance of *P. l. cozumelae* and *O. c. cozumelae* with the longest date of separation being about 125,000 B.P which is the latest date of island submergence (Spaw, 1977). *Oryzomys couesi* is known to be semi aquatic and therefore, could traverse the channel between the mainland and island more effectively than either *Reithrodontomys* or *P. leucopus*. Unfortunately, the IMa2 analysis of gene flow was unable to detect significant differences in gene flow between the three groups.

Meiri (2008) proposed that the island rule does not apply as generally as previously thought. In fact, it may even be clade specific rather than size specific (Meiri et al., 2008). Our results support this conclusion. The “island rule” may be more based on each species evolutionary history rather than a general rule. This is the first study that has compared three different taxa isolated on this same island. The response to isolation was different for all three lineages in term of both morphology and genetic composition. Only *R. spectabilis* followed the island rule of greater size while *P. l. cozumelae* and *O. c. cozumelae* did not. These findings are in line with the findings of Meiri et al. (2008) in which evolution on islands is highly conditional on the history, community composition, and biology of the colonizing species.
REFERENCES


Table 1 – Definition and numbering of dorsal cranial landmarks

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Anterior tip of the nasals</td>
</tr>
<tr>
<td>2</td>
<td>Posterior suture of the nasals with the midline</td>
</tr>
<tr>
<td>3</td>
<td>Suture of the midline with posterior suture of the frontals</td>
</tr>
<tr>
<td>4</td>
<td>Point of contact with midline and anterior portion of the interparietal</td>
</tr>
<tr>
<td>5</td>
<td>Level with the midline, the posterior suture of the interparietal</td>
</tr>
<tr>
<td>6</td>
<td>Furthest point of curvature of the skull</td>
</tr>
<tr>
<td>7</td>
<td>Posterior contact of squamosal and parietal</td>
</tr>
<tr>
<td>8</td>
<td>Point of entry of zygomatic arch</td>
</tr>
<tr>
<td>9</td>
<td>Greatest breadth of zygomatic arch</td>
</tr>
<tr>
<td>10</td>
<td>Interorbital constriction</td>
</tr>
<tr>
<td>11</td>
<td>Slope at anterior portion of zygomatic arch</td>
</tr>
<tr>
<td>12</td>
<td>Zygomatic notch</td>
</tr>
<tr>
<td>13</td>
<td>Anterior contact of nasals and premaxillaries</td>
</tr>
<tr>
<td>Landmark</td>
<td>Description</td>
</tr>
<tr>
<td>-----------</td>
<td>------------------------------------------------------------------</td>
</tr>
<tr>
<td>Landmark 1</td>
<td>Anterior tip of the nasals</td>
</tr>
<tr>
<td>Landmark 2</td>
<td>Anterior sagittal intersection of the incisive alveola</td>
</tr>
<tr>
<td>Landmark 3</td>
<td>Anterior end of the incisive foramen</td>
</tr>
<tr>
<td>Landmark 4</td>
<td>Posterior end of the incisive foramen</td>
</tr>
<tr>
<td>Landmark 5</td>
<td>Posterior end of the suture of the palatines</td>
</tr>
<tr>
<td>Landmark 6</td>
<td>Level with the midline, the suture of the occipital and basisphenoid</td>
</tr>
<tr>
<td>Landmark 7</td>
<td>Anterior limit of the foramen magnum</td>
</tr>
<tr>
<td>Landmark 8</td>
<td>Most posterior point on the occipital</td>
</tr>
<tr>
<td>Landmark 9</td>
<td>Furthest point of curvature of the skull</td>
</tr>
<tr>
<td>Landmark 10</td>
<td>Insertion of the auditory meatus</td>
</tr>
<tr>
<td>Landmark 11</td>
<td>Tip of the Eustachian tube</td>
</tr>
<tr>
<td>Landmark 12</td>
<td>Point of entry of zygomatic arch</td>
</tr>
<tr>
<td>Landmark 13</td>
<td>Greatest breadth of zygomatic arch</td>
</tr>
<tr>
<td>Landmark 14</td>
<td>Slope at anterior portion of zygomatic arch</td>
</tr>
<tr>
<td>Landmark 15</td>
<td>Anterior most protuberance of the maxillary</td>
</tr>
<tr>
<td>Landmark 16</td>
<td>Anterior extremity of the toothrow</td>
</tr>
<tr>
<td>Landmark 17</td>
<td>Posterior extremity of the toothrow</td>
</tr>
<tr>
<td>Landmark 18</td>
<td>Upper extremity of the toothrow</td>
</tr>
<tr>
<td>Landmark 19</td>
<td>Lower extremity of the toothrow</td>
</tr>
<tr>
<td>Landmark 1</td>
<td>Upper extreme anterior part of the incisor alveolus</td>
</tr>
<tr>
<td>--------------</td>
<td>------------------------------------------------------</td>
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<tr>
<td>Landmark 2</td>
<td>Anterior extremity of the maxillary toothrow</td>
</tr>
<tr>
<td>Landmark 3</td>
<td>Anterior point of curvature of the coronoid process</td>
</tr>
<tr>
<td>Landmark 4</td>
<td>Tip of the coronoid process</td>
</tr>
<tr>
<td>Landmark 5</td>
<td>Sigmoid notch</td>
</tr>
<tr>
<td>Landmark 6</td>
<td>Anterior tip of the condyle</td>
</tr>
<tr>
<td>Landmark 7</td>
<td>Tip of the condyle</td>
</tr>
<tr>
<td>Landmark 8</td>
<td>Posterior tip of the condyle</td>
</tr>
<tr>
<td>Landmark 9</td>
<td>Greatest curvature point between angular process and posterior tip of the condyle</td>
</tr>
<tr>
<td>Landmark 10</td>
<td>Posterior extremity of the angular process</td>
</tr>
<tr>
<td>Landmark 11</td>
<td>Greatest point of curvature of the ramus</td>
</tr>
<tr>
<td>Landmark 12</td>
<td>Lower extreme posterior part of the incisor alveolus</td>
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Table 3 – Definition and numbering of mandibular landmarks
Table 4 – Results of the multivariate mixed model analysis for the dorsal view of the skull.

<table>
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<td>Island/Mainland</td>
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Table 5 – Results of the multivariate mixed model analysis for the ventral view of the skull

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Table 6 – Results of the multivariate mixed model analysis for the mandible view.

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<td>Centroid size x Index variable</td>
<td>10.23</td>
<td>11, 1232</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>
Table 7 – Results of the paired t test on centroid size by species

<table>
<thead>
<tr>
<th>Species</th>
<th>Dorsal</th>
<th></th>
<th>Ventral</th>
<th></th>
<th>Mandible</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>p value</td>
<td>DF</td>
<td>T</td>
<td>p value</td>
<td>DF</td>
<td>T</td>
</tr>
<tr>
<td>Reithrodontomys</td>
<td>0.0001</td>
<td>92</td>
<td>12.7464</td>
<td>0.0001</td>
<td>83</td>
<td>7.8718</td>
</tr>
<tr>
<td>Oryzomys</td>
<td>0.0915</td>
<td>95</td>
<td>1.7050</td>
<td>0.6207</td>
<td>91</td>
<td>0.4965</td>
</tr>
<tr>
<td>Peromyscus</td>
<td>0.0001</td>
<td>115</td>
<td>7.9253</td>
<td>0.5233</td>
<td>103</td>
<td>0.6404</td>
</tr>
</tbody>
</table>
Table 8 – Summary diversity estimates of $\theta$ (S) (Watterson, 1975), $\theta$ ($\pi$) (Tajima, 1983), and nucleotide diversity $\pi$ (Tajima, 1993) and their 95% confidence intervals for Cytochrome b (Cytb) and the control region (CR) from Arlequin v. 3.5.1.2 (Excoffier et al., 2005).

All values are statistically significant except those indicated by *.

<table>
<thead>
<tr>
<th></th>
<th>Cytb $\theta$ S</th>
<th>CR $\theta$ S</th>
<th>Cytb $\theta$ $\pi$</th>
<th>CR $\theta$ $\pi$</th>
<th>Cytb nucleotide diversity $\pi$</th>
<th>CR nucleotide diversity $\pi$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reithrodontomys</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Island</td>
<td>4.522102</td>
<td>6.188139</td>
<td>2.193457</td>
<td>4.611664</td>
<td>0.007435</td>
<td>0.025763</td>
</tr>
<tr>
<td></td>
<td>± 1.644104</td>
<td>± 2.136509</td>
<td>± 1.378374</td>
<td>± 2.571374</td>
<td>± 0.004672</td>
<td>± 0.014365</td>
</tr>
<tr>
<td>Mainland</td>
<td>65.345282</td>
<td>38.981841</td>
<td>22.147163</td>
<td>16.865248</td>
<td>0.075075</td>
<td>0.094219</td>
</tr>
<tr>
<td></td>
<td>± 18.407759</td>
<td>± 11.129249</td>
<td>± 11.021753</td>
<td>± 8.476017</td>
<td>± 0.037362</td>
<td>± 0.047352</td>
</tr>
<tr>
<td><strong>Oryzomys</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Island</td>
<td>4.237335</td>
<td>6.426922</td>
<td>* 3.646667</td>
<td>6.358696</td>
<td>* 0.049954</td>
<td>0.019809</td>
</tr>
<tr>
<td></td>
<td>± 1.680623</td>
<td>± 2.408488</td>
<td>± 2.129094</td>
<td>± 3.481255</td>
<td>± 0.029166</td>
<td>± 0.010845</td>
</tr>
<tr>
<td>Mainland</td>
<td>13.494295</td>
<td>61.495428</td>
<td>* 8.391287</td>
<td>146.332079</td>
<td>* 0.114949</td>
<td>0.455863</td>
</tr>
<tr>
<td></td>
<td>± 3.589257</td>
<td>± 15.092702</td>
<td>± 4.337986</td>
<td>± 70.034257</td>
<td>± 0.059424</td>
<td>± 0.218175</td>
</tr>
<tr>
<td><strong>Peromyscus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Island</td>
<td>4.17593</td>
<td>3.131947</td>
<td>1.061457</td>
<td>1.043459</td>
<td>0.006207</td>
<td>0.00509</td>
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<tr>
<td></td>
<td>± 1.403968</td>
<td>± 1.123119</td>
<td>± 0.788921</td>
<td>± 0.779449</td>
<td>± 0.004614</td>
<td>± 0.003802</td>
</tr>
<tr>
<td>Mainland</td>
<td>55.497265</td>
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<td>73.755556</td>
<td>95.711111</td>
<td>0.431319</td>
<td>0.449348</td>
</tr>
<tr>
<td></td>
<td>± 22.658594</td>
<td>± 27.628822</td>
<td>± 39.342633</td>
<td>± 50.940343</td>
<td>± 0.230074</td>
<td>± 0.239157</td>
</tr>
</tbody>
</table>
Table 9 – Results of the Fst calculation from Arlequin v. 3.5.1.2 (Excoffier et al., 2005) for Cytochrome b (Cytb) and the control region (CR) and the gsi estimates for the island and mainland (Cummings et al., 2008). All values are statistically significant from zero.

<table>
<thead>
<tr>
<th>Species</th>
<th>Fst</th>
<th>gsi</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Cytb</td>
<td>CR</td>
</tr>
<tr>
<td><em>Reithrodontomys</em></td>
<td>0.31375</td>
<td>0.32303</td>
</tr>
<tr>
<td><em>Oryzomys</em></td>
<td>0.27822</td>
<td>0.32567</td>
</tr>
<tr>
<td><em>Peromyscus</em></td>
<td>0.67460</td>
<td>0.63683</td>
</tr>
</tbody>
</table>
Table 10 – Results of the IMa2 analyses estimating gene flow between island and mainland. M0 > 1 indicates M = m/µ from island to mainland forward in time. M1 > 0 indicates M=m/µ from mainland to island forward in time. 95% confidence intervals are included in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>M0 &gt; 1</th>
<th>M1 &gt; 0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reithrodontomys</td>
<td>0.07652 (0.009000, 0.1550)</td>
<td>0.03917 (0.0, 0.08300)</td>
</tr>
<tr>
<td>Oryzomys</td>
<td>0.1466 (0.02100, 0.2650)</td>
<td>0.2726 (0.0, 0.7410)</td>
</tr>
<tr>
<td>Peromyscus</td>
<td>0.2043 (0.01300, 0.4890)</td>
<td>0.04368 (0.0, 0.1310)</td>
</tr>
</tbody>
</table>
Figure 1 – Collection localities of *Reithrodontomys gracilis* and *R. spectabilis*. Black squares indicate a tissue sample, open squares indicate a skull/mandible sample, and grey squares are localities where both a tissue and skull/mandible samples were taken. Numbers indicate the numbered localities in Appendix 1.
Figure 2 – Collection localities of *Peromyscus leucopus*. Black triangles indicate a tissue sample, open triangles indicate a skull/mandible sample, and grey triangles are localities where both a tissue and skull/mandible samples were taken. Numbers indicate the numbered localities in Appendix 1.
Figure 3 – Collection localities of *Oryzomys couesi*. Black circles indicate a tissue sample, open circles indicate a skull/mandible sample, and grey circles are localities where both a tissue and skull/mandible samples were taken. Numbers indicate the numbered localities in Appendix 1.
Figure 4 – A. (top) Landmarks for the dorsal view of the skull B. (center) Landmarks for the ventral view of the skull C. (bottom) Landmarks for the mandible
Figure 5 – Scatter plot of relative warp 1 plotted against relative warp 2 for the dorsal view of the skull (A), ventral view of the skull (B), and mandible (C) with standard error bars included. O represents *Oryzomys*, P represents *Peromyscus*, R represents *Reithrodontomys*, M represents mainland, and I represents island.
APPENDIX I

List of tissue and skull samples included in this study with locality number, collecting location and collector/museum number.

<table>
<thead>
<tr>
<th>Genus/species</th>
<th>Cat number</th>
<th>State</th>
<th>Locality</th>
<th>Locality number</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK2506</td>
<td>Campeche</td>
<td>Candelaria, 10 km S of</td>
<td>1</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK2507</td>
<td>Campeche</td>
<td>Candelaria, 10 km S of</td>
<td>1</td>
<td>T</td>
</tr>
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<td><em>Oryzomys couesi</em></td>
<td>ASK2508</td>
<td>Campeche</td>
<td>Candelaria, 10 km S of</td>
<td>1</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK2504</td>
<td>Campeche</td>
<td>Candelaria, 11 km S of</td>
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<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK0210</td>
<td>Campeche</td>
<td>Candelaria, 27 km S of</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK0211</td>
<td>Campeche</td>
<td>Candelaria, 27 km S of</td>
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<td>T</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK2512</td>
<td>Campeche</td>
<td>Candelaria, 39 km S of</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>ASK2513</td>
<td>Campeche</td>
<td>Candelaria, 39 km S of</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29759</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29760</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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</tr>
<tr>
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<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>FN29762</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>T</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29763</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>T</td>
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<tr>
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<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29766</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
</tr>
<tr>
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<td>FN29767</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>T</td>
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<tr>
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<td>FN29768</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29769</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29770</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
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<tr>
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<td>FN29771</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
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<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29772</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29773</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29774</td>
<td>Campeche</td>
<td>Champoton, 16 km N of</td>
<td>5</td>
<td>T</td>
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</tbody>
</table>


<table>
<thead>
<tr>
<th>Species</th>
<th>Accession</th>
<th>Location</th>
<th>Distance</th>
<th>Status</th>
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<tbody>
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<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29776</td>
<td>Campeche Champoton, 16 km N of</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29665</td>
<td>Campeche Champoton, 52 km SW of</td>
<td>7</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29666</td>
<td>Campeche Champoton, 52 km SW of</td>
<td>7</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29669</td>
<td>Campeche Champoton, 52 km SW of</td>
<td>7</td>
<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29670</td>
<td>Campeche Champoton, 52 km SW of</td>
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<tr>
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<td>Campeche Champoton, 52 km SW of</td>
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<tr>
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<td>Campeche Champoton, 52 km SW of</td>
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<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29675</td>
<td>Campeche Champoton, 52 km SW of</td>
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<td>T</td>
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<tr>
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<td>T</td>
</tr>
<tr>
<td><em>Oryzomys couesi</em></td>
<td>FN29668</td>
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<td><em>Oryzomys couesi</em></td>
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<td>10</td>
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</tr>
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<td><em>Oryzomys couesi</em></td>
<td>ASK2555</td>
<td>Campeche Constitucion (9.5 km S of), Escarcega (9.5 km S 70 km E)</td>
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<td>ASK2568</td>
<td>Campeche Constitucion (9.5 km S of), Escarcega (9.5 km S 70 km E)</td>
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<td><em>Oryzomys couesi</em></td>
<td>ASK2569</td>
<td>Campeche Constitucion (9.5 km S of), Escarcega (9.5 km S 70 km E)</td>
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<td>T</td>
</tr>
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<td><em>Oryzomys couesi</em></td>
<td>ASK2617</td>
<td>Campeche Constitucion (9.5 km S of), Escarcega (9.5 km S 70 km E)</td>
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<td>T</td>
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<td><em>Oryzomys couesi</em></td>
<td>FN30495</td>
<td>Campeche Dzibalchen, 60 km SE of</td>
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<td>Campeche Dzibalchen, 60 km SE of</td>
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<td>Oryzomys couesi</td>
<td>FN32792</td>
<td>Campeche</td>
<td>El Remata, 14 km W of Tanuche</td>
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</tr>
<tr>
<td>----------------</td>
<td>--------</td>
<td>----------</td>
<td>--------------------------------</td>
<td>----</td>
</tr>
<tr>
<td>Oryzomys couesi</td>
<td>KU93661</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
</tr>
<tr>
<td>Oryzomys couesi</td>
<td>KU93662</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
</tr>
<tr>
<td>Oryzomys couesi</td>
<td>KU93663</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
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<tr>
<td>Oryzomys couesi</td>
<td>KU93664</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
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<tr>
<td>Oryzomys couesi</td>
<td>KU93665</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
</tr>
<tr>
<td>Oryzomys couesi</td>
<td>KU93666</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
</tr>
<tr>
<td>Oryzomys couesi</td>
<td>KU93670</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
</tr>
<tr>
<td>Oryzomys couesi</td>
<td>KU93671</td>
<td>Campeche</td>
<td>Escarcega, 103 km SE of</td>
<td>14</td>
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