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University of Oklahoma
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A Geography of Extinction:
Patterns in the Contraction of Geographic Ranges

A Dissertation
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
Doctor of Philosophy

By
Robert B. Channell
Norman, Oklahoma
1998

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A Geography of Extinction: Patterns in the Contraction of Geographic Ranges

A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

Y
Paul
Carolyn
Michael
only for
Katherine

Preface

This dissertation is presented as three separate chapters. Each chapter will be submitted to a refereed journal. The first and second chapters will be submitted to *American Naturalist*. The third chapter will be submitted to *Conservation Biology*. Chapters have been formatted as appropriate for the given journal.

Acknowledgments

I would like to acknowledge my major professor Mark Lomolino who has been a model co-investigator on this project. His persistence, patience, and friendship have ably guided me through this project and I am greatly indebted. I also like to thank Dr. Marvin Baker, Dr. Nicholas Czaplewski, Dr. Mike Kaspari, Dr. Kathryn Pandora, and Dr. Caryn Vaughn for serving on my committee. Their comments and suggestions have improved this project immeasurably. I extend my gratitude to Dr. Michael Mares and Dr. Gary Schnell who have both been generous with their time, experience, and equipment. Dr. Victor Hutchison deserves special consideration for his administration of the GAANN fellowships and his valued advice. Dr. Michael Scott, University of Idaho, freely provided quality data and enthusiasm for this project. Melissa Songer and Tabbie Franklin both worked briefly on this project with me and their contributions are appreciated. I also thank the Department of Zoology for providing me a place and the time to grow.

I would like to thank my friends and family for their support throughout my education. Special thanks goes to my parents whose encouragement and love never flagged. I thank my wife Kim for her patience and love. When I felt like it was all falling apart, she held it together.

I was fortunate to receive a Department of Education Graduate Assistance in Areas of National Need Fellowship. Many of the resources that this grant provided me made this work possible. I also received support from the Department of Zoology in a Graduate Teaching Assistantship. Lastly, Dr. Mark Lomolino generously provided support on several of his grants for me.

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Abstract

I examined the contraction of geographic ranges in 245 species. Remnant portions of the geographic range tended to persist in the periphery of the species' historical range. Larger patches of the geographic ranges persisted longer than smaller patches. For species that occurred on both the mainland and islands, islands maintained their populations better than the mainland. All of the continents except Africa, had significantly more species persist in the periphery than near the center of the species' historical range. While continental species had significantly more species persist in their historical periphery, insular species showed no such bias. I suggest that the observed patterns of range contraction may be the result of isolation from human disturbance. Patterns in the contraction of geographic ranges may be of value in guiding the conservation of sensitive species.

I then evaluated two hypotheses of range contraction by contrasting the predicted sequence of range contraction with empirical observations. While the demographic hypothesis suggests the demographic characteristics of the historical populations determine which populations persist, the contagion hypothesis states that the geographic dynamics of the extinction factors determine which populations survive. The results of Monte Carlo simulations and regression analysis were consistent with the contagion hypothesis. These results suggest that most range contraction should

progress from the edge first impacted by the extinction factor, then the central portion of the range, and finally the periphery most distant from the initial impact of the extinction factor.

The influence of different variables on the process of range contraction was investigated using spatial simulation modeling. Actual range contractions of species were also simulated using distributional data of introduced species thought to be responsible for the range declines. The shape of the species' historical range, initial distribution of the extinction factor, and the method of population loss dominated the simulated ranges contractions. These results suggest that the observed patterns of range contraction may be the result of the interaction of many different factors. These simulations also highlight the need for appropriate data on the spread of extinction factors and their influence on susceptible populations.

**Dynamic Biogeography and the Conservation of Species:
Patterns in the Contraction of Geographic Ranges**

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Key words: geographic range, distribution, abundance,
extinction, conservation

Running head: Contraction of Geographic Ranges

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ABSTRACT: We examined patterns of geographic range contraction in 245 endangered or extinct species. Populations tend to be denser and less variable near the center of a species' geographic range. The extinction probability of a population is commonly thought to be inversely correlated with population density and positively correlated with population variability. This combination of patterns has led others to predict that geographic ranges should contract inward, with populations persisting near the center of the species' historical range. Biogeographic theory also predicts that in geographic ranges that are made up of more than one patch, the largest and least isolated patches should persist the longest. We tested these predictions.

Geographic information system analysis revealed that 167 (68%) of 245 species persisted in the periphery, not the center of their historical range ($P < 0.001$, binomial test). For species that occurred solely on continents or on islands, patch size was positively and significantly correlated with persistence ($P = 0.004$, binomial test). However, species that occurred historically on both continents and islands persisted more frequently on islands, relative to their size, than on continents ($P = 0.029$, binomial test). The isolation of islands and other sites along the periphery of a species' historical range from anthropogenic disturbances may confer on them a persistence advantage. Range contractions of insular species ($P = 0.228$, binomial test) and species from Africa ($P = 0.271$, binomial test) did not

demonstrate a peripheral bias. The history and dynamic nature of the disturbances leading to extinction may explain the deviations for the overall pattern of contraction to the range periphery.

Introduction

Biogeographers and ecologists usually acknowledge that geographic ranges are spatially dynamic, sometimes varying dramatically with fluctuations in environmental conditions. Most biogeographic studies, however, focus on range features (e.g., size, shape, and overlap) at some fixed point in time. With the exception of studies of introduced and expanding species, biogeographers have largely ignored the spatially dynamic process of range formation and decline. Ignorance regarding these processes has not been due to a lack of interest, but is instead a product of the paucity of data and a dearth of analytic spatial tools. However, in the last two decades the technical hurdles for spatial analysis have been overcome (Brown et al., 1996; Longley and Batty, 1996; Mikula et al., 1996) and appropriate data have become available (Brown et al., 1996; Stoms et al., 1996). This availability of data and methods is timely, as the deepening biodiversity crisis requires an understanding of how ranges contract. In this paper, we analyze the dynamics of range contraction in endangered and recently extinct species.

There are several patterns we can draw on to predict how ranges should contract. First, the extinction probability of a population declines with increased population size (MacArthur and Wilson, 1967; Goel and Ritcher-Dyn, 1974; Pimm et al., 1988; Tracy and George, 1992; Lawton, 1995) and should rise with increased variation in population size (Pimm et al.,

1988). Second, studies in the emerging field of macroecology have demonstrated that populations tend to be larger and less variable near the center of the geographic range (Brown, 1984; Gaston 1990, 1994; New 1991; Lawton, 1995; Brown et al., 1995; Curnutt et al., 1996). Given these patterns, ecologists and conservation biologists predict that ranges should implode, with the final populations of a species persisting near the center of the species' historical geographic range (Brown, 1995; Lawton 1995).

Other insights on the spatial characteristics of range contraction can be derived from island biogeography theory (MacArthur and Wilson, 1967). For species whose populations occupy isolated patches on the mainland or true islands, persistence should be highest for populations inhabiting the larger patches or islands. In addition, because populations can be rescued from extinction by emigration from other populations (Brown and Kodric-Brown, 1977; Hanski and Gilpin, 1991, Hanski et al., 1995), persistence is predicted to be highest for populations occupying the less isolated patches or islands. Populations that occupy mainland sites should persist more often than those on the more isolated and smaller island sites.

These predictions underlie many conservation guidelines. Researchers have instructed conservationists to favor the center of an endangered species' range and the larger and less isolated patches when surveying for undiscovered populations, planning reintroductions, and allocating resources for in situ management (Wolf et al., 1996; Griffith et al.,

1989; Pearl, 1992). The periphery, on the other hand, is sometimes viewed as a region of the living dead, with little value for conserving biological diversity (see Stevens, 1992; Griffith et al., 1989; Wolf et al., 1996). However, as these recommendations have not been tested, the unjustified restriction of conservation alternatives may waste limited resources and result in the loss of species.

Here, we test five predictions on spatial dynamics of geographic ranges :

1. Remnant populations should be located near the center of the historical range;
2. Populations occupying larger patches of the historical range should persist more often than those occupying smaller patches;
3. For species whose historical range included the mainland and true islands, mainland populations should persist more often than those on islands;
4. The relative persistence of central populations should not vary among the continents; nor between continental species (species that occur only on a continent) and insular species (species that occur only on islands);
5. The relative persistence of central populations should not vary among taxonomic groups.

Methods and Materials

We obtained range maps for 245 species from literature or through personal correspondence with authorities (Appendix 1)(maps are appended on CD-ROM). We included only those species with maps available for both historical and extant ranges (or final site in the case of extinct species), and with extant ranges that were less than 25% of the species' historical distribution. We digitized the range maps into Idrisi (Eastman, 1995), a geographic information system (GIS). For each species, we first located the center, which was the point within the species' historical range that was most distant from all edges of the range (Lomolino and Channell, 1995). The distance from this point to the nearest edge was then calculated (d in Figure 1). We defined the region that was within half of this distance (d/2 in Figure 1) to an edge as periphery and the remaining portion of the range as central. We then calculated an index of centrality (C) which is a measure of the proportion of the extant or final range that fell within the central region of the historical range.

First, the area of the extant range expected to occur within the central region (C_{EE}) was calculated as follows:

$$C_{EE} = \frac{C_H}{T_H} * T_E$$

Where:

T_E = Total area of the extant (or final) range

T_H = Total area of the historical range

C_H = Area of the central region of the historical range

We then calculated C as follows:

If $C_{EO} \leq C_{EE}$

C_{EO} = Area of the extant range observed within the historical central region (Figure 1)

$$\text{Then } C = \frac{C_E}{C_{EE}} * 0.5$$

If $C_{EO} > C_{EE}$

$$\text{then } C = 0.5 + \left[0.5 * \left[\frac{C_{EO} - C_{EE}}{T_E} \right] \right]$$

The index of centrality (C) ranged from 0, where the extant range fell completely outside of the central portion of the historical range, to 1, where the extant range fell completely within the central portion of the historical range. We labeled species with C-values greater than 0.5 as "central species" (consistent with Prediction 1) and those species with C-values less than 0.5 as "peripheral species." We then used a binomial test to determine whether the ratio of central to peripheral species differed significantly from 1:1 (Zar, 1984).

Maps for the 21 continental species with multiple patches in their historical range were used to test whether persistence was higher for populations inhabiting larger patches (Prediction 2). We first assigned

patches to one of two size categories (“large” or “small”) based on their area relative to the median patch size. If a species had an odd number of patches in its historical range, the median-sized patch was excluded from the analysis. For each species, we counted the number of large and small patches with persistent populations (P_l and P_s , respectively). We counted the number of species (S_l) for which P_l was greater than P_s and the number of species (S_s) where P_s was greater than P_l . Species with ties ($P_l = P_s$) were excluded from analysis. We used a binomial test to determine if the ratio of S_l to S_s differed significantly from 1:1. This analysis was done for continental and insular species.

To compare relative persistence of mainland and island patches (Prediction 3), we first counted the number of mainland patches (P_{MH}) and the number of total patches (mainland and island) in the historical distribution (P_{TH}) for each species. To calculate the expected number of patches persisting on the mainland (P_{ME}), we multiplied the total number of patches by P_{MH}/P_{TH} . We classified a species as a mainland species if the number of patches persisting on the mainland was greater than the expected number (P_{ME}). If the number of mainland patches persisting (P_{MP}) was less than expected (P_{ME}), the species was classified as an island species. There were no ties ($P_{MP} = P_{ME}$). We then used a binomial test to determine if the number of mainland and island species differed significantly from a ratio of 1:1.

To account for the often large difference between mainland and island patch sizes we performed a second test of Prediction 3. For each species, we calculated the total area of all of the historical patches (A_{TH}) and the area of the historical mainland patches (A_{MH}). We multiplied A_{MH}/A_{TH} by the total number of persisting patches (P_{TP}) to generate the expected number of patches persisting on the mainland. If the number of patches persisting on the mainland (P_{MP}) was greater than expected, we classified the species as it as a "mainland species," otherwise, it was classified as an "island species." There were no ties (P_{MP} = expected number of patches). We tested whether the ratio of mainland species and island species differed significantly from 1:1 using a binomial test.

For each region (Prediction 4) and taxonomic group (Prediction 5), we used a binomial test (Zar, 1984) to determine whether the ratio of central to peripheral species differed significantly from 1:1. To test for variations in contraction between regions (Prediction 4) or taxonomic groups (Prediction 5) we used a Kruskal-Wallis test (StatView, 1996) to compare C-values. If the Kruskal-Wallis test showed a significant effect for a factor (region or taxonomic group), we used a Tukey's multiple comparison test (Zar, 1984) to determine which regions or taxonomic groups differed from the others.

Results

The African wild dog (*Lycaon pictus*) and the poo uli (*Melamprosops phaesoma*) were among those species that demonstrated the expected pattern of contraction to the range center (Figure 2a-b). However, contrary to Prediction 1, the majority of species contracted to the periphery of their historical range (e.g., western quoll (*Dasyurus geoffroii*), giant panda (*Ailuropoda melanoleuca*), little spotted kiwi (*Apteryx owenii*), American burying beetle (*Nicrophorus americanus*), and black-footed ferret (*Mustela nigripes*)(Figure 2c-g)). Two hundred forty (98.0%) of the 245 species maintained populations in at least a portion of their peripheral range. In fact, 167 (68.2%) of the 245 species maintained a greater than expected portion of their range in the periphery ($p < 0.001$, binomial test), not the center. Populations of 91 species were exclusively limited to the periphery of their historical range ($C = 0.00$) compared to just 5 species limited to the central region of their historical range ($C=1.00$) ($p < 0.001$, binomial test).

Persistence was higher in the larger patches of the historical range, consistent with Prediction 2. Twelve (75%) of 16 continental species exhibited higher persistence in larger patches of their historical ranges ($P=0.038$, binomial test). Fifteen of 18 insular species exhibited higher persistence in larger patches of their historical range ($P=0.004$, binomial test).

Contrary to Prediction 3, we found that mainland patches did not have greater persistence than island patches. Based on the number of

mainland vs. insular patches with persistent populations, 16 species (47.1%) were classified as mainland species and 18 species (52.9%) as island species ($P=0.432$, binomial test). When the area of historical patches is taken into account, this island bias is even more pronounced with only 11 species (32.3%) being classified as mainland and 23 (68.7%) species as island species ($P=0.029$, binomial test). Thus, islands maintain significantly more populations for their size than does the mainland.

Contrary to Prediction 4, patterns of range contraction differed significantly among continents. Too few species were recorded from South America to justify statistical analysis ($n=8$, power of binomial test=0.123). Australian, North American, and Eurasian regions all had significantly more peripheral species than would be expected by chance (Figure 3). However, the proportion of peripheral species for Africa did not differ statistically from the null expectation (14 peripheral species, 10 central; $P=0.271$, binomial test). The Kruskal-Wallis test indicated that these differences among continents were highly significant ($H=14.035$, $df=3$, $P=0.003$), primarily because Africa differed from all other continents with sufficient sample sizes (Tukey's test, $p_{crit}=0.05$)

Also contrary to Prediction 4, the spatial bias in range contraction differed significantly between continental and insular species. Species from mainland regions were much more likely to contract to the peripheral regions of their range (88 of 120 species; $P<0.001$, binomial test) than were

species from islands (45 of 88 species; $P=0.228$, binomial test)(Figure 4). Moreover, the spatial bias in range contraction of insular species differed significantly among archipelagoes (Kruskal-Wallis $H=9.624$, $df=3$, $P=0.022$). While the Mariana Islands (6 of 6 species; $P=0.015$, binomial test) and New Zealand (11 of 12 species; $P=0.003$, binomial test) were significantly more peripheral than expected by chance, the Hawaiian Islands (23 of 54 species; $P=0.171$, binomial test) and other miscellaneous islands (9 of 17 species; $P=0.500$, binomial test) showed no significant bias in range contraction (Figure 4).

Only mammals, birds, mollusks, and plants had enough species to allow comparisons between taxonomic groups (Prediction 5)(amphibians $n=4$, power of binomial test= 0.081 ; arthropods $n=6$, power of binomial test= 0.101 ; reptiles $n=6$, power of binomial test= 0.101)(Figure 5). Mollusks (9 of 22, $P=0.262$, binomial test) and plants (12 of 21, $P=0.332$, binomial test) did not show a significant bias for the periphery of the range. The Kruskal-Wallis test indicated that the difference among taxonomic groups was marginally significant ($H=7.314$, $df=3$, $P=0.063$). However, both of these groups were dominated by insular forms and thus this pattern may be more a reflection of regional (island vs. mainland) differences, discussed above, than differences among taxonomic groups. The mollusks in our data set were derived largely from Hawaiian land snails. Only two of the mollusk species examined were non-Hawaiian and both of these continental species

were maintained entirely in the periphery ($C = 0.00$). The plants were also primarily from Hawaii (15 species) or other islands (2 species). All of the four continental plant species showed a bias for the periphery, and two of these species were maintained entirely in the periphery.

We are confident of the veracity of the patterns we have uncovered. We also believe that there may be potential shortcomings in the data set that should be noted. While these shortcomings may increase the unexplained error, it is unlikely that they are responsible for the patterns that we have uncovered. Geographic ranges of species are notoriously difficult to measure (see Gaston, 1991, 1994a; Brown et al., 1996; Lomolino and Channell, 1998). Despite these difficulties there is a high degree of correlation among different measures of geographic ranges (Quinn et al., 1996). Historical ranges, because it is impossible to resample them, can be even more problematic to determine (Gaston, 1994b; Fisher and Shaffer, 1996; Lennon et al., 1997; Lomolino and Channell, 1998). A systematic over- or under-estimation of historical distribution could alter the results of this study, but is unlikely to generate a significant bias or be responsible for the uncovered patterns. Furthermore, the range of a species tends to be the accumulated records of where the species occurred, but little mention is made of the places where the species is absent (Gaston, 1994a). The resolution of sampling or mapping may miss or ignore holes within the species' range, making the distribution more homogenous than it is actually.

A change in the resolution of sampling or mapping may again alter the results of this study, but this also is unlikely to generate a significant bias in the data set or be responsible for the patterns we have uncovered.

Discussion

Although most of these results are anomalous with respect to macroecological and island biogeography theory, they are totally consistent with the anthropogenic contagion hypothesis that Lomolino and Channell (1995 and 1998) proposed. We hypothesize that range contraction is dominated by the geography of the extinction forces, which overwhelms historical biogeographical and macroecological patterns. We suggest that a suite of anthropogenic disturbances (including habitat degradation, biocides, xerification, and introduced species or pathogens) spread across a landscape like a contagion. Regardless of where the contagion begins, the last place to be impacted will be along an edge of the historical range. Spatial isolation from disturbance may, therefore, convey an advantage to some peripheral populations.

Large patches in the geographic ranges of continental species maintained populations with greater frequency than smaller patches. This may be because a small contraction in a small patch will likely result in its loss while a contraction of equal or greater magnitude may leave a viable remnant in a larger patch (Peters and Lovejoy, 1990).

The high relative persistence of insular vs. mainland populations is contrary to Prediction 3, which was based on biogeographic theory, but is consistent with the contagion hypothesis. Despite their relatively low population sizes and infrequent immigration (rescue effect), insular populations are isolated from and, thus, less likely to be affected by anthropogenic forces that spread rapidly across relatively continuous mainland populations.

The exceptional case for Africa, whose species failed to exhibit any spatial bias in range contraction, is reminiscent of the pattern of extinctions at the close of the Pleistocene. All continents showed marked declines in the numbers of large mammal and bird species at the end of the Pleistocene, except for Africa (Martin, 1984). Martin hypothesized that as early humans moved out of Africa they exterminated the native game species that they encountered (overkill hypothesis; Martin, 1984; Diamond 1984). Over the course of evolution in Africa, other species had adapted in ways that allowed them to coexist with humans, but species from other regions were naïve to the unusual abilities of the human invaders. Africa was never subjected to the expanding wave front of humans that truncated geographic ranges on other continents. Thus, both the contagion and overkill hypotheses expect Africa to be the exception to their respective patterns.

Insular species also serve as instructive exceptions. Although continental species showed a significant tendency to persist in their

historical peripheries, insular species showed no such bias. The size of islands allows them be colonized from many different directions, allowing the extinction front to encircle the island before penetrating the interior. Therefore, the most isolated portion of an island is not at the edge, but rather near the center of the island. Again, the insular-dominated mollusks and plants did not exhibit a peripheral bias in range contraction. Islands should not exhibit a peripheral pattern of range contraction unless the island is too large to be encircled (e.g., New Zealand) or where the contagion is expanding as a single front (e.g., the brown tree snake, *Boiga irregularis*, in Guam, Mariana Islands (Savidge, 1987; Committee on the Scientific Bases for the Preservation of the Mariana Crow, 1997)).

The decline of Guam's vertebrate fauna over the last 50 years represents one of the best studied cases of a contagion-like extinction force and consequent range contraction. Shortly after World War II, the brown tree snake was accidentally introduced to Guam, possibly with returning military equipment (Committee on the Scientific Bases for the Preservation of the Mariana Crow, 1997). The snake rapidly expanded its distribution from the naval magazine on the southern portion of the island (Figure 6a-b). Range expansion and population growth of the brown tree snake closely mirrored the range contractions and numerical declines of the island's indigenous fauna (Committee on the Scientific Bases for the Preservation of the Mariana Crow, 1997; Savidge, 1987). The bridled white-eye (*Zosterops*

conspicillata) and Guam rail (*Rallus owstoni*) are excellent examples of this pattern of decline. Both species initially occupied the entire island, but now persist only on the portion of their range that is most distant from where the brown tree snake was first established (Figures 6a-b). Thirteen of Guam's 23 indigenous species of birds have been extirpated (Committee on the Scientific Bases for the Preservation of the Mariana Crow, 1997). However, many of these species persist on nearby islands that, although smaller, lack the brown tree snake (Savidge, 1987).

The demographic and macroecological patterns from which we generated our initial predictions may be valid for undisturbed systems. Undisturbed systems, however, are not the foci of the extinction crisis. The tendency for population size to peak near the center of the geographic range has been demonstrated for many different species (see Brown, 1984, 1995; Gaston, 1990; Hengeveld, 1990; Brown et al., 1995; Lawton, 1995). Studies of extinction have also consistently shown that small populations have the greatest probability of extinction (MacArthur and Wilson, 1967; Goel and Ritcher-Dyn, 1974; Pimm et al., 1988; Tracy and George, 1992; Lawton, 1995). However, the intensity and pervasive nature of human disturbances overwhelm these patterns: persistent populations are those last to come into contact with the extinction forces. The geography of extinction and extirpation is the geography of humans.

- There is a great deal that we need to learn about the spatial dynamics of extinction factors if we to make best use of these patterns of range contraction. We know surprisingly little about the factors that drive species to extinction (Soulé, 1983; Caughley, 1994; Caughley and Gunn, 1996). How does the speed and method of movement of the contagion influence the contraction process? Does the number, orientation, or shape of contagion fronts have a significant impact on the observed range contraction? Do the features of the affected populations change the expansion of the contagion? How does the extinction factor interact with the population? Are populations eliminated immediately or through attrition? Answers to these questions are needed if we are to understand the spatial dynamics of the extinction factors and range contraction. Furthermore, these answers are needed to help conserve biodiversity.

The pattern of range contraction we described may not be the result of any single cause but may be the result of a number of convergent factors. Peripheral populations tend to be genetically and ecologically dissimilar from each other and from central populations (Brussard, 1984, Hoffman and Blows, 1994). One of these numerous and diverse peripheral populations may be preadapted to the disturbances that drove the more central populations to extinction (Brussard, 1984; Lomolino and Channell, 1995; Nathan et al., 1996). The sheer number of peripheral populations also may give them an advantage. Even if populations of a species go extinct at

random, the majority of the remaining populations will probably be peripheral because of their initial numerical advantage.

Although it may seem obvious that populations would persist longest in that portion of the species' range that is last impacted by extinction factors, we believe these results are especially significant for four reasons. First, currently accepted theory did not predict the pattern of range contraction we uncovered nor did it even consider the distribution of extinction factors. Understanding how populations are impacted by extinction factors must be central to any theory purporting to predict population persistence. Second, predictions derived from this faulty theory had been used to direct conservation efforts. While it can not be proven that these misguided conservation efforts actually harmed species, it is unlikely efforts based on flawed theory would actually benefit species. Third it is not clear that a theory recognizing the importance of extinction factors on individual populations would predict greater persistence in the periphery of species historical ranges. Only when the entire range of a species is considered in concert with the distribution of extinction factors will the population that should persist the longest be clear. Finally, results of this study have identified lines of future research focusing on spatial dynamics of extinction factors (e.g., rate of spread, method of spread, number of extinction fronts, interaction with populations, susceptibility or resistance of different populations to various extinction factors).

Conservation Implications

The results of this study have important implications for conservation biology. Along with more central sites, conservation biologists should consider the periphery of the historical range when searching for undiscovered populations and possible sites for reintroduction. In fact, some of the most successful reintroductions have been to islands that lack the anthropogenic disturbances that drove continental populations to extinction (Burbidge and McKenzie, 1989; Short et al., 1992; Bibby, 1994; Short and Smith, 1994; Franklin and Steadman, 1991; Towns and Daugherty, 1994).

Of course, we are not suggesting that conservationists ignore more centrally located populations. Inclusion of peripheral sites into the conservation plans would not only increase the number of options available to conservationists, but possibly also improve the quality of sites from which to select. Peripheral populations should not be regarded as the "living dead" and abandoned in a rush to save central populations (Lesica and Allendorf, 1995; Nathan et al., 1996; Lomolino and Channell, 1998). We also suggest that conservation biologists be skeptical of generic prescriptions and untested theory. Strategies for conserving biological diversity should be based on a thorough understanding of the species and the particular threats to its survival. Theories regarding population dynamics have led us to an

understanding of the demographic fates of individual populations, but the complex interplay of population, biogeographic, and anthropogenic factors related to range contraction requires as rich and comprehensive a conceptual base and data set as possible. Our study suggests that the best conservation strategy for any species must consider the geographic distribution of those factors that are contributing to the species' decline.

Acknowledgments

We thank N. Czaplewski, T. Franklin, M. Kaspari, K. Pandora, D. Perault, K. Perez, G. Smith, and C. Vaughn for their advice and comments on this paper. We would also like to thank M. Scott, D. Steadman, and L. Carbyn who provided information the distribution of several species.

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Figure Legends

Figure 1. A graphical representation of how geographical range contractions were quantified. The cross-hair represents the range center, the point within the species range that is most distant from all range edges. "d" represents the distance from the center of the range to the nearest edge. "d/2" is the width of the region defined as peripheral. C_{EO} is the portion of the extant range that occurs in the central region. Central and peripheral regions of historical range are depicted in gray and white, respectively.

Figure 2. Historical and extant ranges of seven species. Historical ranges are indicated in dark gray, the extant range in black. The index of centrality (C) is a standardized proportion of the extant or final range which falls within the central region. C ranges from 0 to 1 for species whose extant ranges fall entirely within peripheral or central portions of their historical ranges. The percentage in parentheses indicates how much the range has contracted.

Figure 3. Proportion of species in each of five regions which persisted in the periphery of the historical range ($C < 0.5$). All regions except for Africa had significantly more peripheral species than expected. Sample sizes

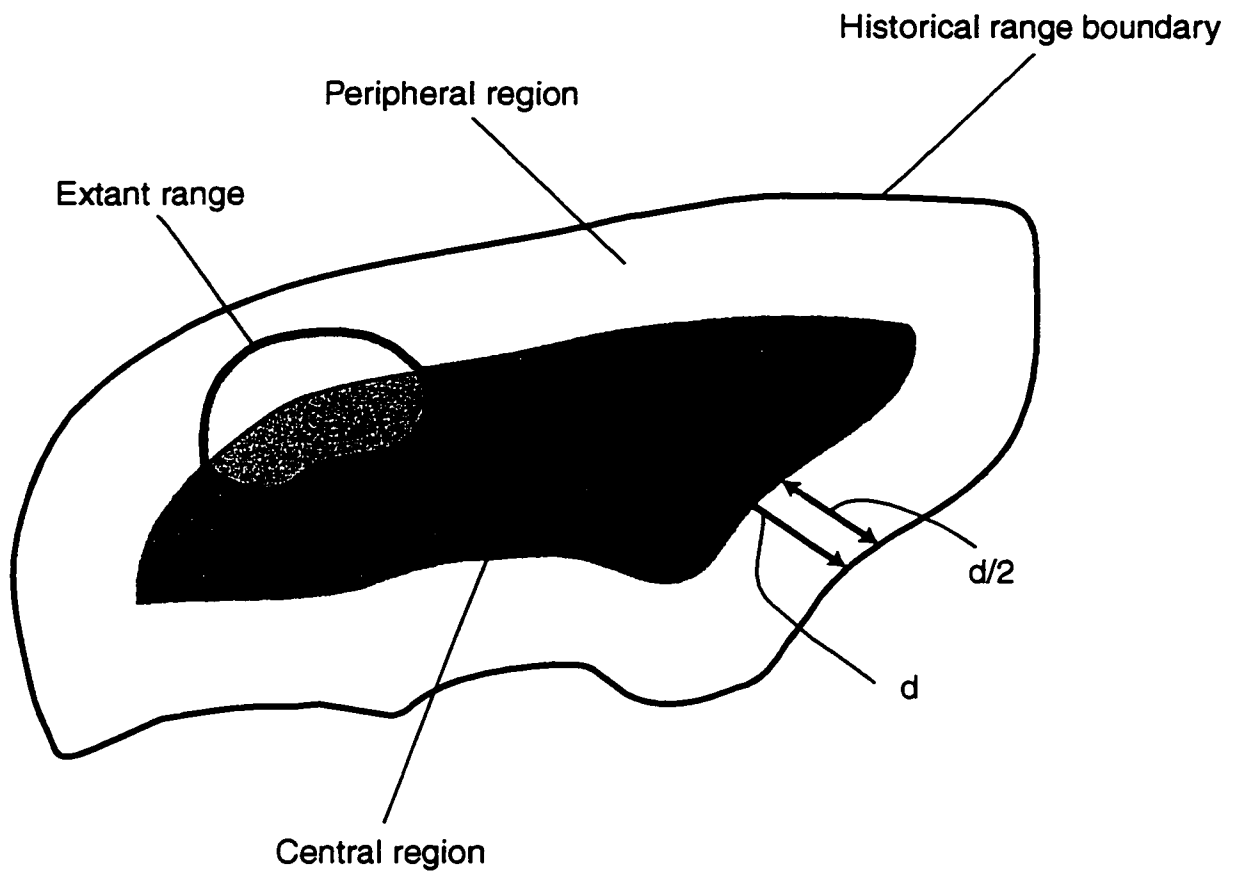
are included in parentheses. († South America had too few species to justify analysis; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Figure 4. Proportion of peripheral species ($C < 0.5$) for those found just on continents, just on islands, and species that historically occupied both. Continental species and species occupying both mainland and islands had significantly more peripheral than central species (binomial test). Insular species showed no significant trend. Samples sizes are included in parentheses. (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

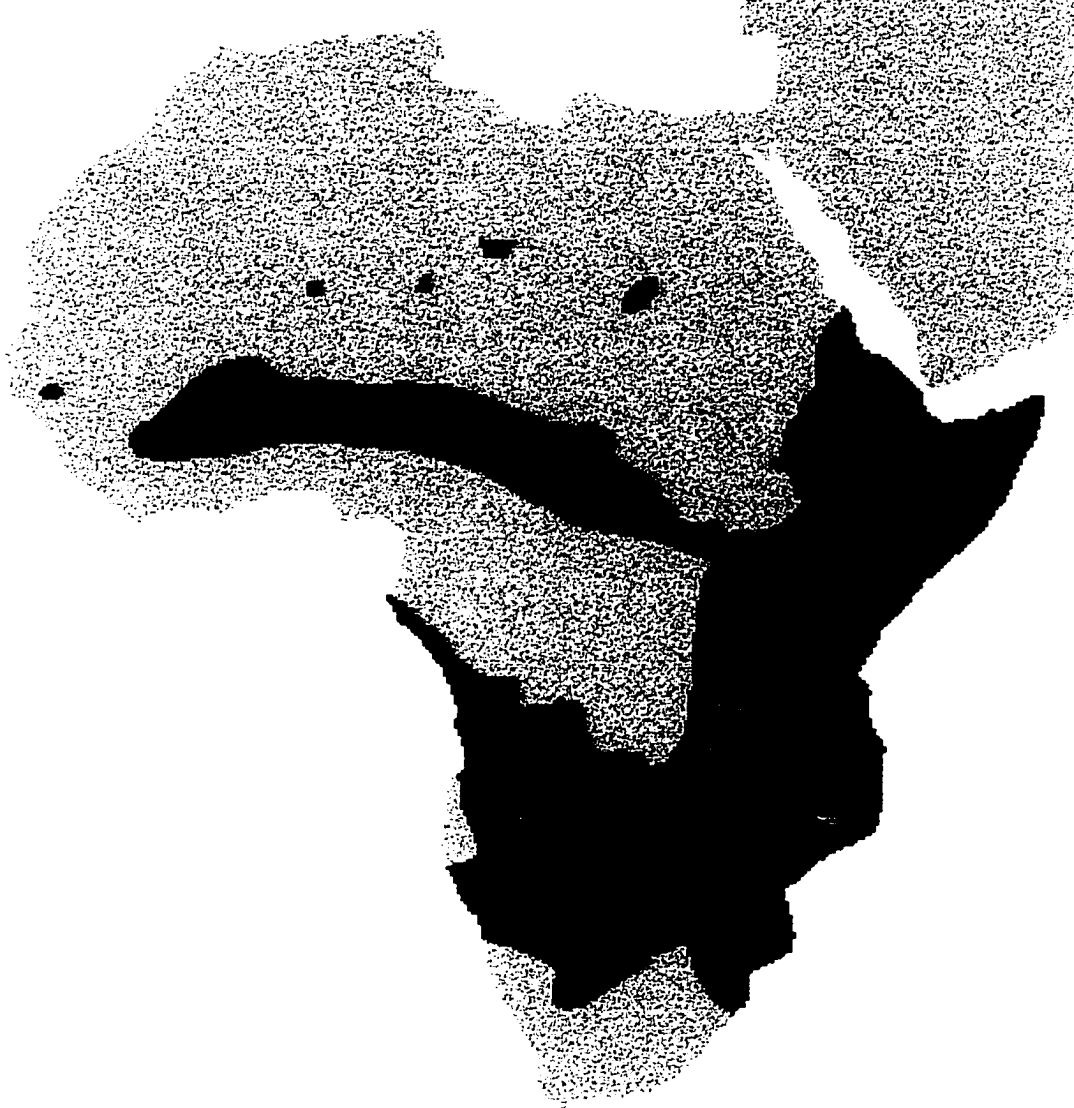
Figure 5. Proportion of peripheral species ($C < 0.5$) for taxonomic groups with sufficient sample sizes. Birds and mammals showed more contractions to the periphery than did plants and mollusks, which were dominated by species from Hawaii. Samples sizes are included in parentheses. (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Figure 6. Historical and extant ranges for two species on Guam. Historical ranges are indicated in dark gray, the extant range in black. The index of centrality (C) is a standardized proportion of the extant or final range that falls within the central region. C ranges from 0 to 1 for species whose extant ranges fall entirely within peripheral or central portions of their historical ranges. The percentage in

parentheses indicates how much the range has contracted. The arrows show how the introduced brown tree snake (*Boiga irregularis*) has spread on the island since its accidental introduction in the late 1940s or early 1950s. The persisting portion of each species' range is that area which was located most distant from the initial establishment of the snake.

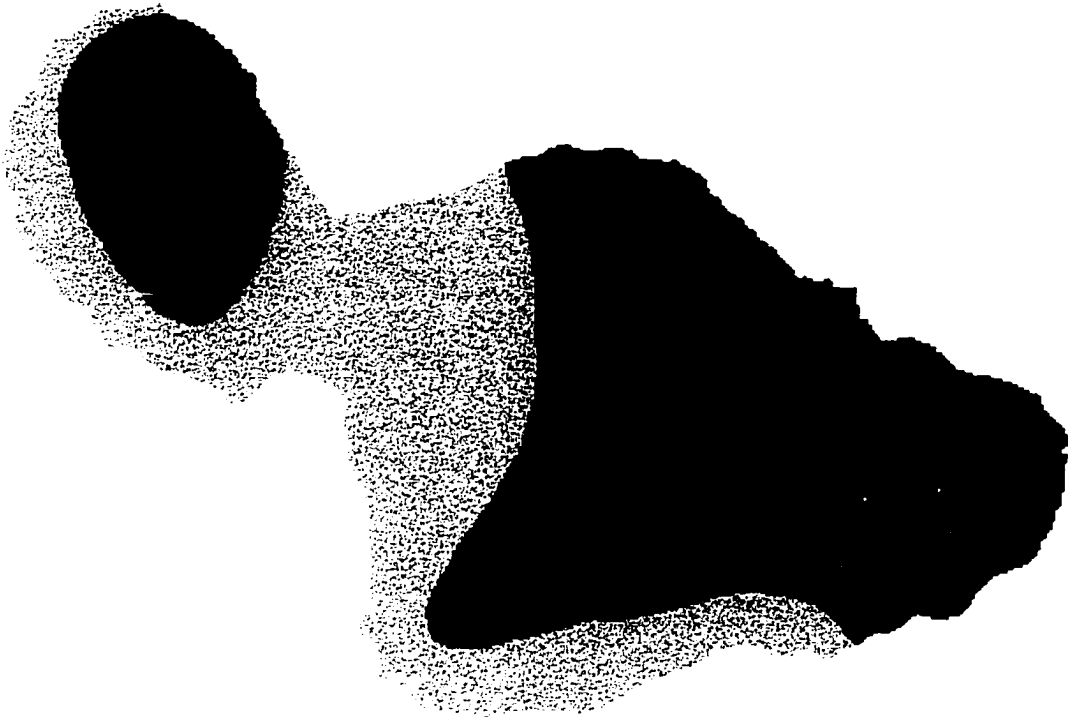


a. African Wild Dog
 $C=0.67$ (81%)



Poo Uli
C=0.99 (99%)

b.



Western Quoll
C=0.00 (98%)

C.



d.

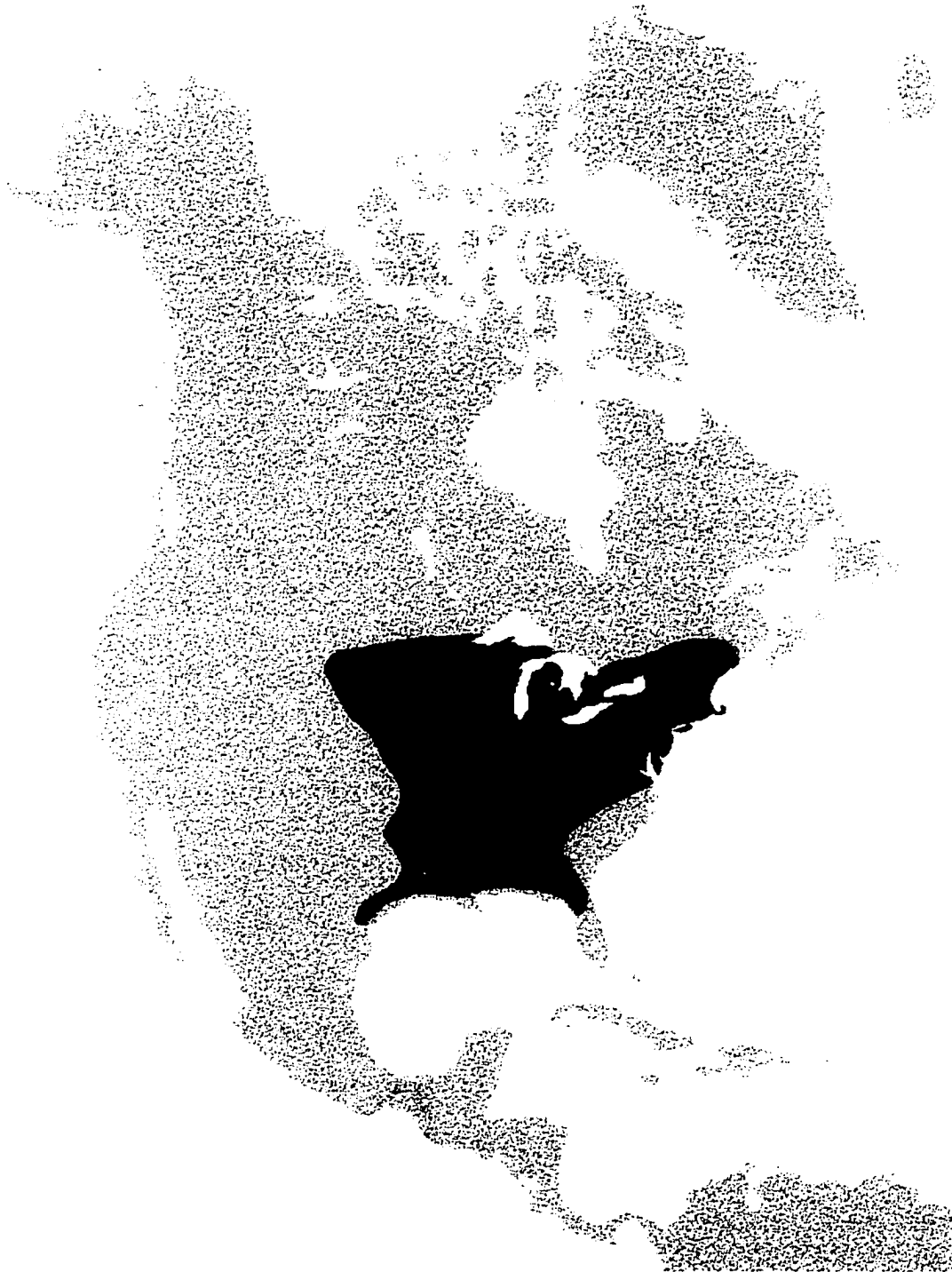
Giant Panda
C=0.00 (98.1%)



e. Little Spotted Kiwi
C=0.00 (99.8%)



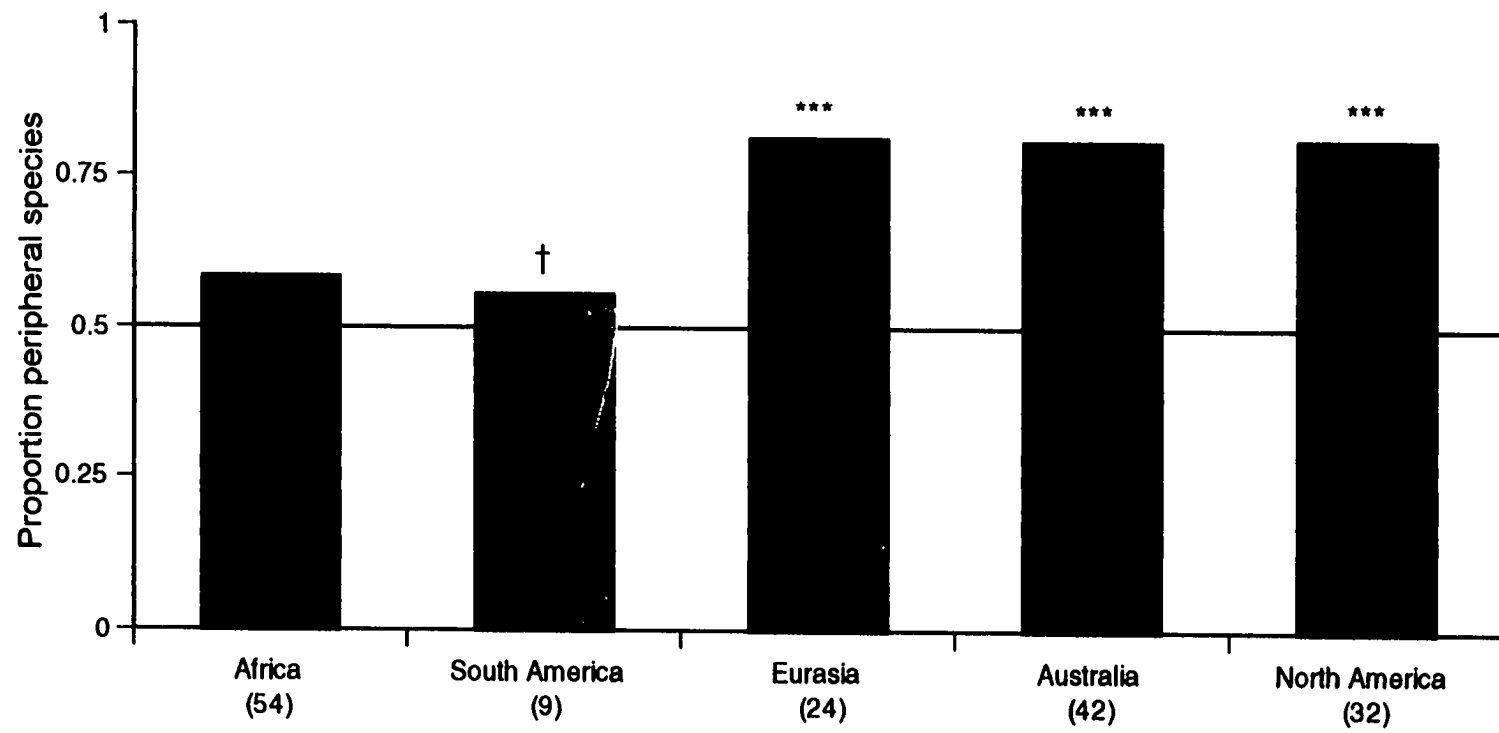
f. American Burying Beetle
C=0.02 (97.6%)

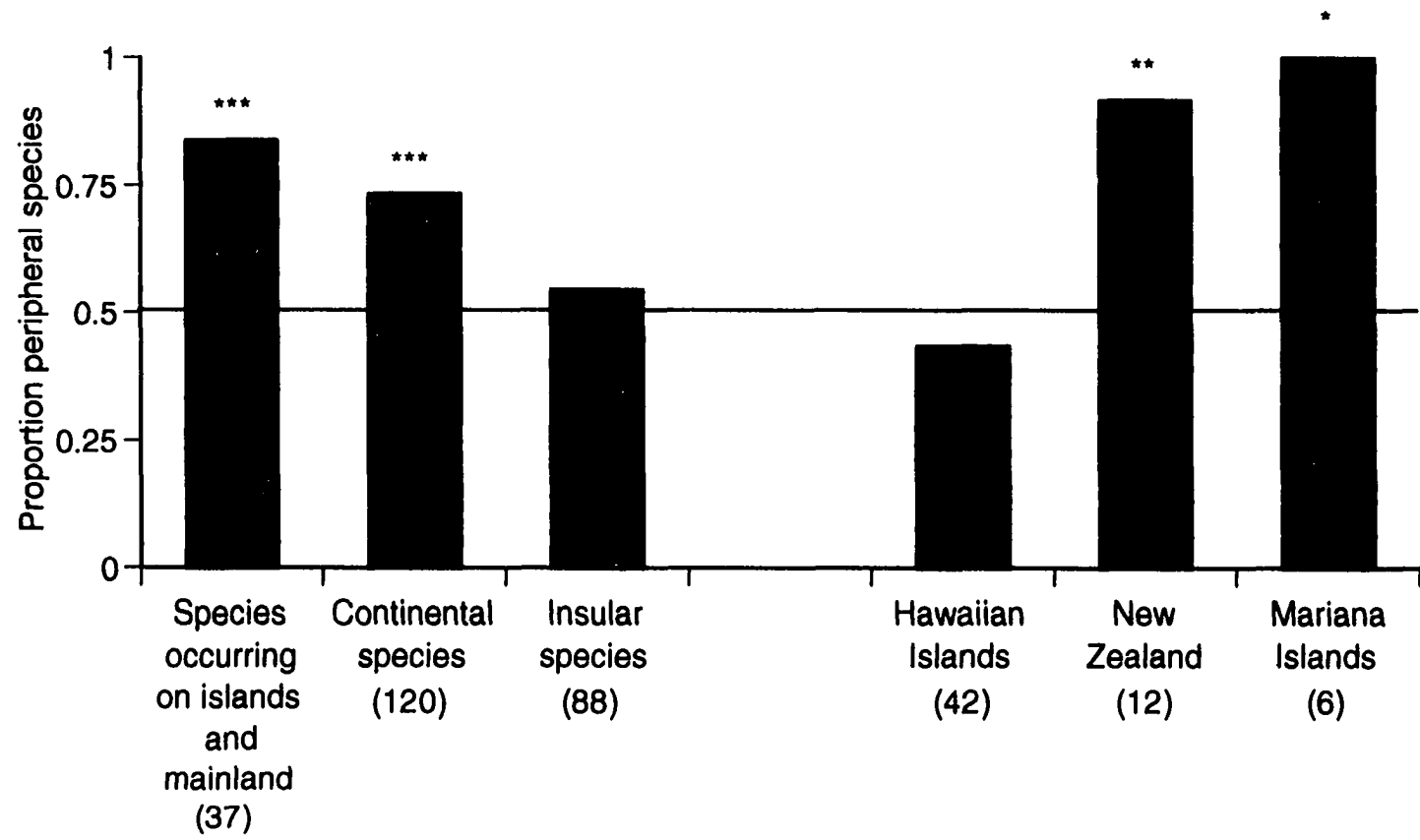


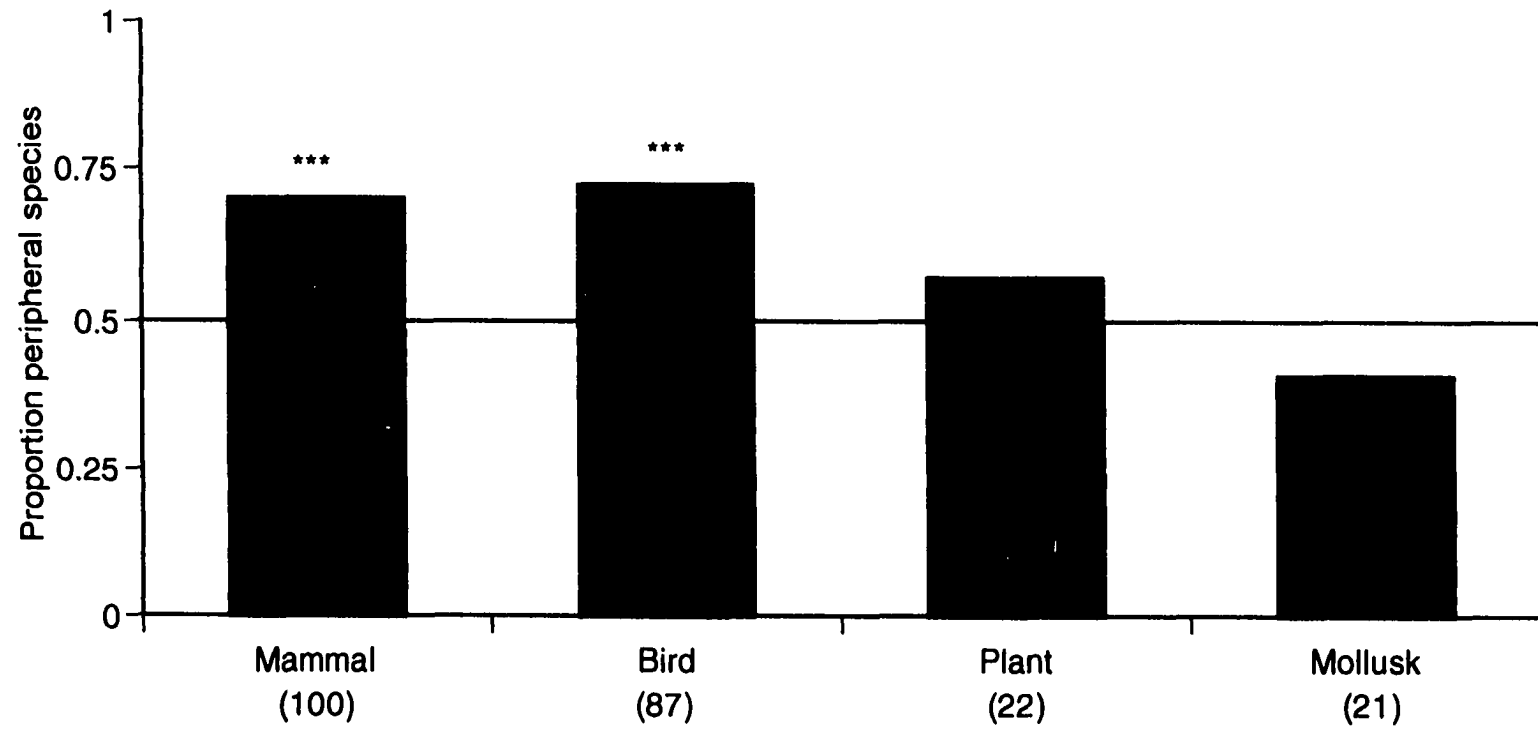
g.

Black-footed Ferret C=0.00 (99%)









a. Bridled White-eye
C=0.13 (90%)



b.

Guam Rail
C=0.18 (94%)



**Trajectories to Extinction:
Spatial Dynamics of the Contraction of Geographic ranges**

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Key words: geographic range, dynamic biogeography,
extinction, conservation

Running head: Contraction of Geographic Ranges

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ABSTRACT: Spatial patterns in the contraction of geographic ranges were examined in 316 declining species of animals and plants. We compared the observed patterns of range contraction with those predicted from two competing hypotheses, one based on the demographic characteristics of historical populations (the demographic hypothesis) and the other based on the contagion-like spread of extinction forces (the contagion hypothesis). These hypotheses were contrasted by examining the sequence of changes in the proportion (C) of the remnant range that fell within the central region of the historical range, over the percent change in range size. The demographic hypothesis predicts that throughout the stages of extinction, from initial decline to loss of the final population, ranges should implode with extinction of central populations occurring only after all peripheral populations have gone extinct. Thus, C should rise above 0.50 and remain there throughout the contraction of the range. The contagion hypothesis, on the other hand, predicts that C should initially rise, but then decline in later stages of range contraction where only the most isolated peripheral populations survive. Two different approaches were employed to examine changes in C during the process of range contraction. First, we compared C -values at intermediate and "final" stages of range contraction with those generated from a Monte Carlo simulation. Second, we used polynomial regression analysis to compare C -values for all species, combined, in different stages of range contraction. The results of the Monte Carlo simulations indicated that

more species had observed range contractions consistent with the contagion hypothesis than expected by chance ($z\text{-score}=2.922$, $P=0.002$). The Monte Carlo analysis also indicated that the number of species whose observed range contractions were consistent with the demographic hypothesis was no greater than expected by chance ($z\text{-score}=0.337$, $P=0.367$). The results of the polynomial regression analysis for both the taxonomic groups (mammals and birds) and all the regions (Australia, Africa, Eurasia, and North America) we examined also supported the contagion hypothesis. We believe these results have important implications for the development of dynamic biogeography and for guiding the conservation of endangered species.

Introduction

In an article reviewing the extent of our knowledge on extinction, Soulé (1983) states:

The extinction problem has little to do with the death rattle of its final actor. The curtain in the last act is but a punctuation mark -- it is not interesting in itself. What biologists want to know about is the process of decline in range and numbers.

Soulé concluded that we knew relatively little about the decline of species' ranges and numbers. An understanding of how and why geographic ranges contract is necessary to develop effective conservation strategies (Simberloff, 1986). Such an understanding could help wildlife managers make better decisions in conserving biodiversity by allowing more efficient allocation of resources for in situ management, suggesting where to survey for undiscovered populations, or planning reintroductions (Lomolino and Channell, 1995, 1998).

Most of the theory regarding extinction has been described as belonging to the small-population paradigm (Simberloff, 1986; Caughley, 1994). It includes the genetic and demographic factors that influence a small population's risk of extinction (e.g., demographic stochasticity, environmental stochasticity, genetic drift, and inbreeding). The small-population paradigm has been contrasted with the declining-species

paradigm that includes those factors that contribute to the decline of species before their populations become rare (e.g., over-exploitation, habitat degradation, and introduced species) (Simberloff, 1986; Caughley, 1994; Green 1994; Hedrick et al., 1996). Hedrick et al. (1996) suggested that this was a false dichotomy, and that processes from both paradigms contribute to extinctions. The factors of the declining-species paradigm reduce distributions and numbers to a point where those of the small-population paradigm can deliver the final blow (Gilpin and Soulé, 1986; Simberloff, 1986; Hedrick et al., 1996). Yet, the factors that reduce a species' range are frequently quite different from those that eliminate the last populations (Soulé, 1983; Vermeij, 1986; Burbidge and McKenzie, 1989; Bibby, 1994). With the exception of extinctions driven by cataclysmic events (e.g., asteroid impact; see Alvarez et. al., 1980) it is unlikely that a numerous and widespread species would become extinct without a prolonged reduction in distribution and number (Raup, 1991). How species interact with environmental changes that lead to extinction is of fundamental interest to conservation biology, but at the scale of the species' range such interactions have been largely ignored. An understanding of this reduction in distribution and accompanying decline in numbers is vital for the preservation of biodiversity, but this understanding does not yet exist (Simberloff, 1986; Bibby, 1994; Caughley, 1994; Raup 1991).

A knowledge of how geographic ranges contract is not only important to conservation biologists, but also to biogeographers. Although acknowledging that geographic ranges are spatially dynamic, most biogeographers have treated them as though they were static features. Most studies of geographic ranges examine a feature of the range (e.g., size, shape, and overlap) at some specific point in time. However, all of these features are influenced by environmental conditions and are subject to change when environmental conditions change (Brown et al., 1996). Most of the research that has treated geographical ranges as dynamic examined how the ranges of introduced species expanded. Most of this work has focused on measuring the expansion rate of the invading species, but has seldom examined other aspects of range formation (Andow et al., 1990; Liebhold et al., 1992; Hasting, 1996a, 1996b; Shigesada and Kawasaki, 1997; but see Taulman and Robbins, 1996).

Very little research has been conducted on the contraction of geographic ranges. Yet, the study of range dynamics should be of fundamental importance to the field of biogeography. How do the geographic ranges of once widely distributed species contract? Are there any directional, latitudinal, regional, or taxonomic biases in the contraction of geographic ranges? More simply put, are there patterns in the contractions of species' geographic ranges?

In this paper, we examine the contraction of geographic ranges of imperiled species, demonstrate a new approach to investigating dynamic biogeography, and provide some important insights for conserving biological diversity.

Currently, there are two different hypotheses that can be used to predict how geographic ranges should contract: one based on demographic characteristics of the historical populations (the demographic hypothesis) and the other based on the geographic dynamics of the extinction factors (the contagion hypothesis – sensu Lomolino and Channell, 1995). These hypotheses rely on different mechanisms, generate different predictions of how ranges should contract, and represent different and competing paradigms within conservation biology.

The demographic hypothesis is derived from the small-population paradigm. It is based on two assumptions. First, the extinction probability of a population should decline with increased population size (MacArthur and Wilson, 1967; Goel and Ritcher-Dyn, 1974; Pimm et al., 1988; Tracy and George, 1992; Lawton, 1995) and should rise with increased variation in population size (Pimm et al., 1988). Second, populations tend to be larger and less variable near the center of the species' geographic range because the environment is more suited to the species (Brown, 1984; Gaston 1990, 1994; New 1991; Lawton, 1995; Curnutt et al., 1996). Given these patterns, ecologists and biogeographers have predicted that ranges should implode,

with final populations of a species persisting near the center of the historical range (Brown, 1995; Lawton 1995; Wolf et al., 1996; Mehlman, 1997).

The demographic hypothesis also makes the implicit assumptions that the environmental change that triggers the species' decline is ubiquitously and uniformly distributed. For this hypothesis to be correct, the environmental trigger or extinction factor must include the entire range of the species, because any portion of the range that is not impacted by the extinction factor would be expected to persist. In addition, the intensity of the extinction factor must be uniformly distributed, or else peripheral populations might persist where the intensity of the extinction factor was low. The demographic hypothesis further requires that the onset of the extinction factor is sudden and synchronous across the entire range of the species. If, however, the onset of the extinction factors are staggered across the range of the species, those populations that are last impacted, regardless of their location, may persist longer than those that were historically large.

The contagion hypothesis is derived from the declining-species paradigm. It emphasizes the geographic dynamics of the extinction factors in determining where populations should persist (Lomolino and Channell, 1995). The contagion hypothesis expects those populations that are last impacted by the extinction force to persist the longest. Furthermore, these extinction factors are thought to spread across the landscape like a contagion (Lomolino and Channell, 1995). Regardless of where the contagion begins,

the last place impacted will be along an edge of the historical range. We and others have suggested that in most cases this contagion is a suite of anthropogenic disturbances, including habitat degradation, biocides, xerification, and introduced species or pathogens (Townes and Daugherty, 1994; Lomolino and Channell, 1995).

The little research that has examined how geographic ranges contract has suggested that the contagion hypothesis may better explain the observed patterns. Townes and Daugherty (1994) studied range contraction and extinction of reptiles and amphibians in New Zealand and found that many species that now persist only in small isolated pockets, particularly smaller islands, once occurred throughout the larger islands. From paleontological and archaeological evidence they concluded that the decline of many of these species coincided with the waves of human colonization of New Zealand (Townes and Daugherty, 1994). They attribute some of the change in distributions to direct human influences (e.g., human predation and habitat degradation), but suggest the largest impact has come from introduced mammals (e.g., dogs, *Canis familiaris*; pigs, *Sus scrofa*; Norway rats, *Rattus norvegicus*; feral cats, *Felis catus*; Townes and Daugherty, 1994). The tendency for species to persist in the isolated portions of their range, frequently the periphery, and on off-shore islands matches what we have found in our previous studies (Lomolino and Channell, 1995, 1998; Chapter 1).

In our initial studies of range contraction, we found a tendency for species from large landmasses to persist in the periphery of their historical range (Lomolino and Channell, 1995, 1998; Chapter 1). To account for this pattern, we proposed the contagion hypothesis – the species persists in the portion of its range that is most isolated from the initial point of contagion. This interpretation was further supported by the observation that species that historically occurred on both the mainland and the off-shore islands persisted more frequently on the islands than one would expect from their small sizes (Lomolino and Channell, 1995; Chapter 1). We suggested that the isolation of the insular populations protected them from the anthropogenic disturbances that extirpated the mainland populations.

Although these examinations of range contraction are important and useful, they were derived from only two snapshots of the entire contraction process. The study of Towns and Dougherty (1994) and our previous work (Lomolino and Channell, 1995, 1998; Chapter 1) looked at the size and location of geographic ranges at two specific times (historical and current or final geographic range), but neither of these studies examined the sequence of range contraction between these extremes. A more comprehensive understanding of dynamic biogeography would include not only the position of the final range, but also the sequence or trajectory that the range may have undergone to reach that position.

Fortunately, the demographic and contagion hypotheses not only predict different positions for final populations, but they also suggest distinctive trajectories to these outcomes. Throughout all stages of range contraction, the demographic hypothesis predicts that ranges should contract from the periphery to the center of the historical range (Figure 1a). In contrast, the contagion hypothesis predicts that range contraction should progress from the edge first impacted by the contagion, then to the central portion of the range, and finally to the periphery most distant from the initial impact of the contagion (Figure 1b). The proportion of the remnant range that falls in the central region of the historical range (C) changes predictably throughout both types of range contraction. If C is graphed against the percent contracted (Figure 2), the two hypotheses are easily distinguished. As the range contracts, the demographic hypothesis suggests that C should rise rapidly to the maximum value (1.0) and remain there through the rest of the contraction. The contagion hypothesis suggests that C should rise initially above 0.50 then gradually decline towards 0.00. In this study, we evaluate these two hypotheses of range contraction by testing these predicted extinction trajectories using empirical contractions of species geographic ranges. We then discuss the relevance of our results, and outline prospective studies that may provide some additional key insights into dynamic biogeography and conservation biology.

Methods and Materials

We obtained range maps for 309 species from literature or through personal correspondence with authorities. Only species with maps available for both the historical and extant ranges (or final site in the case of extinct species) were used. We digitized the range maps into Idrisi (Eastman, 1995), a geographic information system (GIS). For each species, we located the range center, which was the point within the species' historical range that was most distant from all edges (Lomolino and Channell, 1995). We divided the historical ranges into two equal area bands, peripheral and central. These bands were constructed by collapsing the range boundaries toward the range center until the area occupied in the inner polygon equaled half of the area of the historical range. We then calculated an index of centrality (C), which was the proportion of the remnant range that fell within the central portion of the historical range. The index of centrality ranges from 0.0, where the remnant range falls completely outside the central portion of the historical range, to 1.0, where the remnant range falls completely within the central portion of the historical range.

We used two different approaches to examine the dynamics of range contraction: one comparing C-values for each species at an intermediate and "final" stage of range contraction (intermediate stage approach), and one comparing C-values for many species each at different stages of contraction (multi-species approach). For the intermediate stage approach, the

demographic hypothesis predicts C -values should exceed 0.50 for intermediate stages (C_i) and increase or remain the same for the final stages of range contraction (C_f). The contagion hypothesis predicts C_i should be greater than 0.5, but C_f should be less than C_i . There are two other possible scenarios: $0.5 > C_i \geq C_f$ (scenario 1), and $0.5 > C_i < C_f$ (scenario 2).

Our protocol required that the area of the geographic range at the intermediate stage of contraction be greater than 25% of the historical range and that the area of the geographic range at the "final" stage of range contraction be less than or equal to 25% of the historical range. Range maps for 27 species met these requirements. We counted the number of species whose C_f and C_i values supported the prediction of the demographic hypothesis, contagion hypothesis, or one of the two alternative scenarios. We then performed a Monte Carlo simulation to assess the statistical significance of these counts. First, we calculated the function limits, the range of possible C -values at all degrees of contraction (thick lines in Figure 2). While C can range from 0.0 to 1.0, the extreme values are only possible after the range has contracted at least 50%. For degrees of contraction less than 50%, we calculated the possible extreme values. Second, we generated random C_i -values for each species at the observed percent contracted and within the function limits at that degree of contraction. Third, we generated random C_f -values for each species at the observed percent contracted. Since we required the percent contracted for the C_f -value to be greater than or

equal to 75%, the randomly generated C_r -values could vary from 0 to 1. Fourth, we counted how many randomly generated C_i and C_r -values supported each hypothesis or scenario. We repeated these randomizations for 1000 iterations. The observed counts were compared with the generated distributions of counts using z-scores (Zar, 1984).

For the multi-species approach, we graphed the C-value of each species against its percent contracted. We performed a second-order polynomial regression forced through an intercept of 0.50 ($C=0.50$ by definition at 0% contracted)(StatView, 1996). Outliers or points of undue leverage were identified in the regression analysis and the analysis was repeated excluding those points (Systat, 1997). If the resulting regression line initially rises above 0.50 and remains greater than 0.50 in later stages of contraction, then the demographic hypothesis would be supported. However, if the resulting regression line initially rises above 0.50 and then declines toward 0.0, then the contagion hypothesis would be supported. We compared the linear and quadratic terms of the regression lines between regions and between taxonomic groups using an analysis of covariance (ANCOVA)(SAS, 1996) .

Results

Patterns of range contraction in the American chestnut (*Castanea dentata*), the red wolf (*Canis rufus*), and the numbat (*Myrmecobius*

fasciatus) are representative of those for most species. That is, they all show contractions in which the C-value initially rose above 0.50 and then later declined toward 0.00 (Figure 3a-c).

Initial examination of the C-values at intermediate and final stages of range contraction (Figure 4) shows a significant dominance of vectors with negative slopes ($C_i > C_f$; 7 positive slopes, 20 negative slopes, $P=0.01$, binomial test). This suggests a tendency for most species to contract to the periphery of their historical ranges. The intermediate stage analysis indicated that significantly more species demonstrated range contractions consistent with the contagion hypothesis ($C_i > 0.50$ and $C_f < 0.5$) than expected by the simulation ($z\text{-score}=2.922$, $P=0.002$; Figure 5d). In contrast, the number of species that demonstrated range contractions consistent with the demographic hypothesis ($C_i > 0.50$ and $C_f > C_i$) or scenario 1 ($C_i < 0.50$ and $C_f < C_i$) did not differ significantly from their respective simulation means ($z\text{-score}=0.337$, 0.383 , $P=0.367$, 0.352 , respectively; Figures 5a and 5b). Statistically fewer species exhibited the scenario 2 pattern ($C_i < 0.50$ and $C_f > 0.5$) than predicted by the simulation ($z\text{-score}=2.353$, $P=0.009$; Figure 5c).

The initial rise of the regression line of C as a function of the percent contracted and its later decline toward 0.00 is general across species and regions, and is consistent with the prediction supporting the contagion hypothesis (Figures 7-8 and Table 1). Only the birds and mammals had a sufficient number of species at various degrees of range contraction to

warrant separate regression analysis. The regression line of both of these taxonomic groups rose above 0.50 initially and then later declined toward 0.0, consistent with the contagion hypothesis (regression coefficients significant at $P < 0.01$; Figure 7a-b and Table 1). The ANCOVA indicated that there were not significant differences between these regressions' linear terms ($F = 1.995$, $df = 1$, $P = 0.159$) or between the quadratic terms ($F = 1.502$, $df = 1$, $P = 0.221$).

Africa, Australia, Eurasia, and North America had sufficient numbers of species at various degrees of range contraction to allow separate regression analysis (all taxa combined). All of the regression lines resulting from the regional analysis initially rose above 0.5, and then declined toward 0.0, again consistent with the contagion hypothesis (regression coefficients significant at $P < 0.05$; Figure 8a-d and Table 1). The ANCOVA indicated no significant inter-regional differences between the linear terms ($F = 0.620$, $df = 3$, $P = 0.603$) or between the quadratic terms ($F = 0.949$, $df = 3$, $P = 0.417$).

Discussion

All of the results of this study are consistent with the contagion hypothesis. Range contraction in species with well-documented, multi-stage declines all illustrated what we expect from the contagion hypothesis (e.g., Figures 3a-c). Species with information on two stages of decline further supported the contagion hypothesis (Figures 4 and 5a-d). All of the

regression analyses for different taxonomic groups and regions, as well as the overall analysis, demonstrated the pattern of range contraction predicted from the contagion hypothesis.

The particular shape of the regression lines also suggests other important features of range contraction. The initial rise of the regression lines (Figures 6, 7a-b, and 8a-d) indicate that initial range loss occurs in the periphery of the historical range. This may at first seem counter-intuitive. We predict from the contagion hypothesis that remnant populations will be found in the periphery of the historical range, but we also predict from the same hypothesis that the initial loss of the range will occur in the periphery. Therefore, initial loss of some peripheral populations does not contradict the contagion hypothesis (e.g., see Haeck and Hengeveld, 1981; Gaston, 1994; Fuller et al., 1995; Mehlman, 1997). The regression lines also do not indicate a peripheral bias until late in the contraction process (the regression line crosses $C=0.5$) (ranging from 56% contracted for North America to 88% contracted for Africa). Thus, only the examination of geographic ranges at high degrees of range contraction should find the peripheral bias. Furthermore, by the time the peripheral bias becomes apparent, not only is most of the central region gone, but so is most of the periphery. Regional studies (e.g., Nathan et al., 1996) that examine only a portion of a species' range will frequently see the loss of peripheral populations. However, because most of the periphery is lost in range contractions, this again does

not contradict the contagion hypothesis. Even the loss of most of the periphery of the historical range of a species should not disqualify the remaining periphery from conservation efforts. The red wolf (Figure 3b), for example, had lost 72% of its historical range by 1930 and had a relatively high C-value ($C=0.67$), but further range contractions resulted in the species persisting only in the periphery of its historical range (99% contracted, $C=0.00$). These explanations, however, should not be taken to minimize the importance of small or regional declines of species. Observations of small declines in species' ranges (e.g., Short and Smith, 1994; Smith and Quin, 1996; Fisher and Shaffer, 1996) may presage much larger declines in the future (King, 1987).

In our previous work we have shown that although species from most regions showed a significant tendency to contract to the periphery of their historical range, African species did not (Chapter 1). The results of this study also suggest that trajectories of range contraction in Africa differ from that in other regions (Figure 8 and Table 1). The African regression model explained considerably less variation (adjusted $r^2=0.092$) than did the Australian (adjusted $r^2=0.696$), Eurasian (adjusted $r^2=0.390$), and North American (adjusted $r^2=0.429$) regression model. The regression model for Africa was also noticeably flatter than those for other regions, initially rising above 0.50 but then decreasing to only slightly less than 0.50. In the other regions, an initial increase in C-values above 0.50 is followed by a steeper

decline toward 0.00. Africa's predicted C-value at 100% contracted (0.445 ± 0.157) is considerably greater than that predicted for Australia (0.114 ± 0.275), Eurasia (0.262 ± 0.417), or North America (0.227 ± 0.216). This difference in regression lines suggests that in Africa initial range contraction begins along the periphery, but then shifts so that peripheral and central populations are lost in equal proportions. This sequence of range contraction contrasts with the sequence from the other regions, where later stages of range contraction are dominated by the loss of central populations.

We believe that Africa's uniqueness in range contraction is the result of a fundamental difference in the dynamics of the extinction forces that are acting in Africa. Human evolution in Africa allowed species there to adapt to coexist with humans (Martin, 1984). However, as humans expanded their range out of Africa and into the other regions of the world they encountered animals that were naïve to their abilities and made them easy prey (Martin, 1984; Diamond, 1984). African species were never exposed to the colonizing , contagion-like wave front of humans that pushes species to the edge of their ranges and possible extinction.

We believe that the macroecological patterns and the extinction theory on which the demographic hypothesis is based are probably real and general patterns of nature, but that the extinction factors, often the forgotten element in conservation studies, overwhelm these patterns. Furthermore, the demographic hypothesis assumes that the extinction factor has a sudden

onset that quickly covers the entire range of the species. In addition, it assumes that the extinction factor must act uniformly across the range of the species, eliminating equal numbers of individuals from all populations. The extinction factor is also assumed not to interact with other aspects of the biology of the species that could alter the previously optimal regions within the species range. Favorable regions, where the species is abundant prior to the introduction of the extinction factor, "should on average remain relatively more favorable" (Brown, 1995). We submit that these assumptions are somewhat unrealistic. Finally, all of these assumptions must be met if the demographic hypothesis is correct. Relatively minor deviations from these assumptions may radically alter the expected pattern of range contraction. If the extinction factor is not ubiquitous or uniform, those populations that are last or least impacted should persist longer than populations that were initially larger. Interestingly, the persistence of such populations would then depend on the distribution and nature of the extinction force, as predicted by the contagion hypothesis.

This study should not be misinterpreted as implying that all periphery is equal. Isolation from the extinction disturbance determines which populations survive. Only when the distribution and dynamics of the extinction factors are well understood will it become apparent which of the peripheral populations should persist. We, however, know surprisingly little about extinction factors or how they may interact with demographic

characteristics of historical populations. Future research into the nature of the spread of extinction forces will not only further illuminate the patterns we have uncovered, but also aid in the development of conservation strategies. Both biogeography and conservation biology would benefit from understanding not only how these disturbances are distributed, but also how they spread (speed, direction, and ultimate distribution). Studies of this type may benefit by understanding the other end of dynamic biogeography, the range expansion of invading species (see Shigesada and Kawasaki, 1997 for a review). This combination of both aspects of dynamic biogeography may be especially appropriate considering the part that many invading species play in the decline of other species (Burbidge and McKenzie, 1989; Bibby, 1994; Towns and Dougherty, 1994; Short and Smith, 1994; Fisher and Shaffer, 1996; Smith and Quin, 1996; Steadman, 1996). Are these patterns of distribution and spread altered by the characteristics of the environment? Does environmental heterogeneity, for example, accelerate or hinder the spread of the contagion? Do the characteristics of the focal populations (e.g., size, resistance to a particular extinction factor, density, isolation) influence the spread of the contagion? We also do not know how extinction factors interact with populations. An extinction factor may truncate geographic ranges without regard to the characteristics of the constituent populations, or they may slowly decrease the size of populations until populations are lost through attrition. Moreover, there undoubtedly

will be considerable variation among the answers to these questions depending on the extinction factors that are examined (e.g., logging vs. a pathogen). Answering these basic but important questions would help us to understand how geographic ranges and populations decline, and should also suggest how we might better conserve biodiversity.

Much of the information we would need to make use of the described pattern of range contraction does not exist. The actual cause of decline in most species is not well understood (Caughley, 1994). Rarely, even in the few cases where the causes of the decline are known, has the distribution and intensity of the extinction factors been mapped. The identification of the factors causing the decline in a species should be among the first steps in its conservation (Caughley, 1994; Green, 1994; Caughley and Gunn, 1996; Dickman, 1996). Conservation biologists should begin to consider the geographic dynamics of the extinction factors. As we have shown, it is not only the features of the species or populations that determine which populations will survive, but the distribution and dynamic nature of extinction factors. We are not suggesting that sites near the center of the species historical range be excluded from conservation plans. Both central and peripheral populations can play important roles in conservation (Chapter 1; Lesica and Allendorf, 1995; Lomolino and Channell, 1995, 1998).

Caughley (1994) and Green (1994) observed that the small-population paradigm was the current fashion, but stressed that the declining-species

paradigm also had a part to play in conserving biodiversity. Our results emphasize the under-appreciated importance of the declining-species paradigm. The contraction of species' ranges is not the small-population paradigm writ large (the demographic hypothesis), but rather the function of the dynamic geography of extinction factors. This study also suggests the importance of the declining-population paradigm, not only for the identification of declining species, but also to begin to address conservation efforts before the species is critically endangered. If conservation strategies can be implemented before a species' distribution and number have declined to a critical level (where the problems of the small populations become relevant), we may be able to conserve more successfully more species. In closing his paper comparing the small-population and declining-population paradigms, Caughley (1994) stated: "Each has much to learn from the other. In combination they might enlarge our idea of what is possible." We agree that the best conservation plans will incorporate insights from both paradigms. This will require, however, recognition of the part that the declining-species paradigm can play.

Acknowledgments

We thank N. Czaplewski, T. Franklin, M. Kaspari, D. Mehlman, K. Pandora, D. Perault, K. Perez, G. Smith, and C. Vaughn for their advice and comments on this paper. We would also like to thank M. Ashley, L. Carbyn, M. Scott, and D. Steadman who provided information on the distribution of several species.

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Table 1. Linear and quadratic terms of the polynomial least squares regression analyses for birds and mammals from all continents, and for all species on four continents (StatView, 1996). The intercept of each regression line was forced through 0.50. Numbers in parentheses are the standard error of the term, t-test of term differing from 0, and probability associated with the t-test. Also included are the adjusted r^2 of the regression line and sample size (n). Analysis of covariance (ANCOVA) indicated that the regression terms for the birds and mammals did not differ significantly from one another (linear term $F=1.995$, $df=1$, $P=0.159$; quadratic term $F=1.502$, $df=1$, $P=0.221$)(SAS Institute, 1996). The ANCOVA also did not detect significant differences between the regression terms of the continents (linear term $F=0.620$, $df=3$, $P=0.603$; quadratic term $F=0.949$, $df=3$, $P=0.417$).

	Linear (se, t, P)	Quadratic (se, t, P)	adjusted r^2	n
Birds	0.00549 (0.00173, 3.174, 0.002)	-8.387E-5 (1.926E-5, 4.355, <0.001)	0.485	71
Mammals	0.00570 (0.00091, 6.288, <0.001)	-8.022E-5 (1.040E-5, 7.492, <0.001)	0.342	208
Africa	0.00418 (0.00155, 2.703, 0.009)	-4.732E-5 (1.868E-5, 2.533, 0.014)	0.092	56
Australia	0.00496 (0.00099, 5.028, <0.001)	-8.817E-5 (1.130E-5, 7.804, <0.001)	0.696	94
Eurasia	0.00739 (0.00205, 3.612, <0.001)	-9.773E-5 (2.214E-5, 4.415, <0.001)	0.390	78
North America	0.00372 (0.00160, 2.333, 0.023)	-6.451E-5 (1.799E-5, 3.585, <0.001)	0.429	65
Overall	0.00533 (0.00082, 6.491, <0.001)	-7.752E-5 (9.237E-5, 8.393, <0.001)	0.343	309

Figure legends

Figure 1. A graphical representation of the spatial sequence of range contraction suggested by two alternate hypotheses of range contraction: the demographic hypothesis (a) and the contagion hypothesis (b). We divided the historical ranges into two equal area bands, peripheral and central. These bands were constructed by collapsing the range boundaries toward the range center until the area occupied in the inner polygon equaled half of the area of the historical range. The dark gray represents the peripheral half of the historical range, while the light gray represents the central half of the historical range. The black represents the region in which the species is extinct. The index of centrality (C) is the proportion of the remnant range that falls within the central region of the historical range.

Figure 2. Changes in the index of centrality (C), the proportion of the remnant range that falls within the central region of the historical range, with range contraction according to the demographic hypothesis (from Figure 1) and contagion hypothesis (from Figure 2). The thick line represents the function limits of C. Note that according to the demographic hypothesis, C should rise continuously to the maximum value (1.0) and remain there through the rest of the contraction. The contagion hypothesis, on the other hand, suggests

that C should initially rise above 0.50 and then gradually decline to 0.00.

Figure 3. Sequential range contractions of American chestnut (*Castanea dentata*) (a), red wolf (*Canis rufus*)(b), and numbat (*Myrmecobius fasciatus*)(c). Within the range of the species, darker colors represent more recent occurrences. The index of centrality (C), the proportion of the remnant range that falls within the central region of the historical range, has been graphed for each of the species at the corresponding percent contracted. The initial rise of C above 0.50 followed by a decline towards 0.00 is consistent with the contagion hypothesis of range contraction, which predicts that extinction fronts should first impact a peripheral population, but then move to drive more central populations to extinction.

Figure 4. Vectors representing declines of species with two intermediate stages of decline. Consistent with the contagion hypothesis of range contraction, a significant proportion of the slopes are negative (20 negative, 7 positive, $P=0.01$, binomial test) indicating that the more peripheral populations exhibit higher persistence during final stages of range contraction.

Figure 5. Frequency distributions of simulated species exhibiting one of 4 different patterns of range contraction: (a) ranges continually implode with final populations found near center of historical range (demographic hypothesis), (b) ranges explode with final populations found near an edge of the species historical range (scenario 1), (c) populations are lost initially in the central portion of the species historical range and then lost in the periphery with final populations found in the central region, (d) initial population loss occurs in the periphery, then switches to the central region with final populations being found near an edge of the species' historical range (contagion hypothesis). The number of observed species with range contractions consistent with each situation are indicated with appropriate z-scores and probabilities. Note that the number of species with range contractions consistent with scenario 2 was significantly less than expected from the frequency distribution (c). The number of species with range contractions consistent with the contagion hypothesis was significantly greater than expected.

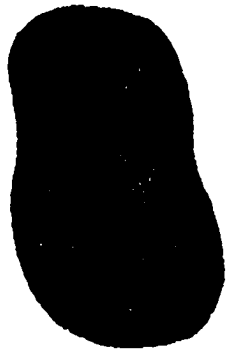
Figure 6. Polynomial least squares regression line of C, the proportion of the remnant range that falls within the central region of the historical range, as a function of percent contracted for all taxonomic groups and regions. The intercept of each regression line was forced through

0.50. The initial rise of C above 0.50 followed by a decline toward 0.0 is consistent with the contagion hypothesis of range contraction.

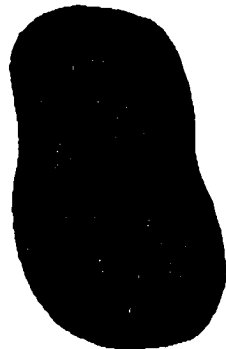
Figure 7. Polynomial least squares regression lines for birds (a) and mammals (b) of C, the proportion of the remnant range that falls within the central region of the historical range, as a function of percent contracted. The intercept of each regression line was forced through 0.50. Regressions for birds and mammals did not differ significantly from each other (ANCOVA linear terms $F=1.995$, $df=1$, $P=0.159$; quadratic terms $F=1.502$, $df=1$, $P=0.221$). The initial rise of C above 0.50 followed by a decline toward 0.00 is consistent with the contagion hypothesis of range contraction.

Figure 8. Polynomial least squares regression lines for Africa (a), Australia (b), Eurasia (c), and North America (d) of C, the proportion of the remnant range that falls within the central region of the historical range, as a function of percent contracted. The intercept of each regression line was forced through 0.50. Regressions for the four regions did not differ significantly from each other (ANCOVA linear term $F=0.620$, $df=3$, $P=0.603$; quadratic term $F=0.949$, $df=3$, $P=0.417$). The initial rise of C above 0.50 followed by a decline toward 0.00 is consistent with the contagion hypothesis of range contraction.

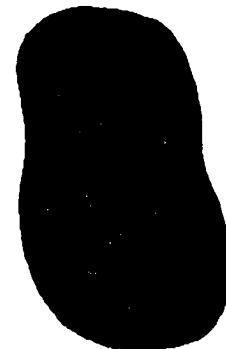
a. Demographic hypothesis



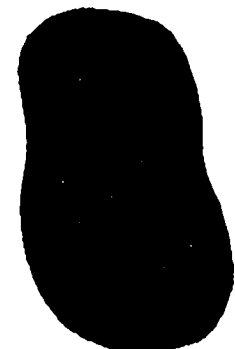
Contracted (%)=0
C=0.5



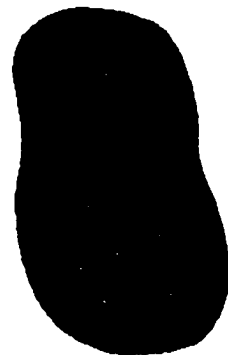
Contracted (%)=13
C=0.56



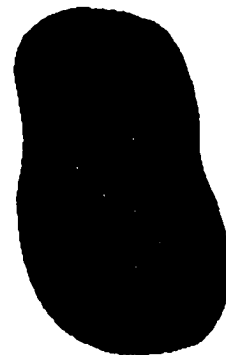
Contracted (%)=28
C=0.67



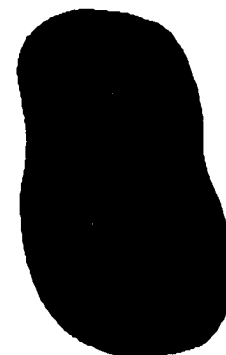
Contracted (%)=42
C=0.86



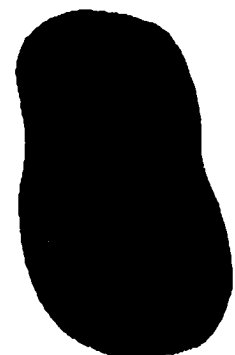
Contracted (%)=57
C=1.0



Contracted (%)=69
C=1.0

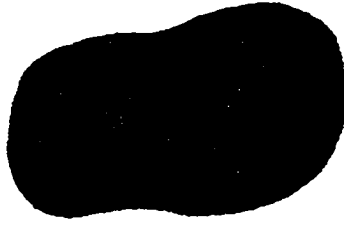


Contracted (%)=84
C=1.0

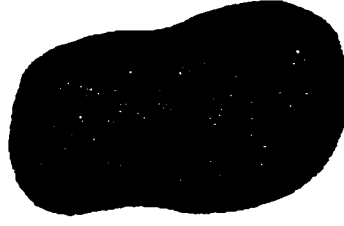


Contracted (%)=98
C=1.0

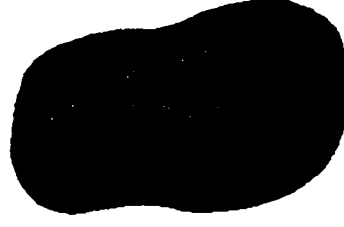
b. Contagion hypothesis



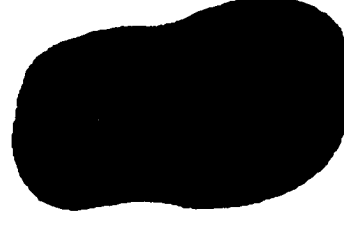
Contracted (%)=0
C=0.5



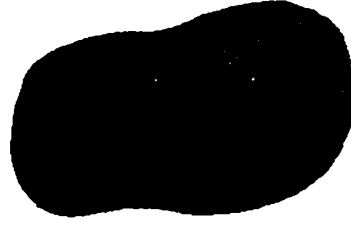
Contracted (%)=14
C=0.58



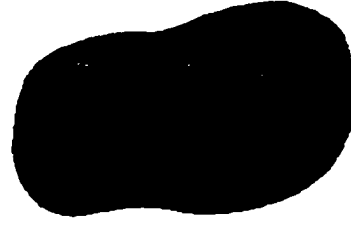
Contracted (%)=28
C=0.57



Contracted (%)=42
C=0.53



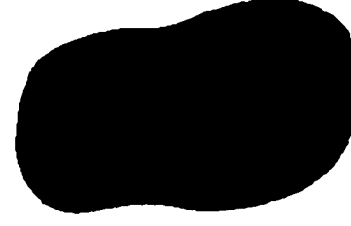
Contracted (%)=57
C=0.44



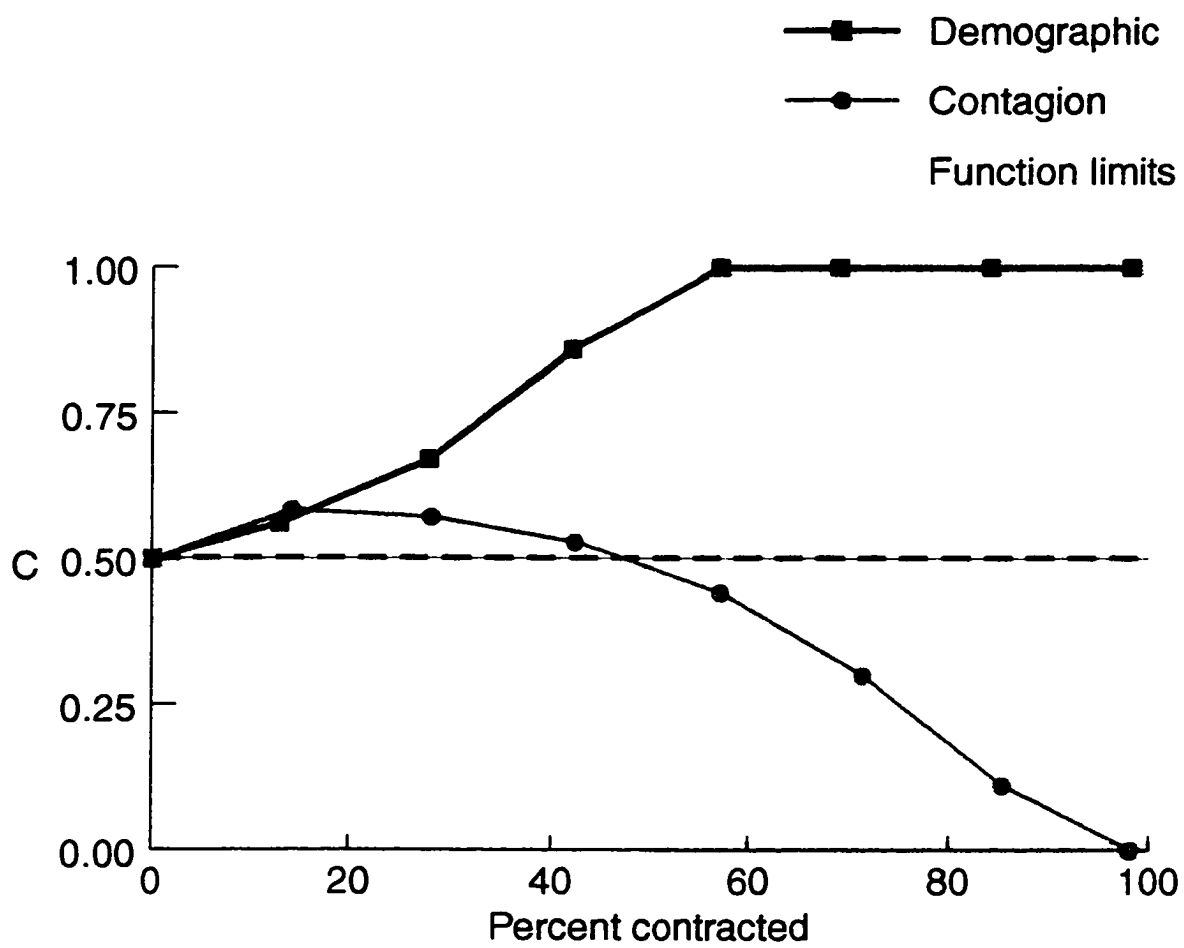
Contracted (%)=71
C=0.30



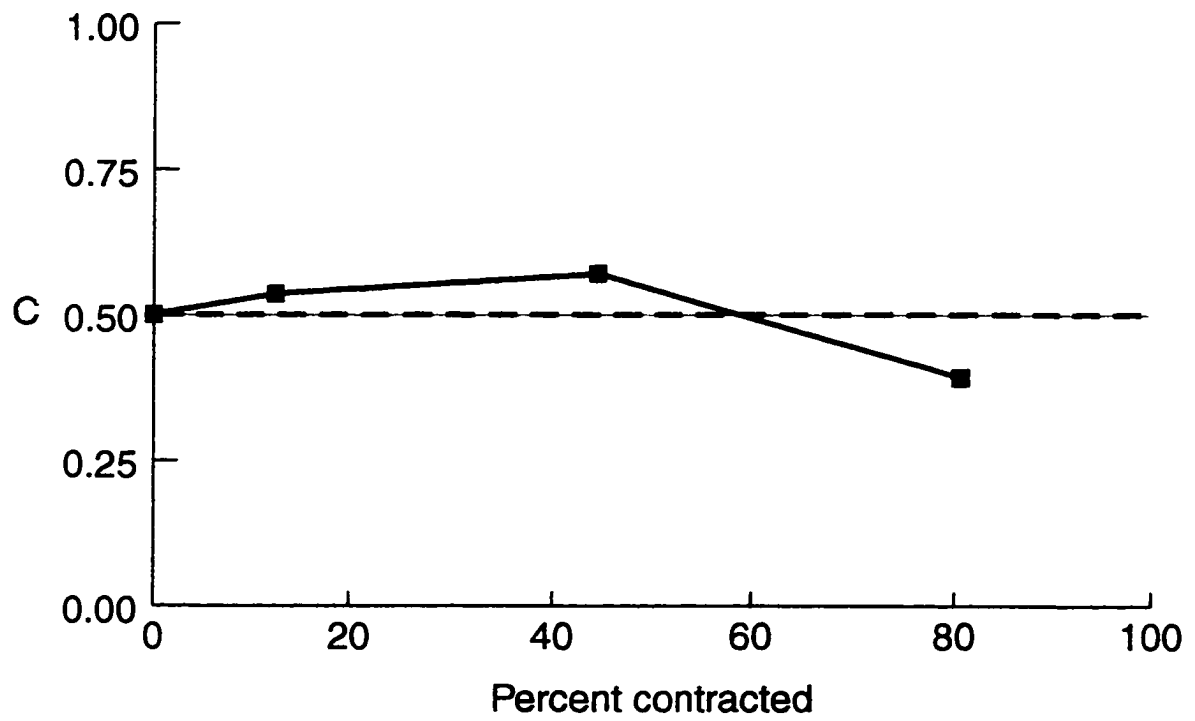
Contracted (%)=85
C=0.11



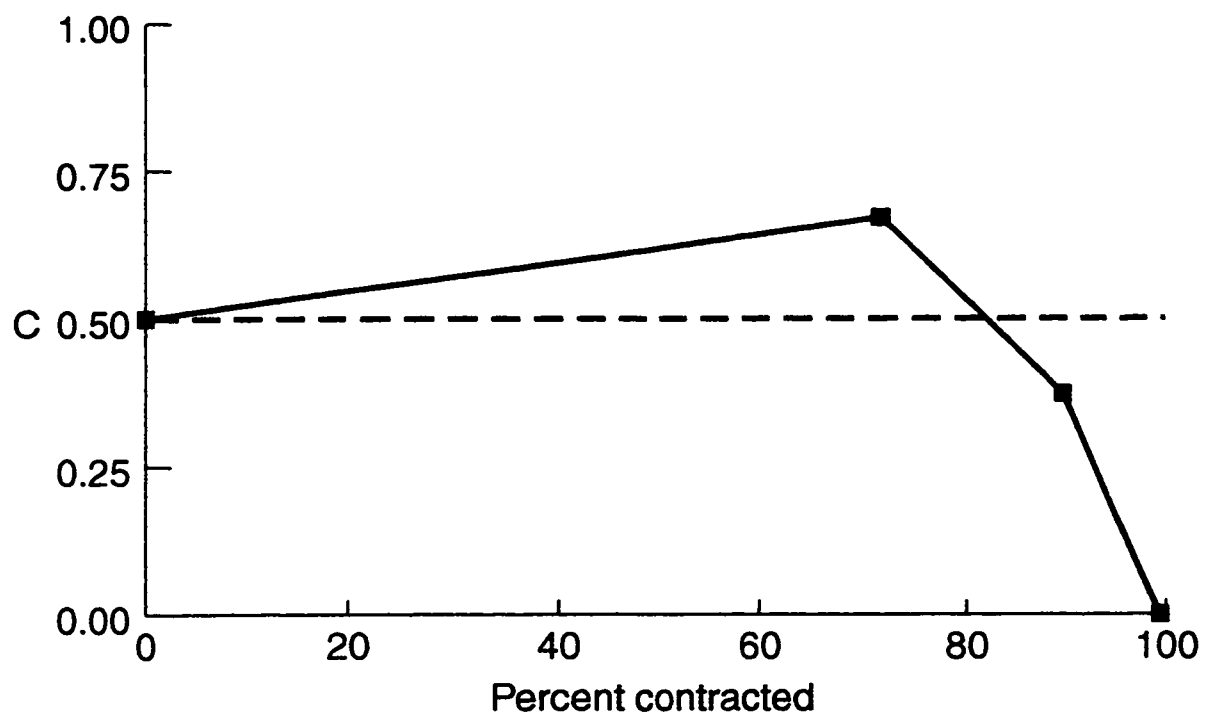
Contracted (%)=98
C=0.0



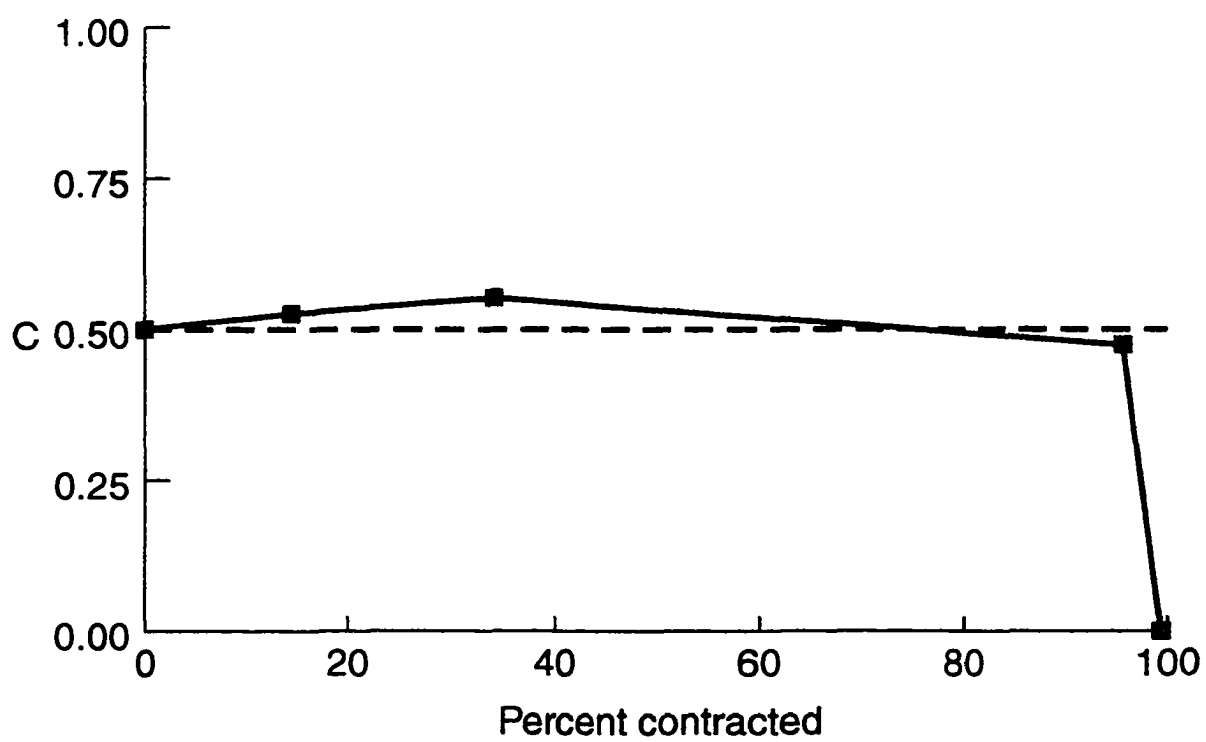
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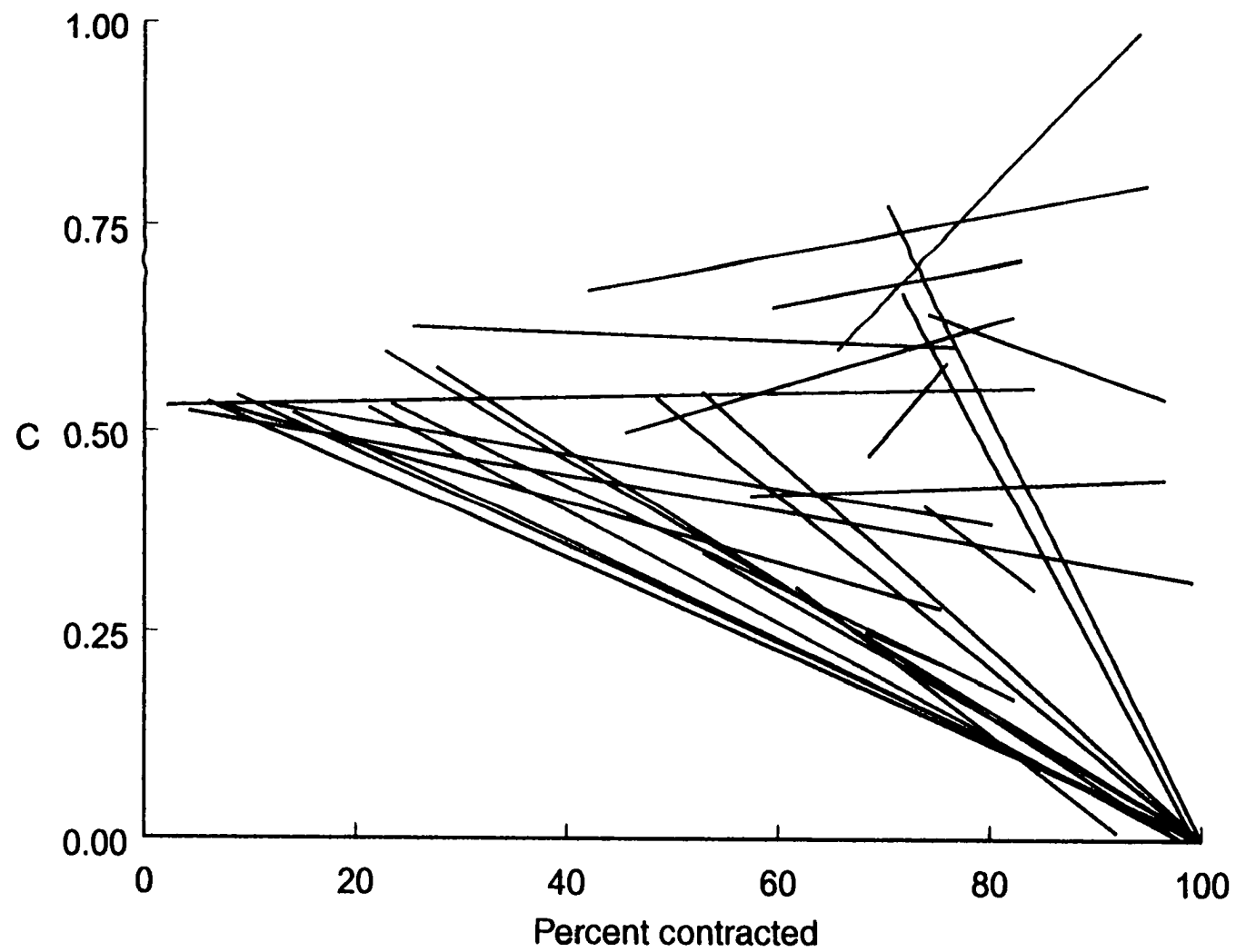


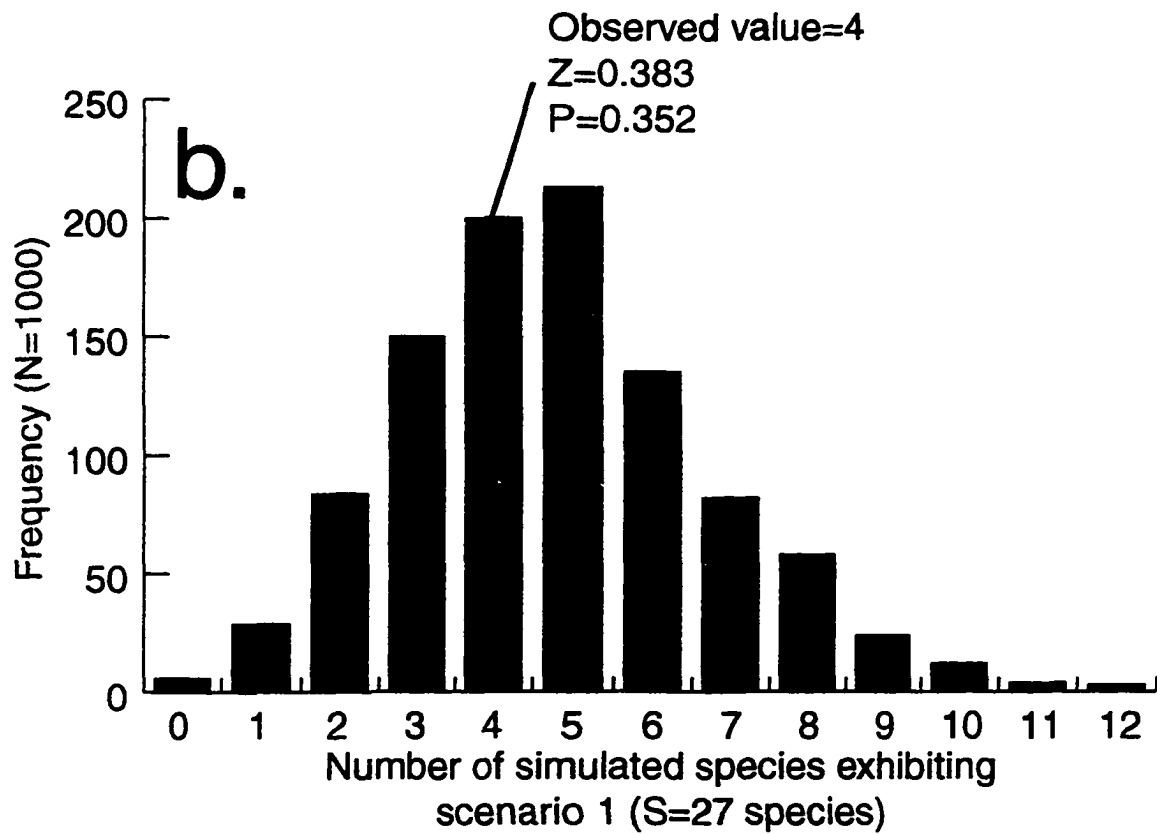
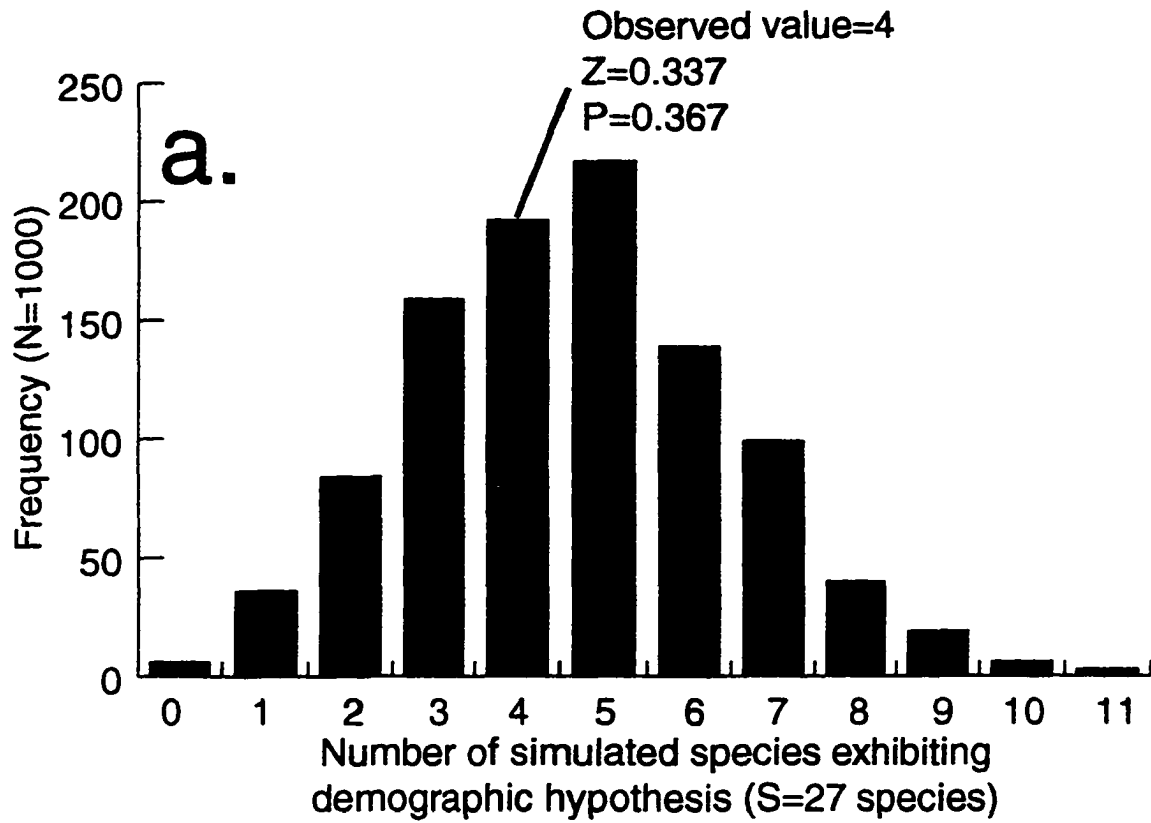
b.

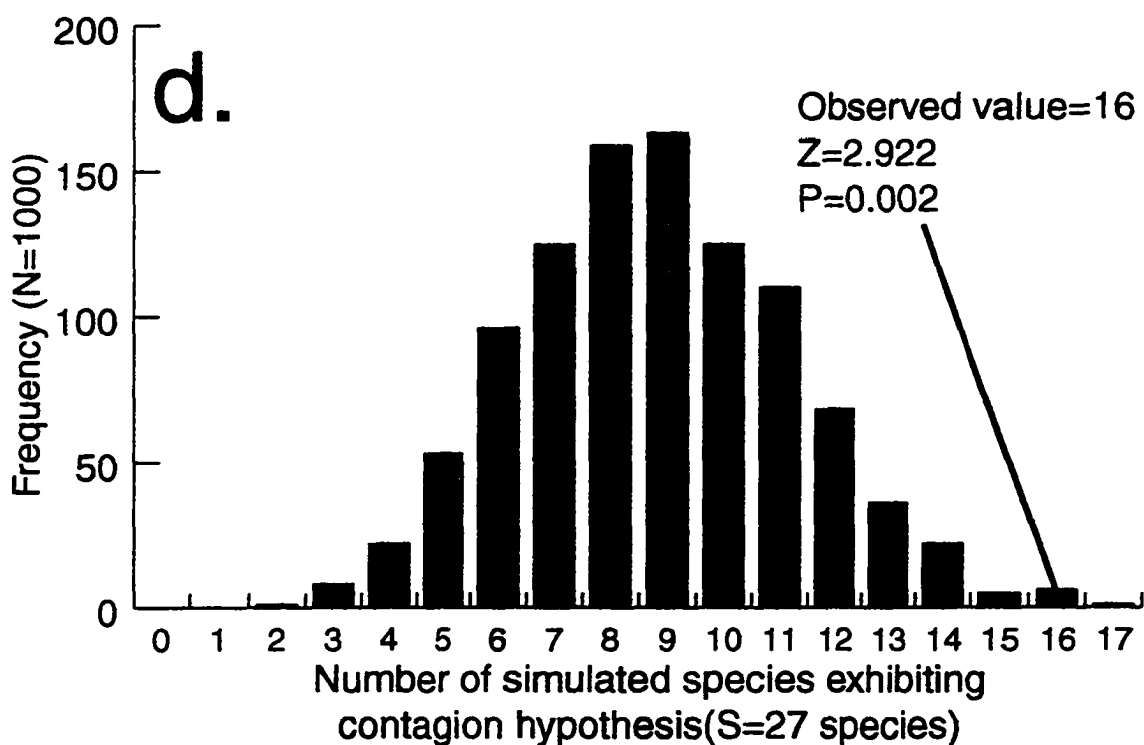
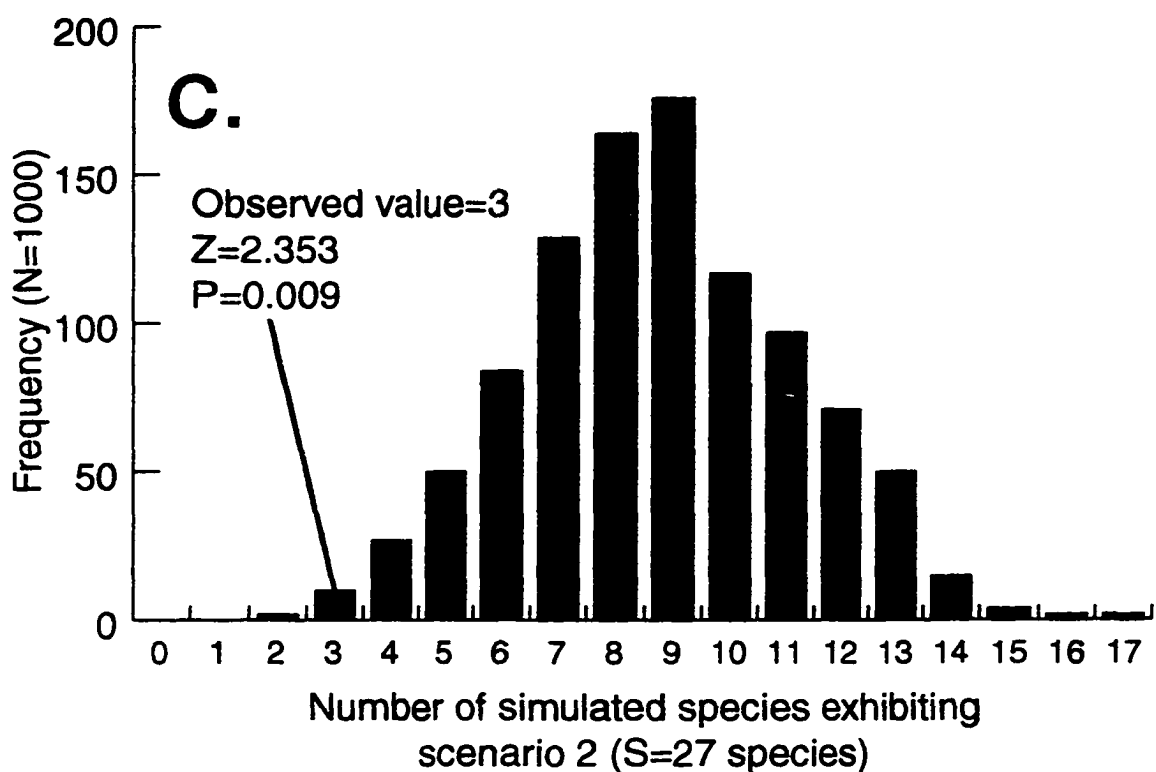


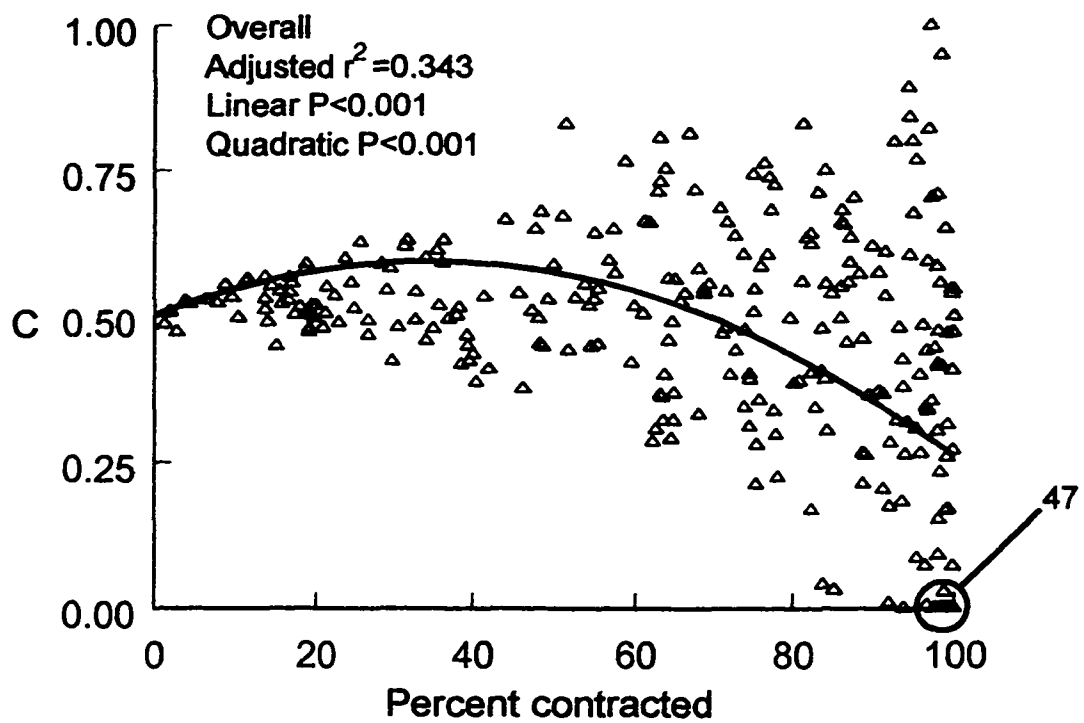
C.

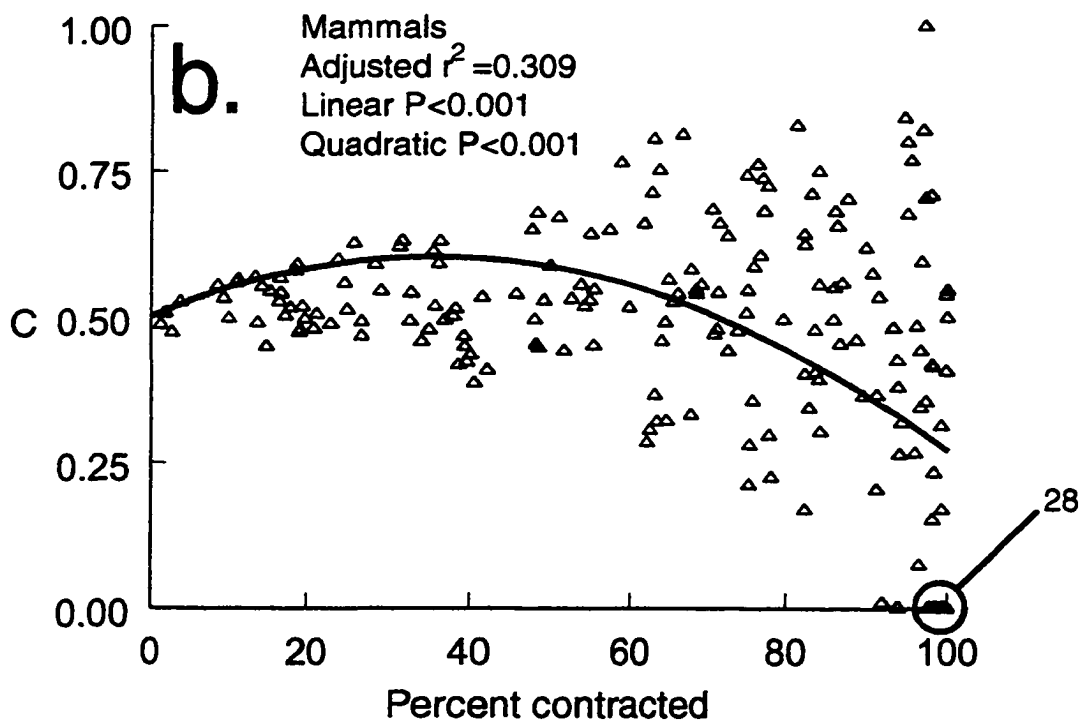
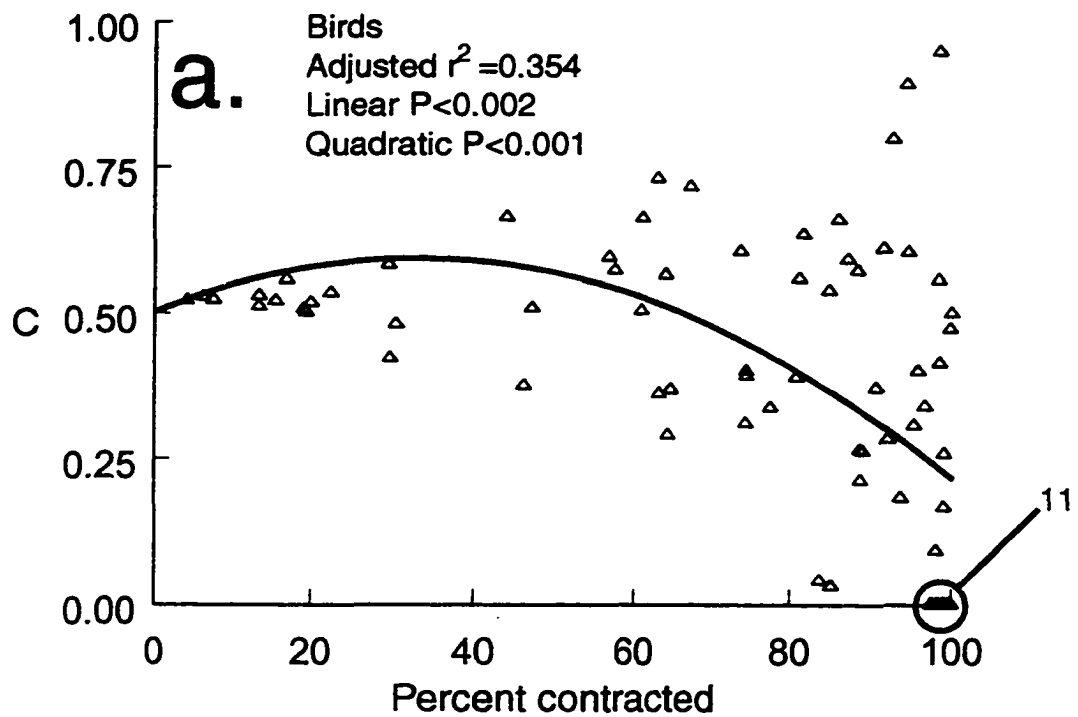


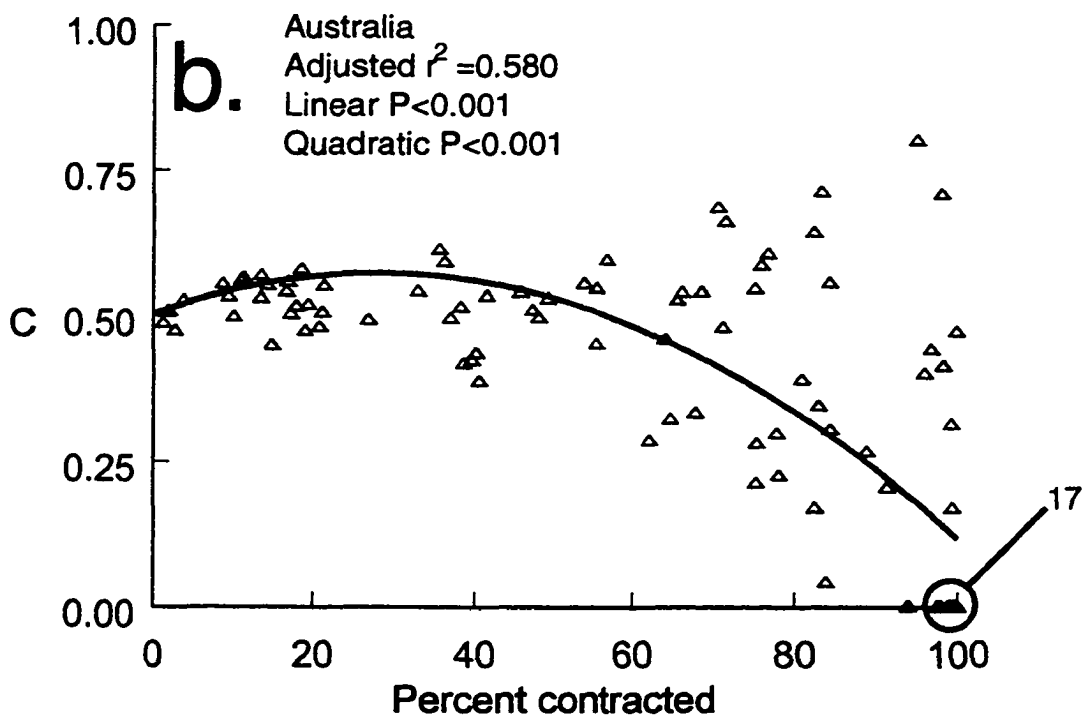
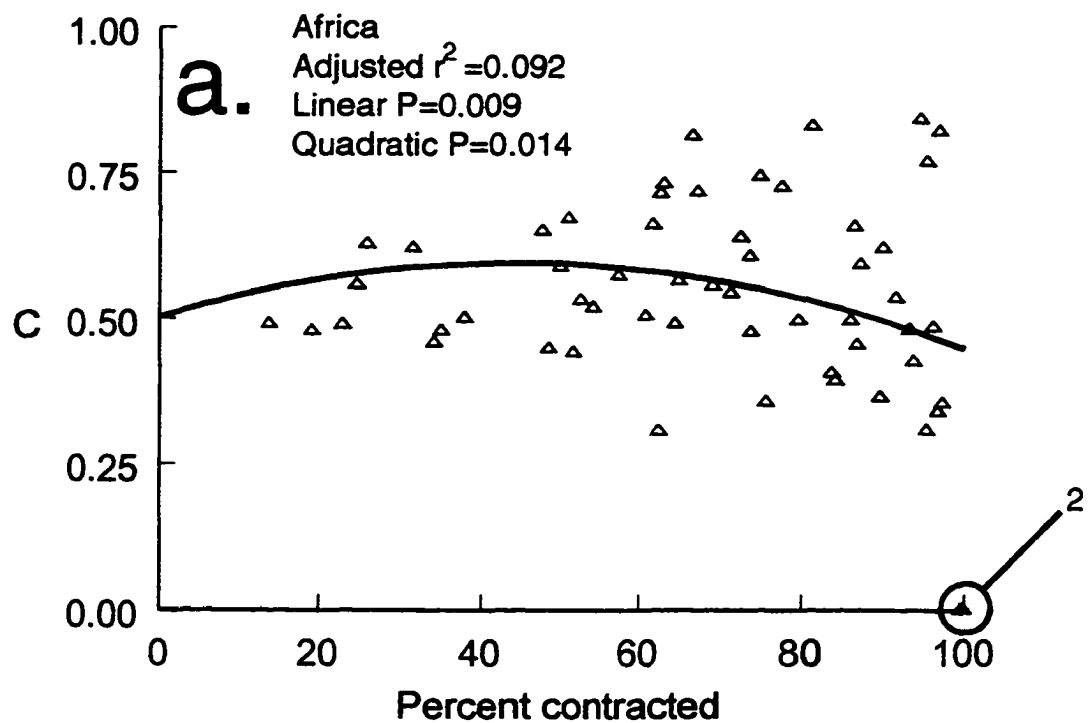


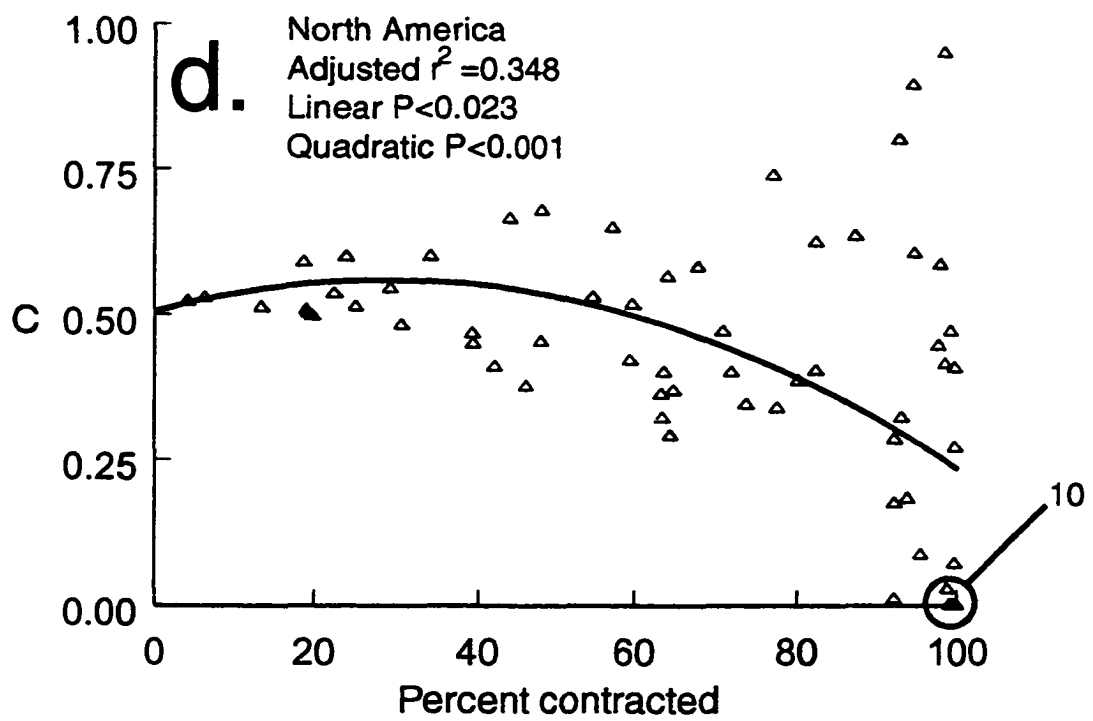
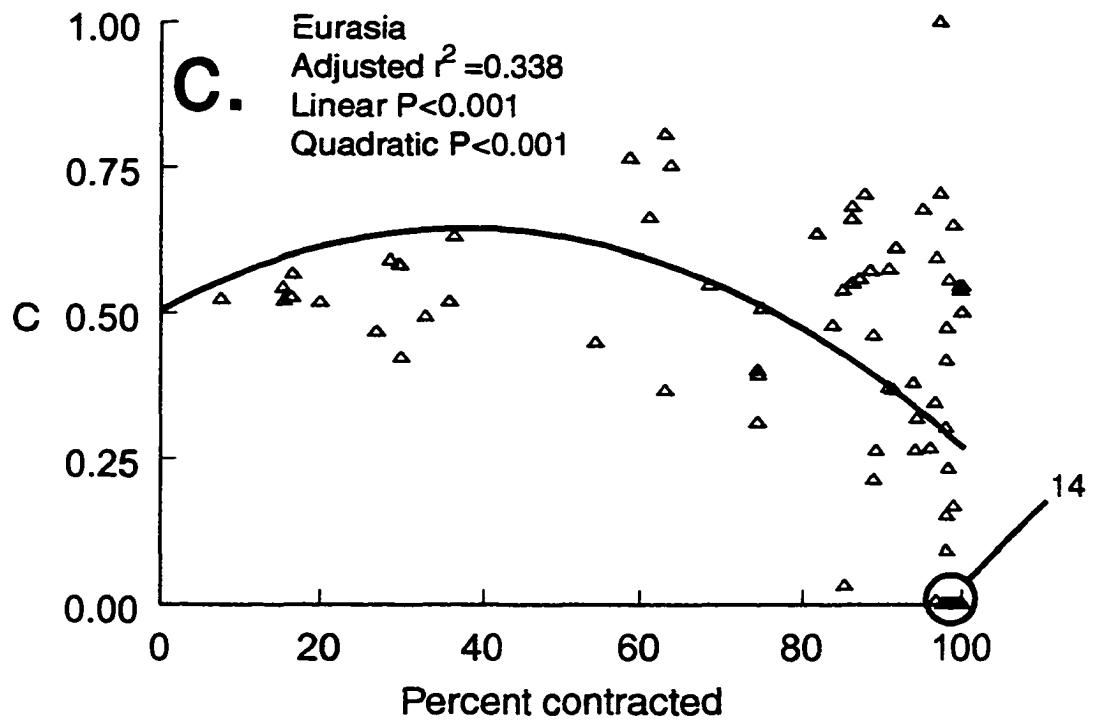












Spatially dynamic models of extinction

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Key words: geographic range, distribution, abundance,
extinction, conservation

Running head: Modeling Contraction of Geographic Ranges

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Abstract: I developed a spatial simulation model to examine how features of the species' geographic range (shape and orientation) and aspects of the extinction causing factor (initial distribution, movement, and method of population loss) combined to influence patterns of range contraction. I found that the process of range contraction was dominated by the initial distribution of the extinction factor, how the extinction factor reduces susceptible populations and the shape of the species' historical range. The results highlight the importance of the interaction between the species' distribution and the extinction causing factor in determining where the final populations of a species are located.

The simulation model was also modified to compare the distribution of three suspected extinction causing factors (Europeans, foxes, and rabbits) on the distribution of five Australian mammals (golden bandicoot, *Isodon auratus*; bilby, *Macrotis lagotis*; numbat, *Myrmecobius fasciatus*; western barred bandicoot, *Perameles bougainville*; and short-tailed hopping-mouse, *Notomys amplius*). I found that the observed range contractions were consistent with those predicted in the model based on degree of overlap and sequence of range contraction. Modeling was hampered by the lack of information on cats, a major agent of extinction in Australia.

This model provides insight into future research needs for examining the contraction of geographic ranges and for developing conservation

strategies. The model also unites two aspects of conservation biology (invasion with extinction) and dynamic biogeography (range contraction with range expansion).

Introduction

Biologists are confronted with an abundance of variables that could influence the patterns or phenomena that interest them. As a result, it can be difficult to determine which variables are responsible for generating these patterns. This difficulty is particularly pronounced for conservation biology for several reasons. First, the nature of the research lends a particular urgency that demands the rapid identification of important variables and the development of conservation strategies. Quickly determining which variables are important in a particular system may allow conservation efforts to be implemented earlier and improve the chances for success. Second, the consequences of misidentification of variables or poorly developed management strategies can harm the focal species or population. While many research programs can rely on trial and error identification of the pertinent variables, conservation biology does not have this luxury because the possible extinction of a population or species may result. Finally, many of the variables that may be important in conservation biology operate at spatial scales that make manipulation difficult. Without direct manipulation of the variables, it can be difficult to establish causality. There are, however, other research tools that allow scientists to identify the variables that are likely to be important in the system.

Although most scientists identify modeling with the development of predictive tools, models can serve other functions (Holling, 1978). One of these functions is the exploration of data and theory (Holling, 1978; Starfield and Bleloch, 1986; Swartzman and Kalunzy, 1987). Exploratory models can help us identify what data we need to collect and can point to flaws in our understanding (Starfield and Bleloch, 1986; Swartzman and Kalunzy, 1987; Forester and Machlis, 1996). By helping guide our collection of data and further refining our theories, models can aid us in focusing our resources more efficiently. Models can also be used to explore the implications of different hypotheses (Swartzman and Kalunzy, 1987). By modeling competing hypotheses, we can examine those features that the hypotheses share and explore where they differ. This examination may lead us to reject or to revise a particular hypothesis.

Human activities are often viewed as the primary cause of the deepening biodiversity crisis (see Forester and Machlis, 1996). Humans are able to rapidly alter the environment across broad spatial scales (Johnson, 1996). These alterations of the environment can affect different species in different ways. Conservation biologists are beginning to appreciate the importance of the spatial setting in developing conservation plans (Dunning et al., 1995; Turner et al., 1995; Skelly and Meir, 1997). Increasingly, scientists are beginning to acknowledge that the development of conservation plans

requires a knowledge of the species' "historical, current, and potential distributions" (Stoms et al., 1996; Lomolino and Channell, 1995, 1998).

Conservation biologists can directly investigate the historical and current distributions of a species, but must often rely on modeling to develop the potential distribution of a species (e.g., see Lindenmayer et al., 1991; Sumner and Dickman, 1988). A more thorough understanding of geographic range contraction can help conservationists efficiently allocate resources for in situ management, plan surveys for undiscovered populations, and select sites for reintroduction (Lomolino and Channell, 1995, 1998).

Understanding potential distributions of species is not only of use to conservationists, it is also a challenge to biogeographers. Although the distribution of organisms are dynamic, biogeographers typically study them as if they were static. Of the studies that have examined the dynamics of species' ranges, the majority have examined how the geographic ranges of introduced or invading species are formed. Very few studies have examined the contraction of a species' geographic range. Work on species' distributions have been limited by the availability of data (Brown et al., 1996; Stoms et al., 1996) and analytical techniques (Brown et al., 1996; Longley and Batty, 1996; Mikula et al., 1996). With recent advances in computer technology, however, scientists have begun to overcome these limitations (Longley and Batty, 1996; Mikula et al., 1996; Stoms et al., 1996). Among the new analytical techniques

available to biogeographers is spatial simulation modeling, which enables them to explore the potential effects of different variables on species' distributions.

In our previous work examining changing distributions of endangered species (Lomolino and Channell, 1995, 1998, Chapters 1 and 2), we identified several patterns that we feel can help guide the conservation of biodiversity and lend insight into predicting the potential distribution of species. We found that the remnant populations of a once widespread species are frequently located in the periphery of the species' historical range (Lomolino and Channell, 1995; Chapter 1). We also found that, for species that originally occurred on both the mainland and on islands, islands, despite their small size, maintained remnant populations better than mainland regions (Lomolino and Channell, 1995; Chapter 1). Species that occurred only on islands, however, showed no bias for contracting to either the peripheral or central region of their historical range (Chapter 1). We attributed these patterns of range contraction to the dynamic geography of the extinction factors (Lomolino and Channell, 1995, 1998; Chapter 1). We hypothesized that anthropogenic changes tend to move across the landscape like a contagion and that the last place impacted by these changes in the geographic range of a species should be the region most isolated from the initial point of contagion (i.e., the contagion hypothesis; Lomolino and

Channell, 1995, 1998; Chapter 1). Spatial isolation from the extinction factor may, therefore, convey an advantage to some peripheral populations. We then generated a predicted sequence of range contractions based on the contagion hypothesis (Chapter 2). This predicted sequence of range contraction was compared with the observed pattern of range contraction for numerous species. We found that ranges tended to contract as hypothesized, retreating from an edge of the range, through the center, and then leaving remnant populations in the periphery of the species' historical range (Chapter 2). Many questions remain, however. Are the patterns of distribution and spread of the contagion altered by the characteristics of the environment? Does environmental heterogeneity, for example, accelerate or hinder the spread of the contagion? Do the characteristics of the focal populations (e.g., size, resistance to a particular extinction factor, density, isolation) influence the spread of the contagion?

In this paper, I use a simulation model of range contraction to explore the causality of the patterns of geographic range contraction. Specifically, I examine how the shape of the historical range, characteristics of the individual populations, and distribution and spread of the extinction factor influence range contraction. Although it is not my goal to develop a model that would necessarily predict potential distributions of species, the insights gained from this paper should serve as a basis for future predictive models.

Also in this paper, I use my model to investigate the impact of suspected extinction factors on the actual range contractions of several Australian species. The results obtained from this modeling may help us direct research to features of the extinction factors that are most important in determining their dynamics and, therefore, suggest how we can better conserve species.

Methods and Materials

The model was programmed in Microsoft Visual Basic 3.0 (Microsoft, 1993), Microsoft Excel 4.0 macro language (Microsoft, 1992), and Idrisi for Windows 1.0 macro language (Eastman, 1995). The overall control and flow of the model was programmed in Visual Basic. Excel was used in the handling of data input and numeric output and in the control of the iterative portion of the model. Idrisi, a geographic information system (GIS), was used for spatial calculations and the mapping of distributions.

Input

Input for the model consisted of a map representing the geographic distribution of a species and an initial distribution of the extinction factor (Figure 1). Also included in the input were settings that determined how the extinction factor moved (conductance and nature of movement) or acted on populations (method of population loss: subtraction or truncation) (Table 1).

Within the model, the geographic distribution of the species and the distribution of the extinction factor were depicted as a series of pixels. Each of these pixels represented a population. Within the geographic range of the species, the pixels stored information regarding the population size and conductance. Pixels in the distribution of the extinction factor stored the presence or absence of the extinction factor in that population.

Setup

Population size was assigned as a function of the pixel's distance to the nearest range boundary, with highest densities near the center of the species' historical range. This distribution of abundance was selected to simulate that observed in actual species where the largest populations are located near the center of the species' historical range (Brown, 1984; Gaston 1990; Lawton, 1995; Brown et al., 1996). To calculate the population size, I first located the range center, which was the point within the species' historical range that was most distant from all edges of the range (Lomolino and Channell, 1995). The distance from the range center to the nearest edge was calculated (d_{max}). The distance of each pixel to the nearest range boundary was then calculated (d_i). Population size for each pixel was then calculated as $1+19*(d_i/d_{max})$. This resulted in a range of population sizes from one to 20 , along the range border and at the range center respectively.

Conductance

Conductance controlled how quickly the extinction factor moved through different portions of the species' geographic range. The extinction factor advanced rapidly in a region with high conductance and slowly in a region of low conductance. I modeled conductance as a function of population size and population position within the historical range of the species (Figure 1). Conductance could be set at a higher level for larger or smaller populations or for central or peripheral populations. Conductance could also be set to neutral. If conductance was to be higher for larger populations, then the conductance for each population was set as equal to the initial population size. If conductance was to be higher for smaller populations, then the conductance for each population was set as 21 minus the initial population size.

To calculate conductance as a function of the population's relative position in the historical range of the species, I divided the historical range into 20 equal area bands by collapsing the range boundaries towards the range center and noting when a particular band contained 1/20th of the historical range. Each of the bands were numbered from (1 on the outside to 20 at the center). Each population was assigned a conductance based on which band it was located within. If conductance was to be higher for peripheral populations, then the conductance for each population was set

equal to 21 minus population's band number. If conductance was to be higher for central populations, then the conductance for each population was set equal to the population's band number. Conductance was set at 10 for all populations if the neutral setting was selected.

Iterations

During the iterative portion of the model, three functions were performed. First, a new distribution of the extinction factor was determined. Second, the new distribution of the extinction factor acted on the demographic profile. Third, data from the modified demographic profile was output. The new distribution of the extinction factor was calculated using the previous distribution of the extinction factor, the population conductance, and the selected nature of movement for the extinction factor (Figure 1). The distance from the previous distribution of the extinction factor to all the pixels of the species' map was calculated. The population's conductance was then divided by the distance to the nearest pixel currently occupied by the extinction factor (the population's conductance to distance ratio).

Movement of the extinction factor

There were three possible ways in which the extinction factor could move: distance, jump, and random. With distance movement, all of the

populations with a conductance to distance ratio higher than a threshold number of 3 were colonized by the extinction factor. Under distance movement, the extinction factor spread smoothly without jumps. With jump movement, populations were colonized by the extinction factor if their conductance to distance ratio was greater than a randomly generated number between 0 and the maximum value of the conductance to distance ratio of all the populations. Under jump movement, the extinction factor spread relatively smoothly but the extinction factor could "jump" to sites beyond the main extinction front. Random movement did not use population conductance. With random movement, a population was colonized by the extinction factor if the reciprocal of the population's distance to the nearest pixel occupied by the extinction factor was greater than a randomly generated number between 0 and 1. Under random movement, the extinction factor did not spread smoothly.

Nature of population loss

The new distribution of extinction factors was then used to alter the population sizes (Figure 1). The extinction factor could either act on the populations through subtraction or truncation. If the subtraction option was selected, then the population size of any pixel that was occupied by the extinction factor was decreased each iteration by one. If the truncation option

was selected, then the population size of any pixel that was occupied by the extinction factor was reduced to zero. The resulting new population sizes were used to calculate the output for that iteration. The species' new distribution was that portion of the historical range with extant populations.

Output

The output for the model consisted of a C-value, a percent contracted, and a species' distribution map for that iteration. The program divided the historical range into two equal area bands: central and peripheral. These bands were constructed by collapsing the range boundaries toward the range center until the area occupied in the inner polygon equaled half of the area of the historical range. The program then calculated an index of centrality (C), which was the proportion of the remnant range that fell within the central portion of the historical range. The index of centrality ranged from 0.00, where the remnant range fell completely outside the central portion of the historical range, to 1.00, where the remnant range fell completely within the central portion of the historical range. The percent contracted was calculated by subtracting from 1 the area of the remnant range divided by the area of the historical range. Maps were produced by the program to illustrate the simulated contraction of the geographic range. All maps produced by the model were stored in both the TIF file format and the Idrisi map format.

The iterative portion of the model repeated until the C-value equaled 1.00 or 0.00. A normal pass through the iterative portion of the model took 10 minutes. A complete simulation averaged 2 1/2 hours under the truncation setting and 72 hours under the subtraction setting.

The behavior of the model was validated by substituting the geographic range of the species with simple geometric shapes at coarse resolutions. The coarse resolutions and simple shapes allowed me to predict the behavior of the model and to compare those predictions with the actual results obtained from the computer model. During the validation, I also frequently stopped the model and examined important intermediate results. Comparisons of the final and intermediate results to the predicted results confirmed that the model behaved as designed.

Exploratory simulations

To explore the behavior of the model and to determine which of the variables were important in generating the patterns of range contraction that we have observed, I ran a series of exploratory simulations. Five species were selected for the exploratory simulations. Three of these species were continental species that differed in the shape of their historical ranges (American burying beetle, *Nicrophorus americanus*; American chestnut, *Castanea dentata*; whooping crane, *Grus americana*). The two other species

were insular species (little spotted kiwi, *Apteryx owenii*; Lord Howe woodhen, *Tricholimnas sylvestris*). The historical geographic range of each of these species was subjected to simulations with varied model settings to examine how the results differed between species and between simulations. A simulation was run on each species as a control for comparison with the other simulations (simulation B, Table 2). In all the other simulations, I varied one or two variables of the model from the settings in the control simulation (Table 2). In this paper the simulations are referred to by a letter (B-N) and by the variable in which they differed from the control (Table 2). These letters were also used to refer to the maps and graph lines resulting from the appropriate simulation.

In some simulations, I varied the geometry and orientation of the extinction factors. Four types of initial distributions of extinction factors were used: points, lines, coastlines, and ubiquitous. In the case of points, the simulated extinction factor was introduced to a single pixel along the edge of the species' distribution. When the extinction factor's initial distribution was described as a line, the extinction factor was introduced as a single line of pixels running north to south along an edge of the species' distribution. When the initial extinction factor was described as coastline, the coastline of the landmass that the species occupied was input as the initial distribution of the extinction factor. The ubiquitous initial distribution of the extinction

factor indicated that the extinction factor occurred throughout the species' range. In other simulations, I varied the nature of population loss, the conductance of populations, or the movement of the extinction factor (Table 2).

Historical simulations

I also conducted simulations on four species of Australian mammals which had undergone range contraction (golden bandicoot, *Isodon auratus*; bilby, *Macrotis lagotis*; numbat, *Myrmecobius fasciatus*; western barred bandicoot, *Perameles bougainville*) and for which the distribution of at least some putative extinction factors were known. These extinction factors were Europeans (Figure 2a), rabbits (*Oryctolagus cuniculus*)(Figure 2b), and red foxes (*Vulpes vulpes*)(Figure 2c). The short-tailed hopping-mouse, *Notomys amplus*, was apparently declining before any of the included extinction factors had entered the species' range and was included in this study as a control. The model was modified to accept the known distributions of the extinction factors at different points in time. All historical simulations used subtraction as the method of population loss. Those populations that overlapped the distribution of the extinction factor were decreased by one each year.

Results

The results of the exploratory simulations are presented in Figures 3-8 and the results of the historical simulations appear in Figures 9-14. In each set of maps (Figures 3-7 and 9-13), the observed range contraction is included for comparison. The American chestnut (Figure 4a), in the exploratory simulations, and the numbat (Figure 11), in the historical simulations, have known sequences of range contraction that are also presented for comparison. In the graphs of the C-values vs. percent contracted (Figures 8 and 14), the observed C-value or observed sequence of C-values is also indicated.

Exploratory simulations

Simulations B (single point, truncation) and C (ubiquitous, subtraction) for all species show distinctly different graphs of C-values (Figure 8a-e) and predict remnant ranges that rarely overlap (Figures 3b,c - 7b,c). All graphs of C-values for simulation B (single point, truncation), except for the whooping crane, initially rise above 0.50 and then decline to 0.00 near 100% contracted. All graphs of C-values for simulation C (ubiquitous, subtraction) rise rapidly from 0.50 to a maximum value of 1.00 near 50% contracted. Of all the simulations conducted, only simulation C (ubiquitous, subtraction) differed in more than one variable from the control, simulation B (single point, truncation; Table 1).

Simulation D (single point, subtraction) differs from simulations B (single point, truncation) and C (ubiquitous, subtraction) only in one variable each. Interestingly, simulation D (single point, subtraction) demonstrates behavior that is intermediate between simulations B (single point, truncation) and C (ubiquitous, subtraction). The graphs of C-values for simulation D (single point, subtraction) demonstrate two different patterns. In simulation D (single point, subtraction), the C-value initially rises rapidly, mirroring simulation C (ubiquitous, subtraction) (Figures 8a-8e). Near 30% contracted, the C-value continues to rise, but at a rate less than in simulation C (ubiquitous, subtraction). Late in the contraction (>80% contracted) the two different patterns become apparent. In the cases of the American chestnut (Figure 8b) and Lord Howe woodhen (Figure 8e), the C-value continues to rise to 1.00 at 100% contracted. In the other cases of the American burying beetle (Figure 8a), the whooping crane (Figure 8c), and the little spotted kiwi (Figure 8d), the C-value precipitously declines to 0.00 at 100% contracted, similar in result to simulation B (single point, truncation). The predicted remnant ranges for simulation D (single point, subtraction) of the American chestnut (Figure 4d) and the Lord Howe woodhen (Figure 7d), while located in the central portion of their historical range, are slightly off-center, being on the side of the center opposite the initial position of the extinction factor.

Simulations B (one point), E (two points), and F (three points) all demonstrate C-value graphs that are roughly similar in shape for a given species (Figure 8a-e). However, inspection of the maps show that the predicted remnant ranges of these simulations rarely overlap.

Simulations G (coastline) and H (line) differ from simulation B (point) in the geometry of the initial extinction factor. Simulations B (point) and G (coastline) predict overlapping remnant ranges for the American burying beetle (Figure 3b,g), the American chestnut (Figure 4b,g), and the little spotted kiwi (Figure 3b,g), but the sequence of range contraction is different, as evidenced by the graphs of C-values for simulations B (point) and G (coastline) for the burying beetle (Figure 8a) and kiwi (Figure 8d). Simulation H (Line) was very similar to simulation B (point) in C-value graphs and predicted remnant ranges for all species, except the whooping crane (Figures 5b,h and 8c).

The predicted remnant ranges for simulations I (higher conductance in large populations), J (higher conductance in small populations), K (higher conductance in peripheral populations), and L (higher conductance in central populations) all overlap the remnant ranges predicted for simulation B (conductance neutral). The shape of the graphs of C-values for simulations I (higher conductance in large populations), J (higher conductance in small populations), K (higher conductance in peripheral populations), L (higher

conductance in central populations) and B (conductance neutral) are all very similar (Figure 8a-e).

The different ways in which the extinction factor could move had little influence on the simulated patterns of range contraction. Remnant ranges for simulations M (distance movement) and N (random movement) overlapped with those from simulation B (jump movement). The C-value graphs for simulations M (distance movement), N (random movement), and B (jump movement) were similar (Figure 8a-e).

Most simulations of the range contraction in the American burying beetle were successful in predicting range remnants along the western edge of the range. Simulations G (coastline), J (higher conductance in small populations), and K (higher conductance in peripheral populations) predicted range remnants close to the position of the western remnants (Figure 3). Simulations C (ubiquitous, subtraction), E (two points) and F (three points) did the poorest job of predicting remnant ranges.

The sequence of range contraction predicted by most of the simulations closely matched the observed sequence of range contraction in the American Chestnut (Figure 4). Most of the models also did a good job predicting the position of remnant populations. Only simulation C (ubiquitous, subtraction) did a poor job of predicting the range remnant. While the predicted range remnant from simulation D (single point, subtraction) does overlap slightly

with the observed range remnant, the sequence of range contraction is completely different (Figure 8b).

Only simulations C (ubiquitous, subtraction), H (Line), and N (random movement) predicted range remnants that overlapped with observed range remnants for the whooping crane (Figure 5). However, simulation C (ubiquitous, subtraction) also predicted a large range remnant in the large central patch of the historical range. All of the simulations, except simulation G (coastline), suggested that the species would persist along the Texas Coast (Figure 5).

None of the remnant ranges predicted by any of the simulations overlapped the observed range remnants of the little spotted kiwi (Figure 6). The majority of the simulations did predict that the populations should persist in the periphery as has been observed for New Zealand (Chapter 1). Predicted remnant ranges of the little spotted kiwi were frequently located on the northern peninsula of North Island and Fjordland, the southwestern corner of South Island. Both of these regions serve as refuges for other species.

Predicted range remnants from simulations C (ubiquitous, subtraction), D (single point, subtraction), and G (coastline) overlap the observed range remnants for the Lord Howe woodhen (Figure 7). All other

simulations, except simulation F (three points), had a high degree of overlap in their predicted range remnants.

Examination of the graphs of C-values during range contraction (Figures 8a-e) indicate that the characteristics of the historical range of the species may play a role in determining the sequence of range contraction. For most simulations, all of the species examined, except for the whooping crane, demonstrate similar graphs of range contraction with an initial increase in C-values above 0.50 and a later, relatively steep decline to 0.00 near 100% contracted. In the whooping crane, most of the C-values from the simulations fall below 0.50 almost immediately and gradually decline to 0.00 near 90% contracted.

It should be noted that the close proximity of an observed C-value to the simulated C-value curves does not necessarily indicate that the mapped remnant ranges are similar. In Figure 8a, for example, the observed C-value lies almost on the line for simulation F (three points); examination of the maps (Figures 3a and 3f), however, shows that not only does the predicted remnant range not overlap the observed remnant range, but that they are at opposite sides of the historical range from each other.

Historical simulations

The predicted remnant ranges generated from the rabbit distributions and the combination of European, rabbit, and fox distributions overlap with that observed for the golden bandicoot (Figure 9). All simulations predicted remnant ranges of the golden bandicoot on the islands along the western coast of Australia (Figure 14). Yet none of the graphs of C-values approached the position of the observed C-value (Figure 14a).

The remnant range of the bilby overlapped well with those predicted from the distribution of Europeans and the distribution of foxes (Figure 10). C-value graphs of foxes, the combination of Europeans and rabbits, and the combination of Europeans and foxes approached the position of the observed C-value (Figure 14b).

Remnant ranges predicted from rabbit distributions and fox distributions overlapped the observed remnant ranges of the numbat (Figure 11). The remnant range predicted from the combination of the rabbit and fox distributions did not overlap the observed range, but it was close in position. The graph of C-values for the observed range contraction of the numbat is similar to that for the combination of rabbits and foxes and the combination of Europeans, rabbits, and foxes (Figure 14c).

All of the historical extinction factors predicted remnant ranges on the islands along the western coast of Australia for the western barred bandicoot

(Figure 12). Similarly, most of the C-value graphs generated from the historical distribution of extinction factors approached the observed C-value of the western barred bandicoot (Figure 14d).

In contrast, none of the predicted remnant ranges broadly overlapped the observed remnant ranges of the short-tailed hopping-mouse (Figure 13). The observed C-value of the short-tailed hopping-mouse was near those generated from rabbit distributions and the combination of rabbit and fox distributions (Figure 14e).

Discussion

Exploratory simulations

Simulations B (single point, truncation) and C (ubiquitous, subtraction) are of particular interest as they represent competing hypotheses about how the geographic ranges of species should contract. Simulation B (single point, truncation) is the simplest version of the contagion hypothesis which predicts that a species should persist in the portion of its geographic range that is most isolated from the spreading extinction factor (Lomolino and Channell, 1995, 1998; Chapter 1). The contagion hypothesis further predicts that the graph of C-values should initially rise above 0.50 and then later decline towards 0.00.

Simulation C (ubiquitous, subtraction) represents the demographic hypothesis which assumes that the extinction factor is distributed

ubiquitously and acts by uniformly decreasing the size of populations (Chapter 2). Because the largest populations are frequently located near the center of the species' range (Brown, 1984; Gaston 1990; Lawton, 1995; Brown et al., 1996), the demographic hypothesis predicts that remnant ranges of a species should also be located near the center of the species' historical range. In addition, the demographic hypothesis predicts that the graphs of C-values should rise rapidly from 0.50 to 1.00.

The results of simulations B (single point, truncation) and C (ubiquitous, subtraction) resemble what their respective theories predicted. In all species, simulation B (the contagion hypothesis) predicted remnant ranges in the periphery of the species' historical range. All of the C-value graphs for simulation B (single point, truncation), except that of the whooping crane, show an initial rise above 0.50 and a later decline to 0.00. In simulation C (the demographic hypothesis), remnant ranges were predicted to be in the central portion of the historical range for all species. Graphs of C-values for simulation C (ubiquitous, subtraction) rose rapidly from 0.50 to 1.00. While these particular simulations can not be used to establish the validity of one hypothesis over the other, the simulations do confirm the expected dynamics of both hypotheses.

Simulation D (single point, subtraction) demonstrated an important feature of range contraction that had not been anticipated prior to the

modeling. In two of the five species (American chestnut and Lord Howe woodhen), simulation D (single point, subtraction) produced range contractions that ended in range remnants found near the center of the species' historical ranges. In the other three species (American burying beetle, whooping crane, and little spotted kiwi), simulation D (single point, subtraction) predicted range remnants to be found in the periphery. Examination of the graphs of C-values for simulation D (single point, subtraction) shows that it can be difficult to distinguish between these two types of range contraction until extremely late in the simulation (>80% contracted, Figure 8a-e). I believe these results are the product of the combination of a contagion-like movement and the subtractive method of population loss. I suggest that if the movement of the extinction factor is fast relative to the intensity of population loss, then the remnant ranges should be found near the center of the species' historical range. If, on the other hand, the movement of the extinction factor is slow relative to the intensity of population loss, remnant ranges should be found near the periphery of the historical range. Within my model, expansion speed of the extinction factor is controlled by the method of movement. Jump movement was used in simulation D (single point, subtraction). Jump movement allows the extinction factor to jump to more distant sites. While extinction factors should

all be moving at the same speed in this simulation, a particularly distant jump in the initial iterations of the model may generate a faster rate of expansion.

This potential interaction between the extinction factor's rate of spread and the method of population loss, while unexpected, has interesting implications for the patterns of range contraction uncovered earlier. Most remnant populations of declining species are located in the periphery of the species' historical range (Lomolino and Channell, 1995; Chapter 1). This suggests that either the extinction factor spreads slowly or spreads quickly and that the method of population loss tends to truncate. This interaction also suggests that a contagion-like extinction factor can, with the correct rate of spread and intensity of population loss, generate a contraction to the central portion of the species' historical range. This is particularly satisfying in that it unites two apparently divergent patterns (contractions to the center or the periphery) under a single hypothesis.

The position of the predicted remnant ranges differed considerably between simulations B (one point), E (two points), F (three points), and G (coastline). All of these simulations vary some aspect of the initial distribution of the extinction factor. The variation in predicted remnant ranges underscores the importance of the initial distribution of the extinction factor in the process of range contraction. For example, if a contagion is introduced at one point in the range of a species, a particular remnant range

may be predicted, but if the same contagion were introduced in another portion of the species' range, a different remnant range may be expected.

The simulation that used the coastline of the landmass as the initial distribution of the extinction factor deserves special attention. When we examined observed range contraction of species, we found that species that occurred on continents or on both continents and islands showed a significant tendency to persist in the periphery of their historical range (Lomolino and Channell, 1995; Chapter 1). Species that occurred only on islands demonstrated no such tendency (Chapter 1). We explained this apparent deviation from the contagion hypothesis as the result of the combination of island geography and human settlement patterns. The small size of islands allows them to be colonized from many different sides. These multiple colonization sites and the human tendency to first settle in the lowlands combine to effectively surround the island. Therefore, the most isolated portion of an island is not at an edge, but rather near the center of the island. In simulation G (coastline), I attempted to reproduce these conditions. While it is unlikely that the conditions necessary for simulation G (coastline) would ever occur on a continent because of its large size, I ran simulation G (coastline) on all five species hoping that the results might serve as instructive examples. Two of the five simulations (little spotted kiwi and Lord Howe woodhen) contracted to the central region of their historical ranges (Figures

6g and 7g). The three other simulations (American burying beetle, American chestnut, and whooping crane) contracted to the periphery of their historical ranges (Figures 3g, 4g, and 5g). The important differences between the contraction to the periphery and the contraction to the central region appears to be the position of the species' range relative to the center of the landmass, the point on the landmass that is most distant from all coastlines. If the center of the landmass occurs in the central region of the species' historical range, then a contraction to the central region is produced by simulation G (coastline). If the center of the landmass lies in the periphery of the species' historical range or outside the range of the species, then a contraction to the periphery is produced by simulation G (coastline). In contractions to the periphery, persisting populations are found along the edge of the species' historical range nearest the center of the landmass. The results of simulation G (coastline) produced contractions both to peripheral and central regions, consistent with observed range contractions of insular species. These results also indicate another way that, given the correct initial conditions, the contagion hypothesis can produce contractions to the center of a species' historical range.

None of the simulations in which I varied conductance (I, higher conductance in large populations; J, higher conductance in small populations; K, higher conductance in peripheral populations; L higher conductance in

central populations) was very different from the control. This suggests that as long as the extinction factor moves in a roughly contagion-like manner, similar results may be obtained regardless of slight variations in the underlying populations. This idea is further supported by noting that the different methods of movement (simulations B, jump movement; M, distance movement; N, random movement) produced remarkably similar predicted remnant ranges. The technical differences in the methods of movement of the extinction factor made little difference in their results, suggesting that contagion-like movement is enough to generate robust patterns.

None of the simulations effectively predicted the remnant ranges for all of the species. Furthermore, a simulation that predicted the range remnants for one species may do poorly for another species (e.g., simulation D for the Lord Howe woodhen and the little spotted kiwi). The diverse responses of species with ranges of different shapes and sizes to the simulations suggests that the historical range of the species and its orientation with the extinction factor can create considerable variation in the simulated range contractions. This diversity of response is best exemplified by the whooping crane. The graphs of C-values for the whooping crane decline much more rapidly than do those for the other species. This result may be related to the geometry of the species' historical range and the way that C-values are calculated. The slender shape of the whooping crane's historical range (Figure 5) means that

the range perimeter is relatively long compared to the area it encloses. This slender range shape results in a peripheral region that is particularly thin. This problem of a thin peripheral region is further aggravated by the multiple patches in the historical range of the whooping crane. The initial impact of the extinction factor may rapidly reach from the edge of the historical range to the central portion of the historical range, causing the C-values to decline almost immediately.

The results of the exploratory simulations suggest that the variables that dominate the model are the initial distribution of the extinction factor, the method of population loss, and the species' historical range,. These variables are likely to play an important role in the contraction of the actual geographic ranges of species. However, the actual cause of decline in most species is not well understood (Caughley, 1994). Among the first steps in the conservation of any species should be the identification of the factors causing its decline (Caughley, 1994; Green, 1994; Caughley and Gunn, 1996; Dickman, 1996). The distribution of the extinction factor and its method of decreasing population size cannot be studied until the extinction factor has been identified. The exploratory simulations suggest that the identification of the extinction factor, the mapping of its distribution, and an understanding of how it decreases populations is vital if we are to predict the contraction of a species' geographic range.

Historical simulations

Although the cause of most species' declines is not well understood, they are known for a few species and have been mapped and whose pattern of spread also is known. In Australia, habitat alteration by European settlers, predation by the introduced red fox, and competition from the introduced rabbit have threatened many native species. In my historical simulations, the remnant range observed for the golden bandicoot best matched the remnant ranges predicted from the distribution of rabbits and the combination of Europeans, rabbits and foxes. None of the C-value graphs approached the observed C-value for the golden bandicoot. Humans and cats (*Felis catus*) have been identified as the major causes of decline in the golden bandicoot (McKenzie et al., 1995). The golden bandicoot is primarily an insectivore and is unlikely to compete with the rabbit (McKenzie et al., 1995). Therefore, the overlap of the predicted and observed remnant ranges for the golden bandicoot may be coincidental.

The observed remnant range of the bilby best matched those predicted from the distribution of Europeans and the distribution of foxes. The graphed C-values from the fox simulation approached the C-value observed for the bilby. Foxes, rabbits, and cats have been implicated in the decline of the bilby (Johnson, 1995). In this case, the model seems to have accurately predicted

the influence of the distribution and spread of the fox on the distribution of the bilby. However, the rabbit, also considered important in the actual decline of the bilby, did not adequately predict the remnant range of the bilby.

The remnant range observed for the numbat overlapped the predicted ranges from the distribution of the rabbit and from the distribution of the fox. The combination of the rabbit and fox distributions also produced a predicted range remnant that was near the observed remnant range. Graphed C-values for the combination of rabbit and fox distributions approached the C-values graphed for the observed sequence of range contractions of the numbat. The fox is considered a major predator of the numbat (Friend, 1995). The diet of the numbat consists almost entirely of termites (Friend, 1995) and, therefore, is not a competitor with the rabbit. Of the extinction factors that I examined, the fox is the most likely to be responsible for the range contraction observed in the numbat.

All of the potential extinction factors and their combinations predicted the observed remnant range of the western barred bandicoot on the islands along the western coast of Australia. The graphed C-values of most of the potential extinction factors also approached the observed C-value. The decline of the western barred bandicoot has been attributed to humans, foxes, and cats (Aitken, 1979). Since all of the extinction factors predicted the same

position for the remnant ranges of the western barred bandicoot, I cannot suggest that one extinction factor or a particular combination of extinction factors as responsible for producing the observed range remnants. Still, the western barred bandicoot nicely illustrates a species that persists only on islands that are isolated from the extinction forces that have spread rapidly across the mainland (Lomolino and Channell, 1995, 1998; Chapter1).

The short-tailed hopping-mouse was declining before any of the extinction factors I examined had reached its geographic range (Thornback and Jenkins, 1982; Dixon, 1995). Thus, the fact that none of the predicted range remnants overlaps significantly with the observed range remnants is not surprising. Cats have been suggested as the primary cause of decline in the short-tailed hopping-mouse (Thornback and Jenkins, 1982).

The observed range contractions of the numbat and golden bandicoot resembled those predicted from the distribution of the rabbit, but neither of these species is a direct competitor with the rabbit. However, the rabbit may indirectly influence the distribution of these species. Rabbits have radically altered vegetation patterns in Australia (see Lever, 1985) and these species may be reacting to changes in their habitat. Changes in habitat structure may also allow predators to capture prey more efficiently. Thus, the changes in habitat structure, acting through predation, may cause alterations in the distribution of prey species. Smith and Quin (1996) have noted that

population declines of many native Australian rodents are most severe in regions where rabbits and an introduced predator (cats, foxes, or dingos; *Canis familiaris*) co-occur. To explain this phenomena they suggested the "hyperpredation" model. In the hyperpredation model, the rabbits, a year-round source of food, enable the introduced predators to reach high densities (Smith and Quin, 1996). The high predator densities also increases the predation on indigenous prey species (Smith and Quin, 1996). While the rabbit is reproductively active throughout the year and, thus, is able to withstand the increased predation load, many of the native species which are reproductively active only seasonally are not (Smith and Quin, 1996). Therefore, rabbits may influence the distribution of native species through competition, alteration of habitats, increased predation via habitat alteration, or increased predation via increased predator densities. Any one of these scenarios may have contributed to the range contractions observed in the numbat and golden bandicoot.

The results of my historical simulations confirm that the pattern of spread of several suspected extinction factors is consistent with the pattern of range contraction exhibited by the declining species that I examined. However, the fit of the predicted range remnants to the observed range remnants is not exact. The limited number of stages of spread for each of the extinction factors restricts the degree to which the predicted geographic

ranges can be contracted. This results in predicted ranges that are much larger than observed ranges and can generate considerably more chance overlap.

The historical simulations could have been improved by including the pattern of spread for the cat. The cat was introduced quite early in the colonization of Australia and has had a profound impact on the native fauna of Australia (Lever, 1985; Smith and Quin, 1996). Cats were suggested to be important in the decline of four of the five species I included in my analysis. My model might have better predicted the range contraction of these four species if the distribution and spread of cats had been included, but I could find no map of the spread of cats in Australia.

In the historical simulations extinction factors acted on populations through subtraction. Wherever the distribution of the extinction factor overlapped the species' geographic range, the species' populations were decreased by a uniform amount (1 per year). It is unrealistic to assume, however, that the intensity or density of the extinction factor is uniformly distributed or that population loss for all populations would be the same. I am not, however, aware of maps of potential extinction factors that show a sequence of spread and the intensity or density at each turn in the sequence. How does the distribution of not only the extinction factor, but also the intensity of the extinction factor contribute to the process of range

contraction? There are also no data on how an extinction factor influences susceptible populations throughout the range of the species. Are there general spatial patterns of population loss associated with different extinction factors?

Comment

Simulation models and sensitivity analyses can identify variables that may be important and they can also suggest areas of future research that may be particularly productive. The model employed herein indicated that the distribution of extinction factors can influence the position of remnant ranges, but the identification of and distribution of most extinction factors is not known. Such information would not only improve the model's predictive power, but could also contribute to better conservation strategies. Similarly, how extinction factors act on a population is not well understood and was indicated to be of importance in the model. Do attributes of the population mediate the method of population loss? Does an extinction factor act uniformly across all populations or is there variation in the extinction factor unrelated to the populations? Answers to these questions will undoubtedly vary with the extinction factor investigated, but we do not currently know the degree or direction of such variation. Incorporation of such knowledge and

an understanding of these parameters can improve our ability to predict and perhaps slow range contraction.

My model did not include the extinction factor's rate of spread as an explicit variable, but my results suggest that this rate may strongly influence the patterns we have observed. Future models of range contraction should incorporate variation in the factor's rate of spread. This improvement in the model should attempt to draw on the work of biogeographers examining the spread of introduced species. Inclusion of this work would furnish realistic parameters and a ready-made body of theory on the variables that influence those parameters (see Shigesada and Kawasaki, 1997).

This simulation study begins to point the way to developing a predictive model of geographic range contraction. Moreover, it also unites two disparate, but related elements within both biogeography and conservation biology. In biogeography, processes influencing geographic ranges are of fundamental importance, but until relatively recently, research on range dynamics has focused only on range expansion -- not contraction. In conservation biology, the preservation of declining species is of primary concern. An understanding of how the geographic range of such species is eroded can help guide the development of conservation strategies (Lomolino and Channell, 1995, 1998; Chapter 1). However, many declining species are threatened by the introduction and subsequent expansion of exotic species.

The current study represents one of the first spatially rigorous attempts to simultaneously investigate both aspects of range dynamics: the expansion of an exotic species and its effect on the contraction of a native species. Such an integration of ideas not only promises to help us develop better conservation strategies, but also to encourage a dialogue between researchers studying the two aspects of dynamic biogeography (expansion and contraction).

Acknowledgements

I thank N. Czaplewski, T. Franklin, M. Kaspari, M. Lomolino, K. Pandora, D. Perault, K. Perez, G. Smith, and C. Vaughn for their advice and comments on this paper. I would also like to thank M. Scott, who provided information on the distribution of the whooping crane, and B. Maurer, who provided early guidance in the spatial modeling of species' distributions.

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Table 1. Definition of terms used in the model.

Initial distribution of the extinction factor – The shape and position of the extinction factor at the beginning of the simulation.

Point – The extinction factor was introduced to a single pixel along the edge of the range.

Two points – The extinction factor was introduced to two pixels along the edge of the range. One of the pixels was the same as in the single point condition.

Three points – The extinction factor was introduced to a three pixels along the range edge. Two of the pixels were the same as in the two point condition.

Line – The extinction factor was introduced as a line running north to south along the edge of the range and through the pixel used in the one point condition.

Coastline – The coastline of the landmass that the species occupied was input as the initial distribution of the extinction factor.

Ubiquitous – The extinction factor occurred throughout the species' range.

Method of population loss – How the extinction factor acts on the individual populations within the range of the species.

Subtraction -- The population size was decreased in each iteration by one in any pixel that was occupied by the extinction factor.

Truncation -- The population size was immediately reduced to zero in any pixel that was occupied by the extinction factor.

Conductance -- How quickly the extinction factor moved through different portions of the species' geographic range. The extinction factor advanced rapidly in a region with high conductance and slowly in a region of low conductance.

Higher conductance in large populations -- The extinction factor moved more rapidly through regions with larger populations than those with smaller populations.

Higher conductance in small populations -- The extinction factor moved more rapidly through regions with smaller populations than those with larger populations.

Higher conductance in peripheral populations -- The extinction factor moved more rapidly through peripheral regions than central regions.

Higher conductance in central populations – The extinction factor moved more rapidly through central regions than peripheral regions.

Method of movement – The different ways that the extinction factor was allowed to move.

Distance – The extinction factor spread evenly as a single wave front with a smooth leading edge.

Jump – The extinction factor spread as a wave front with an irregular leading edge. The extinction factor can also "jump" to pixels beyond the edge of the wave front.

Random – The extinction factor expands to random pixels, but with decreasing probability as the pixel's distance from an occupied pixel increases.

Table 2. The model variable settings for each of the simulations (B-N). Initial distribution of the extinction factor referred to the position and shape of the extinction factor at the start of the simulation. Method of population loss indicated whether the extinction factor truncated geographic ranges (immediate extinction of affected populations) or decreased the population size of the affected populations (decreased by one each turn). Conductance influenced how the extinction contagion moved through the species' range. The extinction factor advanced rapidly in a region with high conductance and slowly in a region of low conductance. There were three ways that the extinction factor could have moved: distance, jump, and random.

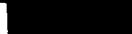
	Initial distribution of the extinction factor	Nature of movement of the extinction factor	Conductance higher in	Method of population loss
C	Ubiquitous	NA	Neutral	Subtraction
H	Line	Jump	Neutral	Truncation
G	Coastline	Jump	Neutral	Truncation
F	3 points	Jump	Neutral	Truncation
E	2 points	Jump	Neutral	Truncation
M	Point		Neutral	Truncation
N	Point		Neutral	Truncation
I	Point	Jump		Truncation
J	Point	Jump		Truncation
K	Point	Jump		Truncation
L	Point	Jump		Truncation
D	Point	Jump	Neutral	
Control -- B	Point			

Figure legends

Figure 1. A diagram illustrating the flow of data through the simulation model. The four thick-bordered boxes (input, setup, iterations, and output) represent the major divisions of the model. The thin-bordered boxes represent an element of spatial data. Diamonds indicate a transformation of spatial data into a new form.

Figure 2. The historical spread of Europeans (a), rabbits (*Oryctolagus cuniculus*)(b), and red foxes (*Vulpes vulpes*)(c) over Australia. Maps were modified from Johnson (1992), Thompson and King (1994), and Jarman (1986) respectively.

Figure 3. Observed (a) and simulated (b-n) range contractions of the American burying beetle, *Nicrophorus americanus*. Within the range of the species, darker shades indicate more recent occurrences. The letter (b-n) associated with each map refers to the simulation that produced that map.

Figure 4. Observed (a) and simulated (b-n) range contractions of the American chestnut, *Castanea dentata*. Within the range of the species, darker

shades indicate more recent occurrences. The letter (b-n) associated with each map refers to the simulation that produced that map.

Figure 5. Observed (a) and simulated (b-n) range contractions of the whooping crane, *Grus americana*. Within the range of the species, darker shades indicate more recent occurrences. The letter (b-n) associated with each map refers to the simulation that produced that map.

Figure 6. Observed (a) and simulated (b-n) range contractions of the little spotted kiwi, *Apteryx owenii*. Within the range of the species, darker shades indicate more recent occurrences. The letter (b-n) associated with each map refers to the simulation that produced that map.

Figure 7. Observed (a) and simulated (b-n) range contractions of the Lord Howe woodhen, *Tricholimnas sylvestris*. Within the range of the species, darker shades indicate more recent occurrences. The letter (b-n) associated with each map refers to the simulation that produced that map.

Figure 8. Changes in the index of centrality (C), the proportion of the remnant range that falls within the central region of the historical range, with

different simulations of range contraction. Each graph represents the simulations for a particular species: American burying beetle (a), American chestnut (b), whooping crane (c), little spotted kiwi (d), and Lord Howe woodhen (e). The letter (B-N) associated with each line refers to the simulation that produced that line. The observed C-value or sequence of C-values also is indicated on each graph.

Figure 9. Observed and predicted range contractions of the golden bandicoot, *Isoodon auratus*. Within the range of the species, darker shades indicate more recent occurrences. The predicted range contractions were generated from the overlapping distribution of suspected extinction instigating factors (Europeans, rabbits, or foxes) or a combination (e.g., Europeans and rabbits).

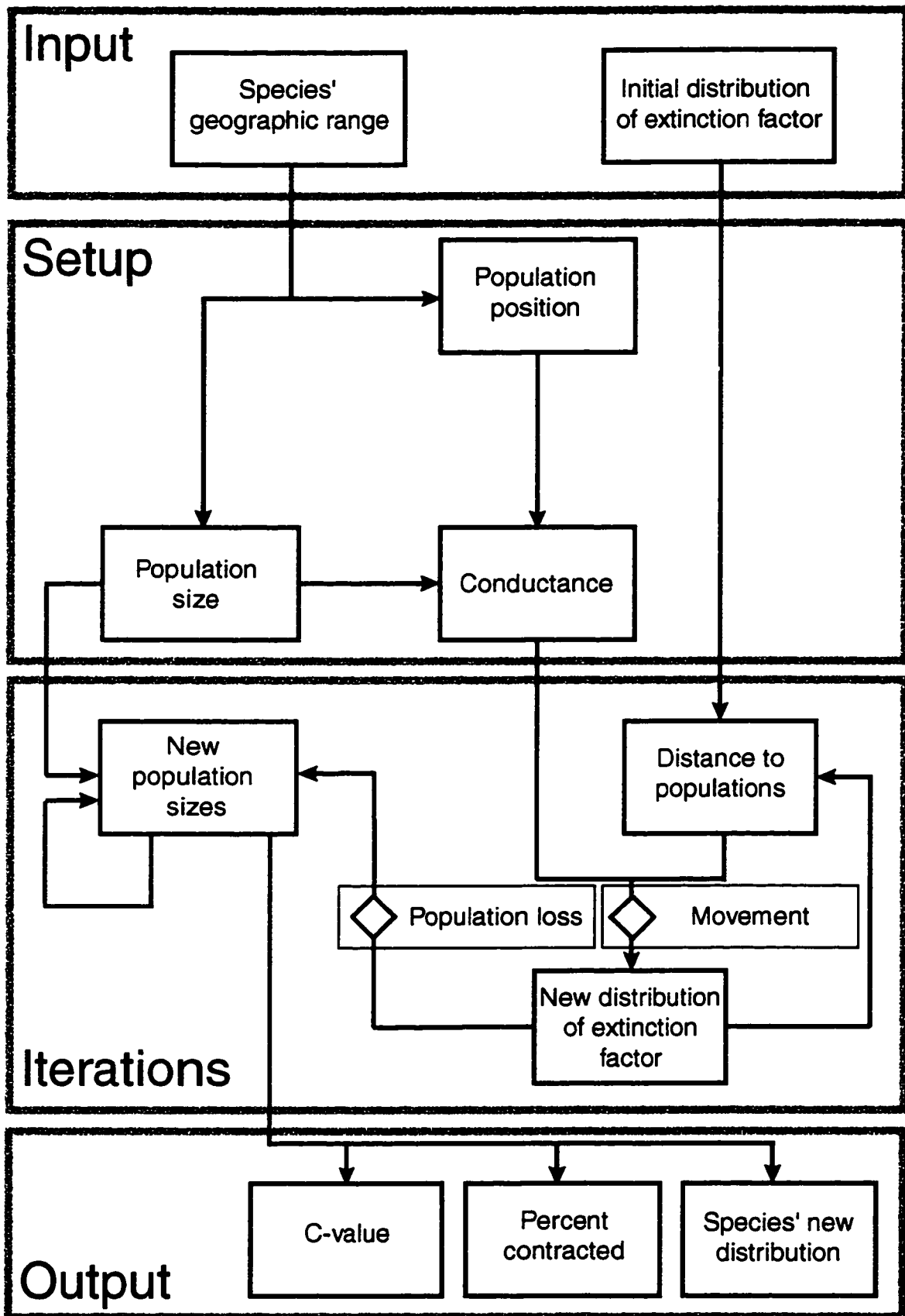
Figure 10. Observed and predicted range contractions of the bilby, *Macrotis lagotis*. Within the range of the species, darker shades indicate more recent occurrences. The predicted range contractions were generated from the overlapping distribution of suspected extinction instigating factors (Europeans, rabbits, or foxes) or a combination (e.g., Europeans and rabbits).

Figure 11. Observed and predicted range contractions of the numbat, *Myrmecobius fasciatus*. Within the range of the species, darker shades indicate more recent occurrences. The predicted range contractions were generated from the overlapping distribution of suspected extinction instigating factors (Europeans, rabbits, or foxes) or a combination (e.g., Europeans and rabbits).

Figure 12. Observed and predicted range contractions of the western barred bandicoot, *Perameles bougainville*. Within the range of the species, darker shades indicate more recent occurrences. The predicted range contractions were generated from the overlapping distribution of suspected extinction instigating factors (Europeans, rabbits, or foxes) or a combination (e.g., Europeans and rabbits).

Figure 13. Observed and predicted range contractions of the short-tailed hopping-mouse, *Notomys amplius*. Within the range of the species, darker shades indicate more recent occurrences. The predicted range contractions were generated from the overlapping distribution of suspected extinction instigating factors (Europeans, rabbits, or foxes) or a combination (e.g., Europeans and rabbits).

Figure 14. Changes in the index of centrality (C), the proportion of the remnant range that falls within the central region of the historical range, with different simulated extinction instigating factors. Each graph represents the simulations for a particular species: golden bandicoot (a), bilby (b), numbat (c), western barred bandicoot (d), and short-tailed hopping-mouse (e). The different lines represent the different extinction factors used to generate that sequence of C-values. The observed C-value or sequence of C-values also is indicated on each graph.



a.



1820s

1840s

1860s

1870s

1880s

1890s

b.



1900s

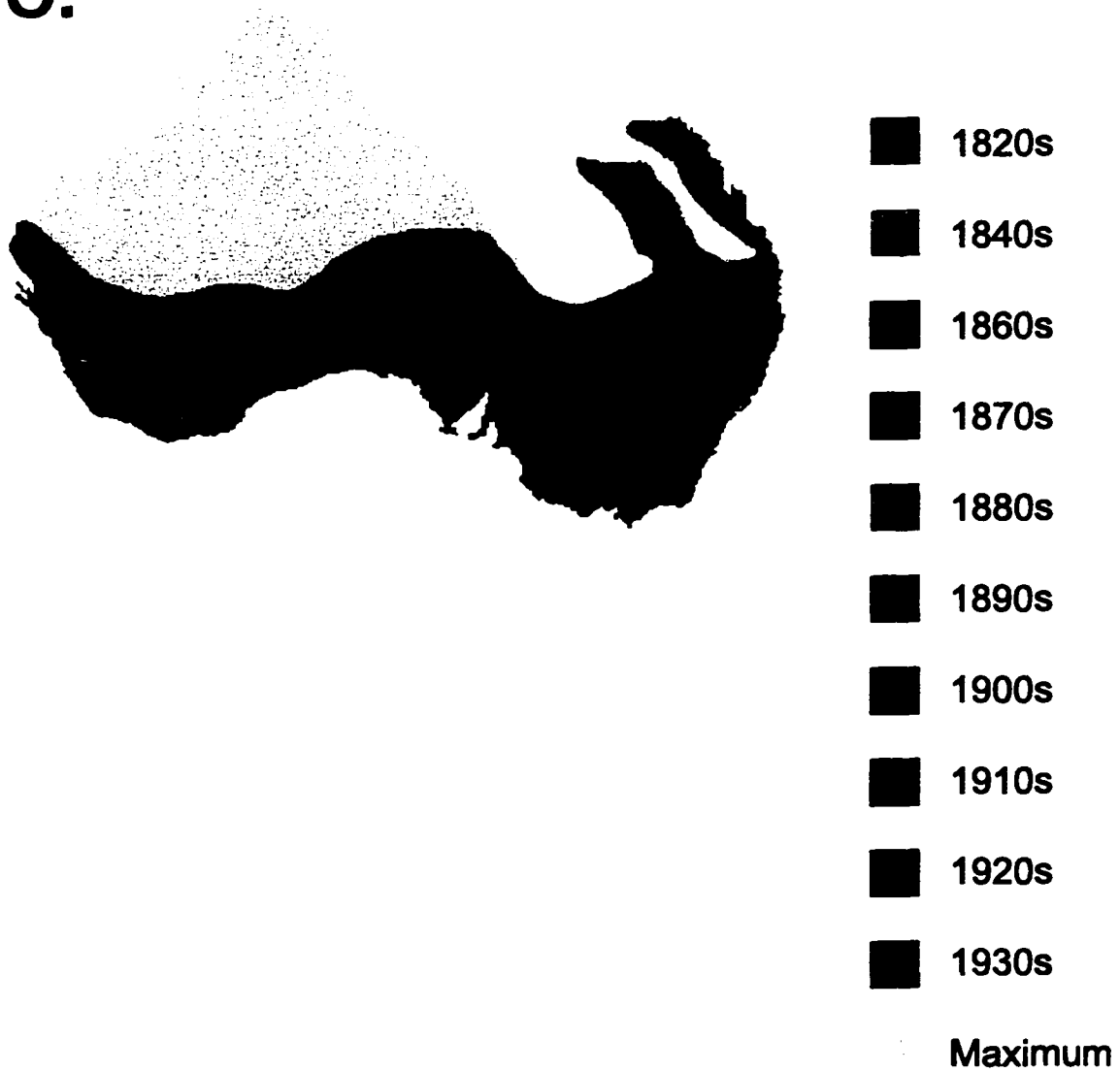
1910s

1920s

1930s

Maximum

C.



a.



b.



c.



d.



e.



f.



g.



h.



i.



j.



k.



l.



m.



n.



a.



b.



c.



d.



e.



f.



g.



h.



i.

j.



k.

l.



m.

n.



a.



b.



c.



d.



e.



f.



g.



h.



i.



j.



k.



l.



m.



n.



a.



b.



c.



d.



e.



f.



g.



h.



i.



j.



k.



l.



m.



n.









j.



i.



i.



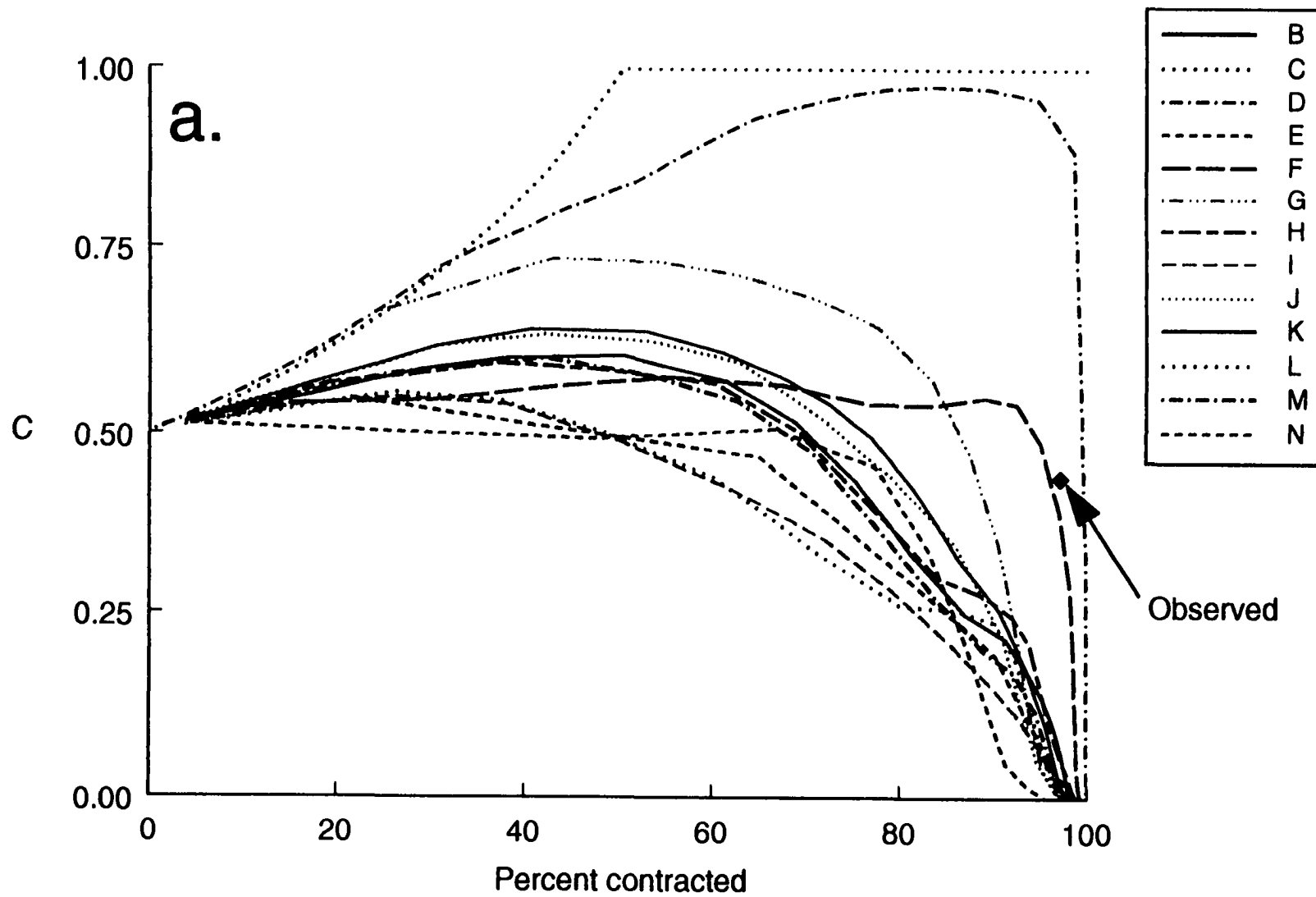
k.

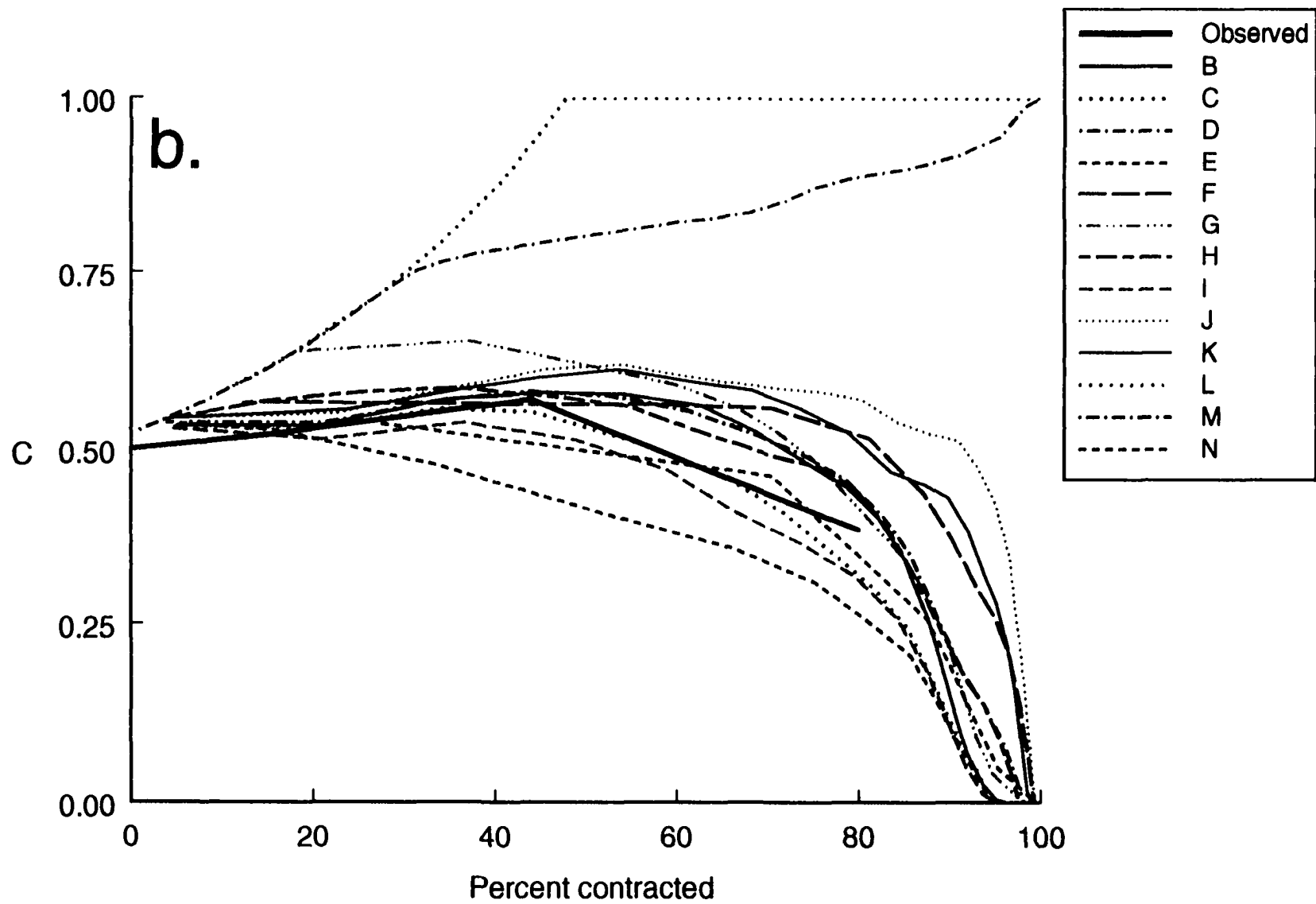


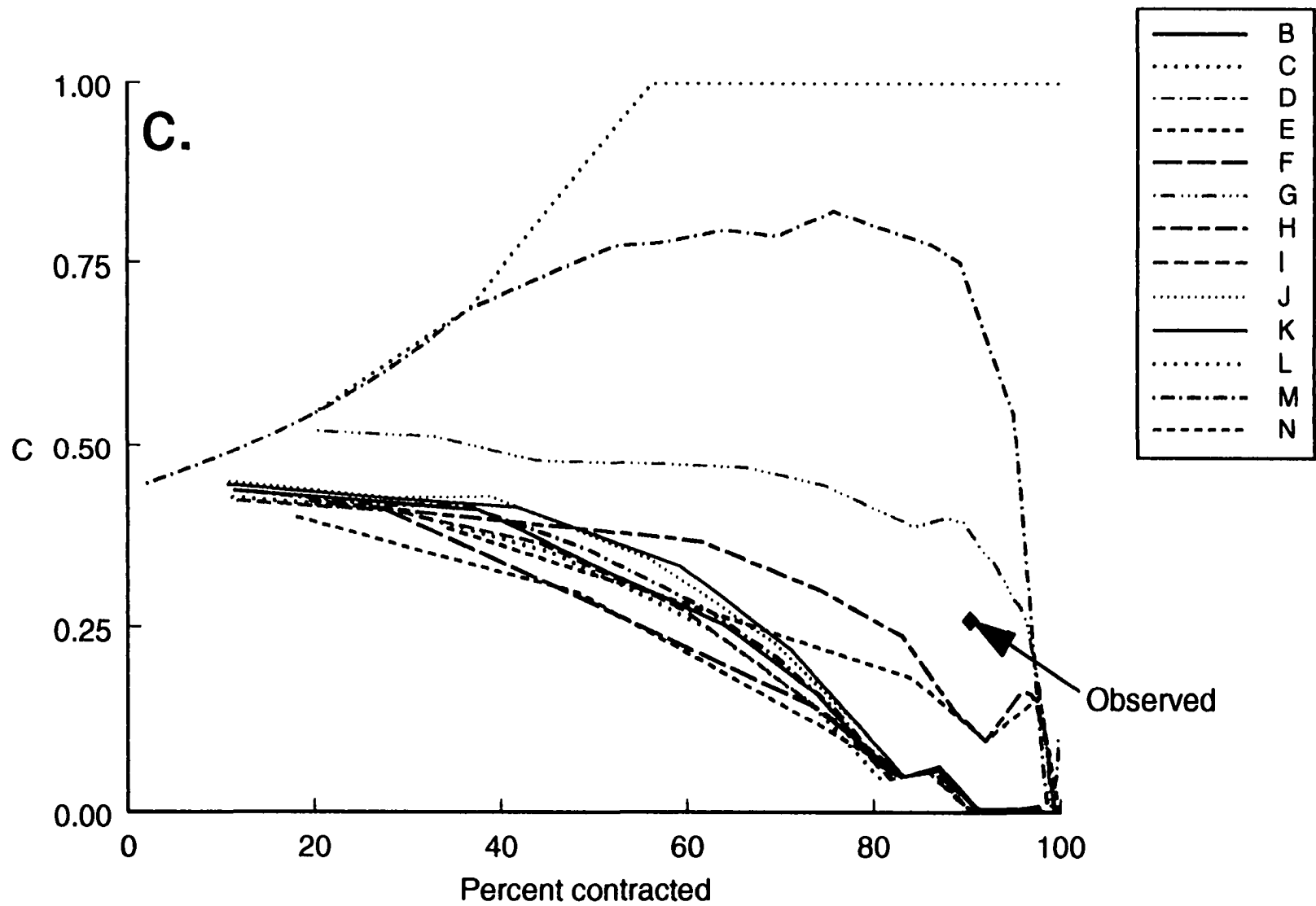
n.

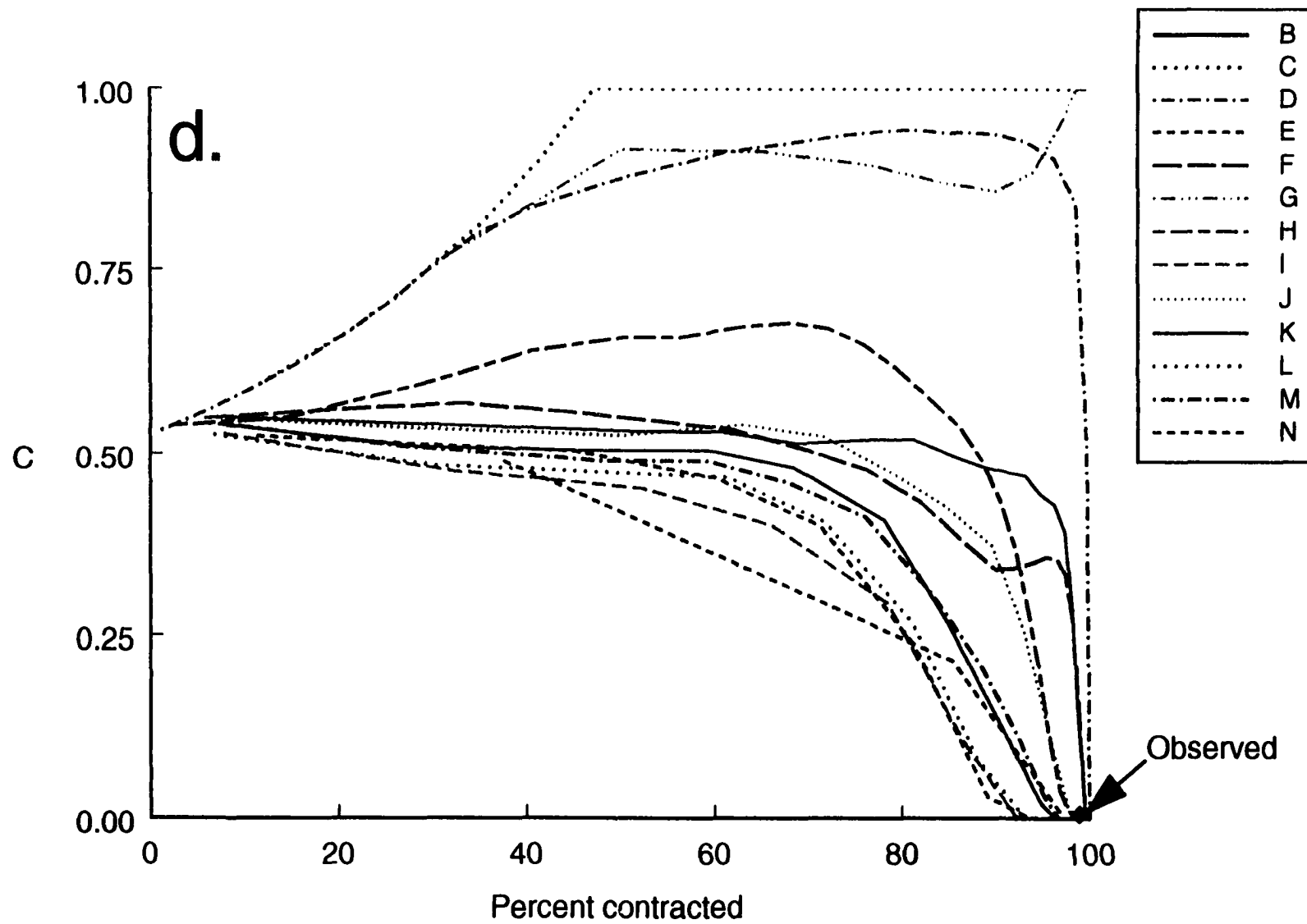


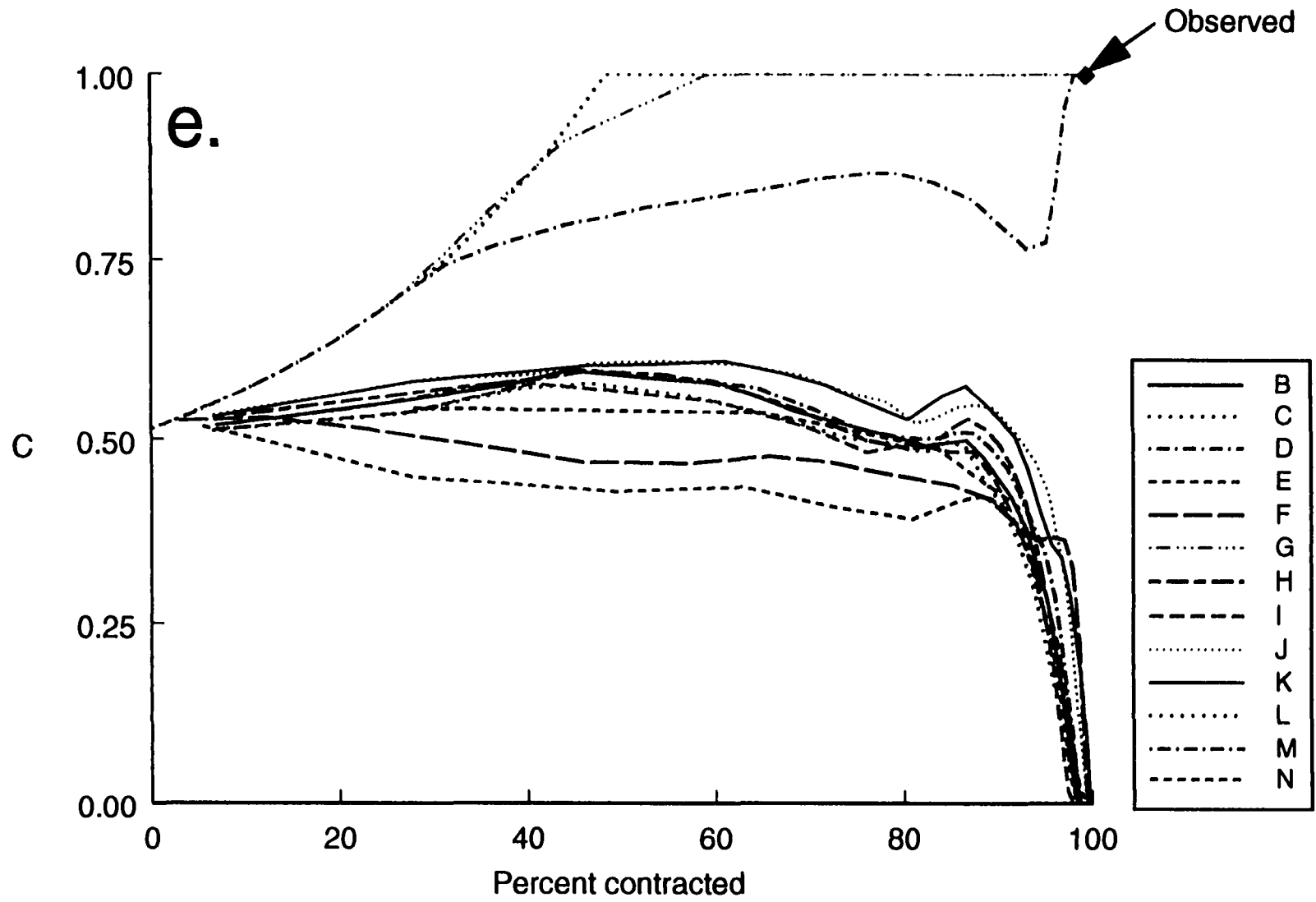
m.













Observed



Europeans



Rabbits



Foxes



Europeans and rabbits



Europeans and foxes

180



Rabbits and foxes



Europeans, rabbits,
and foxes



Observed



Europeans



Rabbits



Foxes



Europeans and rabbits



Europeans and foxes



Rabbits and foxes



Europeans, rabbits,
and foxes



Observed



Europeans



Rabbits



Foxes



Europeans and rabbits



Europeans and foxes



Rabbits and foxes



**Europeans, rabbits,
and foxes**



Observed



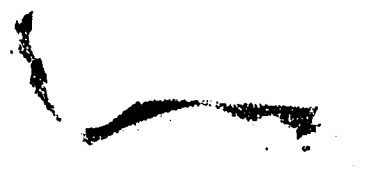
Europeans



Rabbits



Foxes



Europeans and rabbits



Europeans and foxes



Rabbits and foxes



Europeans, rabbits,
and foxes



Observed



Europeans



Rabbits



Foxes



Europeans and rabbits



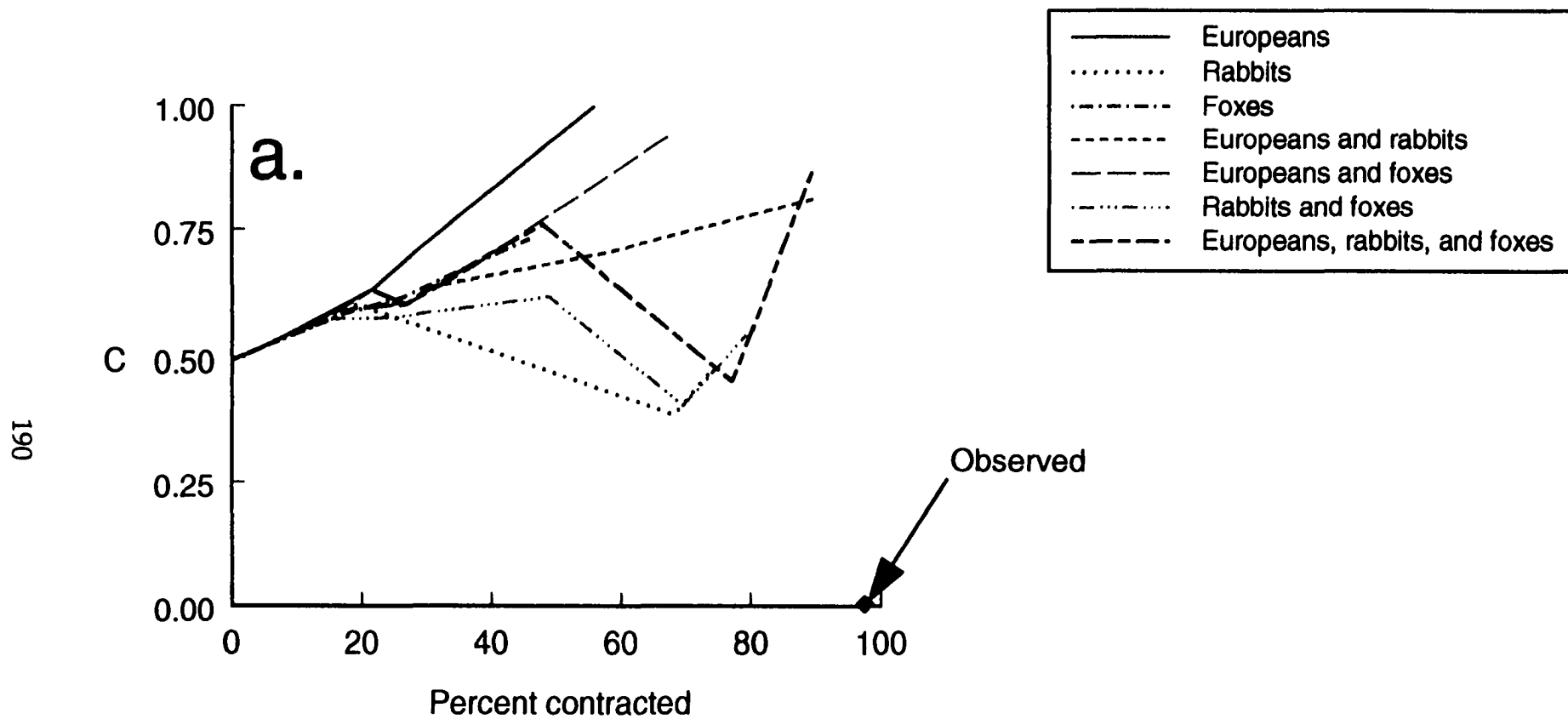
Europeans and foxes

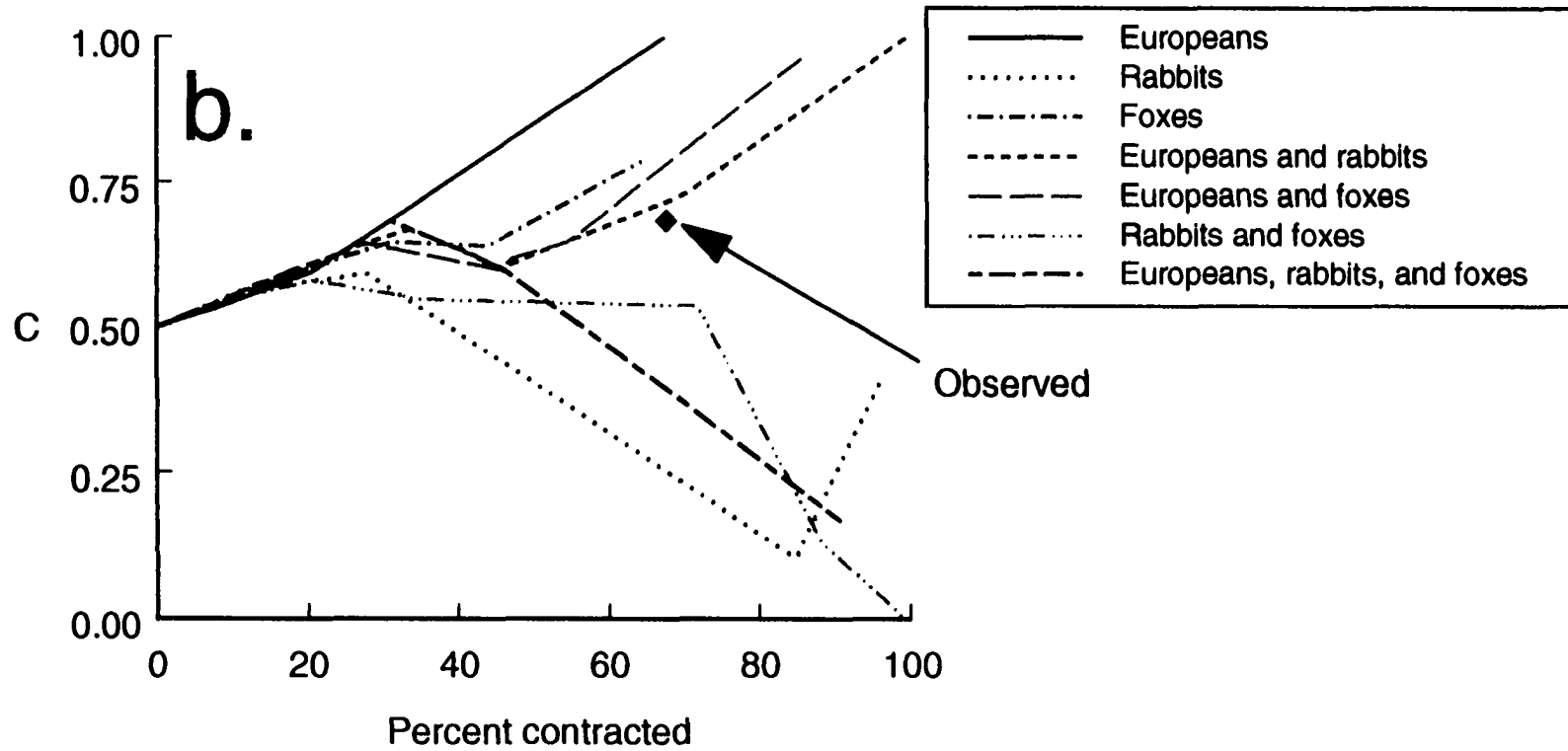


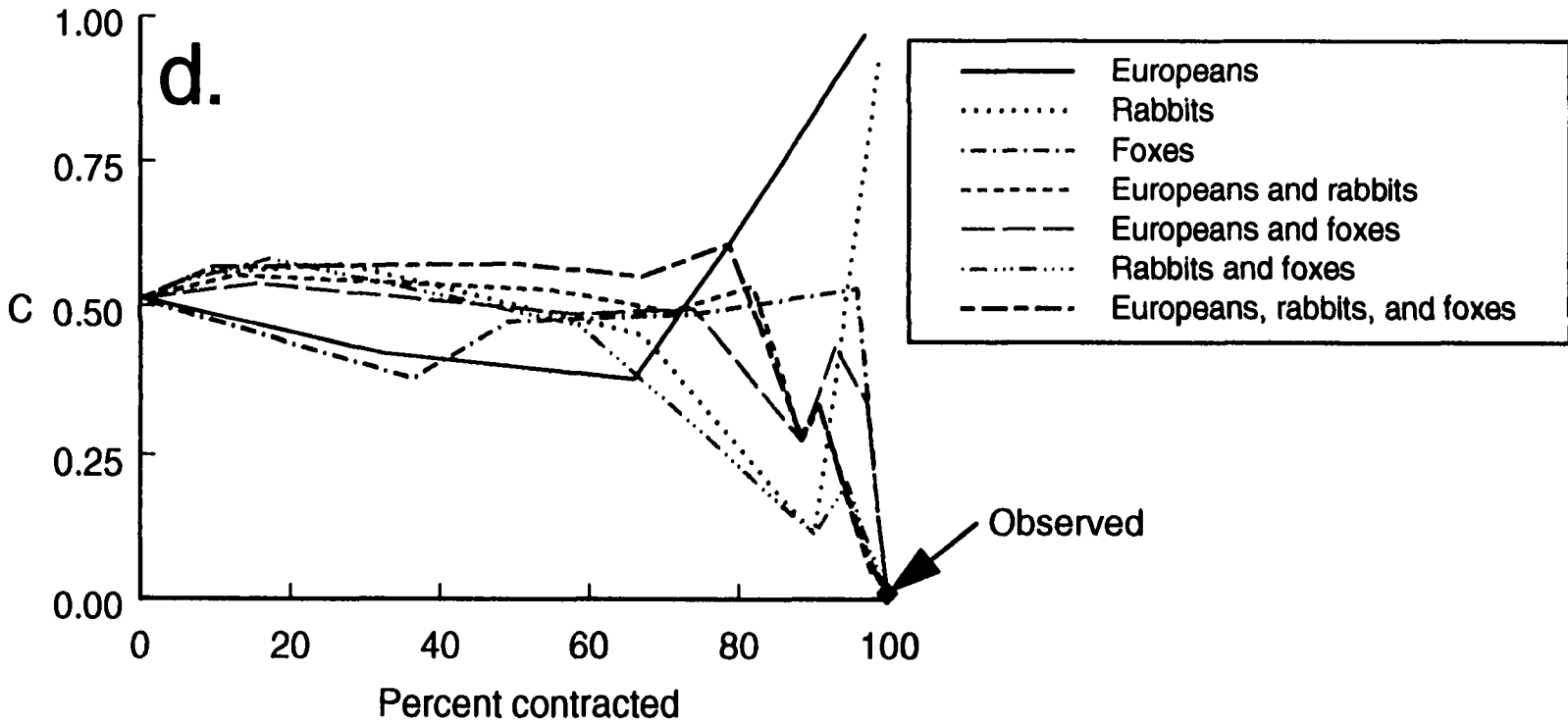
Rabbits and foxes

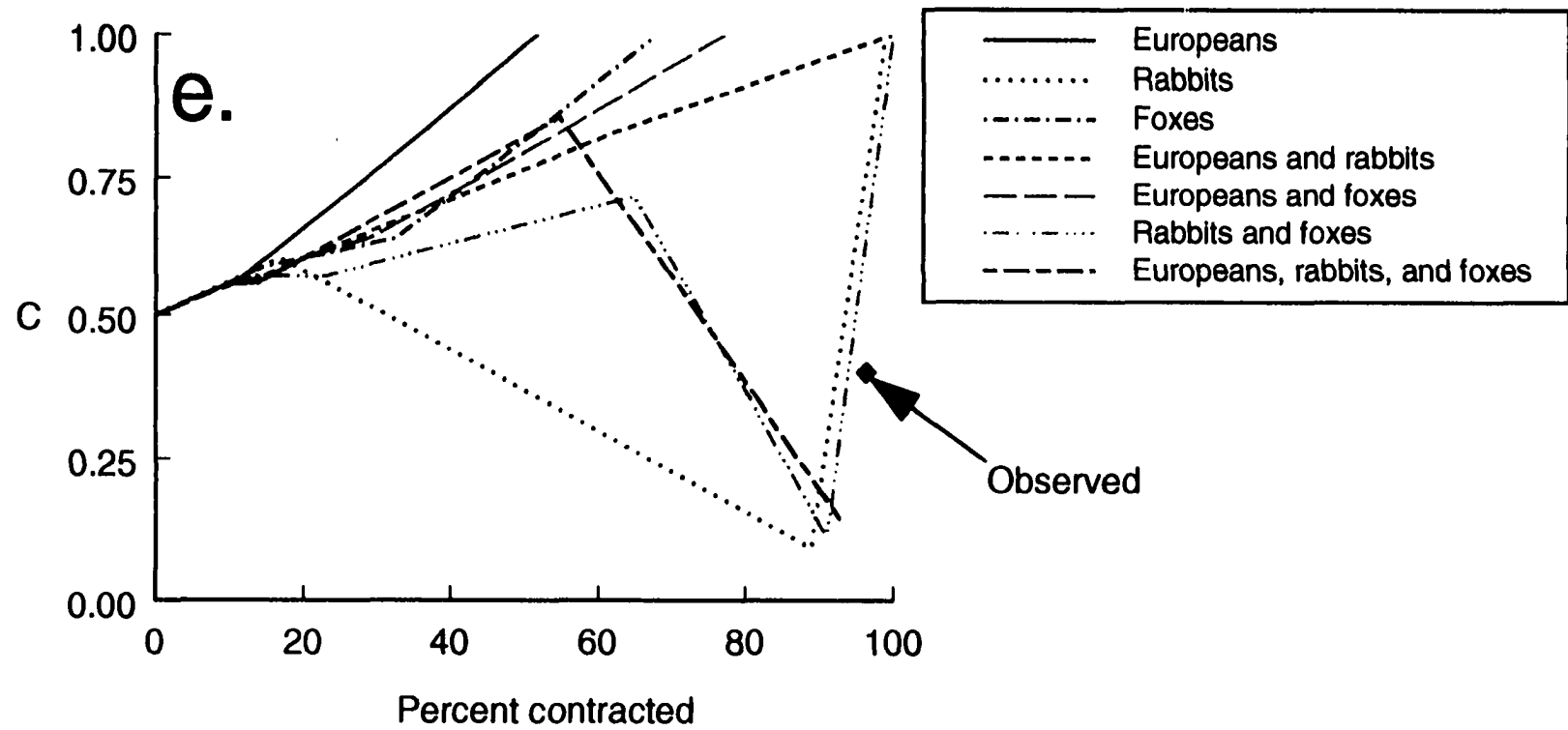


Europeans, rabbits,
and foxes









Appendix 1. Table of data and references. The table is organized by region, taxonomic group, and species name. A tilde (~) in any position indicates that data for that position does not exist or that that category of data can not be applied to that particular species (e.g., number of islands in historical geographic range for a species that only occurred on a continent). Region refers to the geographic region in which the species occurs. Taxonomic group lists how I grouped species for analysis between taxa (Groups of unequal taxonomic ranks were used to maximize the number of species in each taxonomic group and therefore maximize the number of taxa that were included in the analysis.) Species refers to the scientific name of the species. Common name refers to the vernacular name of the species. Fields listed as prediction 1-3 refer to whether that species was used to test the associated predictions in chapter 1 (Yes/No). Any species that was used to test prediction 1 was also used to test predictions 4 and 5. The field titled chapter 2 indicates that that species was used in analyses for chapter two (Yes/No). Type refers to whether the species occurred only on a continent (C), only on islands (I), or on both continents and islands (B). Current and historical ranges indicate the extent (km²) of the species at each time. Contracted indicates the degree of contraction (%) the species

had experienced. C distance is the index of centrality used in chapter 1. P/C distance indicates if the species was classified as Peripheral or Central in chapter 1. C area is the index of centrality used in chapter 2. P/C area indicates if the species was classified as Peripheral or Central in chapter 2. Historical patches refers to the number of patches in the historical range. Extant patches indicates the number of patches in the extant or final range of the species. (Because of increased fragmentation, the number of extant patches may exceed the number of historical patches.) Extinction indicates whether the species is considered extinct (Yes/No). (Species that are extinct in the wild but are maintained in captivity are classified as not being extinct.) Historical mainland and historical island refer to the number of patches that occurred historically on the continent and islands. Current mainland and current island indicate the number of historical patches that are still occupied on the mainland and islands. (Historical mainland, historical island, and current mainland, historical island refer to only species that occurred historically on both mainland and islands.) N/S (North or South) and W/E (West or East) refer to the half of the range in which the majority of the extant or final range fell. Reference is the citation for the source of the species' map. Complete citations are included in the attached

literature cited. All species' maps are appended on the accompanying CD-ROM.

	Region	Taxonomic group	Species	Common name
1	Africa	Arthropod	<i>Circellium bacchus</i>	~
2	Africa	Bird	<i>Agapornis nigrigenis</i>	Black-cheeked lovebird
3	Africa	Bird	<i>Agelastes melearides</i>	White-breasted guineafowl
4	Africa	Bird	<i>Geronticus calvus</i>	Southern bald ibis
5	Africa	Bird	<i>Geronticus eremita</i>	Waldrapp ibis
6	Africa	Bird	<i>Grus carunculatus</i>	Wattled crane
7	Africa	Bird	<i>Gypaetus barbartus</i>	Bearded vulture
8	Africa	Bird	<i>Gypo coprotheres</i>	Cape vulture
9	Africa	Bird	<i>Oxyura leucocephala</i>	White-headed duck
10	Africa	Mammal	<i>Acinonyx jubatus</i>	African cheetah
11	Africa	Mammal	<i>Addax nasomaculatus</i>	Addax
12	Africa	Mammal	<i>Alcelaphus buselaphus</i>	Hartebeest
13	Africa	Mammal	<i>Ammodorcas clarki</i>	Dibatag
14	Africa	Mammal	<i>Antidorcas marsupialis</i>	Springbok
15	Africa	Mammal	<i>Canis simensis</i>	Ethiopian wolf
16	Africa	Mammal	<i>Cephalophus jentinki</i>	Jentinti's duiker
17	Africa	Mammal	<i>Ceratotherium simum</i>	White rhinoceros
18	Africa	Mammal	<i>Crocuta crocuta</i>	Spotted hyaena
19	Africa	Mammal	<i>Damaliscus dorcas</i>	Blesbok
20	Africa	Mammal	<i>Damaliscus lunatus</i>	Topi
21	Africa	Mammal	<i>Diceros bicornis</i>	Black rhinoceros
22	Africa	Mammal	<i>Equus africanus</i>	African wild ass
23	Africa	Mammal	<i>Equus grevyi</i>	Grevy's zebra
24	Africa	Mammal	<i>Equus zebra</i>	Mountain zebra
25	Africa	Mammal	<i>Felis caracal</i>	Caracal
26	Africa	Mammal	<i>Felis serval</i>	Serval

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
1	Y	N	N	Y	C	1,700	3,824,900	99.96
2	N	N	N	Y	C	7,500	17,700	57.48
3	Y	N	N	Y	C	36,500	284,200	87.16
4	N	N	N	Y	C	242,200	656,800	63.13
5	Y	N	N	Y	C	60,300	1,817,300	96.68
6	Y	Y	N	Y	C	217,800	4,637,000	95.30
7	N	N	N	Y	C	1,274,400	3,905,000	67.37
8	N	N	N	Y	C	770,700	2,932,500	73.72
9	N	N	N	Y	C	32,400	82,900	60.93
10	Y	N	N	Y	C	2,248,600	22,190,600	89.87
11	Y	N	N	Y	C	248,200	3,934,900	93.69
12	N	N	N	Y	C	2,527,800	8,213,100	69.22
13	N	N	N	Y	C	152,600	315,700	51.66
14	N	N	N	Y	C	1,336,900	1,801,900	25.81
15	Y	N	N	Y	C	10500	191,900	94.52
16	Y	N	N	Y	C	31,000	194,600	84.09
17	Y	Y	N	Y	C	148,200	3,840,900	96.14
18	N	N	N	Y	C	12,605,800	14,635,400	13.87
19	Y	N	N	Y	C	158,700	2,355,800	93.26
20	N	N	N	Y	C	1,978,800	5,583,600	64.56
21	Y	N	N	Y	C	486,500	10,575,600	95.40
22	N	N	N	Y	C	225,000	362,700	37.96
23	Y	N	N	Y	C	71,300	843,700	91.55
24	Y	N	N	Y	C	105,600	435,700	75.76
25	N	N	N	Y	C	12,052,300	14,916,800	19.20
26	N	N	N	Y	C	12,213,200	23,697,200	48.46

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
1	0.00	P	0.00	P	1	3	N	~
2	0.57	C	0.57	C	1	1	N	~
3	0.52	C	0.59	C	1	7	N	~
4	0.66	C	0.73	C	1	1	N	~
5	0.00	P	0.34	P	1	1	N	~
6	0.42	P	0.31	P	2	40	N	~
7	0.58	C	0.72	C	2	7	N	~
8	0.54	C	0.61	C	1	6	N	~
9	0.51	C	0.50	C	3	1	Y	~
10	0.51	C	0.62	C	1	7	N	~
11	0.33	P	0.43	P	1	4	N	~
12	0.40	P	0.56	C	3	33	N	~
13	0.44	P	0.44	P	1	3	N	~
14	0.56	C	0.63	C	1	1	N	~
15	0.70	C	0.84	C	1	5	N	~
16	0.21	P	0.39	P	1	6	N	~
17	0.49	P	0.49	P	2	21	N	~
18	0.50	C	0.49	P	1	1	N	~
19	0.10	P	0.48	P	1	2	N	~
20	0.37	P	0.49	P	4	19	N	~
21	0.65	C	0.77	C	1	41	N	~
22	0.55	C	0.50	C	1	2	N	~
23	0.50	C	0.53	C	1	4	N	~
24	0.25	P	0.36	P	1	15	N	~
25	0.43	P	0.48	P	2	6	N	~
26	0.30	P	0.45	P	1	4	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
1	~	~	~	S	W
2	~	~	~	~	~
3	~	~	~	S	W
4	~	~	~	~	~
5	~	~	~	N	E
6	~	~	~	S	E
7	~	~	~	~	~
8	~	~	~	~	~
9	~	~	~	~	~
10	~	~	~	S	E
11	~	~	~	S	W
12	~	~	~	~	~
13	~	~	~	~	~
14	~	~	~	~	~
15	~	~	~	N	E
16	~	~	~	S	E
17	~	~	~	S	E
18	~	~	~	~	~
19	~	~	~	S	E
20	~	~	~	~	~
21	~	~	~	S	E
22	~	~	~	~	~
23	~	~	~	S	W
24	~	~	~	N	W
25	~	~	~	~	~
26	~	~	~	~	~

Reference	
1	Chown et al., 1995
2	Stuart and Stuart, 1996
3	Stuart and Stuart, 1996
4	Stuart and Stuart, 1996
5	Hancock et al., 1992
6	Stuart and Stuart, 1996
7	Stuart and Stuart, 1996
8	Stuart and Stuart, 1996
9	Stuart and Stuart, 1996
10	Stuart and Stuart, 1996
11	Stuart and Stuart, 1996; Kingdon, 1997
12	Stuart and Stuart, 1996
13	Stuart and Stuart, 1996; Kingdon, 1997
14	Skinner and Louw, 1996; Kingdon, 1997
15	Stuart and Stuart, 1996
16	Stuart and Stuart, 1996; Kingdon, 1997
17	Penny, 1988; Stuart and Stuart, 1996
18	Stuart and Stuart, 1996
19	Burton et al., 1987
20	Stuart and Stuart, 1996
21	Penny, 1988; Stuart and Stuart, 1996
22	Burton et al., 1987; Duncan, 1992; Stuart and Stuart, 1996
23	Duncan, 1992; Stuart and Stuart, 1996; Kingdon, 1997
24	Duncan, 1992; Stuart and Stuart, 1996
25	Burton et al., 1987
26	Burton et al., 1987; Kingdon, 1997

	Region	Taxonomic group	Species	Common name
27	Africa	Mammal	<i>Gazella cuvieri</i>	Cuvier's gazelle
28	Africa	Mammal	<i>Gazella dama</i>	Dama gazelle
29	Africa	Mammal	<i>Gazella leptoceros</i>	Slender-horned gazelle
30	Africa	Mammal	<i>Gazella rufifrons</i>	Red-fronted gazelle
31	Africa	Mammal	<i>Gazella soemmerringii</i>	Soemmerring's gazelle
32	Africa	Mammal	<i>Gazella spekei</i>	Speke's gazelle
33	Africa	Mammal	<i>Giraffa camelopardalis</i>	Giraffe
34	Africa	Mammal	<i>Gorilla gorilla</i>	Gorilla
35	Africa	Mammal	<i>Hexaprotodon liberiensis</i>	Pygmy hippopotamus
36	Africa	Mammal	<i>Hippotragus equinus</i>	Roan antelope
37	Africa	Mammal	<i>Hippotragus niger</i>	Sable antelope
38	Africa	Mammal	<i>Hyaena brunnea</i>	Brown hyanea
39	Africa	Mammal	<i>Kobus kob</i>	Kob
40	Africa	Mammal	<i>Kobus leche</i>	Lechwe
41	Africa	Mammal	<i>Kobus vardonii</i>	Puku
42	Africa	Mammal	<i>Loxodonta africana</i>	African elephant
43	Africa	Mammal	<i>Lutra lutra</i>	Eurasian otter
44	Africa	Mammal	<i>Lycan pictus</i>	African wild dog
45	Africa	Mammal	<i>Macaca sylvanus</i>	Barbary macaque
46	Africa	Mammal	<i>Okapia johnstoni</i>	Okapi
47	Africa	Mammal	<i>Oryx damali</i>	Scimitar-horned oryx
48	Africa	Mammal	<i>Pan paniscus</i>	Bonobo
49	Africa	Mammal	<i>Pan troglodytes</i>	Chimpanzee
50	Africa	Mammal	<i>Panthera leo</i>	African lion
51	Africa	Mammal	<i>Panthera pardus</i>	Leopard
52	Africa	Mammal	<i>Proteles cristatus</i>	Aardwolf

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
27	Y	N	N	Y	C	222,800	1,685,700	86.78
28	Y	N	N	Y	C	705,500	5,174,500	86.37
29	Y	N	N	Y	C	18,800	5,625,600	99.67
30	N	N	N	Y	C	1,576,800	3,215,000	50.95
31	N	N	N	Y	C	602,100	781,800	22.98
32	N	N	N	Y	C	149,800	399,700	62.52
33	N	N	N	Y	C	2,854,500	10,926,100	73.87
34	N	N	N	Y	C	599,900	1,569,600	61.78
35	Y	N	N	Y	C	15,500	495,400	96.88
36	N	N	N	Y	C	5,023,000	7,332,400	31.50
37	N	N	N	Y	C	1,324,700	2,892,100	54.20
38	N	N	N	Y	C	1,067,100	2,248,600	52.54
39	N	N	N	Y	C	2,633,400	3,496,400	24.68
40	Y	N	N	Y	C	74,600	531,300	85.95
41	Y	N	N	Y	C	322,300	1,971,000	83.65
42	N	N	N	Y	C	5,171,100	20,666,800	74.98
43	Y	N	N	Y	C	65,200	623,700	89.54
44	Y	Y	N	Y	C	1,814,600	9,697,100	81.29
45	Y	N	N	Y	C	63,600	312,900	79.68
46	N	N	N	Y	C	575,000	2,097,600	72.59
47	Y	N	N	Y	C	190,200	6,865,700	97.23
48	N	N	N	Y	C	329,500	1,153,300	71.43
49	N	N	N	Y	C	1,780,300	5,089,900	65.02
50	N	N	N	Y	C	6,035,800	18,127,400	66.70
51	N	N	N	Y	C	16,850,800	25,935,800	35.03
52	N	N	N	Y	C	2,339,300	3,552,800	34.16

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
27	0.43	P	0.45	P	1	3	N	~
28	0.53	C	0.66	C	1	3	N	~
29	0.00	P	0.00	P	1	2	N	~
30	0.58	C	0.67	C	1	3	N	~
31	0.52	C	0.49	P	1	4	N	~
32	0.19	P	0.31	P	1	1	N	~
33	0.37	P	0.48	P	1	17	N	~
34	0.62	C	0.66	C	1	3	N	~
35	0.72	C	0.82	C	1	2	N	~
36	0.54	C	0.62	C	2	26	N	~
37	0.45	P	0.52	C	1	12	N	~
38	0.56	C	0.53	C	1	1	N	~
39	0.53	C	0.56	C	1	4	N	~
40	0.48	P	0.50	P	1	6	N	~
41	0.38	P	0.40	P	1	12	N	~
42	0.68	C	0.74	C	1	70	N	~
43	0.37	P	0.36	P	1	6	N	~
44	0.67	C	0.83	C	6	13	N	~
45	0.54	C	0.50	P	1	4	N	~
46	0.52	C	0.64	C	1	18	N	~
47	0.00	P	0.35	P	1	2	N	~
48	0.52	C	0.54	C	1	1	N	~
49	0.53	C	0.56	C	1	1	N	~
50	0.68	C	0.81	C	1	20	N	~
51	0.48	P	0.48	P	1	2	N	~
52	0.40	P	0.46	P	1	1	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
27	~	~	~	N	E
28	~	~	~	S	W
29	~	~	~	S	W
30	~	~	~	~	~
31	~	~	~	~	~
32	~	~	~	~	~
33	~	~	~	~	~
34	~	~	~	~	~
35	~	~	~	N	W
36	~	~	~	~	~
37	~	~	~	~	~
38	~	~	~	~	~
39	~	~	~	~	~
40	~	~	~	S	W
41	~	~	~	N	E
42	~	~	~	~	~
43	~	~	~	N	W
44	~	~	~	S	W
45	~	~	~	S	W
46	~	~	~	~	~
47	~	~	~	S	E
48	~	~	~	~	~
49	~	~	~	~	~
50	~	~	~	~	~
51	~	~	~	~	~
52	~	~	~	~	~

Reference	
27	Stuart and Stuart, 1996
28	Stuart and Stuart, 1996; Kingdon, 1997
29	Stuart and Stuart, 1996
30	Stuart and Stuart, 1996
31	Stuart and Stuart, 1996; Kingdon, 1997
32	Kingdon, 1997
33	Stuart and Stuart, 1996
34	Schaller, 1963; Goodall et al., 1993
35	Stuart and Stuart, 1996
36	Stuart and Stuart, 1996
37	Stuart and Stuart, 1996
38	Stuart and Stuart, 1996
39	Kingdon, 1997
40	Stuart and Stuart, 1996
41	Kingdon, 1997
42	Stuart and Stuart, 1996
43	Stuart and Stuart, 1996
44	Stuart and Stuart, 1996
45	Stuart and Stuart, 1996; Kingdon, 1997
46	Kingdon, 1997
47	Stuart and Stuart, 1996; Kingdon, 1997
48	Goodall et al., 1993; Kingdon, 1997
49	Goodall et al., 1993
50	Stuart and Stuart, 1996
51	Burton et al., 1987
52	Burton et al., 1987

	Region	Taxonomic group	Species	Common name
53	Africa	Mammal	<i>Synecrus caffer</i>	African buffalo
54	Africa	Mammal	<i>Taotragus derbianus</i>	Great eland
55	Africa	Mammal	<i>Tragelaphus buxtoni</i>	Mountain nyala
56	Africa	Mammal	<i>Tragelaphus eurycerus</i>	Bongo
57	Australia	Arthropod	<i>Astacopsis gouldi</i>	Tasmanian giant freshwater lobster
58	Australia	Bird	<i>Atrichornis clamosus</i>	Noisy scrub-bird
59	Australia	Bird	<i>Cacatua badinii</i>	White-tailed black cockatoos
60	Australia	Bird	<i>Calyptrorhynchus funereus latirostris</i>	Carnaby's cockatoo
61	Australia	Bird	<i>Leipoa ocellata</i>	Malleefowl
62	Australia	Bird	<i>Lichenostomus melanops cassidix</i>	Helmeted honeycreeper
63	Australia	Bird	<i>Pardalotus quadragintus</i>	Forty-spotted pardalote
64	Australia	Bird	<i>Pedionomus torquatus</i>	Plains-wanderer
65	Australia	Bird	<i>Pezoporus occidentalis</i>	Night parrot
66	Australia	Bird	<i>Poephila cincta</i>	Black-throated finch
67	Australia	Bird	<i>Psephotus pulcherrimus</i>	Paradise parrot
68	Australia	Mammal	<i>Aepyprymnus rufescens</i>	Rufous bettong
69	Australia	Mammal	<i>Antechinomys laniger</i>	Kultarr
70	Australia	Mammal	<i>Bettongia gaimardi</i>	Tasmanian bettong
71	Australia	Mammal	<i>Bettongia lesueur</i>	Burrowing bettong
72	Australia	Mammal	<i>Bettongia penicillatus</i>	Brush-tailed bettong
73	Australia	Mammal	<i>Bettongia tropica</i>	Northern bettong
74	Australia	Mammal	<i>Bubalus bubalis</i>	Water buffalo
75	Australia	Mammal	<i>Chaeropus edaudatus</i>	Pig-footed bandicoot
76	Australia	Mammal	<i>Conilurus penicillatus</i>	Brush-tailed tree-rat
77	Australia	Mammal	<i>Dasyercus cristicauda</i>	Mulgara
78	Australia	Mammal	<i>Dasyuroides byrnei</i>	Kowari

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
53	N	N	N	Y	C	7,183,100	14,342,400	49.92
54	Y	N	N	Y	C	622,500	2,791,000	77.69
55	N	N	N	Y	C	19,500	52,400	62.77
56	N	N	N	Y	C	1,586,800	3,025,900	47.56
57	N	N	N	Y	I	8,700	11,000	21.44
58	Y	N	N	Y	C	1,600	63,900	97.57
59	N	N	N	Y	C	128,100	154,300	16.97
60	Y	N	N	Y	C	100	67,500	99.85
61	N	N	N	Y	C	1,121,400	2,591,300	56.72
62	Y	N	N	Y	C	650	15,400	95.80
63	Y	Y	N	Y	I	6,500	39,900	83.77
64	N	N	N	Y	C	1,226,900	2,321,200	47.15
65	Y	Y	N	Y	C	232,500	2,068,000	88.76
66	N	N	N	Y	C	658,200	760,900	13.50
67	Y	N	N	Y	C	51,000	265,900	80.84
68	N	N	N	Y	B	709,300	820,800	13.59
69	N	N	N	Y	C	2,422,300	2,975,000	18.58
70	Y	N	Y	Y	B	30,600	351,300	91.29
71	Y	N	Y	Y	B	1,400	2,669,600	99.95
72	Y	N	Y	Y	B	24,300	3,004,400	99.19
73	N	N	N	Y	C	25,200	42,300	40.49
74	N	N	N	Y	C	70,900	210,100	66.23
75	N	N	N	Y	C	1,867,000	3,192,000	41.51
76	Y	N	Y	Y	B	63,800	361,600	82.36
77	Y	Y	N	Y	C	820,600	3,530,400	76.76
78	N	N	N	Y	C	109,300	348,100	68.60

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
53	0.55	C	0.59	C	1	18	N	~
54	0.63	C	0.72	C	1	4	N	~
55	0.62	C	0.71	C	1	1	N	~
56	0.57	C	0.65	C	1	24	N	~
57	0.53	C	0.55	C	1	2	N	~
58	0.00	P	0.00	P	1	1	N	~
59	0.52	C	0.56	C	1	1	N	~
60	0.16	P	0.47	P	1	11	N	~
61	0.53	C	0.59	C	1	4	N	~
62	0.00	P	0.40	P	1	1	N	~
63	0.00	P	0.04	P	3	3	N	~
64	0.50	P	0.51	C	1	1	N	~
65	0.08	P	0.26	P	3	4	N	~
66	0.51	C	0.53	C	1	1	N	~
67	0.28	P	0.39	P	1	1	N	~
68	0.54	C	0.57	C	2	3	N	1
69	0.53	C	0.58	C	7	4	N	~
70	0.04	P	0.20	P	2	1	N	1
71	0.00	P	0.00	P	6	4	N	2
72	0.00	P	0.31	P	8	3	N	5
73	0.51	C	0.39	P	2	1	N	~
74	0.54	C	0.54	C	1	1	N	~
75	0.53	C	0.53	C	1	3	Y	~
76	0.00	P	0.17	P	4	5	N	1
77	0.56	C	0.61	C	2	8	N	~
78	0.55	C	0.54	C	4	3	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
53	~	~	~	~	~
54	~	~	~	S	E
55	~	~	~	~	~
56	~	~	~	~	~
57	~	~	~	~	~
58	~	~	~	S	E
59	~	~	~	~	~
60	~	~	~	S	W
61	~	~	~	~	~
62	~	~	~	S	W
63	~	~	~	S	E
64	~	~	~	~	~
65	~	~	~	S	E
66	~	~	~	~	~
67	~	~	~	S	W
68	1	1	1	~	~
69	~	~	~	~	~
70	1	0	1	S	W
71	5	0	4	S	W
72	4	1	2	N	W
73	~	~	~	~	~
74	~	~	~	~	~
75	~	~	~	~	~
76	3	1	3	N	W
77	~	~	~	N	W
78	~	~	~	~	~

	Reference
53	Prins, 1996
54	Stuart and Stuart, 1996; Kingdon, 1997
55	Stuart and Stuart, 1996
56	Stuart and Stuart, 1996
57	Horwitz, 1994
58	Smith, 1985; Hermes, 1990
59	Saunders et al., 1985
60	Saunders, 1990
61	Jones et al., 1995
62	Hermes, 1990
63	Hermes, 1990
64	Hermes, 1990
65	Trounson and Trounson, 1987; Hermes, 1990
66	Trounson and Trounson, 1987
67	Ovington, 1978; Hutchins and Lovell, 1985; Hermes, 1990
68	Strahan, 1995
69	McKenzie et al., 1996
70	Strahan, 1995
71	Strahan, 1995
72	McKenzie et al., 1996
73	Strahan, 1995
74	Strahan, 1995
75	McKenzie et al., 1996
76	McKenzie et al., 1996
77	McKenzie et al., 1996
78	McKenzie et al., 1996

	Region	Taxonomic group	Species	Common name
79	Australia	Mammal	<i>Dasyurus geoffroii</i>	Western quoll
80	Australia	Mammal	<i>Dasyurus hallucatus</i>	Northern quoll
81	Australia	Mammal	<i>Dasyurus maculatus</i>	Spotted-tail quoll
82	Australia	Mammal	<i>Dasyurus viverrinus</i>	Eastern quoll
83	Australia	Mammal	<i>Gymnobelideus leadbeateri</i>	Yellow-bellied glider
84	Australia	Mammal	<i>Isodon auratus</i>	Golden bandicoot
85	Australia	Mammal	<i>Isodon macrourus</i>	Northern brown bandicoot
86	Australia	Mammal	<i>Isodon obesulus</i>	Southern brown bandicoot
87	Australia	Mammal	<i>Lagorchestes conspicillatus</i>	Spectacled hare-wallaby
88	Australia	Mammal	<i>Lagorchestes hirsutus</i>	Rufous hare-wallaby
89	Australia	Mammal	<i>Lagorchestes leporides</i>	Eastern hare-wallaby
90	Australia	Mammal	<i>Lagostrophus fasciatus</i>	Banded hare-wallaby
91	Australia	Mammal	<i>Lasiorhinus krefftii</i>	Northern hair-nosed wombat
92	Australia	Mammal	<i>Lasiorhinus latifrons</i>	Southern-hairy nosed wombat
93	Australia	Mammal	<i>Leggadina forresti</i>	Forrest's mouse
94	Australia	Mammal	<i>Leporillus apicalis</i>	Lesser Stick-nest Rat
95	Australia	Mammal	<i>Leporillus conditor</i>	Greater stick-nest rat
96	Australia	Mammal	<i>Macroderma gigas</i>	Ghost bat
97	Australia	Mammal	<i>Macropus eugenii</i>	Tammar wallaby
98	Australia	Mammal	<i>Macrotis lagotis</i>	Bilby
99	Australia	Mammal	<i>Macrotis leucrua</i>	Lesser bilby
100	Australia	Mammal	<i>Melomys burtoni</i>	Grassland melomys
101	Australia	Mammal	<i>Mesembriomys gouldii</i>	Black-footed tree-rat
102	Australia	Mammal	<i>Mesembriomys macrurus</i>	Golden-backed tree-rat
103	Australia	Mammal	<i>Myrmecobius fasciatus</i>	Numbat
104	Australia	Mammal	<i>Notomys amplius</i>	Short-tailed hopping-mouse

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
79	Y	N	N	Y	C	110,200	5,400,700	97.96
80	Y	N	Y	Y	B	465,000	1,887,900	75.37
81	N	N	N	Y	B	390,000	494,900	21.19
82	Y	N	Y	Y	B	73,500	429,400	82.88
83	Y	N	N	Y	C	190	16,100	98.84
84	Y	N	Y	Y	B	86,100	4,267,700	97.98
85	N	N	N	Y	B	993,700	1,106,400	10.18
86	N	N	N	Y	B	287,700	894,900	67.85
87	N	N	N	Y	C	1,757,400	2,859,700	38.54
88	Y	N	Y	Y	B	650	2,060,700	99.97
89	Y	N	N	Y	C	130	445,900	99.97
90	Y	N	Y	Y	B	650	161,800	99.60
91	Y	Y	N	Y	C	3,000	49,000	93.92
92	N	N	N	Y	C	130,400	161,900	19.46
93	N	N	N	Y	C	1,860,400	1,894,100	1.78
94	Y	N	N	Y	C	130	2,103,900	99.99
95	Y	N	Y	Y	B	390	1,393,100	99.97
96	N	N	N	Y	B	1,986,000	3,290,300	39.64
97	N	N	N	Y	B	88,900	302,800	70.62
98	N	N	N	Y	C	1,443,000	5,070,700	71.54
99	Y	Y	N	Y	C	130	1,047,000	99.99
100	N	N	N	Y	B	633,500	651,800	2.80
101	N	N	N	Y	B	344,300	513,100	32.90
102	Y	N	Y	Y	B	108,100	683,400	84.18
103	Y	N	Y	Y	B	16,100	2,797,500	99.43
104	Y	N	N	Y	C	42,200	2,277,000	98.14

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
79	0.00	P	0.00	P	1	1	N	~
80	0.09	P	0.28	P	2	13	N	2
81	0.50	C	0.50	C	3	7	N	2
82	0.24	P	0.34	P	5	4	N	1
83	0.00	P	0.00	P	1	1	N	~
84	0.00	P	0.00	P	4	4	N	1
85	0.50	P	0.50	P	7	7	N	3
86	0.11	P	0.33	P	12	8	N	3
87	0.32	P	0.42	P	1	2	N	~
88	0.00	P	0.00	P	5	2	N	3
89	0.00	P	0.00	P	1	1	Y	~
90	0.00	P	0.00	P	5	2	N	3
91	0.00	P	0.00	P	3	1	N	~
92	0.53	C	0.52	C	7	4	N	~
93	0.50	C	0.51	C	2	1	Y	~
94	0.00	P	0.00	P	1	1	Y	~
95	0.00	P	0.00	P	3	2	Y	1
96	0.33	P	0.42	P	5	2	N	5
97	0.61	C	0.69	C	13	9	N	3
98	0.61	C	0.66	C	2	4	N	~
99	0.00	P	0.00	P	2	1	Y	~
100	0.50	C	0.47	P	8	7	N	2
101	0.50	C	0.54	C	5	5	N	3
102	0.50	C	0.56	C	4	2	N	3
103	0.00	P	0.00	P	6	2	N	1
104	0.06	P	0.41	P	1	1	Y	~

	Historical island	Extant mainland	Extant island	N/S	W/E
79	~	~	~	S	W
80	6	2	6	S	W
81	3	2	3	~	~
82	3	1	4	S	W
83	~	~	~	S	W
84	5	1	3	N	W
85	3	3	3	~	~
86	8	2	8	~	~
87	~	~	~	~	~
88	2	0	2	S	W
89	~	~	~	S	W
90	2	0	2	N	W
91	~	~	~	N	W
92	~	~	~	~	~
93	~	~	~	~	~
94	~	~	~	N	E
95	3	0	3	S	E
96	5	2	4	~	~
97	11	1	9	~	~
98	~	~	~	~	~
99	~	~	~	S	E
100	5	1	5	~	~
101	2	3	2	~	~
102	5	1	0	N	W
103	5	1	0	S	W
104	~	~	~	S	E

	Reference
79	McKenzie et al., 1996
80	McKenzie et al., 1996
81	Strahan, 1995
82	Strahan, 1995
83	McKenzie et al., 1996
84	McKenzie et al., 1996
85	McKenzie et al., 1996
86	McKenzie et al., 1996
87	Strahan, 1995
88	Strahan, 1995
89	Strahan, 1995
90	Strahan, 1995
91	McKenzie et al., 1996
92	McKenzie et al., 1996
93	Strahan, 1995
94	Strahan, 1995
95	Strahan, 1995
96	Strahan, 1995
97	McKenzie et al., 1996
98	McKenzie et al., 1996
99	Strahan, 1995
100	Strahan, 1995
101	Strahan, 1995
102	Strahan, 1995
103	Caughley and Gunn, 1996
104	Strahan, 1995

	Region	Taxonomic group	Species	Common name
105	Australia	Mammal	<i>Notomys fuscus</i>	Dusky hopping-mouse
106	Australia	Mammal	<i>Notomys longicaudatus</i>	Long-tailed hopping-mouse
107	Australia	Mammal	<i>Notomys mitchelli</i>	Mitchells hopping mouse
108	Australia	Mammal	<i>Onychogalea fraenata</i>	Bridled nailtail wallaby
109	Australia	Mammal	<i>Onychogalea lunata</i>	Crescent nailtail wallaby
110	Australia	Mammal	<i>Parantechinus apicalis</i>	Southern dibbler
111	Australia	Mammal	<i>Perameles bougainville</i>	Western barred bandicoot
112	Australia	Mammal	<i>Perameles gunnii</i>	Eastern barred bandicoot
113	Australia	Mammal	<i>Perameles nasuta</i>	Long-nosed bandicoot
114	Australia	Mammal	<i>Petaurus australis</i>	Leadbeater's possum
115	Australia	Mammal	<i>Petaurus breviceps</i>	Sugar glider
116	Australia	Mammal	<i>Petrogale lateralis</i>	Black-footed rock-wallaby
117	Australia	Mammal	<i>Petrogale pencillata</i>	Brush-tailed rock wallaby
118	Australia	Mammal	<i>Petrogale xanthopus</i>	Yellow-footed rock wallaby
119	Australia	Mammal	<i>Phascogale calura</i>	Red-tailed phascogale
120	Australia	Mammal	<i>Phascogale tapoatafa</i>	Brush-tailed phascogale
121	Australia	Mammal	<i>Phascolarctos cinereus</i>	Koala
122	Australia	Mammal	<i>Potorous platyops</i>	Broad-faced potoroo
123	Australia	Mammal	<i>Potorous tridactylus</i>	Long-nosed potoroo
124	Australia	Mammal	<i>Pseudantechinus macdonnellensis</i>	Fat-tailed pseudantechinus
125	Australia	Mammal	<i>Pseudocheirus occidentalis</i>	Western ringtail possum
126	Australia	Mammal	<i>Pseudomys albocinereus</i>	Ash-grey mouse
127	Australia	Mammal	<i>Pseudomys australis</i>	Plains rat
128	Australia	Mammal	<i>Pseudomys bolami</i>	Bolam's mouse
129	Australia	Mammal	<i>Pseudomys chapmani</i>	Western pebble-mound mouse
130	Australia	Mammal	<i>Pseudomys desertor</i>	Desert mouse

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
105	N	N	N	Y	C	157,700	458,500	65.61
106	Y	N	Y	Y	B	65,000	3,148,800	97.94
107	N	N	N	Y	B	716,300	978,600	26.81
108	Y	N	N	Y	C	7,700	1,060,500	99.28
109	N	N	N	Y	C	2,391,500	2,487,300	3.85
110	Y	Y	N	Y	C	20,100	127,700	84.26
111	Y	N	Y	Y	B	1,000	1,518,500	99.93
112	N	N	N	Y	B	39,000	61,200	36.23
113	N	N	N	Y	B	488,700	815,800	40.10
114	Y	N	N	Y	C	130	13,200	99.02
115	N	N	N	Y	B	1,942,600	1,969,100	1.34
116	Y	N	Y	Y	B	311,600	1,408,500	77.88
117	N	N	N	Y	C	117,200	408,200	71.28
118	N	N	N	Y	C	157,400	309,500	49.14
119	Y	Y	N	Y	C	66,400	1,968,300	96.63
120	N	N	N	Y	C	627,000	1,404,000	55.34
121	N	N	N	Y	B	1,037,000	1,909,300	45.68
122	Y	Y	N	Y	C	44,000	176,900	75.15
123	N	N	N	Y	C	100,000	158,600	36.96
124	N	N	N	Y	C	1,061,800	1,199,100	11.45
125	Y	N	N	Y	C	19,100	87,100	78.13
126	N	N	N	Y	B	341,400	377,200	9.49
127	Y	Y	N	Y	C	152,000	855,300	82.23
128	N	N	N	Y	C	648,600	762,500	14.95
129	N	N	N	Y	C	103,200	292,600	64.73
130	N	N	N	Y	C	1,239,300	2,776,600	55.37

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
105	0.51	C	0.53	C	1	1	N	~
106	0.77	C	0.71	C	3	3	Y	2
107	0.49	P	0.49	P	6	7	N	1
108	0.00	P	0.17	P	1	1	N	~
109	0.51	C	0.53	C	1	1	Y	~
110	0.25	P	0.30	P	3	1	N	~
111	0.00	P	0.00	P	3	2	N	1
112	0.54	C	0.59	C	2	4	N	1
113	0.34	P	0.44	P	2	3	N	1
114	0.00	P	0.00	P	1	1	N	~
115	0.50	C	0.49	P	7	6	N	2
116	0.13	P	0.30	P	13	14	N	4
117	0.36	P	0.48	P	2	4	N	~
118	0.53	C	0.53	C	2	3	N	~
119	0.06	P	0.44	P	6	1	H	~
120	0.32	P	0.45	P	7	8	N	~
121	0.54	C	0.54	C	7	13	N	4
122	0.50	C	0.55	C	3	2	Y	~
123	0.30	P	0.50	P	13	13	N	~
124	0.52	C	0.56	C	2	5	N	~
125	0.08	P	0.22	P	1	3	N	~
126	0.52	C	0.53	C	4	4	N	1
127	0.60	C	0.64	C	4	2	N	~
128	0.44	P	0.45	P	1	1	N	~
129	0.06	P	0.32	P	3	4	N	~
130	0.53	C	0.55	C	2	1	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
105	~	~	~	~	~
106	1	2	0	N	E
107	6	1	6	~	~
108	~	~	~	N	E
109	~	~	~	~	~
110	~	~	~	S	E
111	2	0	2	N	W
112	1	1	1	~	~
113	1	1	1	~	~
114	~	~	~	S	W
115	5	1	5	~	~
116	9	4	8	N	E
117	~	~	~	~	~
118	~	~	~	~	~
119	~	~	~	S	W
120	~	~	~	~	~
121	3	4	3	~	~
122	~	~	~	S	W
123	~	~	~	~	~
124	~	~	~	~	~
125	~	~	~	S	W
126	3	1	3	~	~
127	~	~	~	N	W
128	~	~	~	~	~
129	~	~	~	~	~
130	~	~	~	~	~

	Reference
105	Strahan, 1995
106	Strahan, 1995
107	Strahan, 1995
108	Strahan, 1995
109	Strahan, 1995
110	McKenzie et al., 1996
111	McKenzie et al., 1996
112	Strahan, 1995
113	McKenzie et al., 1996
114	Strahan, 1995
115	Strahan, 1995
116	Strahan, 1995
117	Strahan, 1995
118	Strahan, 1995
119	McKenzie et al., 1996
120	McKenzie et al., 1996
121	Strahan, 1995
122	Strahan, 1995
123	McKenzie et al., 1996
124	Strahan, 1995
125	Strahan, 1995
126	Strahan, 1995
127	Strahan, 1995
128	Strahan, 1995
129	McKenzie et al., 1996
130	Strahan, 1995

	Region	Taxonomic group	Species	Common name
131	Australia	Mammal	<i>Pseudomys fieldi</i>	Shark Bay Mouse
132	Australia	Mammal	<i>Pseudomys fumeus</i>	Smoky mouse
133	Australia	Mammal	<i>Pseudomys gouldii</i>	Gould's mouse
134	Australia	Mammal	<i>Pseudomys hermannsburgensis</i>	Sandy inland mouse
135	Australia	Mammal	<i>Pseudomys nanus</i>	Western chestnut mouse
136	Australia	Mammal	<i>Pseudomys shortridgei</i>	Heath rat
137	Australia	Mammal	<i>Rattus fuscipes</i>	Bush rat
138	Australia	Mammal	<i>Rattus tunneyi</i>	Pale field-rat
139	Australia	Mammal	<i>Rattus villosissimus</i>	Long-haired rat
140	Australia	Mammal	<i>Setonix brachyurus</i>	Quokka
141	Australia	Mammal	<i>Sminthopsis dolichura</i>	Little long-haired rat
142	Australia	Mammal	<i>Sminthopsis gilberti</i>	Gilbert's dunnart
143	Australia	Mammal	<i>Sminthopsis granulipes</i>	White-tailed dunnart
144	Australia	Mammal	<i>Sminthopsis ooldea</i>	Ooldea dunnart
145	Australia	Mammal	<i>Sminthopsis psammophila</i>	Sandhill dunnart
146	Australia	Mammal	<i>Thylacinus cynocephalus</i>	Tasmanian tiger
147	Australia	Mammal	<i>Thylogale billardieri</i>	Tasmanian pademelon
148	Australia	Mammal	<i>Trichosurus vulpecula</i>	Common brushtail possum
149	Australia	Mammal	<i>Vombat ursinus</i>	Common wombat
150	Australia	Mammal	<i>Wyulda squamicaudata</i>	Scaly-tailed possum
151	Australia	Mammal	<i>Zyzomys pedunculatus</i>	Central rock-rat
152	Australia	Mammal	<i>Zyzomys woodwardi</i>	Kimberly rock-rat
153	Eurasia	Amphibian	<i>Bufo calamita</i>	Natterjack toad
154	Eurasia	Arthropod	<i>Argynnis adippe</i>	High brown fritillary
155	Eurasia	Arthropod	<i>Melicta athalia</i>	Heath fritillary butterfly
156	Eurasia	Bird	<i>Anser erythropus</i>	Lesser white-fronted goose

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
131	Y	N	Y	Y	B	520	2,217,200	99.98
132	Y	Y	N	Y	C	34,100	141,700	75.94
133	N	N	N	Y	C	50,800	61,500	17.30
134	N	N	N	Y	B	3,614,700	3,687,100	1.96
135	N	N	N	Y	B	1,134,400	1,837,600	38.27
136	Y	N	Y	Y	B	45,800	271,600	83.15
137	N	N	N	Y	B	582,200	709,600	17.96
138	Y	N	Y	Y	B	863,700	3,500,200	75.33
139	N	N	N	Y	C	2,012,500	3,123,800	35.58
140	N	N	N	Y	B	61,900	78,200	20.90
141	N	N	N	Y	C	462,900	521,900	11.30
142	N	N	N	Y	C	70,300	79,100	11.15
143	N	N	N	Y	C	133,800	160,800	16.77
144	N	N	N	Y	C	1,647,000	1,805,000	8.76
145	N	N	N	Y	C	93,400	179,500	47.98
146	Y	N	Y	Y	B	450	8,767,200	99.99
147	N	N	N	Y	B	73,500	205,000	64.14
148	N	N	N	Y	B	2,811,100	7,430,800	62.17
149	N	N	N	Y	B	268,100	579,500	53.73
150	N	N	N	Y	C	44,000	51,300	14.39
151	Y	Y	N	Y	C	26,700	522,300	94.89
152	N	N	N	Y	B	80,300	99,200	19.08
153	Y	Y	N	Y	I	3,700	113,700	96.76
154	N	N	N	Y	I	65,000	142,700	54.43
155	Y	N	N	Y	C	930	45,500	97.95
156	N	N	N	Y	C	994,500	1,178,000	15.58

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
131	0.00	P	0.00	P	3	1	N	1
132	0.54	C	0.59	C	3	3	N	~
133	0.52	C	0.50	C	3	2	Y	~
134	0.50	C	0.51	C	4	4	N	1
135	0.51	C	0.51	C	2	2	N	1
136	0.61	C	0.71	C	5	4	N	4
137	0.51	C	0.52	C	17	13	N	7
138	0.00	P	0.21	P	7	7	N	2
139	0.55	C	0.61	C	1	1	N	~
140	0.53	C	0.48	P	2	2	N	1
141	0.52	C	0.56	C	2	3	N	~
142	0.52	C	0.56	C	2	2	N	~
143	0.52	C	0.54	C	2	2	N	~
144	0.52	C	0.55	C	1	1	N	~
145	0.47	P	0.50	P	6	3	N	~
146	0.00	P	0.00	P	3	1	Y	1
147	0.51	C	0.46	P	5	4	N	1
148	0.21	P	0.28	P	11	15	N	1
149	0.55	C	0.55	C	2	8	N	1
150	0.51	C	0.55	C	2	1	N	~
151	0.54	C	0.80	C	2	1	N	~
152	0.50	C	0.47	P	5	4	N	2
153	0.00	P	0.01	P	3	7	N	~
154	0.41	P	0.45	P	2	3	N	~
155	0.30	P	0.30	P	1	3	N	~
156	0.51	C	0.52	C	3	3	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
131	2	0	1	N	W
132	~	~	~	S	W
133	~	~	~	~	~
134	2	1	2	~	~
135	2	1	2	~	~
136	1	2	0	S	W
137	12	4	12	~	~
138	2	2	1	N	E
139	~	~	~	~	~
140	1	1	1	~	~
141	~	~	~	~	~
142	~	~	~	~	~
143	~	~	~	~	~
144	~	~	~	~	~
145	~	~	~	~	~
146	2	0	1	S	E
147	4	0	4	~	~
148	13	1	13	~	~
149	1	1	1	~	~
150	~	~	~	~	~
151	~	~	~	S	E
152	3	1	3	~	~
153	~	~	~	N	W
154	~	~	~	~	~
155	~	~	~	S	W
156	~	~	~	~	~

	Reference
131	Strahan, 1995
132	Strahan, 1995
133	McKenzie et al., 1996
134	Strahan, 1995
135	McKenzie et al., 1996
136	Strahan, 1995
137	Strahan, 1995
138	Strahan, 1995
139	Strahan, 1995
140	McKenzie et al., 1996
141	McKenzie et al., 1996
142	Strahan, 1995
143	Strahan, 1995
144	McKenzie et al., 1996
145	McKenzie et al., 1996
146	Guiler, 1985
147	Strahan, 1995
148	Strahan, 1995
149	Strahan, 1995
150	Strahan, 1995
151	McKenzie et al., 1996
152	Strahan, 1995
153	Beebee, 1977
154	Warren and Key, 1994
155	Warren et al., 1984
156	Heredia et al., 1996

	Region	Taxonomic group	Species	Common name
157	Eurasia	Bird	<i>Ardeotis nigriceps</i>	Great Indian bustard
158	Eurasia	Bird	<i>Buteo buteo</i>	Buzzard
159	Eurasia	Bird	<i>Cairina scutulata</i>	Whitewinged wood duck
160	Eurasia	Bird	<i>Crex crex</i>	Corncrake
161	Eurasia	Bird	<i>Cursorius bitorquatus</i>	Jerdon's courser
162	Eurasia	Bird	<i>Euopodotis bengalensis</i>	Bengal florican
163	Eurasia	Bird	<i>Eupodotis indica</i>	Lesser florican
164	Eurasia	Bird	<i>Grus antigone</i>	Sarus crane
165	Eurasia	Bird	<i>Leptoptilos javanicus</i>	Lesser adjutant stork
166	Eurasia	Bird	<i>Milvus milvus</i>	Red kite
167	Eurasia	Bird	<i>Ophrysia superciliosa</i>	Mountain quail
168	Eurasia	Bird	<i>Otis tarda</i>	Great bustard
169	Eurasia	Bird	<i>Pavo muticus</i>	Green peafowl
170	Eurasia	Bird	<i>Pelecanus philippensis</i>	Spot-billed pelican
171	Eurasia	Bird	<i>Pitta gurneyi</i>	Gurney's pitta
172	Eurasia	Bird	<i>Pseudibis papillosa</i>	Black ibis
173	Eurasia	Bird	<i>Rhodonessa caryophyllacea</i>	Indian pink-headed duck
174	Eurasia	Bird	<i>Tadorna cristata</i>	Crested shelduck
175	Eurasia	Bird	<i>Tetrao tetrix</i>	Caucasian black grouse
176	Eurasia	Bird	<i>Tetrao urogallus</i>	Sharp-winged grouse
177	Eurasia	Bird	<i>Tetrao urogallus pyrenees</i>	Capercaillie
178	Eurasia	Bird	<i>Tetrax tetrax</i>	Little bustard
179	Eurasia	Bird	<i>Tragopan blythi blythi</i>	Eastern Blyth's tragopan
180	Eurasia	Bird	<i>Tragopan blythi molesworthi</i>	Western Blyth's tragopan
181	Eurasia	Bird	<i>Tragopan melanocephalus</i>	Western tragopan
182	Eurasia	Bird	<i>Vanellus macropterus</i>	Javanese wattle lapwing

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
157	Y	N	N	Y	C	141,700	1,679,400	91.56
158	N	N	N	Y	C	79,000	309,200	74.46
159	Y	N	Y	Y	B	30,200	3,505,700	99.14
160	N	N	N	Y	B	78,200	306,800	74.50
161	Y	N	N	Y	C	49,000	437,600	88.81
162	Y	N	N	Y	C	11,500	599,000	98.09
163	Y	N	N	Y	C	427,100	2,337,800	81.73
164	N	N	N	Y	C	4,883,900	6,104,800	20.00
165	N	N	N	Y	B	4,563,100	6,509,200	29.90
166	Y	N	N	Y	C	20,800	223,000	90.70
167	Y	N	N	Y	C	1,100	68,800	98.33
168	N	N	N	Y	C	1,667,800	6,560,300	74.58
169	Y	N	Y	Y	B	41,700	2,474,300	98.32
170	Y	N	Y	Y	B	68,800	6,874,800	99.00
171	Y	N	N	Y	C	6.01	36,500	99.98
172	Y	N	N	Y	C	309,400	2,825,400	89.05
173	Y	N	N	Y	C	1,000	1,534,600	99.93
174	Y	N	N	Y	C	23	153,100	99.98
175	N	N	N	Y	B	11,019,000	11,936,000	7.68
176	N	N	N	Y	B	920,000	1,308,500	29.69
177	N	N	N	Y	B	323,700	832,800	61.14
178	Y	Y	N	Y	C	321,800	2,761,200	88.35
179	Y	N	N	Y	C	27,100	179,200	84.88
180	Y	N	N	Y	C	6,300	42,700	85.20
181	Y	N	N	Y	C	23,200	166,700	86.06
182	Y	Y	N	Y	I	6,300	629,200	99.01

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
157	0.16	P	0.61	C	1	12	N	~
158	0.08	P	0.31	P	2	5	N	~
159	0.00	P	0.00	P	3	1	N	1
160	0.39	P	0.40	P	26	43	N	2
161	0.14	P	0.21	P	1	6	N	~
162	0.15	P	0.09	P	1	11	N	~
163	0.58	C	0.63	C	1	2	N	~
164	0.51	C	0.52	C	3	3	N	~
165	0.36	P	0.42	P	4	4	N	1
166	0.14	P	0.37	P	1	1	N	~
167	0.35	P	0.56	C	1	2	N	~
168	0.35	P	0.39	P	8	20	N	~
169	0.00	P	0.00	P	2	4	N	1
170	0.00	P	0.00	P	7	1	N	1
171	0.00	P	0.50	C	1	2	N	~
172	0.16	P	0.26	P	1	8	N	~
173	0.00	P	0.00	P	1	1	Y	~
174	0.00	P	0.00	P	1	1	Y	~
175	0.51	C	0.52	C	2	14	N	1
176	0.56	C	0.58	C	2	2	N	1
177	0.57	C	0.66	C	17	18	N	14
178	0.50	C	0.57	C	14	15	N	~
179	0.36	P	0.54	C	1	1	N	~
180	0.00	P	0.03	P	1	1	N	~
181	0.71	C	0.66	C	1	3	N	~
182	0.00	P	0.17	P	3	1	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
157	~	~	~	N	W
158	~	~	~	~	~
159	2	1	0	N	W
160	24	2	24	~	~
161	~	~	~	S	W
162	~	~	~	N	E
163	~	~	~	N	W
164	~	~	~	~	~
165	3	1	3	~	~
166	~	~	~	S	W
167	~	~	~	S	E
168	~	~	~	~	~
169	1	1	1	S	E
170	6	0	1	S	W
171	~	~	~	S	W
172	~	~	~	N	W
173	~	~	~	N	E
174	~	~	~	S	W
175	1	1	1	~	~
176	2	1	2	~	~
177	3	7	1	~	~
178	~	~	~	N	W
179	~	~	~	N	E
180	~	~	~	S	W
181	~	~	~	N	W
182	~	~	~	S	E

	Reference
157	Mukherjee, 1982; Johnsgard, 1991
158	Brown, 1976
159	Mukherjee, 1982
160	Cadbury, 1980; Mayes and Stowe, 1989
161	Mukherjee, 1982
162	Mukherjee, 1982; Johnsgard, 1991
163	Johnsgard, 1991
164	Johnsgard, 1983
165	Hancock et al., 1992
166	Lovegrove, 1990
167	Mukherjee, 1966
168	Johnsgard, 1991
169	van Balen et al., 1995
170	Johnsgard, 1993
171	Lambert and Woodcock, 1996
172	Hancock et al., 1992
173	Delacour, 1954
174	Delacour, 1954; Johnsgard, 1978
175	Johnsgard, 1983
176	Johnsgard, 1983
177	Johnsgard, 1983
178	Johnsgard, 1991
179	Johnsgard, 1986
180	Johnsgard, 1986
181	Johnsgard, 1986
182	Johnsgard, 1981

	Region	Taxonomic group	Species	Common name
183	Eurasia	Fish	<i>Acipenser sturio</i>	European sturgeon
184	Eurasia	Mammal	<i>Acinonyx jubatus</i>	Indian cheetah
185	Eurasia	Mammal	<i>Ailuropoda melanoleuca</i>	Giant panda
186	Eurasia	Mammal	<i>Antilope cervicapra</i>	Blackbuck
187	Eurasia	Mammal	<i>Bison bonasus</i>	European bison
188	Eurasia	Mammal	<i>Bos gaurus gaurus</i>	Gaur
189	Eurasia	Mammal	<i>Bos sauveli</i>	Kouprey
190	Eurasia	Mammal	<i>Bubalus bubalis</i>	Water buffalo
191	Eurasia	Mammal	<i>Canis lupus</i>	Gray wolf
192	Eurasia	Mammal	<i>Capra falconeri falconeri</i>	Markhor
193	Eurasia	Mammal	<i>Capreolus capreolus</i>	European roe deer
194	Eurasia	Mammal	<i>Capreolus pygargus</i>	Siberian roe deer
195	Eurasia	Mammal	<i>Caprolagus hispidus</i>	Hispid hare
196	Eurasia	Mammal	<i>Castor fiber</i>	European beaver
197	Eurasia	Mammal	<i>Cervus alfredi</i>	Philippine spotted deer
198	Eurasia	Mammal	<i>Cervus dama</i>	Fallow deer
199	Eurasia	Mammal	<i>Cervus duvauceli</i>	Swamp deer
200	Eurasia	Mammal	<i>Cervus elaphus hanguli</i>	Kashmir stag
201	Eurasia	Mammal	<i>Cervus elaphus wallichii</i>	Shou
202	Eurasia	Mammal	<i>Cervus eldi</i>	Brown-antlered deer
203	Eurasia	Mammal	<i>Didermocercus sumatrensis</i>	Sumatran rhino
204	Eurasia	Mammal	<i>Elaphas maximus</i>	Asian elephant
205	Eurasia	Mammal	<i>Equus hemionus</i>	Onager
206	Eurasia	Mammal	<i>Felis temminckii temminckii</i>	Golden cat
207	Eurasia	Mammal	<i>Gulo gulo</i>	Wolverine
208	Eurasia	Mammal	<i>Hemitragus hylocrius</i>	Nilgiri thar

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
183	Y	N	Y	Y	B	1,800	665,400	99.72
184	Y	N	N	Y	C	37,500	2,028,400	98.15
185	Y	N	N	Y	C	34,400	1,830,400	98.12
186	N	N	N	Y	C	1,364,800	3,307,700	58.74
187	Y	N	Y	Y	B	31,000	27,288,600	99.89
188	Y	Y	N	Y	C	270,900	1,944,000	86.07
189	Y	N	N	Y	C	270	139,600	99.80
190	Y	N	N	Y	C	9,000	458,200	98.04
191	N	N	N	Y	B	34,115,800	40,866,100	16.52
192	Y	N	N	Y	C	19,800	331,300	94.03
193	N	N	N	Y	B	5,845,900	6,911,800	15.42
194	N	N	N	Y	C	8,677,900	13,634,800	36.35
195	Y	N	N	Y	C	99	136,100	99.93
196	Y	N	Y	Y	B	1,562,300	11,246,000	86.11
197	Y	Y	N	Y	I	28	38,000	99.93
198	N	N	N	Y	B	2,469,800	7,857,400	68.57
199	Y	Y	N	Y	C	112,500	2,226,300	94.95
200	Y	N	N	Y	C	14,600	500,100	97.08
201	Y	N	N	Y	C	9,400	747,000	98.74
202	Y	N	Y	Y	B	60,400	1,773,100	96.59
203	Y	N	Y	Y	B	58,300	3,375,400	98.27
204	Y	N	Y	Y	B	1,755,400	10,707,600	83.61
205	Y	N	Y	Y	B	1,484,800	13,175,400	88.73
206	Y	N	Y	Y	B	138,600	4,249,500	96.74
207	N	N	N	Y	C	10,761,000	12,919,700	16.71
208	Y	N	N	Y	C	10700	379,200	97.18

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
183	0.00	P	0.55	C	18	2	N	14
184	0.00	P	0.00	P	1	1	N	~
185	0.00	P	0.15	P	1	6	N	~
186	0.70	C	0.76	C	1	4	N	~
187	0.00	P	0.00	P	2	1	Y	1
188	0.48	P	0.55	C	2	9	N	~
189	0.44	P	0.54	C	1	24	N	~
190	0.00	P	0.42	P	1	10	N	~
191	0.51	C	0.53	C	12	11	N	1
192	0.11	P	0.26	P	1	1	N	~
193	0.52	C	0.54	C	2	2	N	~
194	0.56	C	0.63	C	1	1	N	~
195	0.00	P	0.55	C	1	11	N	~
196	0.74	C	0.68	C	8	9	N	1
197	0.52	C	0.50	P	7	6	N	~
198	0.53	C	0.55	C	11	7	N	1
199	0.57	C	0.68	C	3	21	N	~
200	0.86	C	1.00	C	1	1	N	~
201	0.00	P	0.00	P	1	1	N	~
202	0.00	P	0.34	P	2	3	N	1
203	0.00	P	0.23	P	3	13	N	1
204	0.48	P	0.48	P	5	19	N	1
205	0.51	C	0.46	P	3	4	N	1
206	0.00	P	0.59	C	2	5	N	1
207	0.53	C	0.57	C	1	2	N	~
208	0.21	P	0.70	C	1	3	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
183	4	2	0	S	E
184	~	~	~	S	E
185	~	~	~	N	W
186	~	~	~	~	~
187	2	1	0	S	W
188	~	~	~	N	E
189	~	~	~	N	W
190	~	~	~	N	E
191	14	1	10	~	~
192	~	~	~	N	W
193	~	~	~	~	~
194	~	~	~	~	~
195	~	~	~	N	W
196	2	1	0	N	W
197	~	~	~	N	W
198	2	1	2	~	~
199	~	~	~	N	E
200	~	~	~	S	W
201	~	~	~	S	W
202	1	1	1	S	E
203	2	1	2	N	W
204	4	1	3	N	E
205	1	1	0	N	E
206	1	1	1	N	W
207	~	~	~	~	~
208	~	~	~	S	W

	Reference
183	Debus, 1996; Keith and Allardi, 1996
184	Burton et al., 1987
185	Schaller et al., 1985; Laidler, 1992; Stirling, 1993
186	Mukherjee, 1982; Corbet and Hill, 1992
187	Burton et al., 1987
188	Mukherjee, 1982
189	MacKinnon and Mackinnon, 1991
190	Sheshadri, 1969; Mukherjee, 1982
191	Burton et al., 1987
192	Mukherjee, 1966
193	Danilkin and Hewison, 1996
194	Danilkin and Hewison, 1996
195	Bell et al., 1990; Caughley and Gunn, 1996
196	Burton et al., 1987
197	Oliver et al., 1991
198	Burton et al., 1987
199	Mukherjee, 1982
200	Mukherjee, 1966
201	Mukherjee, 1966; Mukherjee, 1982
202	Mukherjee, 1966; Burton et al., 1987
203	Penny, 1988; Khan, 1989; Corbet and Hill, 1992
204	Shoshani and Eisenberg, 1982
205	Burton et al., 1987
206	Mukherjee, 1982
207	Schreiber et al., 1989
208	Mukherjee, 1966; Mukherjee, 1982

	Region	Taxonomic group	Species	Common name
209	Eurasia	Mammal	<i>Hylobates sp.</i>	Gibbon
210	Eurasia	Mammal	<i>Macaca silenus</i>	Lion-tailed macaque
211	Eurasia	Mammal	<i>Marmota bobak</i>	Bobak marmot
212	Eurasia	Mammal	<i>Moschus moschiferus moschiferus</i>	Himalayan musk deer
213	Eurasia	Mammal	<i>Mustela lutreola</i>	European mink
214	Eurasia	Mammal	<i>Panthera leo persica</i>	Indian lion
215	Eurasia	Mammal	<i>Panthera pardus</i>	Leopard
216	Eurasia	Mammal	<i>Panthera tigris</i>	Tiger
217	Eurasia	Mammal	<i>Pongo pygmaeus</i>	Orang-utan
218	Eurasia	Mammal	<i>Presbytis johnii</i>	Nilgiri langur
219	Eurasia	Mammal	<i>Procapra gutturosa</i>	Mongolian gazelle
220	Eurasia	Mammal	<i>Rangifer tarandus</i>	Caribou
221	Eurasia	Mammal	<i>Rhinoceros sondaicus</i>	Javan rhino
222	Eurasia	Mammal	<i>Rhinoceros unicornis</i>	Indian rhino
223	Eurasia	Mammal	<i>Saiga tatarica</i>	Siaga
224	Eurasia	Mammal	<i>Sus barbatus</i>	Bearded pig
225	Eurasia	Mammal	<i>Sus salvanius</i>	Pygmy hog
226	Eurasia	Mammal	<i>Sus verrucosus</i>	Warty pigs
227	Eurasia	Mammal	<i>Tapirus indicus</i>	Malayan tapir
228	Eurasia	Mammal	<i>Tetracerus quadricornis</i>	Fourhorned antelope
229	Eurasia	Mollusk	<i>Margaritifera auricularia</i>	~
230	Eurasia	Reptile	<i>Crocodylus palustris</i>	Marsh crocodile
231	Eurasia	Reptile	<i>Gavialis gangeticus</i>	Gharial
232	Hawaiian Islands	Bird	<i>Branta sandvicensis</i>	Nene
233	Hawaiian Islands	Bird	<i>Corvus tropicus</i>	Hawaiian crow
234	Hawaiian Islands	Bird	<i>Hemignathus lucidus</i>	Nukupuu

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
209	N	N	N	Y	B	3,852,600	5,732,000	32.79
210	Y	N	N	Y	C	19,600	211,500	90.74
211	N	N	N	Y	C	3,672,800	5,719,500	35.78
212	Y	N	N	Y	C	162,500	1,249,100	86.99
213	Y	N	N	Y	C	146,900	6,346,900	97.69
214	Y	N	N	Y	C	20,800	1,420,000	98.53
215	N	N	N	Y	B	8,448,500	11,540,400	26.79
216	N	N	N	Y	B	2,970,300	11,869,300	74.97
217	Y	N	Y	Y	B	390,700	6,284,100	93.78
218	Y	N	N	Y	C	9,200	158,400	94.21
219	N	N	N	Y	C	365,300	1,007,000	63.73
220	N	N	N	Y	B	7,570,200	10,593,000	28.54
221	Y	N	N	Y	C	11,500	2,730,600	99.58
222	Y	N	N	Y	C	93,800	1,072,000	91.25
223	Y	N	N	Y	C	185,900	4,552,300	95.92
224	N	N	N	Y	B	505,300	1,366,800	63.03
225	Y	Y	N	Y	C	110	199,400	99.95
226	Y	Y	N	Y	I	8,300	67,000	87.56
227	N	N	N	Y	B	731,300	1,982,500	63.11
228	N	N	N	Y	C	886,600	1,821,100	51.32
229	Y	N	Y	Y	B	1,800	1,852,300	99.90
230	Y	N	N	Y	C	120,800	6,274,800	98.07
231	Y	Y	N	Y	C	20,800	1,877,300	98.89
232	Y	Y	N	N	I	410	7,100	94.30
233	Y	N	N	N	I	180	6,400	97.22
234	Y	Y	N	N	I	41	4,300	99.03

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
209	0.51	C	0.49	P	4	4	N	1
210	0.57	C	0.57	C	1	6	N	~
211	0.52	C	0.52	C	1	1	N	~
212	0.56	C	0.56	C	1	3	N	~
213	0.00	P	0.00	P	1	1	N	~
214	0.00	P	0.00	P	1	1	N	~
215	0.43	P	0.47	P	3	4	N	1
216	0.55	C	0.51	C	3	13	N	2
217	0.00	P	0.38	P	6	2	N	1
218	0.00	P	0.32	P	1	2	N	~
219	0.69	C	0.75	C	1	1	N	~
220	0.54	C	0.59	C	5	4	N	1
221	0.00	P	0.00	P	1	4	N	~
222	0.27	P	0.37	P	1	4	N	~
223	0.36	P	0.27	P	1	8	N	~
224	0.66	C	0.81	C	3	7	N	1
225	0.00	P	0.00	P	3	4	N	~
226	0.55	C	0.70	C	3	13	N	~
227	0.10	P	0.37	P	3	2	N	1
228	0.67	C	0.83	C	1	2	N	~
229	0.00	P	0.00	P	2	1	N	1
230	0.32	P	0.47	P	1	7	N	~
231	0.29	P	0.65	C	3	4	N	~
232	0.34	P	0.64	C	9	3	N	~
233	0.00	P	0.13	P	1	3	N	~
234	0.68	C	1.00	C	4	2	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
209	3	1	3	~	~
210	~	~	~	S	E
211	~	~	~	~	~
212	~	~	~	N	W
213	~	~	~	S	W
214	~	~	~	S	W
215	1	1	1	~	~
216	4	1	1	~	~
217	4	0	2	S	E
218	~	~	~	N	W
219	~	~	~	~	~
220	4	1	2	~	~
221	~	~	~	S	E
222	~	~	~	S	E
223	~	~	~	N	E
224	2	1	2	~	~
225	~	~	~	S	E
226	~	~	~	N	E
227	3	1	1	~	~
228	~	~	~	~	~
229	1	1	0	S	W
230	~	~	~	N	W
231	~	~	~	S	E
232	~	~	~		
233	~	~	~	S	W
234	~	~	~		

	Reference
209	Goodall et al., 1993
210	Mukherjee, 1982; Heltne, 1985
211	Burton et al., 1987
212	Mukherjee, 1966
213	Schreiber, 1989
214	Sheshadri, 1969
215	Burton et al., 1987
216	Perry, 1965; Barnes, 1994
217	Rodman, 1988; Goodall et al., 1993
218	Mukherjee, 1966; Mukherjee, 1982
219	Lhagvasuren and Milner-Gulland, 1997
220	Whitehead, 1972; Syroechkovskii, 1995
221	Penny, 1988; Khan, 1989; Corbet and Hill, 1992
222	Penny, 1988; Khan, 1989; Corbet and Hill, 1992
223	Sokolov, 1974
224	Oliver, 1993
225	Mukherjee, 1966; Oliver, 1993
226	Oliver, 1993
227	M. Ashley, 1994 personal communication
228	Mukherjee, 1982
229	Altaba, 1990
230	Mukherjee, 1982
231	Mukherjee, 1982
232	Kear and Berger, 1980; Scott et al., 1986; Michael Scott, 1995 personal communication
233	Duckworth et al., 1992; Michael Scott, 1995 personal communication
234	Scott et al., 1986; Michael Scott, 1995 personal communication

	Region	Taxonomic group	Species	Common name
235	Hawaiian Islands	Bird	<i>Hemignathus munori</i>	Akiapolaau
236	Hawaiian Islands	Bird	<i>Loxops coccinea</i>	Hawaiian akepa
237	Hawaiian Islands	Bird	<i>Loxops coccinea</i>	Maui akepa
238	Hawaiian Islands	Bird	<i>Melamprosops phaesoma</i>	Poo Uli
239	Hawaiian Islands	Bird	<i>Moho brachicatus</i>	Kauai Oo
240	Hawaiian Islands	Bird	<i>Moho nobilis</i>	Hawaii Oo
241	Hawaiian Islands	Bird	<i>Myadestes langiensis rutha</i>	Molokai thrush
242	Hawaiian Islands	Bird	<i>Myadestes palmeri</i>	Puaiohi
243	Hawaiian Islands	Bird	<i>Myadestes myadestinus</i>	Kamao
244	Hawaiian Islands	Bird	<i>Oreomystis bairdi</i>	Kauai creeper
245	Hawaiian Islands	Bird	<i>Oreomystis mana</i>	Hawaii creeper
246	Hawaiian Islands	Bird	<i>Palmeria dolei</i>	Crested honey creeper
247	Hawaiian Islands	Bird	<i>Paroreomyza montana</i>	Maui creeper
248	Hawaiian Islands	Bird	<i>Pseudonestor xanthophrys</i>	Maui parrotbill
249	Hawaiian Islands	Bird	<i>Psittirostra bailleui</i>	Palila
250	Hawaiian Islands	Bird	<i>Psittirostra psittacea</i>	Ou
251	Hawaiian Islands	Mollusk	<i>Achatinella apexfulva</i>	~
252	Hawaiian Islands	Mollusk	<i>Achatinella bellula</i>	~
253	Hawaiian Islands	Mollusk	<i>Achatinella bulmoides</i>	~
254	Hawaiian Islands	Mollusk	<i>Achatinella byronii</i>	~
255	Hawaiian Islands	Mollusk	<i>Achatinella concavospira</i>	~
256	Hawaiian Islands	Mollusk	<i>Achatinella curta</i>	~
257	Hawaiian Islands	Mollusk	<i>Achatinella decipiens</i>	~
258	Hawaiian Islands	Mollusk	<i>Achatinella fulgens</i>	~
259	Hawaiian Islands	Mollusk	<i>Achatinella fuscobasis</i>	~
260	Hawaiian Islands	Mollusk	<i>Achatinella leucorraphe</i>	~

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
235	Y	N	N	N	I	760	11,000	93.05
236	Y	N	N	N	I	850	7,200	88.19
237	Y	N	N	N	I	7.03	421	98.33
238	Y	Y	N	N	I	10	1,200	99.16
239	Y	N	N	N	I	20	1,500	98.66
240	Y	N	N	N	I	27	11,000	99.76
241	Y	N	N	N	I	16	671	97.65
242	Y	N	N	N	I	160	3,900	95.89
243	Y	Y	N	N	I	19	1,200	98.42
244	Y	N	N	N	I	300	500	94.02
245	Y	N	N	N	I	1,100	7,300	84.92
246	Y	Y	N	N	I	76	1,900	95.90
247	Y	Y	N	N	I	120	2,800	95.73
248	Y	Y	N	N	I	62	2,800	97.79
249	Y	Y	N	N	I	97	6,100	98.40
250	Y	Y	N	N	I	110	12,000	99.09
251	Y	N	N	N	I	24	800	97.04
252	Y	N	N	N	I	5.71	197	97.10
253	Y	N	N	N	I	5.18	772	99.33
254	Y	N	N	N	I	1.86	811	99.77
255	Y	N	N	N	I	7.91	247	96.80
256	Y	N	N	N	I	7.00	1,300	99.47
257	Y	N	N	N	I	6.39	103	93.79
258	Y	N	N	N	I	0.78	167	99.53
259	Y	N	N	N	I	7.38	74	90.08
260	Y	N	N	N	I	3.72	327	98.86

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
235	0.13	P	0.43	P	1	4	N	~
236	0.26	P	0.57	C	1	5	N	~
237	0.80	C	1.00	C	1	2	N	~
238	0.99	C	1.00	C	2	1	N	~
239	1.00	C	1.00	C	1	1	N	~
240	0.00	P	0.69	C	1	1	N	~
241	0.63	C	0.68	C	1	2	N	~
242	0.76	C	0.94	C	1	3	N	~
243	0.94	C	1.00	C	2	1	N	~
244	0.78	C	0.85	C	1	2	N	~
245	0.26	P	0.61	C	1	4	N	~
246	0.00	P	0.18	P	2	1	N	~
247	0.23	P	0.45	P	3	2	N	~
248	0.50	C	0.64	C	3	1	N	~
249	0.18	P	0.47	P	8	1	N	~
250	0.55	C	0.56	C	6	2	N	~
251	0.03	P	0.30	P	1	2	N	~
252	0.52	C	0.65	C	1	2	N	~
253	0.00	P	0.00	P	1	1	N	~
254	0.71	C	1.00	C	1	1	N	~
255	0.54	C	0.59	C	1	1	N	~
256	0.72	C	0.57	C	1	2	N	~
257	0.57	C	0.81	C	1	2	N	~
258	0.00	P	0.88	C	1	1	N	~
259	0.71	C	0.91	C	1	2	N	~
260	0.64	C	1.00	C	1	1	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
235	~	~	~	N	E
236	~	~	~	N	E
237	~	~	~	S	W
238	~	~	~	S	E
239	~	~	~	N	W
240	~	~	~	N	E
241	~	~	~	S	E
242	~	~	~	N	W
243	~	~	~	S	W
244	~	~	~	N	W
245	~	~	~	S	W
246	~	~	~	S	E
247	~	~	~	~	~
248	~	~	~	~	~
249	~	~	~	~	~
250	~	~	~	~	~
251	~	~	~	S	E
252	~	~	~	S	E
253	~	~	~	S	E
254	~	~	~	S	E
255	~	~	~	N	W
256	~	~	~	S	E
257	~	~	~	N	W
258	~	~	~	S	E
259	~	~	~	S	E
260	~	~	~	N	W

	Reference
235	Scott et al., 1986; Michael Scott, 1995 personal communication
236	Scott et al., 1986; Michael Scott, 1995 personal communication
237	Scott et al., 1986; Michael Scott, 1995 personal communication
238	Scott et al., 1986; Michael Scott, 1995 personal communication
239	Scott et al., 1986; Michael Scott, 1995 personal communication
240	Scott et al., 1986; Michael Scott, 1995 personal communication
241	Scott et al., 1986; Michael Scott, 1995 personal communication
242	Scott et al., 1986; Michael Scott, 1995 personal communication
243	Scott et al., 1986; Michael Scott, 1995 personal communication
244	Scott et al., 1986; Michael Scott, 1995 personal communication
245	Scott et al., 1986; Michael Scott, 1995 personal communication
246	Scott et al., 1986; Michael Scott, 1995 personal communication
247	Scott et al., 1986; Michael Scott, 1995 personal communication
248	Scott et al., 1986; Michael Scott, 1995 personal communication
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251	U.S. Fish and Wildlife Service, 1993
252	U.S. Fish and Wildlife Service, 1993
253	U.S. Fish and Wildlife Service, 1993
254	U.S. Fish and Wildlife Service, 1993
255	U.S. Fish and Wildlife Service, 1993
256	U.S. Fish and Wildlife Service, 1993
257	U.S. Fish and Wildlife Service, 1993
258	U.S. Fish and Wildlife Service, 1993
259	U.S. Fish and Wildlife Service, 1993
260	U.S. Fish and Wildlife Service, 1993

	Region	Taxonomic group	Species	Common name
261	Hawaiian Islands	Mollusk	<i>Achatinella lila</i>	~
262	Hawaiian Islands	Mollusk	<i>Achatinella livida</i>	~
263	Hawaiian Islands	Mollusk	<i>Achatinella lorata</i>	~
264	Hawaiian Islands	Mollusk	<i>Achatinella mustelina</i>	~
265	Hawaiian Islands	Mollusk	<i>Achatinella phaeozona</i>	~
266	Hawaiian Islands	Mollusk	<i>Achatinella pulcherrima</i>	~
267	Hawaiian Islands	Mollusk	<i>Achatinella pupukanioe</i>	~
268	Hawaiian Islands	Mollusk	<i>Achatinella sowerbyana</i>	~
269	Hawaiian Islands	Mollusk	<i>Achatinella turgida</i>	~
270	Hawaiian Islands	Mollusk	<i>Achatinella viridans</i>	~
271	Hawaiian Islands	Plant	<i>Argyroxiphium sandwicense sandwicense</i>	Mauna key silversword
272	Hawaiian Islands	Plant	<i>Bidens wiebkei</i>	Ko'oko'olau
273	Hawaiian Islands	Plant	<i>Brighamia rockii</i>	Po'e
274	Hawaiian Islands	Plant	<i>Canavalia molokaiensis</i>	`Awikiwiki
275	Hawaiian Islands	Plant	<i>Cyanea mannii</i>	~
276	Hawaiian Islands	Plant	<i>Cyanea procera</i>	~
277	Hawaiian Islands	Plant	<i>Hedyotis mannii</i>	~
278	Hawaiian Islands	Plant	<i>Hibiscus arnottianus immaculatus</i>	Koki'o ke'oke'o
279	Hawaiian Islands	Plant	<i>Melicope reflexa</i>	Alani
280	Hawaiian Islands	Plant	<i>Phyllostegia mannii</i>	~
281	Hawaiian Islands	Plant	<i>Pritchardia munroi</i>	Loulu
282	Hawaiian Islands	Plant	<i>Schiedea lydgatei</i>	~
283	Hawaiian Islands	Plant	<i>Silene alexandri</i>	~
284	Hawaiian Islands	Plant	<i>Silene lanceolata</i>	~
285	Hawaiian Islands	Plant	<i>Stenogyne bifida</i>	~
286	Hawaiian Islands	Plant	<i>Vicia menziesii</i>	~

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
261	Y	Y	N	N	I	12	225	94.71
262	Y	N	N	N	I	11	1,900	99.44
263	Y	N	N	N	I	3.87	542	99.29
264	Y	Y	N	N	I	110	607	81.80
265	Y	Y	N	N	I	1.18	155	99.24
266	Y	N	N	N	I	1.90	1,000	99.81
267	Y	N	N	N	I	10	183	94.28
268	Y	N	N	N	I	76	100	92.57
269	Y	N	N	N	I	2.32	844	99.73
270	Y	N	N	N	I	8.18	213	96.16
271	Y	N	N	N	I	2.16	193	98.88
272	Y	N	N	N	I	5.24	144	96.36
273	Y	N	N	N	I	6.95	68	89.76
274	Y	N	N	N	I	5.79	119	95.15
275	Y	N	N	N	I	5.34	76	93.00
276	Y	N	N	N	I	2.58	19	86.14
277	Y	Y	N	N	I	22	111	80.16
278	Y	N	N	N	I	2.02	55	96.31
279	Y	N	N	N	I	1.81	107	98.31
280	Y	N	N	N	I	2.23	82	97.26
281	Y	N	N	N	I	1.19	118	99.00
282	Y	N	N	N	I	2.13	69	96.92
283	Y	N	N	N	I	3.18	25	87.31
284	N	N	N	N	I	69	266	74.05
285	Y	N	N	N	I	0.80	124	99.35
286	Y	Y	N	N	I	1.54	201	99.23

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
261	0.67	C	0.81	C	2	4	N	~
262	0.00	P	0.00	P	1	1	N	~
263	0.00	P	0.48	P	1	1	N	~
264	0.56	C	0.68	C	3	6	N	~
265	0.00	P	0.54	C	3	1	N	~
266	1.00	C	1.00	C	1	1	N	~
267	0.77	C	0.94	C	1	2	N	~
268	0.59	C	0.96	C	1	1	N	~
269	1.00	C	1.00	C	1	1	N	~
270	0.30	P	0.66	C	1	1	N	~
271	0.48	P	0.55	C	1	7	N	~
272	0.00	P	0.08	P	1	2	N	~
273	0.27	P	0.39	P	1	3	N	~
274	0.25	P	0.43	P	1	6	N	~
275	0.82	C	0.92	C	1	9	N	~
276	0.88	C	1.00	C	1	3	N	~
277	0.74	C	0.80	C	2	2	N	~
278	0.25	P	0.36	P	1	3	N	~
279	1.00	C	1.00	C	1	2	N	~
280	0.59	C	0.59	C	1	2	N	~
281	0.86	C	1.00	C	1	1	N	~
282	0.87	C	0.97	C	1	4	N	~
283	0.96	C	1.00	C	1	1	N	~
284	0.96	C	1.00	C	1	1	N	~
285	0.00	P	0.26	P	1	1	N	~
286	0.00	P	0.31	P	10	1	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
261	~	~	~	N	W
262	~	~	~	N	E
263	~	~	~	S	E
264	~	~	~	N	W
265	~	~	~	S	E
266	~	~	~	N	W
267	~	~	~	S	E
268	~	~	~	S	E
269	~	~	~	N	W
270	~	~	~	S	E
271	~	~	~	S	W
272	~	~	~	N	E
273	~	~	~	N	W
274	~	~	~	S	W
275	~	~	~	S	W
276	~	~	~	N	W
277	~	~	~	~	~
278	~	~	~	N	E
279	~	~	~	S	E
280	~	~	~	N	W
281	~	~	~	S	W
282	~	~	~	N	W
283	~	~	~	N	W
284	~	~	~	~	~
285	~	~	~	S	W
286	~	~	~	S	E

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262	U.S. Fish and Wildlife Service, 1993
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264	U.S. Fish and Wildlife Service, 1993
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271	Powell, 1994
272	U.S. Fish and Wildlife Service, 1996
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276	U.S. Fish and Wildlife Service, 1996
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280	U.S. Fish and Wildlife Service, 1996
281	U.S. Fish and Wildlife Service, 1996
282	U.S. Fish and Wildlife Service, 1996
283	U.S. Fish and Wildlife Service, 1996
284	U.S. Fish and Wildlife Service, 1996
285	U.S. Fish and Wildlife Service, 1996
286	Warshauer and Jacobs, 1982

	Region	Taxonomic group	Species	Common name
287	Mariana Islands	Bird	<i>Aerodramus vanikorensis</i>	Vanikoro swiftlet
288	Mariana Islands	Bird	<i>Corvus kubaryi</i>	Mariana crow
289	Mariana Islands	Bird	<i>Halcyon cinnamomina</i>	Micronesian kingfisher
290	Mariana Islands	Bird	<i>Myiagra freycineti</i>	Guam broadbill
291	Mariana Islands	Bird	<i>Rallus owstoni</i>	Guam rail
292	Mariana Islands	Bird	<i>Zosterops conspicillata</i>	Bridled white-eye
293	Mariana Islands	Mammal	<i>Pteropus mariannus mariannus</i>	Guam Marianna fruit bat
294	Mariana Islands	Mammal	<i>Pteropus tokudae</i>	Little Mariana fruit bat
295	Miscellaneous islands	Bird	<i>Agelaius xanthomus</i>	Yellow shouldered blackbird
296	Miscellaneous islands	Bird	<i>Amazona dufresniana</i>	Red-browed amazon
297	Miscellaneous islands	Bird	<i>Amazona versicolor</i>	St Lucia parrot
298	Miscellaneous islands	Bird	<i>Amazona vittata</i>	Puerto Rico parrot
299	Miscellaneous islands	Bird	<i>Caprimulgus noctitherus</i>	Puerto Rican whip-poor-whil
300	Miscellaneous islands	Bird	<i>Copsychus sechellarum</i>	Seychelles magpie robin
301	Miscellaneous islands	Bird	<i>Falco punctatus</i>	Mauritius kestrel
302	Miscellaneous islands	Bird	<i>Haliaeetus vociferoides</i>	Madagascar sea eagle
303	Miscellaneous islands	Bird	<i>Synthliboramphus antiquus</i>	Ancient murrelet
304	Miscellaneous islands	Bird	<i>Tricholimnas sylvestris</i>	Lord Howe woodhen
305	Miscellaneous islands	Plant	<i>Commidendrum robustum</i>	St Helena gumwood
306	Miscellaneous islands	Plant	<i>Trochetiopsis erythroxylon</i>	St Helena ebony
307	Miscellaneous islands	Reptile	<i>Geochelone elephantus</i>	Galapagos tortoise
308	New Zealand	Bird	<i>Anas aucklandica</i>	Brown teal
309	New Zealand	Bird	<i>Apteryx australis</i>	Brown kiwi
310	New Zealand	Bird	<i>Apteryx haastii</i>	Great spotted kiwi
311	New Zealand	Bird	<i>Apteryx owenii</i>	Little spotted kiwi
312	New Zealand	Bird	<i>Callaeas cinerea</i>	Kokako

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
287	N	N	N	N	I	240	876	72.36
288	Y	Y	N	N	I	160	634	75.35
289	Y	N	N	N	I	26	539	95.24
290	Y	N	N	N	I	69	539	87.13
291	Y	N	N	N	I	33	539	93.82
292	Y	N	N	N	I	55	539	89.81
293	N	N	N	N	I	150	540	72.02
294	Y	N	N	N	I	0.31	540	99.94
295	Y	N	N	N	I	260	4,300	93.99
296	Y	N	N	N	C	26,500	140,500	81.14
297	Y	N	N	N	I	48	615	92.19
298	Y	Y	N	N	I	270	9,000	97.07
299	Y	Y	N	N	I	28	2,100	98.65
300	Y	Y	N	N	I	1.69	259	99.35
301	Y	N	N	N	I	49	854	94.24
302	Y	N	N	N	I	7,500	91,100	91.75
303	Y	Y	N	N	I	1.04	9	88.78
304	Y	N	N	N	I	0.16	15	98.89
305	Y	N	N	N	I	0.19	774	99.98
306	Y	N	N	N	I	0.10	502	99.98
307	Y	Y	N	N	I	1,700	7,400	76.49
308	Y	Y	N	N	I	2,900	268,700	98.91
309	Y	Y	N	N	I	47,100	268,500	82.47
310	Y	N	N	N	I	6,100	151,700	96.01
311	Y	Y	N	N	I	400	231,400	99.83
312	Y	Y	N	N	I	8,200	239,300	96.58

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
287	0.03	P	0.30	P	4	2	N	~
288	0.04	P	0.26	P	2	2	N	~
289	0.27	P	0.53	C	1	1	N	~
290	0.19	P	0.36	P	1	1	N	~
291	0.18	P	0.36	P	1	2	N	~
292	0.13	P	0.27	P	1	1	N	~
293	0.51	C	0.47	P	1	2	N	~
294	0.00	P	0.00	P	1	1	Y	~
295	0.01	P	0.42	P	1	2	N	~
296	0.55	C	0.56	C	1	1	N	~
297	1.00	C	1.00	C	1	1	N	~
298	0.20	P	0.44	P	3	1	N	~
299	0.00	P	0.00	P	2	2	N	~
300	0.00	P	0.00	P	8	1	N	~
301	0.83	C	0.99	C	1	1	N	~
302	0.64	C	0.83	C	1	1	N	~
303	0.51	C	0.57	C	4	3	N	~
304	0.98	C	1.00	C	1	2	N	~
305	0.52	C	0.33	P	1	6	N	~
306	0.00	P	0.67	C	1	3	N	~
307	0.50	C	0.69	C	7	14	N	~
308	0.00	P	0.00	P	5	2	N	2
309	0.24	P	0.41	P	3	10	N	2
310	0.18	P	0.12	P	1	3	N	~
311	0.00	P	0.00	P	3	2	N	2
312	0.34	P	0.54	C	5	13	N	2

	Historical island	Extant mainland	Extant island	N/S	W/E
287	~	~	~	~	~
288	~	~	~	N	E
289	~	~	~	N	E
290	~	~	~	N	E
291	~	~	~	N	E
292	~	~	~	N	E
293	~	~	~	~	~
294	~	~	~	N	E
295	~	~	~	S	W
296	~	~	~	N	W
297	~	~	~	S	W
298	~	~	~	N	E
299	~	~	~	S	W
300	~	~	~	N	E
301	~	~	~	S	E
302	~	~	~	N	W
303	~	~	~	N	E
304	~	~	~	N	E
305	~	~	~	S	W
306	~	~	~	S	W
307	~	~	~	~	~
308	3	1	1	N	E
309	1	2	1	N	E
310	~	~	~	N	E
311	1	1	1	N	E
312	3	1	0	N	E

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305	Cronk, 1986b
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307	Macfarland et al., 1974
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309	Peat, 1990
310	Peat, 1990
311	Mills and Williams, 1979; Fuller, 1990; Peat, 1990
312	Mills and Williams, 1979; Hay et al., 1985; Gaze, 1994

	Region	Taxonomic group	Species	Common name
313	New Zealand	Bird	<i>Gallirallus australis greyi</i>	North Island weka
314	New Zealand	Bird	<i>Himantopus novaezealandiae</i>	Black stilt
315	New Zealand	Bird	<i>Hymenolaimus malacorhynchos</i>	Blue duck
316	New Zealand	Bird	<i>Mohoua ochrocephala</i>	Yellowhead
317	New Zealand	Bird	<i>Nestor meridionalis</i>	Kaka
318	New Zealand	Bird	<i>Notiomystis cincta</i>	Stitchbird
319	New Zealand	Bird	<i>Notornis mantelli</i>	Takahe
320	New Zealand	Bird	<i>Philesturnus carunculatus</i>	Saddleback
321	New Zealand	Bird	<i>Strigops habroptilus</i>	Kakapo
322	North America	Amphibian	<i>Bufo hemiophrys baxteri</i>	Wyoming toad
323	North America	Amphibian	<i>Bufo houstonensis</i>	Houston toad
324	North America	Amphibian	<i>Rana aurora draytonii</i>	California red-legged frog
325	North America	Arthropod	<i>Gryllotalpa major</i>	Prairie mole cricket
326	North America	Arthropod	<i>Nicrophorus americana</i>	American burying beetle
327	North America	Bird	<i>Ara militaris</i>	Military macaw
328	North America	Bird	<i>Athene cunicularia</i>	Burrowing owl
329	North America	Bird	<i>Bonasa umellus</i>	Ruffed grouse
330	North America	Bird	<i>Buteo swainsoni</i>	Swainson's hawk
331	North America	Bird	<i>Camephilus principalis</i>	Ivory-billed woodpecker
332	North America	Bird	<i>Campephilus imperialis</i>	Imperial woodpecker
333	North America	Bird	<i>Centrocercus urophasianus</i>	Sage grouse
334	North America	Bird	<i>Cygnus buccinator</i>	Trumpeter swan
335	North America	Bird	<i>Dendroica kirtlandii</i>	Kirtland's warbler
336	North America	Bird	<i>Ectopistes migratorius</i>	Passenger pigeon
337	North America	Bird	<i>Elanoides forficatus</i>	Swallow-tailed kite
338	North America	Bird	<i>Falco femoralis</i>	Aplomado falcon

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
313	Y	Y	N	N	I	6,400	114,800	94.41
314	Y	Y	N	N	I	9,100	174,600	94.81
315	N	N	N	N	I	87,200	266,800	67.33
316	Y	N	N	N	I	35,100	151,700	76.90
317	N	N	N	N	I	101,200	268,700	62.13
318	Y	Y	N	N	I	14	114,800	99.99
319	Y	Y	N	N	I	6,700	266,500	97.47
320	Y	Y	N	N	I	220	229,200	99.91
321	Y	Y	N	N	I	6,800	268,700	97.47
322	Y	N	N	Y	C	0.65	77	99.16
323	Y	N	N	Y	C	190	17,100	98.87
324	Y	N	N	Y	C	320	166,900	99.81
325	Y	Y	N	Y	C	8,000	380,100	97.88
326	Y	N	N	Y	C	72,500	3,042,700	97.62
327	Y	N	N	Y	C	88,000	392,400	77.57
328	N	N	N	Y	C	6,505,700	6,791,500	4.21
329	N	N	N	Y	B	6,787,600	7,850,700	13.54
330	N	N	N	Y	C	4,599,100	4,913,500	6.40
331	Y	N	Y	Y	B	250	2,904,800	99.99
332	Y	N	N	Y	C	4,200	74,000	94.33
333	N	N	N	Y	C	845,100	1,508,800	43.99
334	Y	N	N	Y	C	319,900	5,068,700	93.69
335	Y	N	N	Y	C	1,400	87,300	98.41
336	Y	N	N	Y	C	970	858,400	99.89
337	N	N	N	Y	C	882,400	2,511,100	64.86
338	N	N	N	Y	C	1,871,400	2,314,100	19.13

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
313	0.10	P	0.60	C	2	6	N	1
314	0.93	C	1.00	C	2	1	N	~
315	0.52	C	0.63	C	3	2	N	2
316	0.32	P	0.39	P	1	3	N	1
317	0.51	C	0.59	C	5	6	N	2
318	0.00	P	0.00	P	3	1	N	1
319	0.17	P	0.45	P	2	1	N	~
320	0.00	P	0.00	P	6	2	N	2
321	0.00	P	0.03	P	3	2	N	~
322	0.00	P	0.00	P	1	1	N	~
323	0.00	P	0.03	P	1	4	N	~
324	0.14	P	0.27	P	1	74	N	~
325	0.03	P	0.58	C	3	11	N	~
326	0.02	P	0.45	P	1	3	N	~
327	0.01	P	0.34	P	1	1	N	~
328	0.51	C	0.52	C	2	2	N	~
329	0.50	C	0.51	C	5	7	N	1
330	0.51	C	0.53	C	5	5	N	~
331	0.00	P	0.00	P	2	2	Y	1
332	0.78	C	0.89	C	1	3	Y	~
333	0.57	C	0.66	C	1	9	N	~
334	0.04	P	0.18	P	1	7	N	~
335	0.89	C	0.95	C	1	7	N	~
336	0.00	P	0.00	P	1	1	Y	~
337	0.16	P	0.37	P	1	11	N	~
338	0.51	C	0.51	C	1	1	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
313	1	1	1	N	E
314	~	~	~	S	W
315	1	2	0	~	~
316	1	1	1	S	W
317	3	2	3	~	~
318	2	0	1	N	W
319	~	~	~	S	W
320	4	0	2	S	W
321	~	~	~	S	W
322	~	~	~	S	W
323	~	~	~	S	E
324	~	~	~	S	W
325	~	~	~	N	E
326	~	~	~	S	W
327	~	~	~	S	E
328	~	~	~	~	~
329	1	1	1	~	~
330	~	~	~	~	~
331	1	0	2	S	E
332	~	~	~	N	W
333	~	~	~	~	~
334	~	~	~	N	W
335	~	~	~	N	E
336	~	~	~	S	W
337	~	~	~	~	~
338	~	~	~	~	~

Reference	
313	Graeme and Graeme, 1995
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317	Gaze, 1994
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319	Lavers and Mills, 1984; Gaze, 1994
320	Mills and Williams, 1979; Gaze, 1994
321	Mills and Williams, 1979; Best and Powlesland, 1986; Gaze, 1994; Lloyd and Powlesland, 1994
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323	U.S. Fish and Wildlife Service, 1984a
324	Jennings, 1995
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329	Davis, 1970
330	Johnsgard, 1990
331	Tanner, 1942; Bent, 1964; Short, 1982
332	Howell and Webb, 1995
333	Johnsgard, 1983
334	Palmer, 1976
335	Walkinshaw, 1983
336	Schorger, 1955; Michael Scott, 1995 personal communication
337	Palmer, 1988; Johnsgard, 1990
338	Johnsgard, 1991

	Region	Taxonomic group	Species	Common name
339	North America	Bird	<i>Falco peregrinus</i>	Peregrine falcon
340	North America	Bird	<i>Gavia immer</i>	Common loon
341	North America	Bird	<i>Grus americana</i>	Whooping crane
342	North America	Bird	<i>Gymnogyps californianus</i>	California condor
343	North America	Bird	<i>Haliaeetus leucocephalus</i>	Bald eagle
344	North America	Bird	<i>Meleagris gallopore</i>	Wild turkey
345	North America	Bird	<i>Philohela minor</i>	American woodcock
346	North America	Bird	<i>Tympanuchus cupido attwateri</i>	Attwater's prairie chicken
347	North America	Bird	<i>Tympanuchus cupido pinnatus</i>	Pinnated grouse
348	North America	Bird	<i>Tympanuchus cupido cupido</i>	Heath hen
349	North America	Bird	<i>Tympanuchus phasianellus</i>	Sharp-tailed grouse
350	North America	Bird	<i>Vermivora bachmanii</i>	Bachman's warbler
351	North America	Bird	<i>Vireo atricapillus</i>	Black-capped vireo
352	North America	Fish	<i>Cycleptus elongatus</i>	Blue sucker
353	North America	Fish	<i>Cyprinella monacha</i>	Spotfin chub
354	North America	Fish	<i>Notropis girardi</i>	Arkansas River shiner
355	North America	Fish	<i>Poeciliopsis occidentalis</i>	Sonoran topminnow
356	North America	Mammal	<i>Alces alces</i>	Moose
357	North America	Mammal	<i>Antilocapra americana</i>	Pronghorn
358	North America	Mammal	<i>Bison bison</i>	Bison
359	North America	Mammal	<i>Canis lupus</i>	Gray wolf
360	North America	Mammal	<i>Canis rufus</i>	Red wolf
361	North America	Mammal	<i>Cervus elaphus</i>	Wapiti
362	North America	Mammal	<i>Cynomys parvidens</i>	Utah prairie dog
363	North America	Mammal	<i>Dipodomys ingens</i>	Giant kangaroo rat
364	North America	Mammal	<i>Felis concolor</i>	Puma

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
339	N	N	N	Y	B	9,177,600	17,041,500	46.15
340	N	N	N	Y	B	8,656,200	10,738,700	19.39
341	Y	Y	N	Y	C	48,900	624,400	92.16
342	Y	N	N	Y	C	62,400	4,283,700	98.54
343	N	N	N	Y	B	4,902,200	13,798,900	64.47
344	N	N	N	Y	C	1,748,900	4,874,000	64.12
345	N	N	N	Y	B	2,576,000	3,322,100	22.46
346	Y	N	Y	Y	B	2,000	36,400	94.55
347	Y	N	N	Y	C	211,300	2,876,000	92.65
348	Y	N	Y	Y	B	260	109,000	99.76
349	N	N	N	Y	C	4,501,100	6,487,500	30.62
350	Y	N	N	Y	C	500	755,300	99.93
351	N	N	N	Y	C	124,300	338,500	63.29
352	N	N	N	Y	C	698,400	1,921,300	63.65
353	Y	N	N	Y	C	630	82,400	99.24
354	N	N	N	Y	C	61,800	236,500	73.87
355	N	N	N	Y	C	109,200	269,900	59.53
356	N	N	N	Y	C	3,413,300	7,986,800	57.26
357	Y	N	N	Y	C	1,129,500	4,913,600	77.01
358	Y	N	N	Y	C	750	6,759,300	99.99
359	N	N	N	Y	C	10,207,600	17,603,500	42.01
360	Y	N	N	Y	C	11100	1,778,200	99.37
361	Y	N	Y	Y	B	1,337,300	7,554,000	82.30
362	N	N	N	Y	C	4,300	10,700	59.82
363	Y	Y	N	Y	C	12	6,000	99.80
364	N	N	N	Y	B	5,677,400	10,947,800	48.14

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
339	0.13	P	0.38	P	26	42	N	1
340	0.42	P	0.50	C	17	16	N	1
341	0.00	P	0.28	P	3	1	N	~
342	0.15	P	0.41	P	1	1	N	~
343	0.01	P	0.29	P	16	24	N	1
344	0.51	C	0.57	C	2	25	N	~
345	0.53	C	0.53	C	3	3	N	1
346	0.11	P	0.60	C	3	6	N	1
347	0.63	C	0.80	C	1	15	N	~
348	0.00	P	0.00	P	2	1	Y	1
349	0.52	C	0.48	P	1	17	N	~
350	0.00	P	0.00	P	1	1	N	~
351	0.27	P	0.36	P	1	2	N	~
352	0.50	C	0.40	P	1	6	N	~
353	0.33	P	0.47	P	1	17	N	~
354	0.13	P	0.34	P	1	2	N	~
355	0.33	P	0.42	P	1	1	N	~
356	0.56	C	0.65	C	1	4	N	~
357	0.66	C	0.74	C	1	69	N	~
358	0.00	P	0.00	P	1	1	N	~
359	0.17	P	0.41	P	34	34	N	~
360	0.00	P	0.00	P	1	1	N	~
361	0.54	C	0.62	C	2	9	N	1
362	0.35	P	0.52	C	15	17	N	~
363	0.49	P	0.41	P	3	28	N	~
364	0.25	P	0.45	P	2	3	N	1

	Historical island	Extant mainland	Extant island	N/S	W/E
339	25	1	22	~	~
340	15	1	14	~	~
341	~	~	~	N	W
342	~	~	~	N	W
343	15	1	7	~	~
344	~	~	~	~	~
345	2	1	2	~	~
346	1	1	0	S	W
347	~	~	~	S	W
348	1	0	1	N	E
349	~	~	~	~	~
350	~	~	~	N	W
351	~	~	~	~	~
352	~	~	~	~	~
353	~	~	~	N	E
354	~	~	~	~	~
355	~	~	~	~	~
356	~	~	~	~	~
357	~	~	~	N	E
358	~	~	~	S	W
359	~	~	~	~	~
360	~	~	~	S	W
361	1	1	1	N	W
362	~	~	~	~	~
363	~	~	~	S	E
364	1	1	1	~	~

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339	Johnsgard, 1992
340	McIntyre, 1988
341	Ellis et al., 1996; Michael Scott, 1995 personal communication
342	Koford, 1953; Easton, 1964; U.S. Fish and Wildlife Service, 1984b; Palmer, 1988; David Steadman, 1997 person
343	Grossman and Hamlet, 1964; Gerrard and Bortolotti, 1988
344	Hewitt, 1967
345	Mendall and Aldous, 1943
346	U.S. Fish and Wildlife Service, 1991b
347	Johnsgard, 1983
348	Michael Scott, 1995 personal communication
349	Johnsgard, 1983
350	Hamel, 1988
351	Grzybowski, 1995
352	U.S. Fish and Wildlife Service, 1993c
353	Walsh et al., 1995
354	Larson et al., 1991
355	Meffe et al., 1983
356	Peterson, 1955; Hall, 1981
357	Yoakum, 1980; Hall, 1981
358	Park, 1969; Rorabacher, 1970; McHugh, 1972; Banfield, 1974; Hall, 1981
359	Mech, 1974; Hummel and Pettigrew, 1991
360	National Geographic Society, 1995
361	Murie, 1951; Hall, 1981; Thomas and Toweill, 1982; Bauer, 1995
362	Utah Division of Wildlife Resources and U.S. Fish and Wildlife Service, 1991
363	Williams and Kilburn, 1991
364	Hummel and Pettigrew, 1991; Savage, 1993

	Region	Taxonomic group	Species	Common name
365	North America	Mammal	<i>Gulo gulo</i>	Wolverine
366	North America	Mammal	<i>Lutra canadensis</i>	River otter
367	North America	Mammal	<i>Martes americana</i>	Martin
368	North America	Mammal	<i>Martes pennanti</i>	Fisher
369	North America	Mammal	<i>Mustela nigripes</i>	Black footed ferret
370	North America	Mammal	<i>Odocoileus hemionus</i>	Mule deer
371	North America	Mammal	<i>Ovibos moschatus</i>	Muskox
372	North America	Mammal	<i>Ovis canadensis</i>	American bighorn sheep
373	North America	Mammal	<i>Ovis dalli</i>	Dall's sheep
374	North America	Mammal	<i>Panthera onca</i>	Jaguar
375	North America	Mammal	<i>Plecotus townsendii ingens</i>	Ozark big-eared bat
376	North America	Mammal	<i>Rangifer tarandus</i>	Caribou
377	North America	Mammal	<i>Ursus americanus</i>	Black bear
378	North America	Mammal	<i>Ursus arctos</i>	Brown bear
379	North America	Mammal	<i>Vulpes velox</i>	Swift fox
380	North America	Mollusk	<i>Arkansia wheeleri</i>	Oachita rock-pocketbook
381	North America	Plant	<i>Asclepias meadii</i>	Mead's milkweed
382	North America	Plant	<i>Castanea dentata</i>	American chestnut
383	North America	Plant	<i>Cupressus guadalupensis forbesii</i>	Tecate cypress
384	North America	Plant	<i>Isotria medeoloides</i>	~
385	North America	Plant	<i>Sarracenia oreophila</i>	Green pitcher plant
386	North America	Reptile	<i>Crocodylus acutus</i>	American crocodile
387	North America	Reptile	<i>Uma inornata</i>	Coachella Valley fringe-toed lizard
388	South America	Bird	<i>Crax blumenbachii</i>	Red billed curassow
389	South America	Bird	<i>Glaucis dohrnii</i>	Hook billed hermit
390	South America	Mammal	<i>Blastocerus dichotomus</i>	Marsh deer

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
365	N	N	N	Y	B	7,917,500	13,035,000	39.26
366	N	N	N	Y	C	10,914,300	13,605,200	19.78
367	N	N	N	Y	B	6,656,100	8,198,900	18.82
368	N	N	N	Y	B	3,328,600	4,703,000	29.22
369	Y	N	N	Y	C	490	1,721,100	99.97
370	N	N	N	Y	B	5,522,600	7,249,400	23.82
371	N	N	N	Y	B	677,800	1,500,900	54.84
372	N	N	N	Y	C	638,900	2,197,500	70.93
373	N	N	N	Y	C	633,900	1,974,600	67.90
374	Y	N	N	Y	C	538,700	6,748,600	92.02
375	N	N	N	Y	C	58,500	113,200	48.26
376	N	N	N	Y	B	6,676,600	8,901,100	24.99
377	N	N	N	Y	B	9,132,700	15,070,400	39.40
378	N	N	N	Y	B	3,612,000	9,883,800	63.46
379	Y	N	N	Y	C	320,500	1,810,300	82.30
380	Y	N	N	Y	C	37	20,200	99.82
381	Y	N	N	Y	C	16,900	371,400	95.44
382	Y	N	N	Y	C	206,600	1,044,900	80.22
383	N	N	N	Y	C	0.33	1.18	72.00
384	Y	Y	N	Y	C	49,300	624,100	92.10
385	Y	N	N	Y	C	7,900	112,600	92.98
386	Y	Y	N	Y	C	1,500	12,000	87.20
387	N	N	N	Y	C	3,300	5,100	34.18
388	Y	N	N	Y	C	1,900	804,400	99.76
389	Y	N	N	Y	C	1,300	147,300	99.13
390	Y	N	N	Y	C	1,644,800	6,957,800	76.36

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
365	0.42	P	0.47	P	38	41	N	1
366	0.47	P	0.50	P	21	22	N	~
367	0.53	C	0.59	C	13	13	N	1
368	0.51	C	0.54	C	5	5	N	2
369	0.00	P	0.00	P	1	1	N	~
370	0.54	C	0.60	C	13	13	N	1
371	0.53	C	0.53	C	19	18	N	1
372	0.33	P	0.47	P	6	32	N	~
373	0.36	P	0.58	C	1	9	N	~
374	0.00	P	0.01	P	1	4	N	~
375	0.61	C	0.68	C	1	1	N	~
376	0.53	C	0.51	C	28	25	N	1
377	0.12	P	0.45	P	18	29	N	1
378	0.18	P	0.32	P	4	4	N	1
379	0.32	P	0.40	P	1	3	N	~
380	0.00	P	0.07	P	1	14	N	~
381	0.00	P	0.09	P	1	4	N	~
382	0.23	P	0.38	P	1	1	N	~
383	0.20	P	0.40	P	16	19	N	~
384	0.00	P	0.17	P	2	1	N	~
385	0.04	P	0.32	P	1	1	N	~
386	0.59	C	0.63	C	2	1	N	~
387	0.56	C	0.60	C	1	2	N	~
388	0.00	P	0.00	P	1	3	N	~
389	0.14	P	0.26	P	1	2	N	~
390	0.61	C	0.76	C	1	3	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
365	37	1	36	~	~
366	~	~	~	~	~
367	12	1	11	~	~
368	6	2	6	~	~
369	~	~	~	N	W
370	12	1	12	~	~
371	18	1	16	~	~
372	~	~	~	~	~
373	~	~	~	~	~
374	~	~	~	S	E
375	~	~	~	~	~
376	27	1	22	~	~
377	17	1	16	~	~
378	3	1	3	~	~
379	~	~	~	S	W
380	~	~	~	N	W
381	~	~	~	S	W
382	~	~	~	S	W
383	~	~	~	~	~
384	~	~	~	S	E
385	~	~	~	N	W
386	~	~	~	S	E
387	~	~	~	~	~
388	~	~	~	S	E
389	~	~	~	N	E
390	~	~	~	N	W

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365	Schreiber et al., 1989; Hummel and Pettigrew, 1991
366	Burton et al., 1987
367	Gibilisco, 1994
368	Powell, 1981
369	Hall, 1981; Anderson et al., 1986
370	Hall, 1981; Gerlach et al., 1994; Bauer, 1995
371	Barr, 1991
372	Hall, 1981; Valdez, 1982; Burton et al., 1987; U.S. Department of the Interior, 1995
373	Valdez, 1982
374	Seymour, 1989
375	Hensley and Scott, 1993
376	Weintaub, 1996
377	Hummel and Pettigrew, 1991; Stirling, 1993
378	Hummel and Pettigrew, 1991; Stirling, 1993
379	L. Carbyn, 1995 personal communication
380	Martinez, 1994
381	U.S. Fish and Wildlife Service, 1991a and 1978
382	Bell and Walker, 1992
383	Dunn, 1986
384	Mehrhoff, 1989
385	U.S. Fish and Wildlife Service, 1994
386	Grenard, 1991
387	U.S. Fish and Wildlife Service, 1985
388	Michael Scott, 1995 personal communication
389	Michael Scott, 1995 personal communication
390	Pinder and Grosse, 1991

	Region	Taxonomic group	Species	Common name
391	South America	Mammal	<i>Chrysocyon brachyurus</i>	Maned wolf
392	South America	Mammal	<i>Lama guanicoe</i>	Guanicoe
393	South America	Mammal	<i>Leontopithecus chrysomelas</i>	~
394	South America	Mammal	<i>Leontopithecus chrysopygus</i>	~
395	South America	Mammal	<i>Leontopithecus rosalia</i>	Golden lion tamarin
396	South America	Mammal	<i>Panthera onca</i>	Jaguar
397	South America	Mammal	<i>Vicugna vicugna</i>	Vicuna
398	South America	Reptile	<i>Melanosuchus niger</i>	Black caiman

	Prediction 1	Prediction 2	Prediction 3	Chapter 2	Type	Current range (km ²)	Historical range (km ²)	Contracted (%)
391	N	N	N	Y	C	2,467,700	5,473,300	54.91
392	N	N	N	Y	B	1,301,500	4,763,300	72.68
393	Y	N	N	Y	C	3,000	13,000	77.19
394	Y	N	N	Y	C	380	44,400	99.14
395	Y	N	N	Y	C	4,900	31,000	84.08
396	N	N	N	Y	C	10,153,200	14,890,200	31.81
397	Y	N	N	Y	C	59,200	1,675,500	96.47
398	Y	Y	N	Y	C	33,200	6,936,500	99.52

	C Distance	P/C Distance	C Area	P/C Area	Historical patches	Extant patches	Extinct	Historical mainland
391	0.60	C	0.64	C	1	1	N	~
392	0.23	P	0.44	P	3	9	N	2
393	0.64	C	0.68	C	1	1	N	~
394	0.00	P	0.00	P	1	1	N	~
395	0.66	C	0.75	C	1	1	N	~
396	0.57	C	0.63	C	1	2	N	~
397	0.00	P	0.07	P	1	5	N	~
398	0.00	P	0.00	P	2	3	N	~

	Historical island	Extant mainland	Extant island	N/S	W/E
391	~	~	~	~	~
392	5	2	3	~	~
393	~	~	~	S	E
394	~	~	~	N	W
395	~	~	~	S	W
396	~	~	~	~	~
397	~	~	~	S	W
398	~	~	~	N	W

	Reference
391	Burton et al., 1987
392	Burton et al., 1987
393	Kleiman, 1981
394	Kleiman, 1981
395	Kleiman, 1981
396	Seymour, 1989
397	Burton et al., 1987
398	Plotkin, 1983

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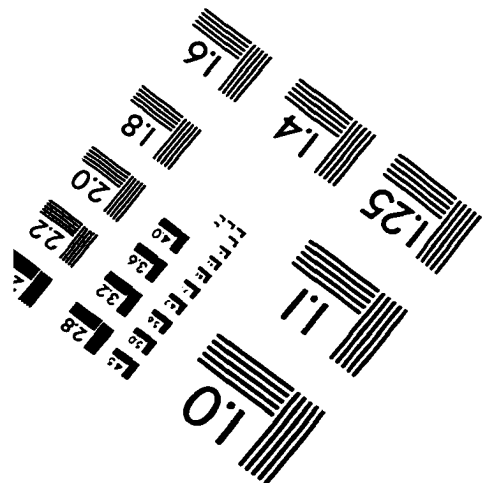
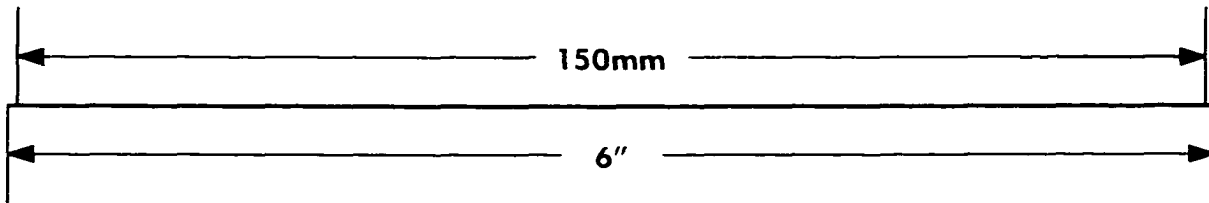
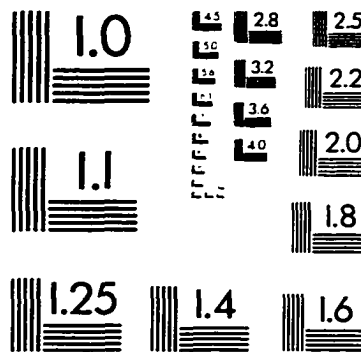
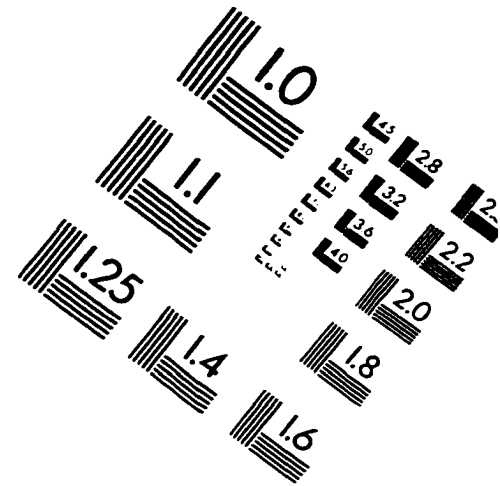
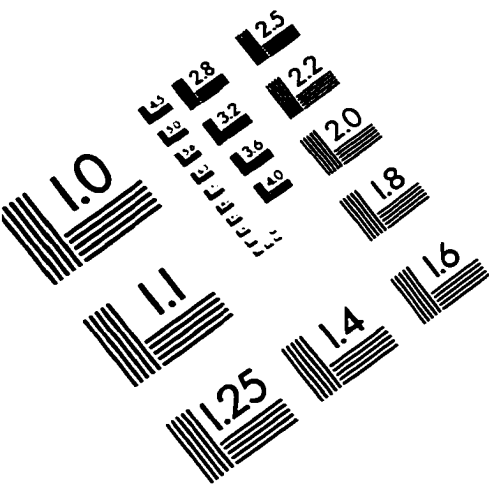
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