Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice

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Geographic studies addressing the role of competition in determining species' macrodistributions have been limited by only simple or subjective means of identifying regions of suitable habitat. Now, ecological-niche models of species' potential distributions present a possible approach to testing for the geographic patterns predicted under competitive exclusion and competitive release. Previously, we modeled the potential distributions of two spiny pocket mice (*Heteromys australis* and *H. anomalus*) in northwestern South America using specimen localities, environmental data, and the Genetic Algorithm for Rule-Set Prediction (GARP). Here we superimpose the models to examine known distributional records in areas of potential sympatry between the two species, thus testing the geographic predictions of competitive exclusion. In addition, we examine environmental characteristics of known localities, testing for data consistent with competitive release. Areas of potential sympatry are minimal, lying in regions of intermediate water balance. Only records of *H. australis* are known from areas of potential sympatry in regions where the species' ranges meet, consistent with exclusion of *H. anomalus* by *H. australis*. *Heteromys anomalus* inhabits areas ecologically suitable for both species only in the isolated Sierra Nevada de Santa Marta, in which *H. australis* is not present (most likely for historical reasons). Furthermore, environmental characteristics of localities of *H. anomalus* in biogeographic regions where *H. australis* is absent fit the pattern predicted under competitive release. In contrast, localities of *H. australis* show no indication of competitive release. Although the results of present analyses do not conclusively demonstrate competitive exclusion or release, they provide directional hypotheses that can now be tested in experimental field and laboratory studies.

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Many interacting factors and forces influence species' distributions (Udvardy 1969, MacArthur 1972). A species' fundamental niche – the intersection of necessary conditions on multiple environmental axes – determines the regions suitable for it (Hutchinson 1957). Biological and historical realities, however, typically modify that ecological potential into a realized geographic distribution (Brooks and McLennan 1991, Brown et al. 1996, Patterson 1999). For example, a species' potential range may be restricted by the presence of competitors, predators, or parasites, reducing its fundamental niche into a fraction or subset that can actually be exploited, the realized niche (Hutchinson 1957).

Because closely related, morphologically similar species commonly share ecological requirements that can prevent their coexistence (Darwin 1859, Gause 1934, MacArthur 1972), a species' realized geographic range may be restricted by related species. For example, where present sympatrically, closely related mammalian species often display behavioral, microhabitat, or macrohabitat segregation (Wilson 1968, Stoecker 1972, Emmons 1980). In some cases, aggressive behavior has been documented, providing a mechanism for the competitive interactions deduced from geographic patterns (Brown 1971, Heller 1971, Murie 1971, Sheppard 1971, Stoecker 1972, Alberico and González-M. 1993). Congeners frequently have parapatric ranges with very narrow contact zones (Hershkovitz 1977, Hall 1981), suggesting that competitive relationships may be common (Miller 1967). Finally, removal experiments have confirmed the ability of certain small mammals to exclude congeners where their ranges come into contact (Koplin and Hoffmann 1968, Stoecker 1972, Chappell 1978, Schoener 1983).

Nevertheless, separating the relative ecological and historical determinants of individual species' distributions has proven difficult from a geographic perspective (Endler 1982). Intriguing studies examining species' macrodistributions have documented patterns suggestive of historical restrictions, competitive exclusion, and competitive release. In most cases, however, interpretation of these examples has been hindered by the lack of objective (or only very simplistic) means for identifying regions of suitable habitat (Miller 1964, Haffer 1967, Terborgh 1971, 1985, MacArthur 1972: 132–142, Hoffmann 1974: 526–531, Terborgh and Weske 1975, Bergstrom and Hoffmann 1991, Remsen and Graves 1995a, b). Recent advances employing geographic information systems (GIS) technology allow niche-based modeling of species' potential macrodistributions, permitting tests of the geographic predictions of competitive exclusion and competitive release in ways not previously possible.

Niche-based modeling of potential distributions

Modeling species' fundamental ecological requirements based on environmental characteristics of known occurrence sites represents a powerful tool for predicting geographic ranges and studying aspects of ecology and evolution (Box et al. 1993, Kadmon and Heller 1998, Yom-Tov and Kadmon 1998, Peterson et al. 1999). One approach, the Genetic Algorithm for Rule-Set Prediction (GARP; http://biodi.sdsc.edu/) has been especially successful in predicting species' distributions (Peterson and Cohoon 1999, Peterson et al. 1999, Chen and Peterson 2000, Godown and Peterson 2000, Sánchez-Cordero and Martínez-Meyer 2000, Peterson 2001, Peterson and Vieglais 2001, Peterson et al. 2001,

Anderson et al. 2002, Stockwell and Peterson 2002, Peterson et al. 2002). GARP is a genetic-algorithm (GA) approach that uses localities of a species' occurrence and environmental data to produce a niche-based model of the species' ecological requirements in those environmental dimensions (Stockwell and Noble 1992, Stockwell and Peters 1999). This complex expert-system model of the species' fundamental niche is then projected into geographic space to create a map of the species' potential distribution. Because GARP is a superset of several approaches (such as logistic regression or bioclimatic-envelope rules; Box et al. 1993, Skidmore et al. 1996) it should always have greater predictive accuracy than any single approach (Stockwell and Peters 1999).

Although encompassing only a few of the possible niche dimensions (sensu Hutchinson 1957), currently available GIS coverages (digital maps) provide environmental data for many major physical variables that commonly influence species' macrodistributions (Root 1988, Brown and Lomolino 1998: 72). Under clear assumptions and given the varying community contexts present across a species' range, a model indicates areas potentially habitable for a species – at least as indicated by the examined niche dimensions (Peterson et al. 1999). Nonetheless, few species actually occupy all areas with suitable conditions. For example, some areas of potential presence may be occupied by closely related species, or may represent suitable areas to which the species has failed to disperse or in which it has gone locally extinct. Furthermore, depending on the scale of analysis, the species will not necessarily be found in all macro- or microhabitats within a map pixel of predicted potential distribution.

Geographic predictions of competitive exclusion and competitive release

In addition to morphological similarity and a credible hypothesis of close phylogenetic relationship, focal species must meet several requirements to permit valid tests of the geographic predictions of competitive exclusion and competitive release (Hutchinson 1957, Miller 1964, 1967). First, prior studies should indicate that the species do not co-occur broadly in sympatry, but rather show narrow contact zones. This allows for the hypothesis that competition may exist and yield geographic manifestations in their realized distributions. Additionally, environmental tolerances of the two species must differ significantly but show partial overlap, providing some regions of potential sympatry where competitive exclusion could occur. Finally, records for each species should include localities in biogeographic regions where both species are present (where competitive exclusion could occur), as well as in regions where the other species is not present, such as due to historical restric-

tions (creating the possibility for competitive release). At least in the context of this two-species system, and given that models are developed based on large regions with varying biotic contexts, the respective models will then approximate the species' fundamental niches. Finally, of the regions indicated as potentially habitable by the models, known distributional records identify the particular regions of suitable conditions that the species actually occupy.

Clear distributional predictions of competitive release exist for species pairs with ecological requirements that overlap but that do not exist in broad zones of sympatry (Hutchinson 1957, Miller 1964, 1967, Chappell 1978, Begon et al. 1996). If one species competitively excludes another from areas that both could potentially inhabit, then the inferior competitor would be predicted to inhabit different environmental conditions in biogeographic regions where the other species is not present – in comparison with the conditions it inhabits in regions where both species exist. Specifically, in biogeographic regions where the superior competitor is not present (e.g. for historical reasons), the inferior competitor should inhabit broader environmental conditions more similar to those typical of the superior competitor. Conversely, the superior competitor would be predicted to inhabit similar environmental conditions regardless of the presence or absence of the inferior competitor in a region. These predictions can be tested with environmental data for sites that the respective species inhabit.

In such species pairs, explicit geographic predictions of competitive exclusion also follow from niche theory (Hutchinson 1957, Miller 1967, Begon et al. 1996). Areas where both species are predicted to be present represent zones of potential sympatry, or overlap between their fundamental niches. Occurrences in areas of potential sympatry may reflect the outcome of exploitation or interference competition, but only in regions where both species are present adjacent to the geographic zone of potential overlap. Hence, regions of potential sympatry should be separated into those along likely contact zones between the species (areas adjacent to known distributional records for both species) and those where only one species is present adjacent to the zone of potential sympatry. If neither species consistently excludes the other, and both show similar average densities and capture probabilities, records of the two species should be present in approximately equal proportions in areas of potential sympatry along real contact zones. However, if one species consistently excludes the other, all known records in areas of potential sympatry along contact zones will be of that species. Herein, we use GIS techniques to test the environmental and geographic predictions of competitive exclusion and competitive release in South American spiny pocket mice.

Methods

Study species

Two species of spiny pocket mice in northwestern South America represent excellent candidates for research testing the geographic predictions of competition. Spiny pocket mice (Rodentia: Heteromyidae: Heteromyinae) originated in North America, with extant species known from Texas to Ecuador (Wood 1935, Rogers 1990, Patton 1993). Throughout the subfamily, congeneric species are seldom syntopic. Where species' ranges meet, they generally segregate into distinct macrohabitats, suggesting a partitioning of their realized niches in such situations (Genoways 1973, Rogers and Engstrom 1992, Sánchez-Cordero and Fleming 1993). Although most heteromyines inhabit parts of Mexico and Central America, these two species of *Heteromys* are widespread in northwestern South America (Fig. 1, Anderson 1999). Other *Heteromys* in this region are locally restricted and only marginally affect these analyses (Paraguaná Peninsula – Handley 1976; Serranía del Darién and two localities in Antioquia – Anderson 1999).

Previously, we successfully modeled the potential macrodistributions of *Heteromys australis* Thomas and *Heteromys anomalus* (Thompson) using GARP modeling technology (Anderson et al. 2002, Fig. 2). The base environmental data (GIS coverages) used in creating those models included physical, biotic, and climatic variables, as well as seasonal values for some of the climatic ones. In total, the models were based on 19 coverages for northern South America (9° S–13° N, 51–82° W): elevation, slope, aspect, soil conditions, coarse vegetation zones, and a series of coverages for solar radiation, temperature and precipitation. For the latter three, both upper and lower bounds of the isopleth intervals were included (for mean annual solar radiation, mean annual temperature, mean monthly temperature in January and July, mean annual precipitation, and mean monthly precipitation in January and July). The coverages, with a pixel size of 0.04° on a side (about 4.5×4.5 km), are available at the GARP website.

Anderson et al. (2002) produced the models using georeferenced localities of both species from Colombia and Ecuador as well as the lone Venezuelan locality for *Heteromys australis*. This data set derived from a systematic review of the species in Colombia and Ecuador (Anderson 1999), and included 56 unique collection localities for *H. australis* and 40 of *H. anomalus*. It excluded known distributional points for *H. australis* in eastern Panama (outside the scope of the environmental data) and for *H. anomalus* in Venezuela and Trinidad & Tobago (because georeferenced localities there were not yet available). If peripheral populations occupy environmental conditions outside those typified by the sam-

ple, the exclusion of records in these distributional areas might have led to an underestimation of the species' fundamental niches. However, characteristics of Panamanian collection localities for *H. australis* (Anderson 1999) and Venezuelan localities of *H. anomalus* examined to-date (Anderson and Soriano 1999) appear to agree well with environmental patterns of known sites in Colombia. Finally, by using records from a
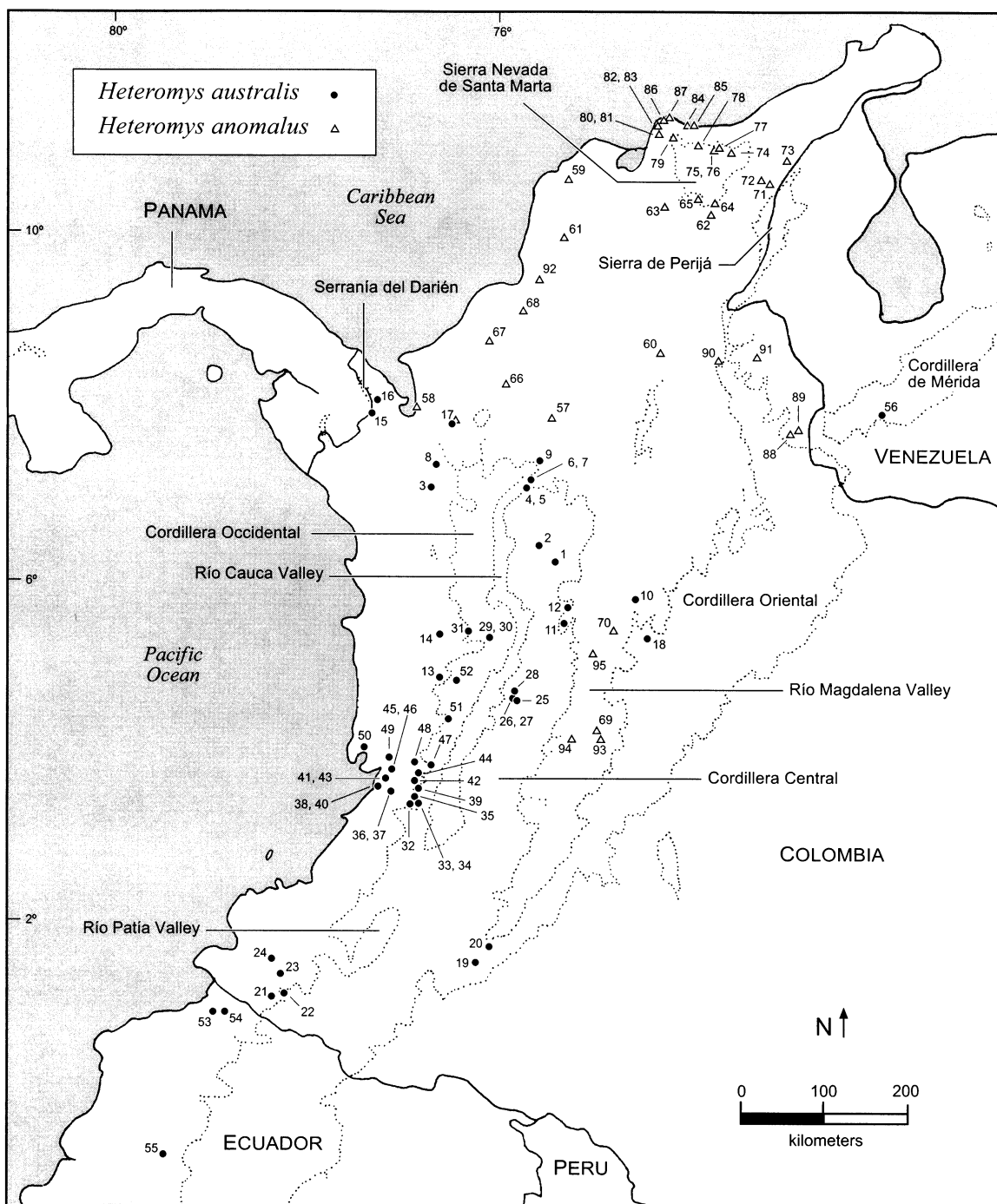

Fig. 1. Collection localities of *Heteromys australis* (solid circles) and *H. anomalus* (open triangles) used in this study (data from Anderson 1999). *Heteromys australis* extends slightly west into Panama, and *H. anomalus* also ranges east throughout northern Venezuela and Trinidad & Tobago (not shown). Dotted lines denote regions over 1500 m. Localities are numbered to correspond with data given in the appendices.
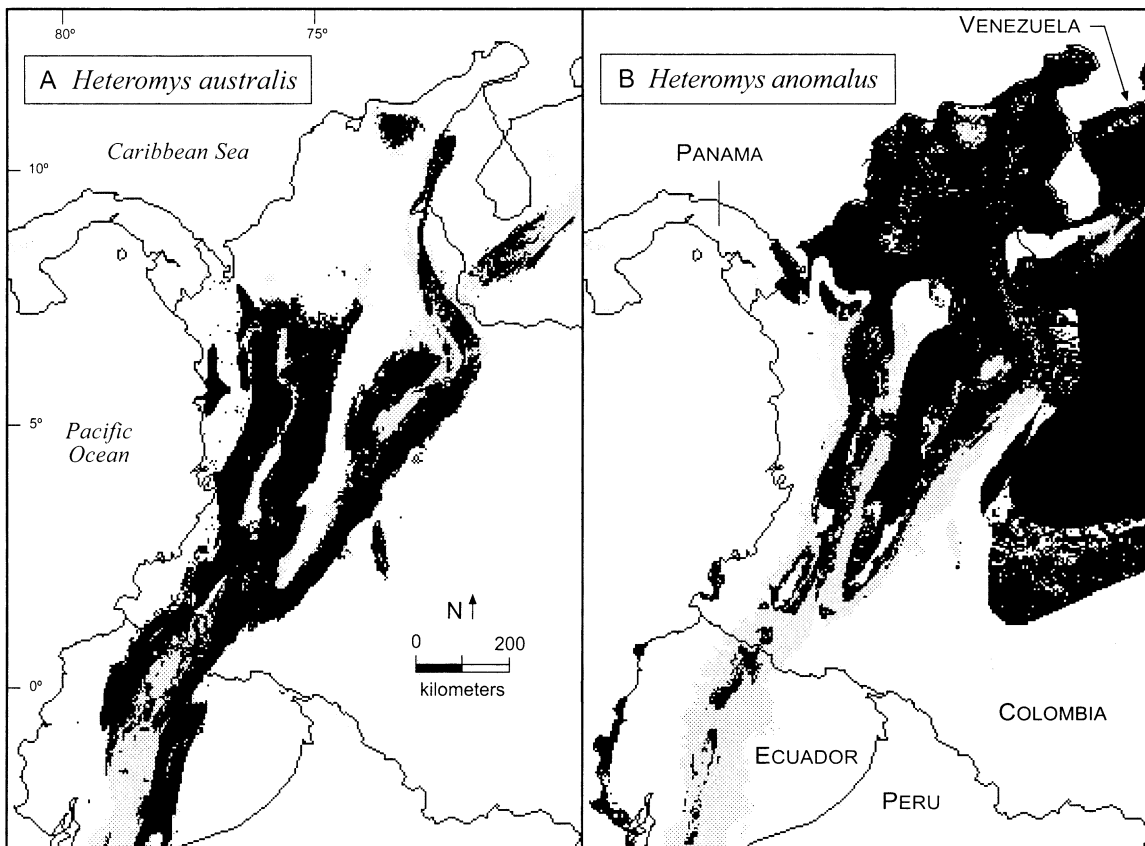
Fig. 2. Models of predicted potential distributions for *Heteromys australis* (A, left) and *H. anomalus* (B, right) in northwestern South America. Potential distributions are shown in black over gray shading representing regions over 1500 m (from Anderson et al. 2002).

variety of museums and collectors, possible collecting biases that might have favored particular regions or biomes and thus adversely affected the models were minimized. We here examine these models and locality records in the Colombian and Ecuadorian ranges of the species and present maps for northwestern South America (3° S–13° N, 70–81° W).

Necessary conditions for the tests

Previous work has shown that the species meet most of the criteria necessary for such tests (see above), and we here further assess one of them. Regarding the first condition, *Heteromys australis* and *H. anomalus* possess parapatric distributions, which probably come into contact along narrow zones in several regions (Anderson 1999, Anderson et al. 2002). *Heteromys australis*, the southern spiny pocket mouse, inhabits rainforests in the Pacific lowlands of Ecuador, Colombia, and eastern Panama and continues its distribution eastward in montane forests of the Colombian and Venezuelan Andes, up to about 2500 m (Anderson 1999, Anderson

and Soriano 1999, Fig. 1). In contrast, *Heteromys anomalus*, the Caribbean spiny pocket mouse, is generally found below 1500 m in drier forests and agricultural areas of the Caribbean coastal lowlands and montane foothills of northern Colombia and Venezuela, as well as at low elevations of the upper Río Magdalena Valley (Anderson 1999, Anderson and Soriano 1999, Fig. 1). These two species are only known to be sympatric at one locality (Locality 17 in Fig. 1, Appendix 1, Anderson 1999), suggesting that contact zones are probably narrow (although the field notes of the collector did not indicate whether they were collected in the same habitat). Because related species of heteromyines typically show parapatric ranges (Patton 1993, Williams et al. 1993, Anderson 1999) and segregate by macrohabitat type in ecotone regions (Genoways 1973: 313–314, Rogers and Engstrom 1992), *H. australis* and *H. anomalus* may compete in transitional zones that both could potentially occupy. Little has been reported, however, on the ecology or natural history of these species (but see González-M. and Alberico 1993 for *H. australis* and Pirlot 1963, August 1984, and Soriano and Clulow 1988 for *H. anomalus*).

Secondly, the two species appear to possess largely, but not entirely, complementary environmental requirements. In previous analyses, *Heteromys australis* was predicted to range throughout wet areas of the northern Andes at all but the highest elevations, as well as some lowland areas of intermediate rainfall (Fig. 2A, Anderson et al. 2002). Conversely, appropriate conditions were predicted for *H. anomalus* in the dry to moderately mesic Caribbean lowlands of northern Colombia and Venezuela, as well as in most arid rainshadowed enclaves of the northern Andes (Fig. 2B). Those models appeared to represent the species' potential distributions adequately, except for overpredicting *H. australis* in some regions over ca. 2500 m, and predicting *H. anomalus* throughout areas of *llanos* (tropical savannas) where the resolution of the base environmental data was not sufficient to discriminate between gallery forest habitat and open grasslands (August 1984, Soriano and Clulow 1988). Here we confirm the criterion of marginally overlapping ecological requirements in two ways. First, we superimposed models of the species' potential distributions in northwestern South America (Fig. 2; 3° S–13° N, 70–81° W) from Anderson et al. (2002), to identify regions of potential sympatry (if any). Secondly, we examined mean annual temperature, mean annual precipitation, elevation, and the potential evapotranspiration (PET) ratio for known localities (see below), testing for differences between the two species (two-tailed Mann-Whitney U-test).

Finally, the modeled potential distribution of each species (Anderson et al. 2002) shows some regions of suitable environmental conditions where the respective species is not known to be present, likely due to historical restrictions. For example, although suitable conditions for *Heteromys anomalus* occur in the upper Río Cauca Valley according to its predictive model, this species has never been collected there in spite of surveys at several sites near Cali (Fig. 1, 2, Alberico 1983, Anderson 1999 reidentified all specimens from the region as *H. australis*). Likewise, *H. australis* is not known from potential distributional areas in the isolated Sierra Nevada de Santa Marta, even though the rodents of that massif are well-collected and many occurrences of *H. anomalus* have been documented (Fig. 1, 2, Bangs 1900, Allen 1904, Anderson 1999).

Testing for predicted geographic patterns

Environmental characteristics of known localities

Values for mean annual temperature, mean annual precipitation, and elevation were extracted from the GIS coverages of Anderson et al. (2002) for the map pixel in which each collection locality fell (upper bounds of isopleth intervals were used for temperature and precipitation). In addition, we calculated an approximation of the potential evapotranspiration (PET)

ratio for those sites. The PET ratio is equal to mean annual biotemperature (°C) divided by total annual precipitation (mm) and multiplied by an empirically derived constant of approximately 60 (Holdridge et al. 1971). Because both low and high extreme temperatures inhibit physiological activity in plants, Holdridge et al. (1971: 8) defined biotemperature as the "mean of unit-period temperatures with the substitution of zero for all unit-period values below 0°C and above 30°C." At a PET ratio of 1.00, potential evapotranspiration equals total precipitation for the long-term average year. Ratios greater than 1.00 indicate increasing aridity, whereas those less than 1.00 correspond to increasingly humid environments. We approximated the PET ratio by dividing the upper bound of mean annual temperature by the upper bound of mean annual precipitation and multiplying by 60.

To test for patterns consistent with competitive release, we divided vouchered localities of each species into two groups: those in areas of possible contact with the other species, and those in areas of possible competitive release. Localities of *Heteromys australis* from the middle and southern Chocó (Pacific coast) and the slopes of the upper Cauca Valley constituted the sample of *H. australis* potentially under competitive release (Anderson et al. 2002). Likewise, localities in the region surrounding the Sierra Nevada de Santa Marta and the Serranía de Perijá (both highland and lowland records) formed the sample of *H. anomalus* in biogeographic regions devoid of *H. australis*. Because these environmental data were not normally distributed, we used nonparametric one-tailed Mann-Whitney U-tests to test for differences between sample medians, in the direction predicted for competitive release (i.e. more similar to the conditions usually inhabited by the congener).

To facilitate interpretation, we plotted precipitation and elevation for known localities as well as the distribution of available combinations of those two variables in northwestern South America (3° S–13° N, 70–81° W). Temperature was not graphed, as it represents a negative correlate of elevation (Holdridge et al. 1971). Likewise, patterns related to the PET ratio should be evident in diagonal "humidity provinces" of the logarithmic precipitation/elevation graph (Holdridge et al. 1971).

Species records in areas of potential sympatry

We tested whether actual records of either species predominated in areas of potential sympatry. Deviations from random expectations were determined using two-tailed tests (χ^2 statistic or exact binomial probability, depending on the available sample size). Probabilities used for generating expected values reflected overall proportions of unique species localities (56 of *Heteromys australis*; 40 for *H. anomalus*). The lone Venezuelan locality for *H. australis* was excluded from these analyses, as the current data set does not include

known localities for *H. anomalus* in that region (Anderson and Soriano 1999). These tests were conducted both before and after trimming the species' potential distributions to include only known distributional areas (Anderson et al. 2002). Proportions of species records before trimming represent the overall pattern of occurrences in areas of potential sympatry in the study region. In contrast, the analysis of proportions of species records in areas of potential sympatry along real contact zones (after trimming) directly tests the geographic pattern predicted under competitive exclusion.

Results

Ecological overlap

Superimposition of the two species' models revealed limited areas of potential sympatry (Fig. 3A). Pixels of potential sympatry represented 38% of the potential distribution of *Heteromys australis*, 18% of that of *H. anomalus*, and approximately 8% of the land area in the present study region (3° S–13° N, 70–81° W). The

models predicted sympatry in a ribbon-like area: the lowlands immediately north of the Cordillera Occidental and Cordillera Oriental and continuing south at intermediate elevations of the valleys of the Río Cauca, Río Patía, and Río Magdalena. These areas thus encompass the eastern versant of the Cordillera Occidental, both flanks of the Cordillera Central, and the western slope of the Cordillera Oriental (Fig. 3A). Areas of potential sympatry also existed in the Serranía de Perijá, the Sierra Nevada de Santa Marta, and the southwestern portion of the Cordillera de Mérida.

Similarly, clear differences in environmental characteristics existed between the localities of *Heteromys australis* and *H. anomalus*, although their tolerances overlapped widely (Table 1, Fig. 4). Medians for the two species were different in all four environmental variables examined (elevation, $P = 0.0033$; precipitation, $P < 0.0001$; temperature, $P = 0.0036$; PET ratio, $P < 0.0001$). On average, *H. australis* inhabits higher, wetter, cooler, and more mesic conditions, but much overlap was observed for each variable. Thus, the pattern of ecological overlap for these two species fits the
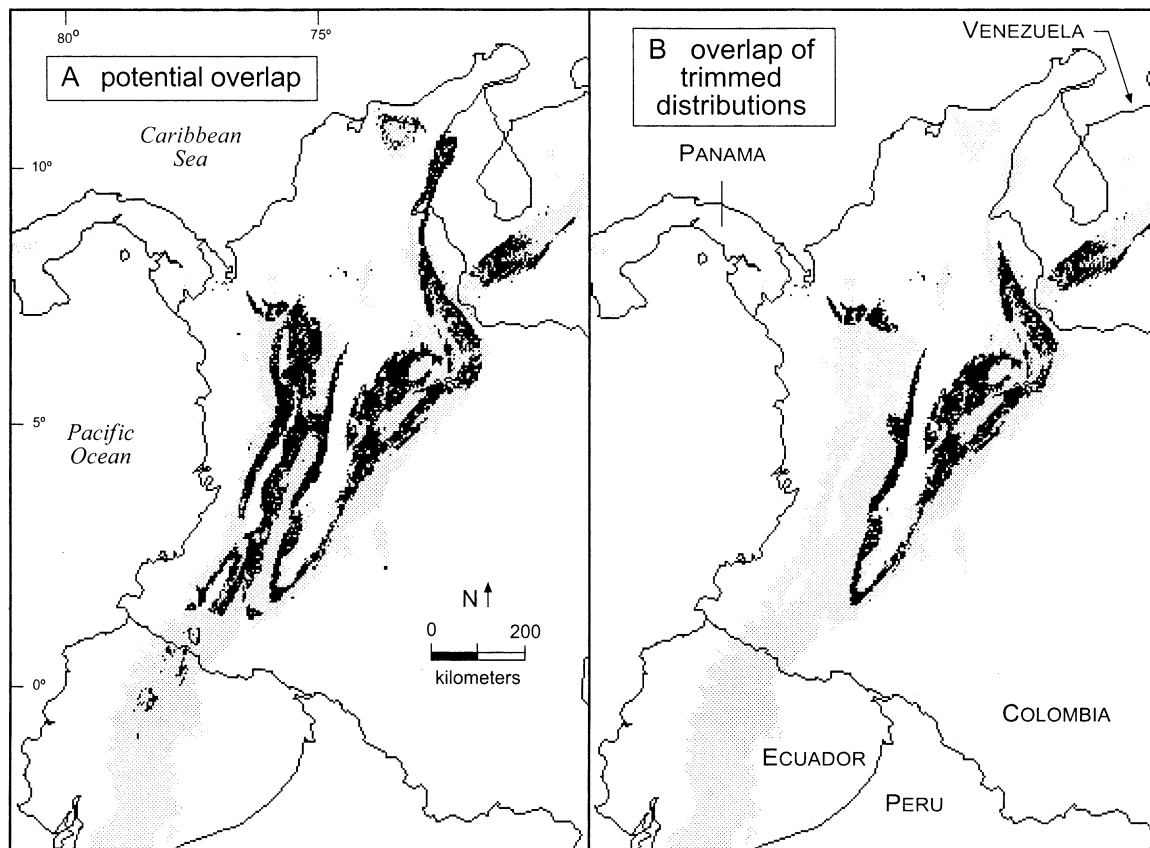

Fig. 3. Areas of potential sympatry between *Heteromys australis* and *H. anomalus* in northwestern South America, indicated by the overlap (in black) between predictive models of the two species. Potential sympatry was calculated both before (left) and after (right) trimming the species' potential distributions by removing regions of potential distribution in which the species are not known (see Anderson et al. 2002). Gray shading denotes other areas over 1500 m.

Table 1. Descriptive statistics for selected environmental variables at known collection localities of *Heteromys australis* and *H. anomalus* used in this study. Mean ± standard deviation and minimum–median–maximum are given for each species in the first two columns. The same statistics are then presented for localities of each species in areas of potential contact with the other species versus localities in biogeographic regions in which the other species is not present. Note that in regions where *H. australis* is absent, *H. anomalus* inhabits higher, wetter, cooler, and more mesic conditions on average. See Methods for details on the calculation of the PET ratio.

	H. australis all records (n=56)	*H. anomalus* all records (n=40)	*H. australis* potential contact outside southern Chocó and upper Cauca (n=19)	*H. australis* potential release southern Chocó and upper Cauca (n=37)	*H. anomalus* potential contact outside Sierra Nevada and Perijá (n=19)	*H. anomalus* potential release Sierra Nevada and Perijá (n=21)
Elevation (m)	998.0±782.0 4–863–2947	528.6±576.2 1–295–1992	980.0±566.0 44–885–1870	1008.0±880.0 4–743–2947	320.4±338.9 1–184–1276	717.0±682.0 1–511–1992
Mean annual precipitation (mm)	4130±2030 1400–4000–8000	2180±830 1000–2000–4000	3170±1170 1400–2800–5600	4620±2200 2000–4000–8000	1880±830 1000–1400–4000	2450±750 1400–2000–4000
Mean annual temperature (°C)	24.5±5.2 15–25–30	27.5±4.2 15–30–35	24.0±6.1 10–25–30	24.7±4.7 20–25–30	28.9±2.7 25–30–35	26.2±5.0 15–30–30
Potential evapotranspiration ratio (°C/mm)	0.42±0.16 0.15–0.43–0.90	0.90±0.44 0.30–0.90–2.10	0.50±0.17 0.15–0.54–0.90	0.38±0.14 0.21–0.38–0.64	1.11±0.49 0.45–1.07–2.10	0.72±0.28 0.30–0.90–1.29

conditions necessary for tests of the geographic patterns predicted by competitive exclusion and release.

Tests of predicted geographic patterns

Environmental characteristics of known localities
The environmental characteristics of localities of *Heteromys anomalus* matched the predictions of competitive release, but those for *H. australis* did not. Environmental characteristics of localities of *H. australis* in biogeographic regions where *H. anomalus* is not present did not fit the pattern of competitive release when compared with those of localities in regions of potential contact with *H. anomalus* (elevation, $P = 0.4655$; precipitation, $P > 0.5$; temperature, $P = 0.4053$; PET ratio, $P > 0.5$). In contrast, the environmental characteristics of localities of *H. anomalus* in regions not inhabited by *H. australis* differed from those of *H. anomalus* in regions of potential contact with *H. australis*, in the direction predicted by competitive release (elevation, $P = 0.0550$; precipitation, $P = 0.0072$; temperature, $P = 0.0467$; PET ratio, $P = 0.0070$).

Species records in areas of potential sympatry
Records of *Heteromys australis* predominated in areas of potential sympatry. Twenty-one collection localities lay in regions of potential sympatry (Fig. 3A, Appendix 2). Seventeen of those localities represented collections of *H. australis*, significantly more than expected by chance ($\chi_1^2 = 4.420$, $P = 0.0355$). All localities in regions of potential sympatry in the Andes were sites of *H. australis* (17 localities, Fig. 1, Appendix 2). In contrast, *H. anomalus* was found in areas of potential sympatry only in the Sierra Nevada de Santa Marta (four localities).

More importantly, all five collection localities falling in areas of potential sympatry along real contact zones represented localities of *Heteromys australis* (binomial probability, $P = 0.0801$, Appendix 3). After trimming, the geographic extent of potential sympatry along real contact zones was even more restricted (4% of land area; Fig. 3B). Two of the localities in such regions lay at the northern end of the Cordillera Central, another was at the headwaters of the Río Magdalena, and the last two derived from middle elevations of the western slope of the Cordillera Oriental (Fig. 1, Appendix 3).

Discussion

Characteristics of areas of potential sympatry

The complex geographic pattern of areas of potential sympatry between *Heteromys australis* and *H. anomalus* corresponds in large part to climatic factors. *Heteromys australis* appears restricted to mesic combinations (above the solid line in Fig. 4C) and can survive at
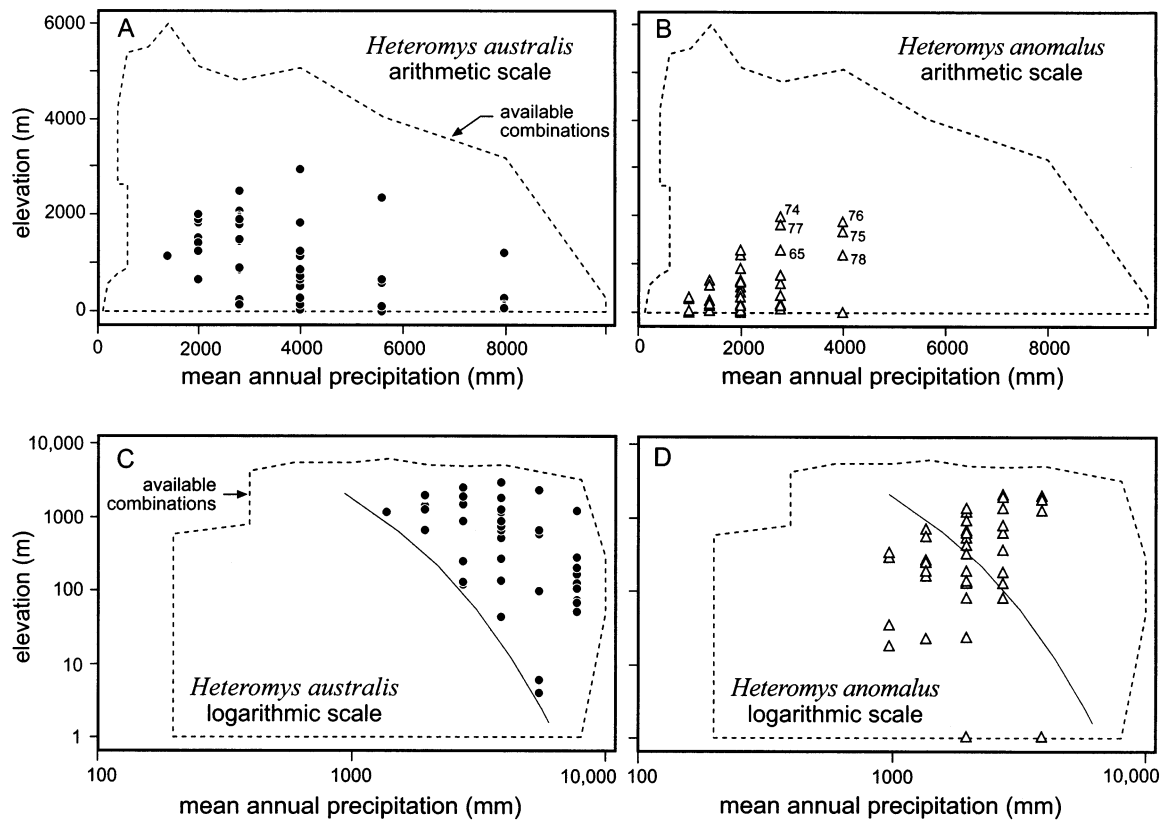
Fig. 4. Plots of elevation versus mean annual precipitation for localities of *Heteromys australis* (left) and *H. anomalus* (right) compared with available combinations of these two variables in northwestern South America. A and B show plots of elevation versus mean annual precipitation on arithmetic scales; C and D present the same data on logarithmic scales. Available combinations of those variables are delimited by dashed lines, and the solid line in C and D approximates the lower limit of habitable conditions for *H. australis*. In B and D, the localities of *H. anomalus* farthest into the niche space of *H. australis* represent sites in regions of potential sympatry in the Sierra Nevada de Santa Marta (Localities 74–76, 78) and two nearby sites (Localities 65 and 77). *Heteromys australis* is not present in the Sierra Nevada de Santa Marta.

localities receiving less precipitation if at higher elevations. Such regions are cooler, with concomitantly lower potential evapotranspiration, and hence they are functionally more mesic than lowland areas receiving the same amount of precipitation (Holdridge et al. 1971). In contrast, *Heteromys anomalus* shows tolerances for more xeric conditions (Fig. 4). This interpretation is supported by the environmental characteristics of the two species' collection localities, with *H. australis* inhabiting higher, wetter, cooler, and more mesic conditions on average (Table 1).

Overlap between the composite models for the two species indicates that both could inhabit middle elevations of the inter-Andean valleys of Colombia (Fig. 3A). Only *Heteromys australis* is predicted for the outer slopes of the Andes facing the Chocó and Amazonia (Fig. 2), however, suggesting that intermediate elevations per se do not determine areas of potential sympatry between the species. The outer slopes of the Andes face mesic lowland regions too wet for *H. anomalus*, whereas the inner slopes contact dry vegetation types suitable for it.

Thus, intermediate elevations of the inner flanks of the Andes facing the Río Cauca and Río Magdalena represent zones of intermediate water balance transitional between the dry lowland valleys and the mesic, cloud-covered montane forests above.

Other areas of potential sympatry also meet the intermediate-moisture criterion. The three additional major mountain ranges containing areas of potential sympatry (Sierra Nevada de Santa Marta, Serranía de Perijá, Cordillera de Mérida, Fig. 1, 3A) lie to the north, in regions where the surrounding lowlands are generally drier than the Chocoan or Amazonian rainforests that abut the Andes. Thus, these northern lowland regions support *Heteromys anomalus* (Anderson 1999, Anderson and Soriano 1999), and middle elevations of those mountain ranges represent areas of intermediate water balance. Most tellingly, potential sympatry also exists in some lowland areas of intermediate precipitation north of the Cordillera Occidental and Cordillera Central (Fig. 3A). This region (the Nechí) comprises a transitional zone between the pluvial rainforests of the Chocó and

the deciduous forests of the Caribbean coast (Cracraft 1985). Hence, we conclude that *Heteromys australis* and *H. anomalus* separate ecologically along a moisture gradient. This pattern is especially clear in the upper Magdalena Valley, where *H. australis* inhabits the wet slopes of the Andes and *H. anomalus* occupies the dry floor of the valley (Fig. 1).

Geographic patterns consistent with competitive exclusion and release

Competitive exclusion

Where the two species' ranges actually meet, specimen records in areas of potential sympatry show a clear pattern: *Heteromys australis* has been found in those areas and *H. anomalus* has not (Appendix 3, Fig. 1, 3B). The existence and consistency of these documented localities thus matches the geographic pattern predicted if *H. australis* competitively excludes *H. anomalus* from regions that satisfy the environmental requirements of both species. Conversely, the observed pattern counters a hypothesis of competitive exclusion of *H. australis* by *H. anomalus* in such regions.

Thus, five localities where *H. australis* has been collected in zones of potential sympatry in the Cordillera Central and Cordillera Oriental of Colombia underscore the possibility of competitive exclusion. These localities lie in three regions of the two cordilleras and vary in collection effort (Fig. 1). La Frijolera (Locality 6) and Quebrada Valdivia (Locality 7) in northern Antioquia are fairly well-collected localities (Allen 1916; Field Museum collection), as is San Adolfo (Locality 20), at the headwaters of the Río Magdalena where the Cordillera Central and Cordillera Oriental meet in southern Huila (Field Museum collection). Paime (Locality 18) and Serranía de Las Quinchas (Locality 10) are poorly collected sites at middle elevations on the western slopes of the Cordillera Oriental (Voss 1988, 1991; American Museum of Natural History and Instituto de Ciencias Naturales collections). Because heteromyines are easily captured in standard inventories but so rarely collected sympatrically, the presence of *Heteromys anomalus* at these places – especially the well-sampled ones – is unlikely (Genoways 1973, Rogers and Engstrom 1992, Anderson 1999). Furthermore, *H. anomalus* is often collected in much larger numbers than *H. australis*, making its collection alone more probable than that of *H. australis* (see specimens reported in Anderson 1999). Hence, although only five localities are known from these areas (yielding marginal statistical significance), the results are consistent with the geographic prediction of competitive exclusion of *H. anomalus* by *H. australis*. Future fieldwork should sample extensively in these regions identified as critical by the predictive models.

Competitive release

Concordant with the test for competitive exclusion, results regarding environmental characteristics of known localities fit the pattern of competitive release for *Heteromys anomalus*. In the absence of *H. australis*, *H. anomalus* inhabits environmental conditions more similar to those of *H. australis* (higher, wetter, cooler, and more mesic) than in regions where both are present (Table 1). In contrast, environmental conditions of the localities of *H. australis* show no indication of competitive release in the absence of *H. anomalus*. The four localities of *H. anomalus* in areas of potential sympatry in the Sierra Nevada de Santa Marta (where *H. australis* is not present) also fall farthest into the niche space of *H. australis* for elevation and precipitation (Fig. 4, Appendix 3).

Interpretations and recommendations for future work

Despite the clear patterns presented above, the present analyses do not conclusively demonstrate competitive exclusion or competitive release. Observational and experimental field studies in zones of contact between *Heteromys australis* and *H. anomalus* are necessary to determine their micro- and macrohabitat usage, behavior, and food habits, in order to confirm any exploitative or interference competition between the two. For example, behavioral studies and removal experiments showed that species of chipmunks in the western United States segregate by habitat type and elevation through both physiological limitations and competitive exclusion (Brown 1971, Chappell 1978). Similarly, removal of one species of vole, *Microtus pennsylvanicus* (Ord), from mesic grasslands in western Montana allowed its congener *Microtus montanus* (Peale) to move into the vacated habitat, whereas the latter was formerly restricted to adjacent xeric habitats (Koplin and Hoffmann 1968). Murie (1971) documented aggressive behavior between these species in laboratory trials and attributed the competitive exclusion to dominance of *M. pennsylvanicus* over *M. montanus*.

No such obvious mechanism for competitive dominance of *Heteromys australis* over *H. anomalus* is currently known. To date, no experimental studies have been attempted for the *Heteromys* here studied, and little is known on their natural history (but see Pirlot 1963, August 1984, Soriano and Clulow 1988, González-M. and Alberico 1993). Often, larger species are competitively dominant over smaller ones (Schoener 1983), but *H. anomalus* has a larger average body size than *H. australis* (Anderson 1999). Population densities also can affect competitive relationships (Stoecker 1972). However, *Heteromys anomalus* has generally been collected in larger numbers than *H. australis*. Even if that pattern reflects higher densities of the former

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throughout most of the species' ranges, it is not necessarily true at the intermediate elevations typical of regions of potential sympatry between the two; population densities vary widely in heteromyines at different localities, even within a single species (Sánchez-Cordero 1993, Sánchez-Cordero and Fleming 1993). No comparative diet studies have been conducted, and little is known of the species' microhabitat use (but see Anderson 1999). Finally, we cannot discount the possibility that other species (mammalian or otherwise) may compete with these pocket mice, affecting their macrodistributions. Similarly, the geographic distributions of unknown parasites, mutualists, or key food resources not examined here may play critical roles in their distributions. Future field work should examine all of these potential factors.

Hence, while they are not sufficient to demonstrate competitive interactions, the present geographic analyses illustrate a new method of testing for the geographic patterns predicted by competitive exclusion and release, and provide explicit, directional hypotheses to be tested in future field investigations. We hope that this study will stimulate similar geographic analyses for other groups. Predictive modeling may reveal geographic patterns in cases where competition has already been documented on the ground (Koplin and Hoffmann 1968, Stoecker 1972, Chappell 1978). Modeling can also be employed for groups in which geographic distributions suggest competition, but prior studies lacked objective criteria of environmental suitability (Haffer 1967, Terborgh and Weske 1975, Bergstrom and Hoffmann 1991, Remsen and Graves 1995a, b). Finally, our results suggest that predictive models of species' distributions should be interpreted in the context of models for closely related or ecologically similar species, considering the restrictions they may place on the target species' realized distributions. Thus, this work represents a first step toward integrating biotic interactions into models of species' potential distributions.

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Appendix 1

Localities of *Heteromys australis* and *H. anomalus* used in this study (Fig. 1). Abbreviated locality names are followed by elevation (when available) and geographic coordinates. Localities are numbered to correspond to those plotted in Fig. 1. Degrees and minutes north of the equator and west of Greenwich are given in parentheses without punctuation – e.g., (0614/7510) for 6°14′ N, 75°10′ W. The lone site south of the equator is denoted by an S following the digits for latitude. Within secondary political division, localities are arranged from south to north. For complete locality information, sources for coordinates, and museum catalog numbers of specimens examined, see Anderson (1999).

Heteromys australis. – 56 unique georeferenced localities, 189 total specimens examined – COLOMBIA: Antioquia: 1. Guatapé, 1880 m (0614/7510); 2. Bellavista, 1200 m (0626/7520); 3. Alto Bonito, 1500 ft (0705/7630); 4. Ventanas, 2000 m (0705/7527); 5. Valdivia, 1200–1900 m (0706/7528); 6. La Frijolera, 5000 ft (0710/7525); 7. Quebrada Valdivia, 900 m (0710/7526); 8. Villa Arteaga, 130 m (0720/7626); 9. Purí, 200 m (0725/7520); Boyacá: 10. Las Quinchas, 1175 m (0549/7418); Caldas: 11. El Estadero, 1850 m (0531/7504); 12. Río Hondo, 1100–1400 m (0542/7501); Chocó: 13. San José del Palmar, 1000 m (0454/7623); 14. Bagadó, 1000 ft (0525/7624), 15. Alto Limón, 600 m (0756/7710); 16. Río Ipetí, ca. sea level (0801/7707); Córdoba: 17. upper Río Sinú, 100–150 m (0751/7617) – sympatry with *H. anomalus*; Cundinamarca: 18. Paime, 1038 m (0522/7410); Huila: 19. Río Suaza, 1400–1600 m (0137/7559); 20. San Adolfo, 1400 m (0149/7552); Nariño: 21. Maindés, 870 m (0115/7810); 22. Río Ñambí, 1300 m (0118/7803), 23. Buenavista, 1200 ft (0129/7805); 24. Barbacoas, 35 m (0141/7809); Quindío: 25. Salento, 7000–7100 ft (0438/7534); 26. Filandia, 1950 m (0440/7537); 27. El Roble, 7200 ft (0441/7536); Risaralda: 28.

La Suiza, 1950 m (0444/7535); 29. La Jalea, 1720 m (0521/7553); 30. Empalado, 1900 m (0522/7553), 31. Puerto de Oro, 1300 m (0527/7604); Valle del Cauca: 32. Peñas Blancas, 1800 m (0327/7643); 33. Pichindé, 1800–1900 m (0327/7637); 34. San Antonio, 2000 m (0330/7638); 35. El Jordán, 2450 m (0332/7640); 36. Alto Anchicayá, 600 m (0336/7654); 37. Bajo Anchicayá, 230 m (0337/7656); 38. Virology Station, 30 m (0338/7705); 39. Las Lomitas, 5000 ft (0338/7638); 40. Río Raposo, ca. sea level (0341/7705); 41. Llano Bajo, 50 m (0342/7658); 42. Morro Frío (0344/7640); 43. Zabaletas, 50 m (0347/7659); 44. El Silencio, 1500 m (0348/7637); 45. Río Escalerte, 50 m (0350/7654); 46. Río Dagua, 50 m (0352/7657); 47. Yotoco, 1500 m (0353/7628); 48. Estación Río Azul, 500 m (0357/7640); 49. Bajo Calima, 40 m (0400/7656); 50. Bahía Málaga, 0–60 m (0407/7714), 51. Bolívar (0426/7619); Valle del Cauca-Chocó: 52. Alto de Galápagos, 2000 m (0453/7613). ECUADOR: Esmeraldas: 53. San Javier, 60–120 ft (0104/7847); 54. Bulím, 50 m (0105/7840); Los Ríos: 55. Río Palenque, 220 m (0034 S/7920). VENEZUELA: Táchira: 56. Pregonero, 1100 m (0757/7142).

Heteromys anomalus. – 40 unique georeferenced localities, 214 total specimens examined – COLOMBIA: Antioquia: 57. Caucasia, 250 m (0753/7512); 58. Río Currulao, 50 m (0800/7644); Atlántico: 59. Ciénaga de Guájaro, 15 m (1037/7502); Bolívar: 60. Norosí, 180 m (0838/7404); 61. San Juan Nepomuceno, 167 m (0958/7504); Cesar: 62. El Guaimaral, 140 m (1014/7330); 63. Caracolicito, 400 m (1018/7400); 64. El Salado, 430 m (1022/7329); 65. Pueblo Bello, 1067 m (1024/7339); Córdoba: 17. upper Río Sinú, 100 m (0751/7617) – sympatry with *H. australis*; 66. Catival, 120 m (0817/7541); 67. Montería, 15 m (0846/7553); 68. San Andrés de Sotavento (0908/7532); Cundinamarca: 69. Ricaurte, 350 m (0418/7443); 70. Volcanes, 250 m (0527/7431); La Guajira: 71. Sierra Negra, 1500 m (1036/7255); 72. Villanueva, 280 m (1037/7258); 73. Las Marimondas, 1000 m (1052/7243); 74. Mamorongo, 3000 ft (1057/7318); 75. San Miguel, 1700 m (1058/7329); 76. Pueblo Viejo, 8000 ft (1059/7327); 77. San Francisco, 6000 ft (1100/7326); Magdalena: 78. Palomino, 600 m (1102/7339); 79. Alto de Mira, 1050 m (1108/7354); 80. Minca, 1000–2000 ft (1109/7407); 81. Onaca, 680 m (1111/7404); 82. Bonda, 150 ft (1114/7408); 83. Mamatoca, 100 ft (1114/7410); 84. Buritaca, ca. sea level (1115/7346); 85. Don Diego, 5 m (1115/7342); 86. Masinga Vieja, 500 ft (1116/7405); 87. El Cedro, 420 m (1119/7401); Norte de Santander: 88. Durania (0743/7240); 89. La Donjuana, 1100 m (0745/7235); 90. Guamalito, 600 m (0834/7327); 91. Río Tarrá, 200 m (0836/7301); Sucre: 92. Colosó, 175–350 m (0930/7521); Tolima: 93. Melgar, 430 m (0412/7439); 94. Chicoral, 1800 ft (0413/7459); 95. Honda, 600 ft (0512/7445).

Appendix 2

Colombian locality records of *Heteromys australis* and *H. anomalus* in areas of potential sympatry between the two species. Conventions follow Appendix 1.

Heteromys australis. – COLOMBIA: Antioquia: 2. Bellavista, 1200 m (0626/7520); 6. La Frijolera, 5000 ft (0710/7525); 7. Quebrada Valdivia, 900 m (0710/7526); Boyacá: 10. Las Quinchas, 1175 m (0549/7418); Cundinamarca: 18. Paime, 1038 m (0522/7410); Huila: 20. San Adolfo, 1400 m (0149/7552); Quindío: 25. Salento, 7000–7100 ft (0438/7534); 26. Filandia, 1950 m (0440/7537); 27. El Roble, 7200 ft (0441/7536); Risaralda: 28. La Suiza, 1950 m (0444/7535); 29. La Jalea, 1720 m (0521/7553); 30. Empalado, 1900 m (0522/7553), Valle del Cauca: 33. Pichindé, 1800–1900 m (0327/7637); 35. El Jordán, 2450 m (0332/7640); 39. Las Lomitas, 5000 ft (0338/7638); 47. Yotoco, 1500 m (0353/7628); 51. Bolívar (0426/7619).

Heteromys anomalus. – COLOMBIA: La Guajira: 74. Mamorongo, 3000 ft (1057/7318); 75. San Miguel, 1700 m (1058/7329); 76. Pueblo Viejo, 8000 ft (1059/7327); Magdalena: 78. Palomino, 600 m (1102/7339).

Appendix 3

Colombian locality records of *Heteromys australis* and *H. anomalus* in areas of potential sympatry along real contact zones. Conventions follow Appendix 1.

Heteromys australis. – COLOMBIA: Antioquia: 6. La Frijolera, 5000 ft (0710/7525); 7. Quebrada Valdivia, 900 m (0710/7526); Boyacá: 10. Las Quinchas, 1175 m (0549/7418); Cundinamarca: 18. Paime, 1038 m (0522/7410); Huila: 20. San Adolfo, 1400 m (0149/7552).