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RESEARCH ARTICLE

Geographical distributions of spiny pocket mice in South America: insights from predictive models

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ABSTRACT

Aim Predictive models of species' distributions use occurrence records and environmental data to produce a model of the species' requirements and a map of its potential distribution. To determine regions of suitable environmental conditions and assess biogeographical questions regarding their ranges, we modelled the potential geographical distributions of two spiny pocket mice (Rodentia: Heteromyidae) in north-western South America.

Location North-western South America.

Methods We used the Genetic Algorithm for Rule-Set Prediction (GARP), environmental data from GIS maps and georeferenced collection localities from a recent systematic review of *Heteromys australis* and *H. anomalus* to produce the models.

Results GARP models indicate the potential presence of *H. australis* throughout mesic montane regions of north-western South America, as well as in some lowland regions of moderately high precipitation. In contrast, *H. anomalus* is predicted to occur primarily in drier areas of the Caribbean coast and rain-shadowed valleys of the Andes.

Conclusions The models support the disjunct status of the population of *H. australis* in the Cordillera de Mérida, but predict a continuous distribution between known populations of *H. anomalus* in the upper Magdalena Valley and the Caribbean coast. Regions of suitable environmental conditions exist disjunct from known distributional areas for both species, suggesting possible historical restrictions to their ranges. This technique holds wide application to other study systems.

Key words biogeography, Colombia, disjunct distributions, distribution model, GARP, GIS, genetic algorithm, *Heteromys*, pocket mice.

INTRODUCTION

Geographical distributions

Many factors affect a species' geographical distribution (Udvardy, 1969; MacArthur, 1972). Foremost, the species' autecological requirements constitute its fundamental niche — the intersection of necessary conditions for multiple environmental variables, such as temperature, precipitation or availability of refuge sites and other key resources (Hutchinson, 1957). Suitable conditions may exist in many regions, but other biological and historical realities typically prevent a species from existing throughout its full potential geographical distribution (Brooks & McLennan, 1991; Brown *et al.*, 1996). For example, a species' utilization of this ecological potential may be modified by interactions with other species (e.g. competitors, predators, or parasites), reducing its fundamental niche into a fraction or subset that can be exploited — the realized niche (Hutchinson, 1957). Additionally, historical factors have often acted to restrict a species' distribution (Brown & Lomolino, 1998; Patterson, 1999; Peterson *et al.*, 1999).

Distributional records document species' geographical ranges, which constitute the basis for subsequent levels of biogeographic research. Shortcomings exist, however, to the most common portrayals of geographical ranges in field guides and taxonomic revisions (Rapoport, 1982; Brown & Lomolino, 1998: 61–64). Shaded outline maps attempt to extrapolate a species' range between and beyond known localities, but do not specify the resolution of the underlying data and are highly dependent on subjective knowledge of the group and study region. In general, their broad-stroke approach probably grossly overestimates most species' distributions. At the other

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end of the spectrum, dot maps (documented localities plotted on a map) depict the species' range very conservatively, leaving the reader to draw conclusions regarding the true distribution. This problem is especially severe in poorly sampled tropical regions. For these reasons, analyses of the ecological and historical factors affecting species' distributions often have been hindered by the lack of an objective means of identifying regions with suitable environmental conditions (Haffer, 1967; Terborgh, 1971, 1985; Hoffmann, 1974: 526–531; Terborgh & Weske, 1975; Endler, 1982; Carleton & Musser, 1989: 55–65; Remsen & Graves, 1995a,b). Niche-based modelling provides a new method for depicting and studying species' ranges.

Predictive modelling

Recent studies have created predictive models of species' distributions in a geographical information systems (GIS) environment, motivated by questions of biogeography and conservation (Bojórquez-Tapia *et al.*, 1995; Yom-Tov & Kadmon, 1998; Godown & Peterson, 2000; Peterson *et al.*, 2000), faunal responses to climatic factors (Walker, 1990; Kadmon & Heller, 1998), effects of global climate change (Malanson *et al.*, 1992; Box *et al.*, 1993; Samways *et al.*, 1999), and evolutionary ecology and speciation (Peterson *et al.*, 1999). One method, the Genetic Algorithm for Rule-Set Prediction (GARP; http://biodi.sdsc.edu/), has been especially successful in predicting species' distributions (Peterson & Cohoon, 1999; Peterson *et al.*, 1999; Godown & Peterson, 2000; Sánchez-Cordero & Martínez-Meyer, 2000; Peterson, 2001; Peterson *et al.*, in press). GARP is a genetic algorithm (GA) approach that uses localities of a species' occurrence and environmental data from geographical coverages (digital maps) to produce a niche-based model of the species' environmental requirements (Stockwell & Noble, 1992; Stockwell & Peters, 1999). This complex expert-system model is then projected into geographical space as a map of the species' potential distribution (see Methods). Because GARP is a super-set of other approaches — e.g. logistic regression or bioclimatic-envelope rules (Box *et al.*, 1993; Skidmore *et al.*, 1996) — it should always have greater predictive ability than any one of them alone (Stockwell & Peters, 1999). It has shown superior performance in head-to-head tests vs. other common approaches (Peterson, unpublished, for BIOCLIM; Peterson and D. Kluza, unpublished, for vegetation-surrogate GAP analysis).

Although encompassing only a few of the possible niche dimensions (*sensu* Hutchinson, 1957), currently available digital environmental coverages provide data for the major physical variables that commonly influence species' macro-distributions (Root, 1988; Brown & Lomolino, 1998: 72; Peterson & Cohoon, 1999). Under a clear set of assumptions (Peterson *et al.*, 1999), a GARP model indicates areas potentially habitable by a species. None the less, few species actually occupy all areas of suitable environmental 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. Although the discrepancy between potential and realized distributions at first appears to be an unacceptable defect, this consequence of the niche-based nature of the models actually allows for synthetic studies of evolutionary ecology and biogeography (Peterson *et al.*, 1999).

Interpreting predictive models

These ecological-niche models use the environmental characteristics of a species' known distributional points and provide a means of assessing the environmental suitability of regions currently lacking records of the species. Do such cases represent areas of unsuitable environmental conditions, appropriate regions where the species is not present owing to historical restrictions or biotic interactions, or simply artefacts of inadequate collection effort? GARP models provide an answer to the first possibility, at least in the environmental dimensions examined: regions of predicted absence do not fulfil the niche requirements of the species.

On the other hand, areas of suitable climatic and physical conditions lacking species records may have several interpretations. Where collection effort has been sparse, further conclusions must await new field efforts. However, two possibilities exist in regions of high collection effort lacking species records. One is that the species' requirements on an unexamined niche dimension may not be met. For species with clear association with other organisms (known mutualisms, obligate food sources, etc.), the distribution of that requisite resource should be included either in the environmental data used to create the model or in the process of interpreting the model. For generalists such as *Heteromys* (see below), however, identification of additional important niche dimensions is problematic, and models are more likely to represent the species' fundamental niche adequately.

Conversely, if sufficient niche dimensions are examined, regions of potential presence that lack species records may highlight instances where either historical causes or biotic interactions (e.g. competition, predation, parasitism) have played a role in restricting the species' realized distribution. Although knowledge of the group's biogeographic history aids in assessing these possibilities, field studies are necessary to interpret biotic hypotheses, and historical restrictions remain difficult to document — especially without a well-documented fossil sequence that lacks records of the species. Despite these caveats, predictive modelling presents a significant step forward in the portrayal of species' distributions and investigation of the factors that affect them. Consequently, we here model the potential distributions of two spiny pocket mice to identify areas matching their basic environmental requirements and interpret those models following the framework outlined above.

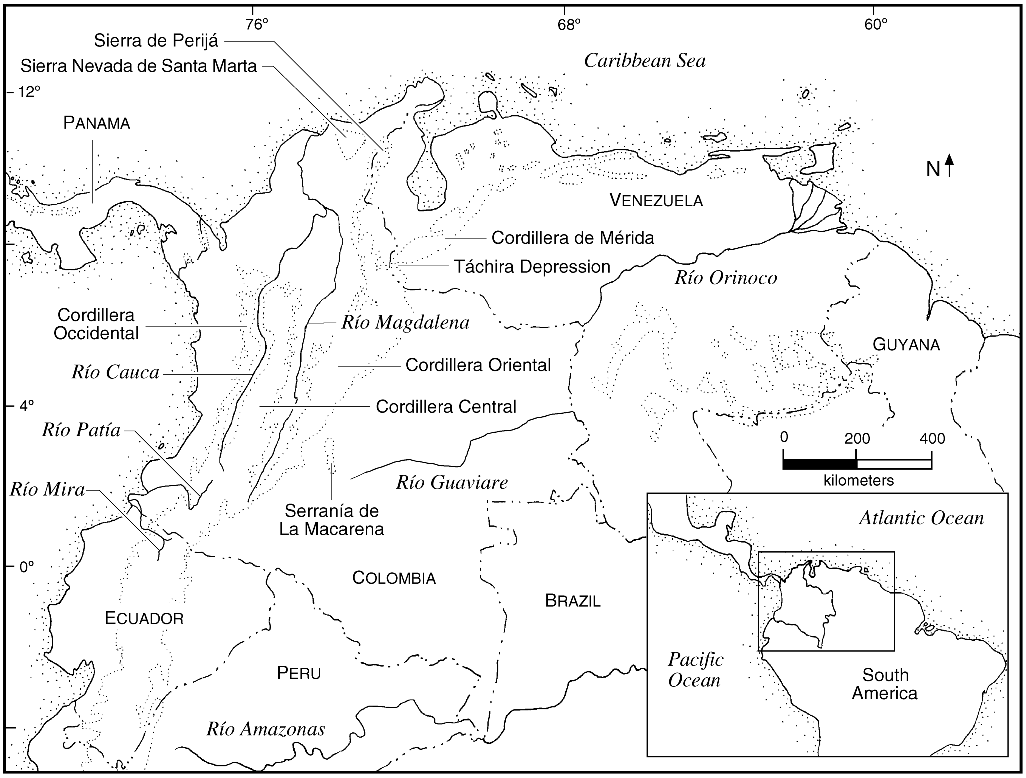

Fig. 1 Major geographical features of north-western South America discussed in the text. Dotted lines over land show approximate 1000 m contours of elevation.

METHODS

Study group: spiny pocket mice

History and distributions

Two species of spiny pocket mice constitute an excellent study system for distributional-modelling research. Spiny pocket mice (Rodentia: Heteromyidae: Heteromyinae) originated in North America, with fossil forms known from the Miocene of Nebraska and South Dakota (Wood, 1935; Rogers, 1990). *Heteromys* and *Liomys* are monophyletic sister genera that form the subfamily (Patton, 1993; Anderson, unpublished). *Heteromys* represents a North American group that has achieved only limited colonization of South America (Hershkovitz, 1972; Simpson, 1980), although the timing of its arrival remains controversial (Anderson & Soriano, 1999; Anderson, 1999). Faunal filters have often been invoked to describe the exchange between the two continents (Haffer, 1970; Hershkovitz, 1972; Simpson, 1980; Marshall *et al.*, 1982; Alberico, 1990; Webb & Rancy, 1996). No obvious barrier limiting further colonization of South America exists for spiny pocket mice, however, which have already surmounted three significant biogeographic barriers: the Bolívar Geosyncline (Hershkovitz, 1972), the Río Magdalena and even the Andes (Fig. 1). However, spiny pocket mice remain restricted to the north-western reaches of the continent. Predictive models provide an objective means by which to assess the potential suitability of various regions and thus assist in interpreting *Heteromys* distributions in South America.

In contrast to the rest of the family Heteromyidae (Schmidly *et al.*, 1993), congeneric species of spiny pocket mice (subfamily Heteromyinae) are seldom syntopic or even collected sympatrically (Genoways, 1973; Anderson, 1999). Where ranges meet, species typically segregate into distinct habitats (Genoways, 1973; Rogers & Engstrom, 1992; Sánchez-Cordero & Fleming, 1993). A recent taxonomic review showed that *Heteromys australis* Thomas (1901) and *Heteromys anomalus* (Thompson, 1815) are both widespread in north-western South America and possess geographically and ecologically complementary ranges (Anderson, 1999; Fig. 2). *Heteromys australis*, the southern spiny pocket mouse, inhabits wet rain forests in the Pacific lowlands of Ecuador, Colombia and eastern Panama and continues its distribution eastward throughout montane forests of the Colombian Andes — up to about 2500 m (Anderson, 1999; Fig. 2). The species is also known from one locality in the Cordillera de Mérida in western Venezuela

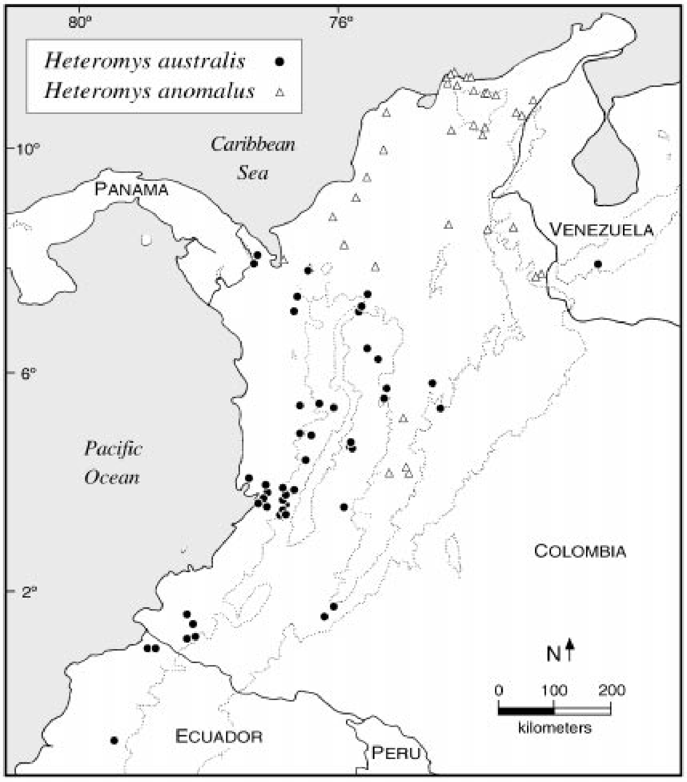

Fig. 2 Collection localities of *Heteromys australis* Thomas (1901) (solid circles) and *Heteromys anomalus* (Thompson, 1815) (open triangles) used in this study. Data were taken from Anderson (1999); some adjacent localities are not visible as distinct symbols. In addition to these distributional points, *H. australis* extends slightly west into Panama, and *H. anomalus* ranges eastward throughout northern Venezuela and Trinidad & Tobago (not shown). Dotted lines denote regions over 1500 m.

(Anderson & Soriano, 1999; Fig. 2). In contrast, *Heteromys anomalus*, the Caribbean spiny pocket mouse, is found primarily in deciduous and semideciduous forests and agricultural areas of the Caribbean coastal lowlands and montane foothills of northern Colombia and Venezuela (Anderson & Soriano, 1999; Anderson, 1999; Fig. 2). It also inhabits similar habitats in the upper Río Magdalena Valley. In Colombia, *H. anomalus* is generally restricted to low elevations, but occasionally ranges up to about 1500 m. Despite a large number of confirmed records for both species, they are known to be sympatric at only one locality (100 m on the upper Río Sinú, Socorré, Córdoba, in north-western Colombia; Anderson, 1999). Other species of *Heteromys* in north-western South America are locally restricted and only marginally affect these analyses of the two widespread species in Colombia, Ecuador, and western Venezuela (Paraguaná Peninsula – Handley, 1976; Serranía del Darién and two Antioquia localities – Anderson, 1999).

Biogeographic questions

The details of these two species' distributions pose biogeographic questions that can be addressed with predictive models. Some populations of each species are thought to be disjunct, presumably as a result of climatic changes that fragmented formerly continuous distributions (Anderson & Soriano, 1999; Anderson, 1999). For example, *Heteromys australis* has been found in the Cordillera de Mérida, a disjunct mountain range that lies east of the Táchira Depression (an area of low hills and ridges that separates the Cordillera de Mérida from the Cordillera Oriental; Anderson & Soriano, 1999; Figs 1, 2). Anderson & Soriano (1999) hypothesized that the Táchira Depression, which represents an important faunal barrier for montane taxa (Cracraft, 1985; Renjifo *et al.*, 1997; Soriano *et al.*, 1999), is currently too xeric for *H. australis*. Similarly, the population of *H. anomalus* in the upper Magdalena Valley (Figs 1, 2) may be disjunct from coastal populations, as the intervening area is wetter (Anderson, 1999).

Some regions lack records altogether. For example, *Heteromys australis* is not known from the humid lowlands of Amazonia, in spite of the apparent similarity of those forests to wet rain forests of the Chocó in western Colombia, where the species has been documented (Fig. 2). Potential source populations of *H. australis* exist near a low pass at the southern end of the Cordillera Oriental in forests historically contiguous with

Amazonian forests to the east (Miller, 1918; Anderson, 1999). Similarly, *H. anomalus* has not been collected from the upper Río Cauca or Río Patía valleys in western Colombia, areas with vegetation similar to the upper Magdalena, where the species is present (Figs 1, 2).

Data sources

We modelled the environmental requirements of *Heteromys australis* and *H. anomalus* using georeferenced localities for Colombia and Ecuador as well as the lone locality for *H. australis* in Venezuela (see Anderson, 1999; for complete data sources). This data set consists of 56 unique collection localities for the former species and 40 of the latter (Fig. 2), an adequate sample for such analyses (Stockwell & Peterson, in press). It excludes known distributional points for *H. australis* in eastern Panama (outside the scope of our environmental data) and for *H. anomalus* in Venezuela and Trinidad & Tobago (because a full set of verified, georeferenced localities is not yet available there). If peripheral populations occupy environmental conditions outside those typified by our sample, exclusion of records from these distributional areas may lead to an underestimation of the species' fundamental niches. However, Panamanian collection localities of *H. australis* (Anderson, 1999) and Venezuelan collection localities of *H. anomalus* examined to date (Anderson & Soriano, 1999; Anderson, unpublished) appear to agree with the environmental patterns of those species in Colombia. Here, we focus on the Colombian and Ecuadorian ranges of these species and present maps only for north-western South America (3°S–13°N, 70–81°W). Finally, by using records from a variety of museums and collectors, we minimize possible collecting biases that might favour particular regions or biomes and thus adversely affect the models.

The base environmental data (GIS coverages) that we used in creating the models included physical, biotic and climatic variables, as well as seasonal values for some of them. 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, separate coverages representing the upper and lower bounds of 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. We used the 1 km^2 digital elevation model for South America from the EROS Data Center (http://edcwww.cr.usgs.gov/) to prepare the elevation, slope and aspect coverages in latitude–longitude projections in ArcInfo 7.2.1 (ESRI, 1998a) and then generalized them to 0.04° pixels in ArcView GIS 3.1 (ESRI, 1998b). For the remaining 16 variables, we cut and then rasterized coverages for South America from ArcAtlas (ESRI, 1996) to coincide with the elevation, slope and aspect coverages.

Modelling

For the modelling effort, we employed the Genetic Algorithm for Rule-Set Prediction (GARP). GARP searches for non–random associations between environmental characteristics of localities of known occurrence vs. those of the overall study region (Stockwell & Noble, 1992; Peterson & Cohoon, 1999; Stockwell & Peters, 1999). It works in an iterative process of rule selection, evaluation, testing and incorporation or rejection to produce a heterogeneous rule set summarizing the species' ecological requirements (Peterson *et al.*, 1999). First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic-envelope rules). Then it is applied to the data, and a rule is developed. Predictive accuracy is evaluated based on points resampled both from the known distribution and from the study region as a whole. Change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model. The algorithm runs either 2500 iterations or until convergence. The final expert-system ecological model is a complicated series of if–then statements used to determine whether a particular pixel will be predicted present or absent (see Peterson & Cohoon, 1999; for a rarefaction experiment investigating the contribution of various coverages to model performance). The final model is then projected into geographical space as a digital map of areas with environmental characteristics suitable for the species.

Preliminary models

To examine model validity, we assessed both model significance and accuracy. First, to test for significance, we compared the predictive power of preliminary models against a random null hypothesis. We randomly divided the unique occurrence points for each species into two pools: *training data* (75% of points) used to develop the model, and *test data* (the remaining 25%) used to test the model. After developing the model, we tested whether test points fell into areas predicted present more often than expected at random, given the overall proportion of pixels predicted present vs. predicted absent for that species. Because expected values were not large enough in all cells to employ a χ^2 statistic (Zar, 1996), we calculated exact one-tailed binomial probabilities of observed proportions of test points falling in pixels of predicted presence and absence, respectively. This test of significance thus incorporated aspects of both omission of true distributional areas (as indicated by the test points) and inclusion of areas not inhabited (via the proportions of pixels predicted present, which influenced the expected binomial probabilities).

In addition to model significance (departure from random predictions), we assessed model accuracy by examining the proportion of test points falling into regions of predicted presence. Significant models are possible without correctly predicting an acceptable proportion of test points, if the predicted area represents a small proportion of the study area (in the species' core ecological region). Conversely, models can attain high accuracy without achieving significance by including an excessively large proportion of the study area. A good model should be both significant and accurate. Thus, after demonstrating significance, we interpreted the proportion of test points falling into regions of predicted presence, a measure of model accuracy.

Final models

After demonstrating that the preliminary model predicted test points significantly better than random, we modelled the species' potential geographical distribution *using all available localities*. Because GARP is an artificial-intelligence application with strong stochastic elements, it produces no unique solution. To temper among-model variation, we made three models per species and developed a composite prediction for each species: any pixel where the species was predicted present by at least two of the three models was considered predicted present. All further analyses were based on these composite models.

RESULTS

Preliminary models

The training data yielded models that predicted the distribution of test points significantly better than random for both species. For *Heteromys australis*, the preliminary model predicted potential presence for the species in 20.4% of the map pixels of land area. Of the 14 test points, 12 fell in pixels of predicted presence, and two lay in pixels of predicted absence (binomial probability, $P < 0.0001$). The two that fell in predicted absence were within 3 km of areas of predicted presence. Similarly, the preliminary model for *H. anomalus* predicted presence in 22.0% of the map pixels. Five of the 10 test points were located in pixels of predicted presence (binomial probability, $P = 0.0482$), and the other five points lay within 10 km of areas of predicted presence.

Composite models

The composite models predicted largely complementary potential ranges for the two species (Fig. 3). *Heteromys australis* (Fig. 3a) was predicted to range throughout wet montane regions of the northern Andes, including the Cordillera de Mérida, as well as some lowland areas of intermediate

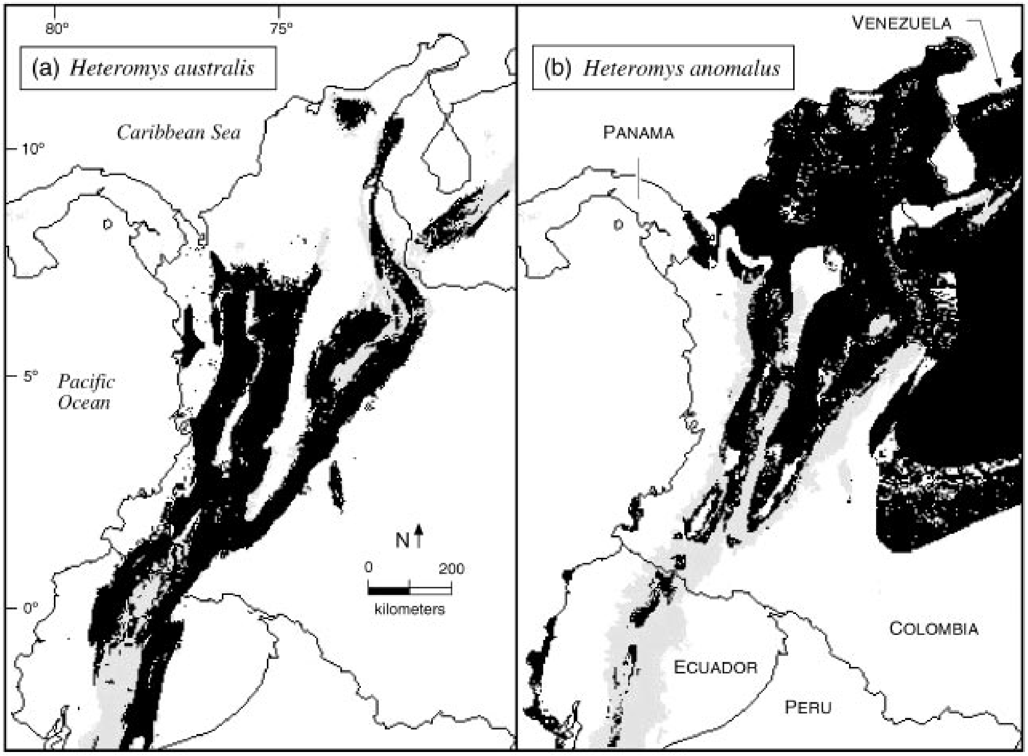

Fig. 3 Composite models of predicted potential distributions for *Heteromys australis* (a, left) and *H. anomalus* (b, right) in north-western South America. Potential distributions are shown in black over grey shading representing regions over 1500 m.

rainfall. The model also predicted presence in other disjunct mountain ranges: the Sierra Nevada de Santa Marta, the Serranía de Baudó and the Serranía de La Macarena. Outside the principal study area, potential distribution was also indicated on various *tepui* formations, the table-like mountains of the Guianan highlands (not shown). Drier areas of the Caribbean coast; rain-shadowed valleys of the Río Magdalena, Río Cauca, and Río Patía; the dry Táchira Depression; and most of the humid lowlands of the Chocó and Amazonia were predicted absent.

Conversely, appropriate conditions were predicted for *Heteromys anomalus* (Fig. 3b) throughout the dry to moderately mesic Caribbean lowlands of northern Colombia and Venezuela, as well as in most arid enclaves in the northern Andes — most notably the Río Magdalena Valley, the Río Cauca Valley, the perimeter of the valley of the Río Patía, and the upper Río Mira Valley and adjacent rain-shadowed areas of northern Ecuador. Additionally, the model indicated suitable habitat in some parts of the *llanos* (tropical savannas) of Venezuela and Colombia (north of Amazonian forests beginning at approximately the Río Guaviare and Río Orinoco). Extrapolating outside the main study area, the models predicted presence in the interior Guianan savannas and some adjacent forests, as well as in dry coastal areas of south-western Ecuador and north-western Peru (not shown). This species was generally predicted absent from wet lowland areas and mesic high montane regions.

DISCUSSION

Preliminary models

The preliminary models demonstrated both significance and acceptable accuracy. They predicted test points significantly better than random despite low statistical power. That low power derived from the division of training and test points (75%/25%), which provided only moderate numbers of localities for the tests. In addition to the significance demonstrated by the binomial probabilities, the proportions of test points properly predicted showed acceptable accuracy for both species. For *Heteromys australis*, the two localities that fell in pixels of predicted absence were within three km of predicted presence. Similarly, all five test points of *H. anomalus* not falling into pixels of predicted presence fell within 10 km of predicted presence. Clearly, 50% accuracy would not be acceptable if the test points fell far from regions of predicted presence. In this case, however, the test points that did not enter into predicted pixels fell very close to them.

Although geographical coordinates were conscientiously assigned to these localities from a variety of sources (Anderson, 1999), the low level of geographical detail provided by some collectors precluded exact location of all localities. Furthermore, collecting typically occurs within a radius of walking distance around a field camp. For these reasons, the coordinates for many localities are probably only accurate to 5 or 10 km. Thus, accuracy of test points to within 10 km is acceptable in the present case. Below, we conservatively interpret the composite models at a much coarser level.

Potential distributions and disjunct populations

Heteromys australis

The composite model for *H. australis* includes few wet lowland regions, *contra* Anderson (1999), who suggested that Amazonian rain forest east of the Andes might support this species. Those forests are seemingly similar to areas that the species inhabits in parts of the wet lowland Chocó in western Colombia and north-western Ecuador. Rather than being a species of mesic lowlands that can tolerate intermediate elevations (Anderson, 1999), the model characterizes *H. australis* as a species of wet montane regions that can descend to mesic lowlands under some circumstances. The model fails, however, by overpredicting the species to extend to higher montane regions, as *H. australis* is not known from above about 2500 m.

The models support the hypothesis that the population of *Heteromys australis* in the Cordillera de Mérida is disjunct (Fig. 3a). All three models for *H. australis* predicted presence there, yet none identified suitable habitat in the Táchira Depression that separates the Cordillera de Mérida from the species' range in the Cordillera Oriental. If this disjunction originated with Pleistocene glacial episodes (Anderson & Soriano, 1999), then the models provide evidence that the species was already present in South America before the Holocene. This interpretation rejects the Recent (Holocene) entry of South America for heteromyines assumed by Marshall *et al.* (1982), based on the lack of a fossil record for the group in South America. Populations in the Darién region of Colombia and Panama may also be disjunct from the central distribution of *H. australis*, with the poorly drained Atrato-San Juan lowlands currently blocking contact with populations in the western foothills of the Andes (see Haffer, 1970; Hershkovitz, 1972; Alberico, 1990). One of the three models predicted presence in the lowlands of the northern Chocó, however, so further sampling and analysis are necessary.

Heteromys anomalus

The model for *Heteromys anomalus* predicts that it could inhabit parts of the *llanos* of Colombia and Venezuela and the interior Guianan savannas. However, this species is not known to inhabit open grassland habitats (Handley, 1976; August, 1984; Soriano & Clulow, 1988). Thus, only gallery forests represent truly habitable environments within the areas of *llanos* where the species was predicted to occur. The resolution of the base vegetational coverage was likely insufficient to discriminate between these two habitat types effectively.

The models do not support the idea that the population of *Heteromys anomalus* in the upper Magdalena Valley (south of Honda and Caparrapí) is disjunct, *contra* Anderson (1999; Fig. 3b). All three models for *H. anomalus* indicate continuous potential distribution through the middle Magdalena region, linking known localities from the upper Magdalena to those in the Caribbean lowlands. Additional fieldwork in the region is needed to confirm the presence of *H. anomalus* in the middle Magdalena and the low Serranía de San Lucas north-west of Barrancabermeja.

Areas of potential distribution without known records

Heteromys australis

The composite model for *Heteromys australis* (Fig. 3a) suggests that it could inhabit the eastern slopes of the Cordillera Oriental of the Andes, where *Heteromys* has not been collected. Because no obvious barriers exist to prevent colonization of the eastern versant of the Cordillera Oriental from known localities at the headwaters of the Río Magdalena, historical restrictions seem unlikely. Hence, the lack of records there may be due to low collection effort in this region or to an unexamined biotic interaction (such as a predator, parasite, or competitor; Anderson, 1999: 623). The species' distribution in areas of continuous suitable environmental conditions present on the eastern slope of the Andes in Ecuador and extreme northern Peru is less certain, but it is doubtful that the species crosses the Huancabamba Depression in northern Peru. That region holds unsuitable habitat according to our models (not shown) and, along with xeric areas of the Río Marañón Valley, represents an important zoogeographic barrier for species adapted to wet forests (Chapman, 1926; Duellman, 1979; Parker *et al.*, 1985).

Environmental characteristics in the disjunct Sierra Nevada de Santa Marta, Serranía de La Macarena, and various *tepui* mountains of the Guianan highlands match this species' requirements (Figs 1, 3a). *Heteromys australis* is not known for any of those regions, all of which are separated from the Andes by areas lower and wider than the Táchira Depression. The Sierra Nevada de Santa Marta has been sufficiently well-collected to conclude that *H. australis* is not present there (Bangs, 1900; Allen, 1904). Similarly, extensive inventories in the Guianan region have failed to collect any *Heteromys* (Tate, 1939; Ochoa-G. *et al.*, 1988, 1993; Ochoa-G., 1995). To the extent that the examined niche dimensions accurately portray the species' requirements, failure to disperse to these regions constitutes a more parsimonious explanation than dispersal subsequently followed by local extinction. Thus, given the northern origin of heteromyines (see Introduction), historical restrictions seem quite likely in these instances. In contrast, although some rodents have been reported from the Serranía de La Macarena, general sampling effort has been inadequate to discount the presence of *H. australis* there (Voss, 1991, 1992; Musser *et al.*, 1998). The model also indicates suitable habitat for *H. australis* in the Sierra de Perijá, a northern extension of the Cordillera Oriental (Figs 1, 3a), but only *H. anomalus* is known from the lower slopes (Anderson, 1999; Anderson & Soriano, 1999; Fig. 2). Fieldwork at higher elevations in this range is necessary to address this question properly.

Heteromys anomalus

In addition to the species' known distribution, the composite model for *Heteromys anomalus* predicts potential distribution in low areas of the Cauca Valley, part of the Patía Valley, and several rain-shadowed interior basins of montane Ecuador (Fig. 3b). As the region of the Cauca Valley near Cali has received notable collection effort for mammals (Alberico, 1983), the easily captured *H. anomalus* would surely have been encountered there by now if present (Anderson (1999) reidentified all specimens from this region as *H. australis*). Its presence is even less likely in other peripheral valleys to the south, such as those of the Río Patía and Río Mira. The model also indicates that suitable conditions exist in the xeric lowlands of coastal Ecuador and Peru, far from any known records of the species. Because heteromyines entered South America from Central America, these examples probably represent historical restrictions to the species' distribution. Similarly, *Heteromys* is not known from south of the Río Orinoco in Venezuela, and virtually all records from that country derive from areas north of the *llanos* (Handley, 1976; Linares, 1998). Regions indicated as potential habitat in the interior Guianan (Rupununi) savannas and adjacent forested areas appear presently unreachable for *H. anomalus*, and its absence there probably stems from historical restrictions related to the northern origin of heteromyines.

Uses of predictive modelling

Although doubts remain regarding the distributions of these pocket mice, our analyses illustrate the kind of research that can now be accomplished with a large-scale geographical perspective using reliable species occurrence records and electronic maps of environmental variables. In particular, the objective criterion of suitable environmental conditions holds application both to studies assessing connectivity of known populations as well as research examining the ecological and historical factors affecting species' distributions. The utility of predictive modelling will vary according to the locality records and environmental data available, however (for data requirements see Stockwell & Peterson, in press; Peterson & Cohoon, 1999). In temperate regions with relatively well-documented species distributions and higher-quality environmental coverages, more accurate predictive models with greater spatial resolution should be possible. Nevertheless, modelling may actually prove more useful in tropical areas where species' distributions are poorly known due to inadequate sampling. There, these approaches allow evolutionary, biogeographic and conservation research based on data from specimens present in natural history collections when fieldwork is not possible or timely.

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