

DISTRIBUTION OF CAPYBARAS IN AN AGROECOSYSTEM, SOUTHEASTERN BRAZIL, BASED ON ECOLOGICAL NICHE MODELING

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Southeastern Brazil has seen dramatic landscape modifications in recent decades, due to expansion of agriculture and urban areas; these changes have influenced the distribution and abundance of vertebrates. We developed predictive models of ecological and spatial distributions of capybaras (*Hydrochoerus hydrochaeris*) using ecological niche modeling. Most occurrences of capybaras were in flat areas with water bodies surrounded by sugarcane and pasture. More than 75% of the Piracicaba River basin was estimated as potentially habitable by capybara. The models had low omission error (2.3–3.4%), but higher commission error (91.0–98.5%); these “model failures” seem to be more related to local habitat characteristics than to spatial ones. The potential distribution of capybaras in the basin is associated with anthropogenic habitats, particularly with intensive land use for agriculture.

Key words: Brazil, ecological niche models, genetic algorithm for rule-set prediction (GARP), geographic distribution, *Hydrochoerus hydrochaeris*, Piracicaba River basin

Habitat fragmentation is one of the more dramatic processes of landscape modification (Forman and Godron 1986) and causes of biodiversity loss (Bisbal 1988; Collinge 1996; Hannah et al. 1995; Lacher et al. 1999; Noss and Csuti 1994). Southeastern Brazilian habitats have suffered extensive fragmentation due to agriculture and urbanization in recent decades. Deforestation in São Paulo State, Brazil, totaled $\sim 4.1 \times 10^6$ ha during 1962–1992 (Kronka 1994). Indeed, the Piracicaba River basin in São Paulo State ranks among the most developed and impacted regions of Brazil, due to both urban and agricultural expansion (Lara et al. 2001), with 70% of its area occupied by pasture and sugarcane (Ballester 2001). Habitat fragmentation that frequently accompanies deforestation further influences species’ distributions and abundances (Kalkhoven 1993; Savard et al. 2000; Wiens 1996).

Ecological niche modeling allows identification of environmental factors affecting species’ distributions and abundances (Morrison et al. 1998). Ecological niche modeling is receiving considerable attention from the scientific community because it permits objective characterization of species–habitat relationships on broad scales (Jackson et al. 2000; Leemans 1999). Ecological niche models developed using the genetic algorithm for rule-set prediction (GARP—Stockwell and Noble 1992) have proven useful in diverse applications (Feria and Peterson 2002; Illoldi et al. 2004; Levine et al. 2004; Martínez-Meyer et al. 2004, 2006; Nakazawa et al. 2004; Peterson 2006a; Peterson et al. 2002, 2006; Peterson and Vieglais 2001; Wiley et al. 2003).

Capybaras (*Hydrochoerus hydrochaeris*), the largest living rodents, are social mammals widely distributed in diverse habitats, from riparian forest habitats to seasonally flooded savannas (Moreira and Macdonald 1997; Ojasti 1973, 1991). They have apparently been favored by landscape alteration in southeastern Brazil (Ferraz et al. 2007), because the highest densities have been recorded in anthropogenic habitats

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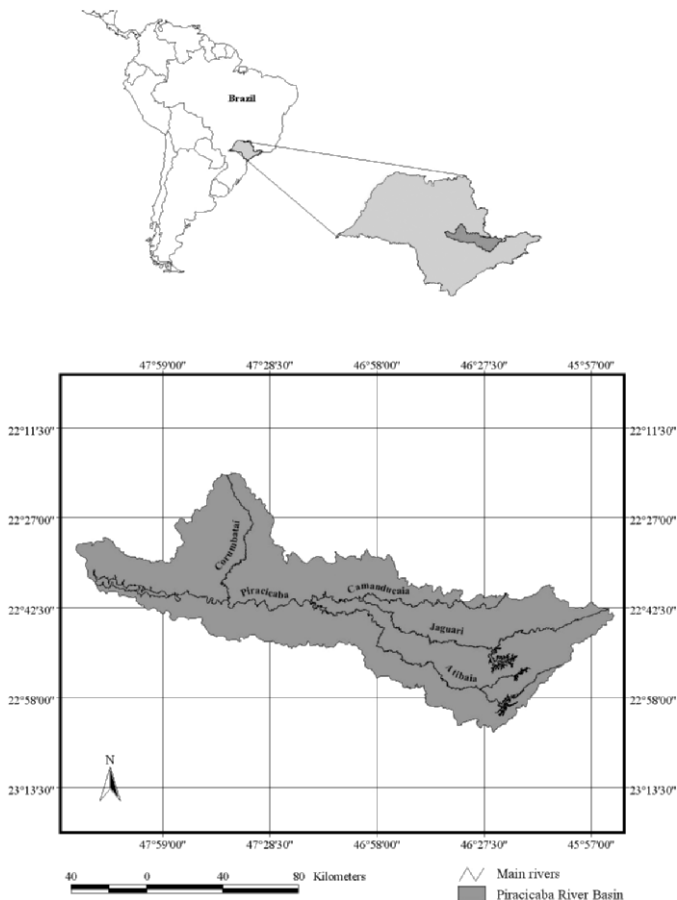


FIG. 1.—Piracicaba River basin with insets indicating location in São Paulo State, southeastern Brazil.

(Verdade and Ferraz 2006). Great availability of food from agricultural activities, open areas created by deforestation, and local elimination of predators have possibly permitted capybara population increases, as with some ungulates (McCullough 1997). Crop damage (Ferraz et al. 2003), as well as risk to human health, is associated with high capybara densities. Capybaras are the main host of *Amblyomma cajennense*, an important vector of spotted fever in Brazil (Labruna et al. 2001, 2004; Pereira and Labruna 1998). Considering the importance of capybaras to wildlife management and conservation, we aimed to understand factors affecting the distribution of capybaras in an anthropogenically modified river basin where the species is widespread and abundant.

MATERIALS AND METHODS

The study was carried out in the Piracicaba River basin, a mesoscale drainage basin located in southeastern Brazil (22°00'–23°30'S, 45°45'–48°30'W; Fig. 1). The basin comprises ~12,400 km² (4.7% of São Paulo State), has ~3 million inhabitants, and includes 61 municipalities, some of which reported crop damage and spotted fever incidence associated with capybaras (Ferraz et al. 2003; Labruna et al. 2004).

The basin is elongated (~250 × 100 km), with a highly dense drainage of ~7,850 km of watercourses, including the

Piracicaba (137 km), Jaguari (180 km), Atibaia (170 km), Corumbataí (112 km), and Camanducaia (100 km) rivers. The basin is covered by agroecosystems, predominantly C4 plants (43.20% pasture, 33.66% sugarcane), with only 10% of the original forest cover remaining (Krusche et al. 2003).

We selected 155 study sites (spatial accuracy ~30 m) at random by videography and by interpretation of Landsat5 Thematic Mapper (TM) images (Instituto Nacional de Pesquisas Espaciais, São José dos Campos, São Paulo, Brazil—Anthony et al. 1995; Sidle and Ziewitz 1990). In addition to being low-cost, videography allows location of small habitat patches not detectable in the coarser satellite images. We analyzed the images from the videography by eye and identified water bodies for sampling. All the study sites had at least 1 water body considered a vital resource for the capybara (Ojasti 1973). Study sites with no water body were not included in sampling because we knew beforehand that it was impossible for capybaras to occur there. Hence, it is important to note that we sampled only sites of likely presence, which has implications for evaluations of commission error rates. We checked the occurrence of capybaras at these sites via observation of individuals, detection of tracks and feces, or both (Thompson et al. 1998). As observed by Pinto et al. (2006), detectability of capybaras varies among study sites mainly due to the presence of vegetation, but capybara signs are conspicuous.

Ecological niche models were based on capybara occurrence points and raster geographic information system layers (environmental variables) describing aspects of the environment: unclassified and classified Landsat5 TM images (both from 1997, composition 3, 4, 5), land use–land cover (Martinelli et al. 1999), soil type, elevation, slope, curvature of terrain, and gradient distance from drainage (all developed as part of the Piracena Project; <http://www.cena.usp.br/piracena/>). We resampled all maps to a pixel resolution of 100 m for analysis (the original resolution was 30 m for all maps).

We used GARP (Stockwell 1999; Stockwell and Noble 1992) to model potential distribution of capybaras. GARP acts in an iterative process of rule selection, evaluation, testing, and incorporation or rejection to produce a heterogeneous rule-set characterizing the species' ecological requirements (Anderson et al. 2003; Peterson 2006b). We carried out all of the modeling via a desktop implementation of GARP (Scachetti-Pereira 2001), available for public download (<http://www.lifemapper.org/desktopgarp/>).

We produced 2 models, 1 based on a random sample of 50% of known-presence points ($n = 45$) and another based on all available occurrence data ($n = 89$). Within GARP processing, we split available occurrence points randomly (50–50) into training and testing data sets for both models. We used a jackknife procedure (Peterson and Cohoon 1999; Peterson et al. 2003) to select subsets of variables that best explained distributions of capybaras in the study area, in which each variable was omitted sequentially to explore the positive and negative effects of inclusion of particular variables in the analysis. We calculated Pearson correlation coefficients between a binary variable representing inclusion and exclusion

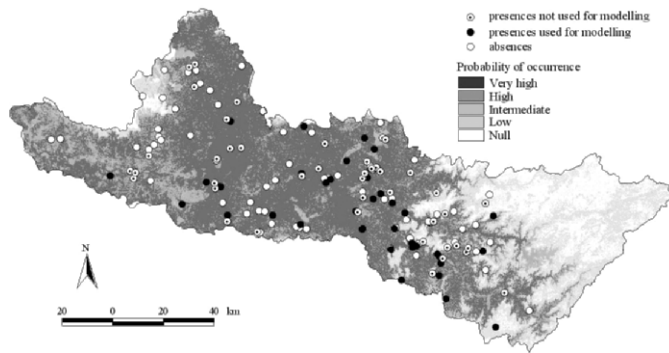


FIG. 2.—Predictive distribution model of capybaras (*Hydrochoerus hydrochaeris*) based on a 50% random subsample of known-presence points, Piracicaba River basin, southeastern Brazil.

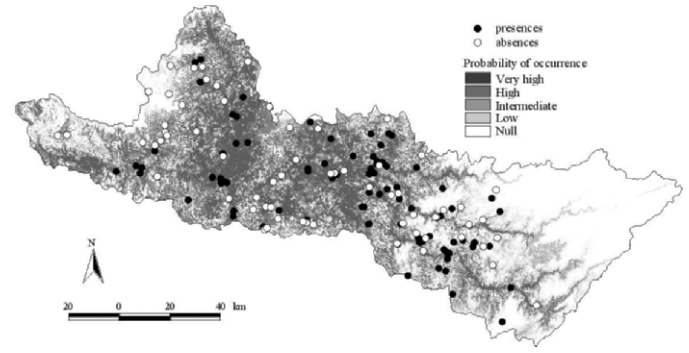


FIG. 3.—Predictive distribution model of capybaras (*Hydrochoerus hydrochaeris*) based on all presence points, Piracicaba River basin, southeastern Brazil.

of each variable and measured omission error rates, and variables for which these correlations were $r > 0.1$ were omitted from further analysis. We repeated the jackknife procedure until all remaining variables were either unassociated or negatively associated with omission error rates. Based on this reduced set of variables, we conducted a final model run, and projected the final ecological niche model across the entire basin to produce a digital map of the species' hypothesized potential distribution.

We performed 1,000 replicate models of capybara ecological niches with the chosen subset of variables for each model. We used the best subsets procedure of Anderson et al. (2003) to select the "best" 20 from these models, based on optimal combinations of error statistics. We summed these 20 models so each pixel in the composite map had values ranging from 0 to 20, indicating levels of model agreement in predicting presence or absence (Anderson et al. 2003). Then, we grouped predictive levels in 5 classes of model agreement in predicting potential presence (very high, ≥ 16 ; high, 11–15; medium, 6–10; low, 1–5; and null, 0) to facilitate interpretation.

We performed an independent test of model predictivity using a random sample of 50% of known-presence points to establish whether models have significant predictive ability. We tested model predictivity by a 1-tailed chi-square statistic to test against a null hypothesis of no association between prediction and testing data points (Anderson et al. 2003), indicating whether testing points fell into areas predicted as present more often than expected at random. Model performance was assessed by a confusion matrix tabulating predictions for testing data, and by quantitative measurements derived from it: omission or false negative rate, where the species has been observed on a site but is not predicted (type II error); and commission or false positive rate, where the species is predicted to occur on a site but has not been observed (type I error). The correct classification rate indicates the overall accuracy of prediction (Fielding and Bell 1997).

RESULTS

In field surveys, 89 presences and 66 absences were detected for capybaras ($n = 155$). Capybaras were observed directly in

only 8.4% of presence sites; in the rest, the species' presence was verified indirectly based on tracks and feces. Most sites where capybaras were present were anthropogenic habitats characterized by flat topography (0–6% slope), with a water body surrounded by sugarcane and pasture.

The jackknife procedure identified a subset of environmental variables that best explained capybara occurrences: reflectance on the unclassified Landsat5 TM image, gradient distance from drainage, elevation, curvature of terrain, and soil type. Other variables tested were eliminated because of positive correlations with overall omission error of models.

The GARP models predicted much of the Piracicaba River basin as potential distributional area for capybaras (Figs. 2 and 3). Most predicted areas were in the midwestern portion of the basin, characterized predominantly by agricultural areas with slopes of $\sim 3\%$. A total of 72.4% of the basin (9,071 km²) presented intermediate-to-high probability of capybara occurrence in the GARP model based on 50% of observations, of which about 51.8% were areas of very high probability, concentrated in sugarcane (3,251 km²) and pasture (1,943 km²). The GARP model based on all observations resulted in a total of 53.3% of the basin (6,681 km²) with intermediate-to-high probability of capybara occurrence, of which about 33.1% were areas of very high probability, concentrated in sugarcane (2,323 km²) and pasture (976 km²).

The performance of the models based on one-half of available data and on all data showed overall 40% and 59.4% correct classification rates, respectively, the latter being higher likely because it was not based on independent testing data. More than 95% of known-presence points were observed in areas predicted by the model as present (97.7% for the model based on a subset of data, and 96.6% for the model based on all data). Both models had low omission error: $\sim 2.3\%$ for the model based on a subset of data, and $\sim 3.4\%$ for the model based on all data, with 88.6% and 85.4% of the study area predicted as highly suitable for the species, respectively, by the 2 models. Although models were accurate (i.e., predictions better than random expectations) in predictions of presence (both $P < 0.001$), predictions of absence were equivocal, with commission errors of 98.5% for the subset data and $\sim 91\%$ for the all-data model. In evaluating the models, 95.5% and 74.2%

of absence points were in areas with predicted medium-to-high probability of presence for the 2 models, respectively; just 1.5% and 9.1% of the absence points were predicted to have null probability of species occurrence, respectively.

DISCUSSION

Capybara habitat in the Piracicaba River basin can be described as open, flat areas associated with agricultural fields and herbaceous vegetation near water bodies and strong human presence (Ferraz et al. 2007). Most of the variability (85%) of land cover in the study sites was explained by the 2 variables—pasture and sugarcane—highly correlated with the 1st component and inversely correlated with one another (Ferraz et al. 2007). This habitat type reflects the largely anthropogenic nature of the basin (Krusche et al. 2003), and capybaras can reach high densities in this region (Verdade and Ferraz 2006). Capybaras are large, generalist herbivores with diets composed predominantly of C4 plants (Barreto and Herrera 1998; Escobar and González-Jiménez 1976; Quintana et al. 1994, 1998). Vegetation type can influence the species' distribution, because high densities are associated with habitats with C4 plants (Aldana-Domínguez et al. 2002; Ferraz et al. 2007). The great availability of food provided by agricultural activities in this basin has likely contributed to increasing habitat carrying capacity and promoting colonization of new areas.

The proximity of capybara populations to water bodies reflects their strong relationship with water as a resource for many activities, such as predator avoidance and reproduction (Herrera and Macdonald 1989). Because streams and rivers are used as dispersal corridors by capybaras, regions holding numerous drainages should hold high populations. Capybaras should colonize suboptimal habitat close at hand or disperse over greater distances (Herrera and Macdonald 1987). Competition for resources—water and grass—under a social system involving group living and territoriality should be the main cause of dispersal of capybaras (Herrera 1992). Topographic complexity, on the other hand, seems to be a limiting factor for capybaras, because they prefer flat regions with lentic water bodies.

The GARP presence-only-based ecological niche models of capybara distribution predicted >75% of the basin as potential area for capybara occurrence. Environmental variables selected by the jackknife procedure were closely related to known details of the species' biology. Elevation and curvature are both physical attributes of landscape related to drainage distribution and configuration, vital resource for capybaras (Herrera and Macdonald 1989; Ojasti 1973). Gradient distance from drainage reemphasizes the importance of water for the species. The satellite image reflects land cover and land use, and the soil map focuses on ground characteristics (both related to food resources and habitat type).

The model of capybara occurrence seemed to be accurate given its low omission error or type II error (about 2.3% and 3.4%), suggesting that this model is highly accurate for capybaras in the study area. However, absence predictions presented low accuracy in the form of high commission error or

type I error (about 98.5% and ~91%). However, it is important to note that areas of likely presence were chosen for sampling a priori based on the video imagery, so many areas that probably would have been predicted correctly as "absent" were excluded from the analysis before testing or even sampling. As such, the commission error index presented above is not a realistic evaluation of model performance. Besides that, most sites at which capybaras were predicted as present, but were actually absent, seemed adequate for capybaras, containing all habitat attributes (e.g., food, cover, water, etc.) essential for their occurrence. Although these sites seemed adequate for capybaras, some specific and local characteristics (e.g., hunting pressure, recent land cover modification, physical barriers such as roads or fencing, etc.), not "visible" in the ecological niche modeling procedures, could explain their absence and the high commission error rates, or they could simply be unoccupied appropriate sites.

Areas predicted as high probability for capybara occurrence coincided with the most heavily developed regions of the basin, with intensive agriculture and with extensive anthropogenic habitats. This area also coincides with sites at which most problems associated with capybaras have occurred in recent years, including crop damage (Ferraz et al. 2003), sanitary and health risks for humans (especially spotted fever and leptospirosis—Labruna et al. 2001, 2004; Pereira and Labruna 1998), car accidents, and other minor conflicts with humans. The greatest potential for sustainable use of capybaras in South America should be considered (Moreira and Macdonald 1996, 1997; Ojasti 1991), and sustainable management should be used to control overabundant populations (Sit and Taylor 1998). However, because hunting of capybaras has been forbidden in Brazil since 1967 (Federal Law 5.197 from January 1967), alternatives for control should be discussed. Landscape management, especially near water courses, replacing C4 plants by other species might be an effective alternative to reduce habitat carrying capacity, and thus capybara abundance indirectly.

The predictive models could be used to indicate priority areas for management to reduce capybara-human conflicts. Ecological niche models could be used to project the species' potential for colonization or expansion in areas with the potential for expansion as cultivated land replaces natural habitats.

RESUMO

O sudeste do Brasil tem sofrido drásticas modificações da paisagem nas últimas décadas devido à expansão da agricultura e de áreas urbanas. Tais mudanças tem influenciado a distribuição e abundância de vertebrados. Nós geramos modelos preditivos de distribuição espacial e ecológica da capivara (*Hydrochoerus hydrochaeris*) usando modelos de nicho ecológico. A maioria das ocorrências de capivaras ocorreram em áreas planas com corpos d'água margeados por cana-de-açúcar ou pasto. Mais de 75% da bacia do rio Piracicaba foi estimada como potencialmente adequada à capivara. Os modelos apresentaram baixos erros de omissão (2,3–3,4%), mas altos erros de comissão (91,0–98,5%); tais "falhas do

modelo” parecem relacionar-se mais às características locais do que espaciais. A distribuição potencial da capivara na bacia está associada a habitats antrópicos, particularmente com intensivo uso agrícola.

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