



Effects of global climate change on geographic distributions of Mexican Cracidae

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Abstract

Although climate change and its implications are a frequent subject of detailed study, the effects of these changes on species' geographic distributions remain little explored. We present a first cross-species analysis of the effects of global climate change on the distributions of one bird family, the Cracidae, in Mexico, based on projecting models of ecological niches from present conditions to modeled future conditions taken from general circulation models of climate change. Based on two different scenarios of climate change and on three assumptions regarding species' dispersal abilities, effects on species' distributions range from drastic reduction to modest increases. These results illustrate the complex nature of species' geographic responses to environmental change, and emphasize the need for detailed analysis of individual species' ecological requirements. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Global climate change is increasingly recognized as a complex phenomenon involving shifts in many dimensions of Earth's atmospheric functions. Particularly prominent among these changes is the broad trend towards global warm-

ing and concomitant environmental changes, apparently a result of elevated levels of the so-called greenhouse gases in the atmosphere (Houghton et al., 1995). Although physical dimensions of these shifts have been analyzed in detail (for example, Crowley, 2000), effects on biodiversity are particularly poorly understood, with estimates of effects available only for single species or habitat types (for example, Loehle and LeBlanc, 1996; Parmesan, 1996; Allen and Breshears, 1998; Lindgren, 1998; Visser et al., 1998; Iverson et al., 1999). A

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broader view, including responses to change in distributions of *sets* of species, based on the ecological characteristics of each one individually, has yet to be produced (Loehle and LeBlanc, 1996).

Three general expectations exist for species' responses to climate change: movement, adaptation (either in terms of evolutionary change or of physiological acclimatization), or extirpation (Holt, 1990). If species are sufficiently mobile, they may track the geographic position of their ecological niches (environmental conditions within which they are able to maintain populations). If species are capable of rapid evolutionary change, or have a wide range of physiological tolerances, adjustment to changing conditions and landscapes may be possible. Failing both mobility and adaptability, extirpation is the likely result (Holt, 1990; Melillo et al., 1995). Because the critical component is change, herein we explore the geographic dimensions of species' responses to global climate change—under different assumptions of ability to move, and neglecting the possibility of evolutionary adaptation, what are the consequences of global climate change for elements of biodiversity?

In this paper, we apply a quantitative methodological framework to modeling species' distributional responses in the face of climate change (Peterson et al., 2001b) for the eight cracid species found in Mexico. This family is of particular interest owing to its usually threatened or endangered conservation status, generally small distributional areas, and wide diversity of habitat types. The approach consists of four steps: (1) accumulation of large sets of present-day distributional data in the form of primary point-occurrence information (Peterson et al., 1998; Peterson and Stockwell, 2001); (2) developing ecological niche models that are then tested using part of the distributional data (Guisan and Zimmerman, 2000; Kobler and Adamic, 2000); (3) projecting regional shifts in geographic and ecological dimensions onto the landscape of interest based on the results of general circulation models of climate change; and (4) modeling distributional shifts by projecting species' modeled ecological niches onto the transformed landscapes.

2. Methods

Locality data associated with scientific specimens of the eight cracid species were obtained via direct consultation of 26 scientific collections (Peterson et al., 1998; Navarro-Sigüenza et al., 2001), now under development as a relational database for all bird species in Mexico (Navarro-Sigüenza et al., 2001). These data were then georeferenced to the nearest minute of latitude and longitude via direct consultation of various map series.

The fundamental ecological niche of a species—defined here as the conjunction of ecological conditions within which it is able to maintain populations—can be depicted as a polyhedron or polyhedrons in multidimensional ecological/environmental space (MacArthur, 1972). Several approaches have been used to approximate species' fundamental ecological niches, including BIOCLIM (Nix, 1986) and logistic multiple regression (Austin et al., 1990). Herein, we employ the Genetic Algorithm for Rule-set Prediction¹ (GARP), which includes both of the latter methods, among others, in an iterative, artificial-intelligence-based approach (Stockwell and Noble, 1992; Stockwell and Peters, 1999). Individual algorithms are used to produce component 'rules' in a broader rule-set, and hence portions of the landscape may be identified as inside or outside of the niche based on different algorithms. GARP therefore represents a superset of the other approaches, and should generally have greater predictive ability than any one of them. Extensive testing of GARP has indicated excellent predictive ability for species' geographic distributions (Peterson, 2001; Peterson and Cohoon, 1999; Peterson and Stockwell, 2001; Peterson et al., 2001a).

GARP models provide a heterogeneous rule-set defining one or more polyhedrons in ecological niche space that are hypothesized to be habitable by a particular species. Quality of such models is usually assessed by dividing point occurrence data into training (for building models) and test (for testing models) data subsets (Fielding and Bell, 1997). However, the relatively small numbers of

¹ <http://biodi.sdsc.edu/>

specimens and localities in the present example make such statistical evaluation of model adequacy impossible.

We used a set of digitized categorical climate maps summarizing annual average temperature and precipitation (acquired from Mexico's Comisión Nacional para el Uso y Conocimiento de la Biodiversidad, CONABIO²) and digital elevation models (processed into maps of elevation, slope, aspect, and solar radiation) from the Defense Mapping Agency.³ These maps were divided in 15 classes for temperature and 19 for precipitation, with a 4 km × 4 km grid cell size. To permit incremental changes to a classified value map, we converted categorical temperature and precipitation maps into pseudo-continuous maps using pycnophylactic interpolation (Tobler, 1979), a mass-preserving spatial interpolation for categorical data available as an extension for ESRI's ArcView GIS program.⁴

The general circulation model used (HadCM2)⁵ includes several different scenarios of climate change. We assessed the implications of both a conservative and a less conservative view of how climates could change over the next 50 years using the HHGSDX50 and HHGGAX50 scenarios, respectively. The HHGSDX50 scenario assumes 0.5%/year CO₂ increase (IS92d), and incorporates sulphate aerosol forcing, making it a relatively conservative estimate of expected climate change. The HHGGAX50 scenario assumes a 1%/year CO₂ increase (IS92a) and does not include the effects of sulfate aerosols, and so is less conservative. Results are based on a 30-year average (2040–2069), and are provided at a spatial resolution of 2.5 × 3.75°. Expected percent change in annual mean temperature and precipitation under each scenario was extracted; to increase resolution,

we interpolated to 0.5 × 0.5° cells using a nearest-neighbor contouring algorithm.

The ecological niche models developed using GARP can be projected onto both current and projected landscapes. In effect, we take the ecological regimes identified based on current distributions, and seek those sets of conditions on the future maps; hence, this step involves no new modeling, but simply identification of sets of conditions on a changed landscape (Peterson et al., 2001b). It is important to bear in mind that GARP models are models of ecological requirements; for a variety of historical and ecological reasons, species rarely inhabit the entire spatial manifestation of their ecological niches (Peterson et al., 1999). Hence, we trimmed raw predictions to include only those ecoregions⁶ from which a particular species was actually known to occur, and took this reduced map as a prediction of species' actual geographic distributions. Coincidence of these reduced maps with independent range descriptions (for example, Howell and Webb, 1995) was generally quite close.

For each climate change scenario, we evaluated expected change in species' distributions under three assumptions regarding dispersal abilities. First, assuming no dispersal capabilities, which may be appropriate for extremely habitat-restricted and sedentary species, we took the intersection of each species' predicted distribution after climate change with its present geographic distribution. This procedure identifies the portions of current distributional areas that will remain habitable by the species after modeled climate change. At the other end of the dispersal spectrum, assuming universal dispersal ability (i.e. the species can inhabit any appropriate habitat anywhere in Mexico), we compared total area of predicted suitable habitat in Mexico under current and changed scenarios (Loehle and LeBlanc, 1996). Finally, we sought an intermediate solution, probably more realistic in general, constraining possible post-change distributions to areas contiguous with current distributional areas. This scenario assumes that species are able to move through appropriate habitat, but not jump over unfavorable areas.

² <http://www.conabio.gob.mx/>

³ <http://edcdaac.usgs.gov/gtopo30/hydro/namerica.html>

⁴ USGS-BRD, Alaska Biological Science Center of the Glacier Bay Field Station: <http://www.absc.usgs.gov/glba/gis-tools/index.htm>

⁵ http://ipcc-ddc.cru.uea.ac.uk/cru_data/examine/HadCM2-info.html; acquired from Data Distribution Centre (DDC) of the Intergovernmental Panel on Climate Change (IPCC); <http://ipcc-ddc.cru.uea.ac.uk/index.html>

⁶ <http://www.conabio.mx/>

3. Results

In general, our modeling efforts indicated substantial shifts in distributional areas for species, and broad reorganization of habitable versus uninhab-

itable sites (Fig. 1). Range shifts were most visible at northern and southern range limits, although no tendency was apparent in one direction or the other. In some cases, changes occurred far from range limits, in central areas of species' distributions.

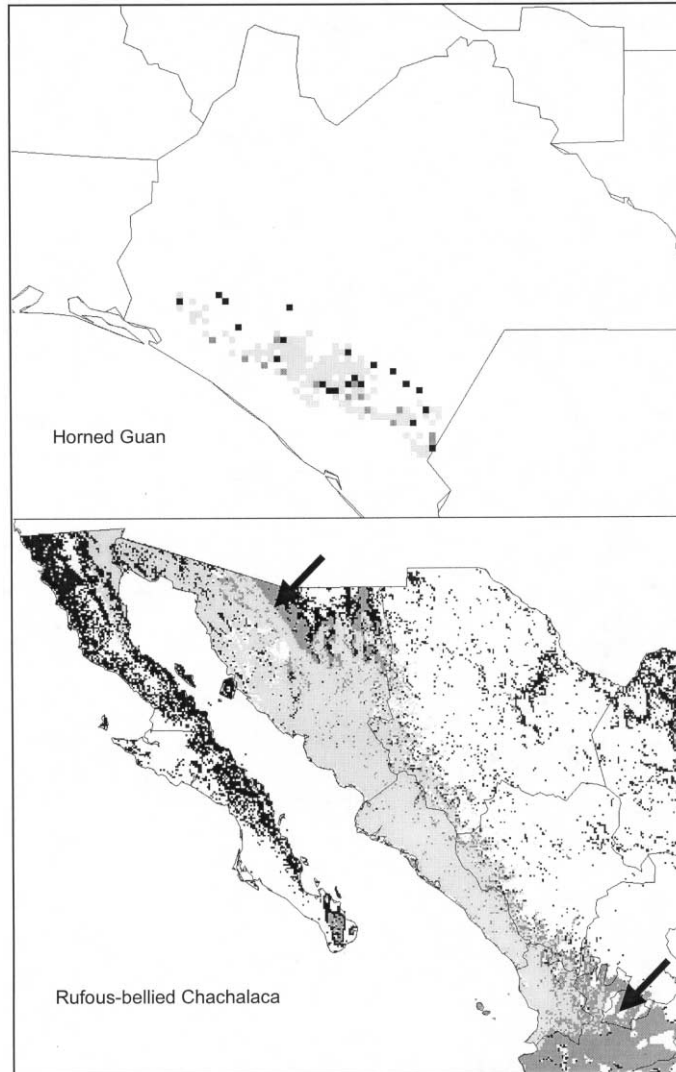


Fig. 1. Current geographic distributions (light gray) and distributions under the HHGSDX50 (dark gray) and HHGGAX50 (black) climate change scenarios for Horned Guans (*Oreophasis derbianus*) (in Chiapas, southern Mexico) and Rufous-bellied Chachalacas (*Ortalis wagleri*). Note that, for clarity of visualization, the Horned Guan (a species declining in the face of modeled changes) is depicted with HHGSDX50 layered on top of HHGGAX50 on top of pre-change distribution, whereas the Rufous-bellied Chachalaca (a species expanding in the face of modeled changes) is depicted with pre-change distribution layered on top of HHGSDX50 on top of HHGGAX50. The arrows on the Rufous-bellied Chachalaca map indicate zones of expected range expansion for the species.

Some species were predicted to experience only mild range shifts, whereas others were predicted to see drastic changes (Table 1). For example, projections for the Great Curassow (*Crax rubra*) suggest that it will experience only subtle adjustments in its potential distributional area: declines of 3.3–7.1% under the no dispersal assumption, and increases of 9.5–11.0% under the contiguous areas assumption. In contrast, the Horned Guan (*Oreophasis derbianus*) is projected to experience very drastic reductions in distributional area regardless of the set of assumptions: declines of 86.0–89.3% under the no dispersal assumption and of 73.3–85.3% under the contiguous areas assumption. This species would experience such serious fragmentation effects (Fig. 1) that extinction would be quite likely. These two examples bracket the range of effects projected for the cracid species treated herein (Table 1 and Fig. 2).

An interesting aspect of these explorations is whether scenarios of climate change differ in their implications for species' distributional shifts. In this case, we examined one scenario that is relatively conservative in its predictions (HHGSDX50), and another that is less conservative (HHGGAX50). Comparing the projected consequences of the two scenarios for species' distributions (Fig. 3), however, the degree of seriousness was comparable: changes under HHGSDX50 tended to be more harsh under the universal dispersal assumption, whereas those under HHGGAX50 were harder under the other two assumptions (the more realistic ones). In general, however, *both* climate change scenarios predicted serious consequences for cracids over the next 50 years.

4. Discussion

The approach developed herein has some limitations, which are explored elsewhere (Peterson and Cohoon, 1999; Peterson, 2001; Peterson and Stockwell, 2001; Peterson et al., 2001a,b; Stockwell and Peterson, 2001). Most of these concerns center on model validation and sample size, as well as on issues of data quality in terms of geographic resolution and inclusion of appropri-

ate ecological dimensions. Nevertheless, the modeling procedures, as well as projections over scenarios of change (for example, Peterson and Vieglais, 2001), appear robust to broad sets of assumptions, and thus projections developed likely bracket probable outcomes of expected environmental changes.

Another, more fundamental criticism of our approach is that interactions of species under climatic change will probably be altered, thus influencing potential distributions much more than species' autecology (Davis et al., 1998). This effect has been demonstrated in laboratory experiments with fruit flies and a parasitoid wasp (Davis et al., 1998), although under rather severe experimental conditions. This criticism, nevertheless, flies in the face of the fact that, at certain scales, bioclimatic models *do* predict current geographic distributions (Peterson and Cohoon, 1999; Peterson, 2001; Peterson et al., 2001a), as well as paths of species invasions (Higgins et al., 1999; Peterson and Vieglais, 2001). The question posed by Davis et al. (1998) is thus far from settled, and more empirical studies at diverse spatial scales and for various taxonomic groups will be required.

This study represents a first-pass assessment of implications of global climate change for elements of biological diversity. Other modeling approaches have been used to the same end (for example, Iverson et al. (1999) with regression tree analysis; Lindgren (1998) with graphical dynamic simulations) for other taxa and regions. Although all of these approaches converge on the same general approach (model ecological niches, project niche model onto changed climate scenarios), at present, the relative predictive abilities of each approach have not been compared. These detailed comparisons of modeling approaches will represent an important step towards development of a truly robust predictive approach.

Herein, we develop the example of Mexican Cracidae, a family that exhibits diversity in dimensions of ecology and geography. In general, under the assumption of no dispersal, all species declined somewhat, whereas with contiguous dispersal, only two of the species declined in distributional area, and others even expanded distributional areas broadly. The species most af-

Table 1

Summary of results of predictions of effects of two scenarios of global climate change on distributions of Cracidae in Mexico under three scenarios of dispersal ability

Species	Universal				No dispersal		Contiguous	
	Current	DX	AX	Actual current	DX	AX	DX	AX
Great Curassow, <i>Crax rubra</i>	1 009 768	598 351 (−40.7)	595 994 (−41.0)	313 821	291 500 (−7.1)	303 321 (−3.3)	343 575 (9.5)	348 346 (11.0)
Horned Guan, <i>Oreophasis derbianus</i>	31 163	37 175 (19.3)	20 505 (−34.2)	1692	180 (−89.3)	237 (−86)	248 (−85.3)	451 (−73.3)
White-bellied Chachalaca, <i>Ortalis leucogastra</i>	92 847	128 330 (38.2)	181 363 (95.3)	7726	4207 (−45.5)	7579 (−1.9)	4872 (−36.9)	10 489 (35.8)
West Mexican Chachalaca, <i>Ortalis poliocephala</i>	707 462	547 101 (−22.7)	1 233 235 (74.3)	240 374	178 228 (−25.9)	148 700 (−38.1)	224 403 (−6.6)	180 461 (−24.9)
Plain Chachalaca, <i>Ortalis vetula</i>	841 849	969 311 (15.1)	1 009 407 (19.9)	388 171	350 511 (−9.7)	375 291 (−3.3)	420 203 (8.3)	493 041 (27.0)
Rufous-bellied Chachalaca, <i>Ortalis wagleri</i>	852 801	925 763 (8.6)	937 381 (9.9)	240 408	152 422 (−36.6)	224 516 (−6.6)	248 743 (3.5)	311 227 (29.5)
Crested Guan, <i>Penelope purpurascens</i>	931 234	1 330 920 (42.9)	1 393 450 (49.6)	648 598	520 234 (−19.8)	636 665 (−1.8)	689 360 (6.3)	808 938 (24.7)
Highland Guan, <i>Penelopina nigra</i>	814 994	281 011 (−65.5)	821 062 (0.7)	53 360	51 916 (−2.7)	38 348 (−28.1)	53360 (0)	63 195 (18.4)

HHGSDX50 and HHGGAX50 are abbreviated ‘DX’ and ‘AX,’ respectively, and dispersal scenarios are described in the text. Data are presented in km²; percent changes from current modeled distributional areas are given in parentheses.

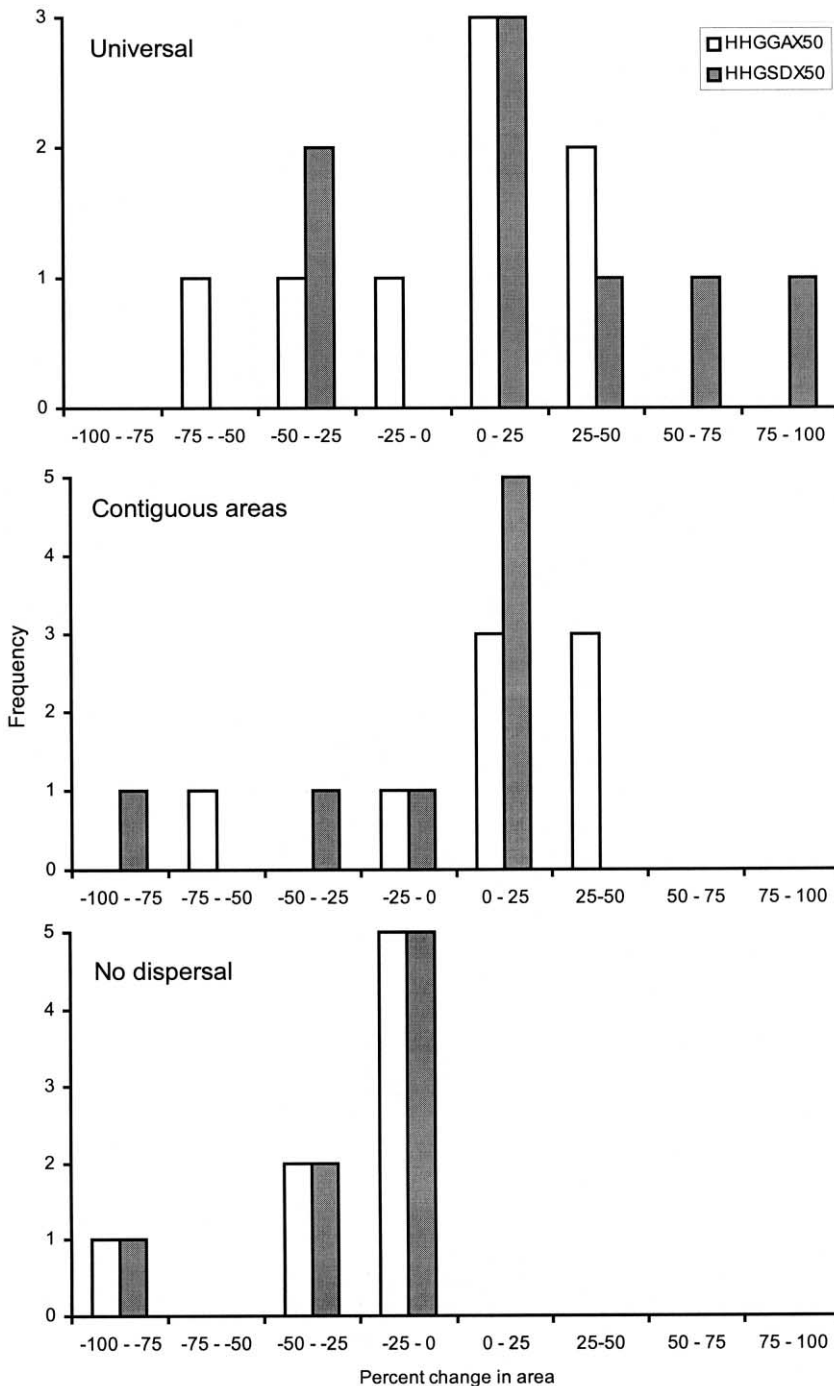


Fig. 2. Frequency histograms of projected percent changes in species' distributional areas under two scenarios of global climate change and three assumptions regarding dispersal capabilities.

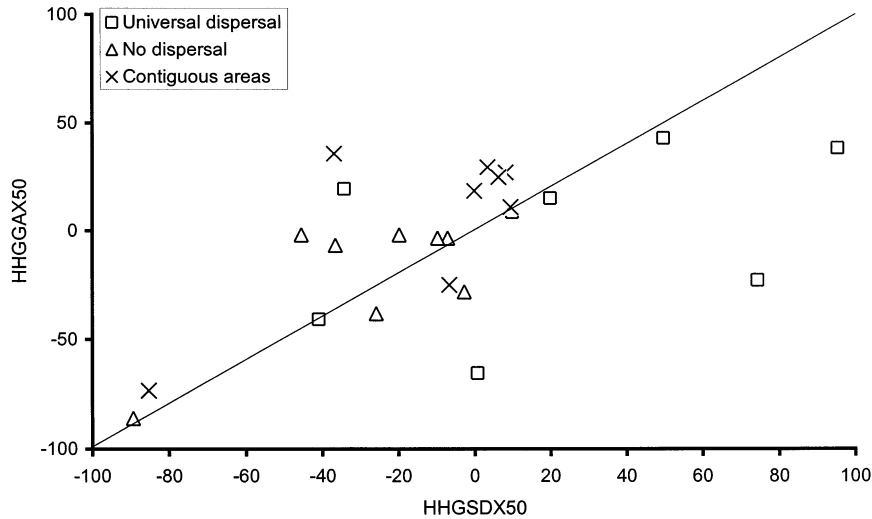


Fig. 3. Comparison of projected changes in species' distributional areas between two scenarios of global climate change under three distinct assumptions regarding dispersal abilities.

ected in these explorations was the Horned Guan, a montane species. However, the other montane species analyzed, the Black Guan (*Penelopina nigra*), which has a geographic distribution closely mirroring that of Horned Guans, was not predicted to decline substantially (Table 1). This point is important, as it suggests that broad generalizations regarding the fate of species in particular habitats or biotic regions (for example, Manne et al., 1999; Chapin et al., 2000; Sala et al., 2000) are likely to be inaccurate. Rather, the particulars of the ecology of each species are key to determining which species will decline or expand its area of distribution.

Returning to the initial framework of movement, adaptation, or extinction (Holt 1990), we have analyzed the potential interaction of global climate change with different assumptions regarding capacity for movement. Badly needed are parallel theoretical analyses of potential for adaptation, the foundations of which have already been laid (for example, Case and Taper, 2000). The combination of these distinct views of species and environmental change offers the possibility of a detailed, predictive understanding of the implications of such phenomena for biodiversity (Loehle and LeBlanc, 1996).

The general approach developed herein has broad implications for biodiversity conservation in general. Under two scenarios of global climate change, one conservative and the other less so, implications for species were pronounced. Species' distributions were predicted to rearrange, and consequences for natural communities are likely to be serious. One of the eight species studied would probably become extinct, suggesting that consequences for numerous individual species may include extinction. Understanding the implications of these results will await broader analyses, already in process, and will include analyses of additional taxa, tests of differences among regions, habitats, higher taxa, guilds, etc., and analyses of implications for reserve system design.

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