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Endemism and local rarity in birds of neotropical montane rainforest

Jill E. Jankowski[1], *Kerry N. Rabenold*[*]

Department of Biological Sciences, Lilly Hall, Purdue University, 915 W. State Street, West Lafayette, IN 47907, USA

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ABSTRACT

Species' rarity is expressed and measured at a variety of spatial scales, and rarity at different scales could be correlated. Considerable empirical evidence has supported a positive correlation between spatial distribution and local numerical abundance of species, which could create a syndrome of rarity for species limited in geographic distribution and occurring at low densities even in their primary habitats. We used auditory-count data and range information for birds in the Tilarán mountains of Costa Rica to examine the abundance–distribution relationship in cloud forest species and to determine if endemic species (limited to Costa Rican–Panamanian highlands or Central America) are locally rare or restricted in ecological distribution. We found a positive correlation between abundance and distribution at the smallest spatial scale: species occupying few sites in the study area had low abundances where they occur. At larger scales, geographical distribution measured categorically was correlated with local ecological amplitude (zones occupied). Local abundance, however, was not correlated across all species with estimates of range size (km^2), although most endemics exhibited below-median abundance. Within families with endemics and cosmopolitan species, 72% of narrow endemics were among the rarest species. For most narrow endemics, we rejected the possibility that they are sufficiently specialized within their habitats to reach relatively high densities. A conclusive test of the abundance–distribution relationship at large spatial scales and evaluation of global population size for endemics will require a comprehensive analysis using abundance data from throughout species' ranges. Such analyses for tropical species will be a long time coming, but it is meanwhile prudent to recognize that many endemics are threatened at several spatial scales, including the risks of small local populations.

1. Introduction

The causes and consequences of rarity are fundamental issues in ecology and conservation biology, including attempts to understand the local determinants of abundance, the variety of ecological specializations among species, the evolutionary histories of geographical ranges, and the prospects of extinction for limited-range species (Brown, 1995; Gaston and Blackburn, 2000). Rarity is expressed and measured at a variety of spatial scales, and expressions at different scales could be correlated. Species that are globally rare, in the sense of having small geographical ranges, could nonetheless be locally common. Alternatively, if species with small geographic ranges also had narrow ecological distributions and low local

[*] *Corresponding author:* Tel.: +1 765 494 8120; fax: +1 765 494 0876.
E-mail addresses: jjankow2@ufl.edu (J.E. Jankowski), rabenold@purdue.edu (K.N. Rabenold).
[1] Present address: Department of Zoology, University of Florida 223 Bartram Hall, P.O. Box 118525, Gainesville, FL 32608, USA. Tel.: +1 352 392 1721x510.

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densities, then they could have very small global populations. Such a positive association of rarity on different scales would make some species extremely vulnerable to extinction because of the common threats to small populations, including demographic stochasticity and loss of genetic diversity (Kattan, 1992; Johnson, 1998a). Endemism (limitation in geographical distribution to a small region) is an often-used early-warning criterion for identifying threatened species and priority habitats or regions for conservation efforts (Bibby et al., 1992; Stotz et al., 1996; Lombard et al., 1999; Brooks et al., 2002; de Klerk et al., 2002; Pimm and Jenkins, 2005; Orme et al., 2005; Das et al., 2006; Ribon et al., 2006). If endemic species are rare at every scale, they may be especially vulnerable, and habitats with concentrations of endemics especially fragile.

There is considerable empirical evidence, from a variety of taxa, for a positive correlation between spatial distribution and local numerical abundance (Bock and Ricklefs, 1983; Brown, 1984; Lacy and Bock, 1986; Bock, 1987; Hanski et al., 1993; Brown, 1995; Gaston, 1996; Blackburn et al., 1997; Johnson, 1998a,b; Gaston and Blackburn, 2000). This relationship has been shown to apply across spatial scales and to be unattributable to sampling artifact. Among the biological mechanisms proposed to generate this correlation is resource specialization that results in narrow distributions at the landscape and geographical scales, as well as numerical scarcity even within optimal habitats (Brown, 1984, 1995). More simply, dependence upon narrowly distributed resources could produce narrow distribution in consumers (Hanski et al., 1993), and density-dependence of movement and demography could also produce abundance–distribution correlations (Hanski et al., 1993 on metapopulation dynamics; O'Connor, 1987 on density-dependent habitat selection; Holt et al., 1997 on variation in intrinsic growth rates). The descriptions, associated predictions, and empirical support for these mechanisms are reviewed in detail elsewhere (Gaston et al., 1997). It can be practically and logically difficult to distinguish among these hypotheses on a local scale, and the evolutionary history of rarity in a particular species is generally inaccessible. The possibility, however, of "syndromes" of rarity produced by whatever mechanism is of immediate concern to conservation biologists. There is ample evidence that narrow endemics (especially island species) account for most historical extinctions (Diamond, 1984) and evidence in some lineages that locally rare endemics are especially extinction-prone (Johnson, 1998a,b).

While the interspecific abundance–distribution relationship has been explored in over 40 published studies of temperate regions, it has seldom been examined for the tropics (Gaston, 1996), where most biodiversity resides and where restricted-range species are concentrated (but see Arita et al., 1990 and Johnson, 1998a,b for mammals; Kattan, 1992; Goerck, 1997; Poulsen and Krabbe, 1997; Thiollay, 2002; and Ribon et al., 2006 for birds; and Pitman et al., 1999 for plants). Tropical species tend to have smaller ranges than related temperate species (Stevens, 1989), to be less numerically abundant (Terborgh et al., 1990; Johnson, 1998b), and to be threatened by rapidly expanding human impact. The combination of high levels of both species richness and endemism in many tropical habitats offers substantial opportunity for testing abundance–distribution hypotheses. In addition, conservation needs in "megadiversity" areas are often compelling, although there are obstacles to addressing these hypotheses in tropical communities. Investigators are limited to studying the best known taxa (e.g., trees, butterflies, birds and mammals), and even for these taxa, estimates of abundance and range size necessary at landscape, regional and geographic spatial scales may be inaccurate or simply unavailable. Low population densities of tropical species hamper accurate measurement of local abundance and limit the range of variation across species. Tropical studies have often used simple categorical measures of population size, habitat restriction and geographic distribution to identify the various "forms of rarity" (Kattan, 1992; Goerck, 1997; Pitman et al., 1999), though quantitative measures of relative abundance and distribution permit better tests of the hypotheses.

This study assesses the relationship between abundance and distribution for cloud forest birds in the Tilarán mountains of Costa Rica. The highlands of Costa Rica and Panamá harbor the greatest avian species richness in Central American montane forests (Hernández-Baños et al., 1995) and one of the highest levels of avian endemism in the world (Bibby et al., 1992). Costa Rican birds are also comparatively well known in the Neotropics (Stiles and Skutch, 1989; Young and McDonald, 2000). In the Tilarán mountains, nearly 10% (41 species) of the forest avifauna is narrowly endemic to Costa Rica and Panamá and many more are limited to Central America. Most of these narrow endemics are included in the current study. We use quantitative measures of abundance, compensating for detectability, on the Pacific slope of the Tilarán range, a qualitative measure of abundance for Pacific and Caribbean slopes, and measures of distribution on three spatial scales: within our study area (<100 km^2); within Costa Rica and Panamá (100–10,000 km^2); and over species' geographic ranges (>10,000 km^2). We test hypotheses suggesting a positive relationship between local abundance and distribution across all species as well as within families and genera, including other studies, and address the practical issue of whether the extent of a species' geographical range is a reliable indicator of its global population size and vulnerability to extinction.

2. Methods

2.1. *Study site*

The humid montane forests of Central America (Mexico-Panamá) contain 147 avian species endemic to that habitat. Avian species diversity and narrow endemism peak in the highlands of Costa Rica and Panamá, and these highlands have been recognized as a global conservation priority (Bibby et al., 1992; Hernández-Baños et al., 1995; Stotz et al., 1996; Orme et al., 2005). The mountain ranges of Costa Rica, from smallest to largest and northwest to southeast, are the Cordilleras Guanacaste, Tilarán, Central and Talamanca; these ranges harbor 28, 41, 45, and 54 species respectively that are narrowly endemic to the highlands of Costa Rica and Panamá (Stiles and Skutch, 1989; Sánchez, 2002; G. Barrantes, personal communication).