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## Species-specific traits associated to prediction errors in bird habitat suitability modelling

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#### Abstract

Although there is a wide range of empirical models applied to predict the distribution and abundance of organisms, we lack an understanding of which ecological characteristics of the species being predicted affect the accuracy of those models. However, if we knew the effect of specific traits on modelling results, we could both improve the sampling design for particular species and properly judge model performance. In this study, we first model spatial variation in winter bird density in a large region (Central Spain) applying regression trees to 64 species. Then we associate model accuracy to characteristics of species describing their habitat selection, environmental specialization, maximum densities in the study region, gregariousness, detectability and body size.

Predictive power of models covaried with model characteristics (i.e., sample size) and autoecological traits of species, with 48% of interspecific variability being explained by two partial least regression components. There are species-specific characteristics constraining abundance forecasting that are rooted in the natural history of organisms. Controlling for the positive effect of prevalence, the better predicted species had high environmental specialization and reached higher maximum densities. We also detected a measurable positive effect of species detectability. Thus, generalist species and those locally scarce and inconspicuous are unlikely to be modelled with great accuracy. Our results suggest that the limitations caused by those species-specific traits associated with survey work (e.g., conspicuousness, gregariousness or maximum ecological densities) will be difficult to circumvent by either statistical approaches or increasing sampling effort while recording biodiversity in extensive programs. © 2005 Elsevier B.V. All rights reserved.

Keywords: Birds; Density; Habitat distribution models; Interespecific differences; Modelling errors; Regression trees

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#### 1. Introduction

The aim of modelling the distribution and abundance of organisms, which roots the modern concept of habitat suitability modelling, is far from new in ecology and conservation biology (MacArthur, 1972; Walter,

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1973; Cody, 1985; Caughley and Gunn, 1996). However, practitioners of these disciplines have recently acquired a wide range of modelling methodologies, based on modern statistical approaches that benefit from continuous developments on both geographical information systems and remote sensing (Guisan and Zimmermann, 2000; Scott et al., 2002). Several empirical models to analyze distribution and abundance have been spreading during the last decade, such as generalized additive models (Leathwick, 1998; Lehmann, 1998; Seoane et al., 2004), classification and regression trees (De'Ath and Fabricius, 2000; Dzeroski and Drumm, 2003), neural networks (Lek et al., 1996; Özesmi and Özesmi, 1999; Dedecker et al., 2004) and distance-based models such as ecological niche factor analysis (ENFA) and climatic envelopes (e.g., Hirzel et al., 2002; Pearson and Dawson, 2003; Huntley et al., 2004; Remm, 2004). These techniques have been compared in terms of predictive accuracy and ease of use (Guisan et al., 1999; Manel et al., 1999; Olden and Jackson, 2002; Segurado and Araújo, 2004; Yen et al., 2004), with the conclusion that there is not a single best method. In fact, predictive accuracy varies more among species than among modelling techniques (Elith and Burgman, 2002; Thuiller et al., 2003).

Nevertheless, little is known about whether ecological traits of species may predict the errors in habitat suitability modelling (but see, Boone and Krohn, 1999; Kadmon et al., 2003). For example, among groups of animal species, the success of several modelling techniques relates inversely with spatial variability (mobility and nomadism) and niche width, but there are some effects which are not consistent across all biological groups (Pearce and Ferrier, 2000; Pearce et al., 2001). Similar effects have been found within particular groups of species, with negative effects of niche width and positive effects of commoness, abundance and detectability (Boone and Krohn, 1999; Kadmon et al., 2003). Nevertheless, among-species differences are often less clear-cut (see, for example, Elith and Burgman, 2002, who in a study of vascular plants did not find associations between specific traits and model discrimination ability). The analysis of the association between species biological traits and model accuracy is useful because if we knew the effect of specific traits on modelling results, we could improve the sampling design for some particular species (e.g., modifying survey intensity). We could also know the maximum accuracy attainable with the analytical approach, which would enable us to make informed judgements on model performances.

Birds are a suitable biological group to assess among-species differences in modelling accuracy because they show a wide range of ecological traits and they may be surveyed in large areas. Bird species differ greatly in stenotopy, abundance, geographical range, mobility and detectability, the main factors that could help to explain variation in modelling accuracy. These interspecific differences increase dramatically in winter, when birds are not constrained to a nest site or a fixed territory, and they may gather in nomadic flocks tracking feeding resources (Fretwell, 1972). In this paper, we study the effect of species' autoecological traits on predictability of habitat suitability models, working with wintering birds of Central Spain. First, we model spatial variation in bird density using regression trees. Second, the predictive power of these models are related to biological characteristics of species describing environmental preferences and specialization, maximum densities attained in the study region, gregariousness, detectability and body size.

### 2. Methods

### 2.1. Study area

The study area is located in the centre of the Iberian Peninsula, comprising Madrid province and surrounding areas of Segovia and Guadalajara (less than 50 km from the province border). Altitude ranges from 450 to 2450 m a.s.l. The climate is Mediterranean continental, with cold winters near the Guadarrama mountains and milder weather in the valleys of the Tajo basin. There is a wide variety of habitats in this region: autochthonous forests (pinewoods of Pinus sylvestris L., riparian woods, deciduous oakwoods of Quercus pyrenaica Willd. and evergreen holm-oakwoods of Q. ilex subsp. ballota [Desf.] Samp.), open wooded habitats (ash and holm-oaks parklands), scrublands, artificial and natural pasturelands, marshlands, rock outcrops, various agricultural formations (vineyards, olive plantations, extensive cereal croplands) and urban areas (from small villages to large cities) (Fig. 1).

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