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Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis



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ABSTRACT

The densities and survival of many wild animals are presently at risk. Crucial for improving conservation actions is an understanding on a large scale of the relative importance of human and ecological factors in determining the distribution and densities of species. However, even for such charismatic species as the African elephant (*Loxodonta africana*), spatially explicit, large-scale analyses are lacking, although various local-scale studies are available. Here we show through continent-scale analysis that ecological factors, such as food availability, are correlated with the presence of elephants, but human factors are better predictors of elephant population densities where elephants are present. These densities strongly correlate with conservation policy, literacy rate, corruption and economic welfare, and associate less with the availability of food or water for these animals. Our results suggest that conservation strategies should be organized in a socioeconomic context. The successful conservation of large animal species could depend more on good human education, greater literacy, good governance, and less corruption, than merely setting aside areas for conservation.

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1. Introduction

Many empirical studies that relate the distribution and density of species to ecological factors determining habitat suitability have been carried out to understand the reasons why species become endangered (Rodrigues et al., 2004). Obviously, human factors, such as land use and resource management, strongly interfere with these ecological factors, leading to problems like habitat fragmentation and overexploitation of food and water resources (Adams et al., 2004; Kareiva et al., 2008). Hence, conservation policies need analyses that include both ecological and human factors, in the knowledge that human factors are becoming dominant in determining the quality of the Earth's ecosystems (Vitousek et al., 1997). Crucial for improving conservation actions is an understanding on a large scale of the relative importance of human and ecological factors in determining the occurrence and densities of species. Many studies that investigate the distribution of species and their population density have a regional focus (Hoare and Du Toit, 1999; Khaemba and Stein, 2000), whereas spatially explicit, continent-wide analyses are often lacking.

Here we use the African elephant (*Loxodonta africana*, Fig. 1) to analyze the relation between both ecological and human factors and the spatial distribution and density of a large-bodied and charismatic species. We distinguish the occurrence (presence/absence) of the elephant as well as the densities at which it occurs. Besides the present-day distribution, we also analyze the historic distribution of elephants. We analyze a continent-wide data set of elephants and determine the relation with 19 ecological variables, including forage availability, rainfall, and water, and 15 human variables, including human density, welfare, literacy rate, and habitat fragmentation. Our choice of the African elephant arose from its indisputable importance to nature conservation.

2. Methods

The African Elephant Database supplied the data for the distribution and densities of elephants over the whole African continent (Blanc et al., 2007). The historic distribution was based on Dorst and Dandelot (1972) and Carruthers et al. (2009). The presence and absence of elephants (ELEPRES) and the mean elephant density



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Fig. 1. Distribution of African elephants (*Loxodonta africana*). Current distribution of African elephants is illustrated by hatched areas if elephant presence was confirmed. Differences in known density estimates (n/km²) are illustrated by gradients of shading (source: Blanc et al., 2007). Hatched areas without shading represent areas where elephant presence was confirmed but where elephant densities were unknown. Inset: historic distribution of elephants. *Source*: Dorst and Dandelot, 1972; Carruthers et al., 2009

(ELEDENS; numbers/km²) for each grid cell south of the Sahara were calculated at a resolution of 0.5° latitude-0.5° longitude (Fig. 1). This was the smallest cell size at which the data could be analyzed without spatial interpolation. Moreover, elephants have large home ranges (Shannon et al., 2010), their distribution is influenced by decisions taken over tens of kilometers (De Knegt et al., 2011), and the elephant survey data are subject to spatial uncertainty (Blanc et al., 2007), so that an analysis at a finer resolution is not justified. The analysis was based on 2932 and 3778 grid cells for elephant presence and absence, respectively, and 1370 grid cells with estimated elephant densities. The latter estimated elephant densities were obtained from a variety of methods, such aerial counts, road transects and dung counts, and for more information regarding methods, estimates and reliability we refer to Blanc et al. (2007). We took elephant range and density estimates at face value, although their reliability is undoubtedly influenced by survey method (Blanc et al., 2007). These estimates were regressed on several predictor variables at a similar resolution, obtained from different sources (Table A1). The sizes of the grid cells were not equal, because of the geographic coordinate system used, but 95.4% of all cells were within ±4% of the mean cell size $(3025 \text{ km}^2 \pm 132 \text{ km})$. Where the original data were available at finer resolutions in a $0.5^{\circ} \times 0.5^{\circ}$ grid cell, we calculated mean values weighted for the proportion of the grid cell. The probability of recording elephants depends to some extent on the proportion of a grid cell that is covered by land. To correct for these differences in land area, we used the variable LAND (land area in%) as a covariate. Several variables were only available per country; these variables were converted to grid cell values.

2.1. Vegetation and soil characteristics

Elephants are bulkfeeders and therefore have lower densities in areas with low plant biomass (Parker and Graham, 1989; Olff et al., 2002). We used Net Primary Production (NPP) and the Normalized Difference Vegetation Index (NDVI) as proxies for the amount of forage for elephants (Young et al., 2009). NDVI measures the reflection of green vegetation, and we calculated mean NDVI over the period 1981-1994. NDVI has been successfully correlated to elephant densities and distribution in other studies at smaller scales (Young et al., 2009; Murwira and Skidmore, 2010). It has the potential problem that it saturates at higher reflectance levels and can thus less accurately measure high levels of forage availability. NPP is highly correlated with NDVI but is more linearly related to plant biomass (Lu, 2006), and could therefore be a better predictor variable for forage biomass. In areas with high amounts of plant biomass, like rainforests, a relatively large part of the vegetation is inaccessible for elephants, which could result in lower elephant densities (Olff et al., 2002). Therefore, we anticipated a unimodal relationship between elephant density and both NDVI and NPP and added their squared terms as predictor variables (NDVI2 and NPP2).

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