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Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards

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ABSTRACT

A species' vulnerability to extinction depends on extrinsic threats such as habitat loss, as well as its intrinsic ability to respond or adapt to such threats. Here we investigate the relative roles of extrinsic threats and intrinsic biological traits in determining extinction risk in the lizard fauna of New Zealand. Consistent with the results of previous studies on mammals and birds, we find that habitat specialization, body size and geographic range size are the strongest predictors of extinction risk. However, our analyses also reveal that lizards that occupy areas with high levels of annual rainfall and are exposed to exotic predators and high human population densities are at greater risk. Thus, while the intrinsic traits that render species prone to extinction appear largely congruent across vertebrate taxa, our findings illustrate that both extrinsic threats and intrinsic traits need to be considered in order to accurately predict, and hence prevent, future population declines.

1. Introduction

There is an emerging consensus that we are in the midst of a mass extinction event that rivals those of the geological past (Pimm et al., 1995; Wake and Vredenburg, 2008; Maclean and Wilson, 2011). However, not all species are equally at risk of extinction (Bennett and Owens, 1997). Indeed, analyses of past and projected extinctions have frequently reported highly non-random patterns in extinction risk (McKinney, 1997; Purvis et al., 2000; Duncan et al., 2002; Olden et al., 2007; Anderson et al., 2011; Murray et al., 2011; Thuiller et al., 2011). Investigating the mechanisms that render species vulnerable to extinction can assist in the identification, and hence mitigation, of threatening processes and can ultimately lead to the development of better preventative approaches and more strategic allocation of conservation funds (Cardillo and Meijaard, 2012). For example, statistical relationships between threatening processes and extinction risk can allow conservation managers to assess the threat statuses of poorly understood species, or assist in the identification of stable species that are prone to future declines (Reed and Shine, 2002; Fisher and Owens, 2004). In contrast to reactive management strategies, which are typically time-consuming and expensive, preventative approaches based on statistical models can provide a rapid, cost-effective means to assess the conservation statuses of large numbers of species (Anderson et al., 2011; Murray et al., 2011; Cardillo and Meijaard, 2012).

A species' vulnerability to extinction depends on extrinsic threats such as habitat loss and invasive species, as well as its intrinsic ability to respond or adapt to such threats (Fisher et al., 2003; Cardillo et al., 2004; Collen et al., 2011; Murray et al., 2011). Because the life-history, behavior, and ecology of a species dictates its demography (and thus its resilience to extrinsic threats: Olden et al., 2007), most previous studies of extinction risk have focused solely on intrinsic characteristics of species. These studies have frequently revealed that large-bodied, range-restricted, and ecologically specialized taxa are at greater risk (Fisher and Owens, 2004; O'Grady et al., 2004), although there is evidence that such relationships may be sensitive to taxonomic or spatial scale (Gage et al., 2004; Cardillo et al., 2008). Fewer studies of extinction risk have considered both intrinsic traits and extrinsic threats simultaneously. This is surprising, in that the impacts of extrinsic threats depend not only on a species' intrinsic characteristics, but also on the geographic distribution and severity of such threats (Collen et al., 2011; Murray et al., 2011). Accounting for both types of characteristics may therefore reveal spatial

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contingencies in extinction risk that are not apparent when either type of variable is considered in isolation.

Here we investigate how intrinsic traits and extrinsic threats influence extinction risk in the lizard fauna of New Zealand. To date, there have been comparatively few studies that have investigated correlates of extinction risk in reptiles (Fisher and Owens, 2004; but see Siliceo and Díaz, 2010; Mitchell and Janzen, 2010), despite the fact that reptile declines mirror those of other vertebrate groups in terms of severity and taxonomic and geographic breadth (Gibbons et al., 2000; Böhm et al., 2013). New Zealand has a diverse terrestrial lizard fauna consisting of ~100 species and undescribed entities (Chapple et al., 2009; Hay et al., 2010; Nielsen et al., 2011), but many of these taxa have experienced substantial range contractions in recent decades. In fact, ~75% of the New Zealand lizard fauna is either at risk or threatened with extinction (Hitchmough et al., 2010). Exotic mammals have been implicated as a major driver of lizard declines in New Zealand and many lizard taxa are now restricted to mammal-free offshore islands (Daugherty et al., 1994; Towns and Daugherty, 1994; Towns et al., 2001, 2003; Towns and Ferreira, 2001). In addition, New Zealand lizards are typically more abundant on predator-free islands (Whitaker, 1973) and previous studies have suggested that large, nocturnal taxa that overlap with the small mammal niche have undergone more substantial declines (Towns and Daugherty, 1994; Hitchmough et al., 2010). However, much of the evidence surrounding impacts of exotic mammals on New Zealand's lizard fauna remains correlative and circumstantial (Towns et al., 2003).

We use a comprehensive dataset on the life-history, ecology, and geographic distributions of New Zealand lizards to evaluate the effects of extrinsic threats suspected to have caused lizard declines in New Zealand (e.g., exotic mammals, habitat loss), as well as intrinsic traits that have been shown to influence endangerment in reptiles and other vertebrate taxa (e.g., range size, habitat specialization). We then use our model of extinction risk to predict the conservation statuses of data deficient lizards in New Zealand and to identify taxa which are currently listed as stable, but have the potential to become threatened due to their intrinsic traits and geographic distributions.

2. Methods

Data on the threat status of 99 described New Zealand reptile species and undescribed entities (hereafter 'species') were taken from a recent conservation assessment (Hitchmough et al., 2010). This assessment ranked species in one of five threat categories: (i) not evaluated, (ii) not threatened, (iii) at risk, (iv) threatened, and (v) extinct. We excluded marine species and those that were deemed extinct, introduced, or were not evaluated, leaving a total of three threat categories for our analysis (not threatened: $n = 21$; at risk: $n = 47$; and threatened: $n = 17$). We also excluded the tuatara (*Sphenodon punctatus*) from our analysis due to its unique life-history and large body size relative to the remainder of the New Zealand reptile fauna. The Chathams skink (*Oligosoma nigriplantare*) was also excluded, as this species is endemic to the Chatham Islands (~800 km east of New Zealand) and we lacked environmental data for this region. Our final dataset included 87 lizard species.

Data on the distribution of each species were taken from the New Zealand Department of Conservation's Herpetofauna Atlas, which collates all verified locality records collected by researchers, museums, government agencies and the general public in New Zealand (Department of Conservation, 2009). Fossils, translocations, and duplicate records were removed from the atlas database prior to conducting our analysis. We did not exclude historic records, as the majority of the atlas data are relatively recent. In fact, the median date across all records is 1989, and less than 5% of all records are from earlier than 1965. Distribution data were used to calculate geographic range size and habitat specialization (see Section 2.1), and to estimate environmental parameters across each species' geographic range (see Section 2.2).

2.1. Intrinsic threats

We compiled a comparative dataset of the life-history and ecological traits of New Zealand lizards (Table A1) from the Landcare Research NZ Lizards Database (Bell, 2010) and recent molecular phylogenetic studies of the endemic skink (Chapple et al., 2009) and gecko faunas (Nielsen et al., 2011). Our dataset included mean body size (there is no substantial sexual size dimorphism in New Zealand lizards), habitat use, habitat specialization, activity phase, diet, maximum reproductive output, phylogenetic longevity (i.e., time since divergence [mya] from its most closely related extant species), reproductive mode, and biogeographic affinity. Occurrence records of each species were also used to calculate geographic range size. To reduce the effects of survey bias and georeferencing errors, range size was approximated as the number of occupied equal-area 1-km grid cells.

2.2. Extrinsic threats

We calculated the mean value of seven variables within each species' geographic range: mean annual temperature, annual precipitation, temperature seasonality (standard deviation), precipitation seasonality (coefficient of variation), human population density, human influence, and extent of habitat loss. These variables were chosen because they characterize the main drivers of reptile declines worldwide (Foufopoulos and Ives, 1999; Reed and Shine, 2002; Whitfield et al., 2007; Sinervo et al., 2010; Böhm et al., 2013). Climate data were taken from the WorldClim database (~1-km resolution) (Hijmans et al., 2005). Data on human population density were taken from the GRUMP v1 dataset (based on United Nations-adjusted census data from 2000; ~1-km resolution; http://sedac.ciesin.columbia.edu/gpw, accessed 22/01/2012), whereas human influence data were extracted from the global human footprint v2 (~1-km resolution; http://ciesin.columbia.edu/wild_areas, accessed 22/01/2012). Extent of habitat loss within each species' range was based on the New Zealand Land Cover Database 2 (LCDB2), which is derived from satellite imagery taken from September 2001 to March 2002 (Terralink, 2004). Following Walker et al. (2008), we re-classified LCDB2 into indigenous and non- indigenous classes and calculated the proportion of all occurrence records in indigenous classes for each species as an estimate of habitat loss. We also determined whether species were represented on at least one offshore island that was free of introduced mammalian predators/competitors. Although several of these variables (e.g., climate, human influence and population density) are indirect measures of extrinsic threats, these variables correlate with extinction risk in other taxonomic groups (Cardillo et al., 2004; Davies et al., 2006; Sodhi et al., 2008), and represent the best data available at the national scale.

2.3. Statistical analyses

To facilitate interpretation and avoid overfitting our models, we used a subset of the life-history, ecological, and environmental variables described above to develop models of extinction risk: (i) geographic range size (ln-transformed), (ii) body size (quadratic relationship), (iii) habitat use (categorical: terrestrial, arboreal, or terrestrial-arboreal), (iv) habitat specialization (number of land-cover types occupied, corrected for range size), (v) activity phase (categorical: diurnal versus nocturnal), (vi) representation on at