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

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2 **ABSTRACT**

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

14

15 *Keywords:* body size, conservation status, geographic range, habitat specialization,
16 population decline, reptiles, threat status

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, behaviour, 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 specialised 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 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 & 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; Towns and Ferreira 2001; Towns et al., 2003). In addition, New Zealand lizards are typically more abundant on predator-free islands (Whitaker 1973) and previous studies have suggested

67 that large, nocturnal taxa that overlap with the small mammal niche have undergone more
68 substantial declines (Towns and Daugherty 1994; Hitchmough et al., 2010). However, much
69 of the evidence surrounding impacts of exotic mammals on New Zealand's lizard fauna
70 remains correlative and circumstantial (Towns et al., 2003).

71
72 We use a comprehensive dataset on the life-history, ecology, and geographic distributions of
73 New Zealand lizards to evaluate the effects of extrinsic threats suspected to have caused
74 lizard declines in New Zealand (e.g., exotic mammals, habitat loss), as well as intrinsic traits
75 that have been shown to influence endangerment in reptiles and other vertebrate taxa (e.g.,
76 range size, habitat specialization). We then use our model of extinction risk to predict the
77 conservation statuses of data deficient lizards in New Zealand and to identify taxa which are
78 currently listed as stable, but have the potential to become threatened due to their intrinsic
79 traits and geographic distributions.

80

81 **2. Methods**

82

83 Data on the threat status of 99 described New Zealand reptile species and undescribed entities
84 (hereafter 'species') were taken from a recent conservation assessment (Hitchmough et al.,
85 2010). This assessment ranked species in one of five threat categories: (i) not evaluated, (ii)
86 not threatened, (iii) at risk, (iv) threatened, and (v) extinct. We excluded marine species and
87 those that were deemed extinct, introduced, or were not evaluated, leaving a total of three
88 threat categories for our analysis (not threatened: n = 21; at risk: n = 47; and threatened: n =
89 17). We also excluded the tuatara (*Sphenodon punctatus*) from our analysis due to its unique
90 life-history and large body size relative to the remainder of the New Zealand reptile fauna.
91 The Chathams skink (*Oligosoma nigriplantare*) was also excluded, as this species is endemic

92 to the Chatham Islands (~800 km east of New Zealand) and we lacked environmental data for
93 this region. Our final dataset included 87 lizard species.

94
95 Data on the distribution of each species were taken from the New Zealand Department of
96 Conservation's Herpetofauna Atlas, which collates all verified locality records collected by
97 researchers, museums, government agencies and the general public in New Zealand
98 (Department of Conservation 2009). Fossils, translocations, and duplicate records were
99 removed from the atlas database prior to conducting our analysis. We did not exclude historic
100 records, as the majority of the atlas data are relatively recent. In fact, the median date across
101 all records is 1989, and less than 5% of all records are from earlier than 1965. Distribution
102 data were used to calculate geographic range size and habitat specialization (see 2.1. *Intrinsic*
103 *threats*), and to estimate environmental parameters across each species' geographic range
104 (see 2.2. *Extrinsic threats*).

105
106 2.1. *Intrinsic threats*

107
108 We compiled a comparative dataset of the life-history and ecological traits of New Zealand
109 lizards (Table A1) from the Landcare Research NZ Lizards Database (Bell 2010) and recent
110 molecular phylogenetic studies of the endemic skink (Chapple et al., 2009) and gecko faunas
111 (Nielsen et al., 2011). Our dataset included mean body size (there is no substantial sexual size
112 dimorphism in New Zealand lizards), habitat use, habitat specialization, activity phase, diet,
113 maximum reproductive output, phylogenetic longevity (i.e., time since divergence [mya]
114 from its most closely related extant species), reproductive mode, and biogeographic affinity.
115 Occurrence records of each species were also used to calculate geographic range size. To

116 reduce the effects of survey bias and georeferencing errors, range size was approximated as
117 the number of occupied equal-area 1-km grid cells.

118

119 2.2. *Extrinsic threats*

120

121 We calculated the mean value of seven variables within each species' geographic range:
122 mean annual temperature, annual precipitation, temperature seasonality (standard deviation),
123 precipitation seasonality (coefficient of variation), human population density, human
124 influence, and extent of habitat loss. These variables were chosen because they characterize
125 the main drivers of reptile declines worldwide (Foufopoulos and Ives 1999; Reed and Shine
126 2002; Whitfield et al., 2007; Sinervo et al., 2010; Böhm et al., 2013). Climate data were taken
127 from the WorldClim database (~1-km resolution) (Hijmans et al., 2005). Data on human
128 population density were taken from the GRUMP v1 dataset (based on United Nations-
129 adjusted census data from 2000; ~1-km resolution; <http://sedac.ciesin.columbia.edu/gpw>,
130 accessed 22/01/2012), whereas human influence data were extracted from the global human
131 footprint v2 (~1-km resolution; http://ciesin.columbia.edu/wild_areas, accessed 22/01/2012).
132 Extent of habitat loss within each species' range was based on the New Zealand Land Cover
133 Database 2 (LCDB2), which is derived from satellite imagery taken from September 2001 –
134 March 2002 (Terralink 2004). Following Walker (2008), we re-classified LCDB2 into
135 indigenous and non- indigenous classes and calculated the proportion of all occurrence
136 records in indigenous classes for each species as an estimate of habitat loss. We also
137 determined whether species were represented on at least one offshore island that was free of
138 introduced mammalian predators/competitors. Although several of these variables (e.g.,
139 climate, human influence and population density) are indirect measures of extrinsic threats,
140 these variables correlate with extinction risk in other taxonomic groups (Cardillo et al., 2004;

141 Davies et al., 2006; Sodhi et al., 2008), and represent the best data available at the national
142 scale.

143

144 2.3. Statistical analyses

145

146 To facilitate interpretation and avoid overfitting our models, we used a subset of the life-
147 history, ecological, and environmental variables described above to develop models of
148 extinction risk: (i) geographic range size (ln-transformed), (ii) body size (quadratic
149 relationship), (iii) habitat use (categorical: terrestrial, arboreal, or terrestrial-arboreal), (iv)
150 habitat specialization (number of land-cover types occupied, corrected for range size), (v)
151 activity phase (categorical: diurnal versus nocturnal), (vi) representation on at least one
152 predator-free offshore island (categorical: no predator-free island population versus at least
153 one predator-free island population), (vii) mean annual temperature (quadratic relationship),
154 (viii) annual precipitation (quadratic relationship), (ix) mean human population density (ln-
155 transformed), and (x) extent of habitat loss (quadratic relationship). Because the number of
156 habitat types that a species occupied was positively correlated with its geographic range size
157 (Spearman's $\rho = 0.907$), we regressed range size on the number of habitat types occupied and
158 used the residuals of this regression as an estimate of habitat specialization. The final set of
159 explanatory variables used in our analysis was chosen on the basis of multicollinearity, data
160 heterogeneity (e.g., only one species was oviparous), and the results of previous studies.
161 Whenever possible, we avoided using variables with many missing values to reduce the
162 probability of biasing our results (González-Suárez et al., 2012). If two variables with no
163 missing data were correlated with each other, the variable with the highest explanatory power
164 in a univariate model was retained.

165

166 We used cumulative link models with a logit link (i.e., proportional odds models) and the
167 Bayesian Information Criterion adjusted for small sample sizes (BICc) to assess the strength
168 of evidence for models containing all possible subsets of the ten variables outlined above. In
169 all models, threat status was the response (coded as an ordinal variable: *not threatened* = 1, *at*
170 *risk* = 2, *threatened* = 3), and intrinsic traits and extrinsic threats were included as fixed
171 effects. BIC is similar to the more widely used Akaike's Information Criterion (AIC), but
172 tends to fit fewer parameters than AIC, and is thus suitable for identifying main effects. The
173 relative importance of each explanatory variable was estimated by summing the BIC weights
174 across all models that contained a given variable. Nagelkerke's R^2 was used as a measure of
175 the explanatory power of each model.

176
177 We initially included a taxonomic random effect in all models to account for clustering of
178 species within genera; however, accounting for taxonomic dependence did not qualitatively
179 influence variable importance and genus explained an insignificant amount of the variance in
180 extinction risk (BICc was 4.47 units lower when genus was excluded from the global model).
181 Furthermore, only two families of lizards are represented in New Zealand, and extinction risk
182 does not vary between families (Hitchmough et al., 2010). We therefore present the results of
183 our analysis using fixed-effects cumulative link models only. All statistical analyses were
184 conducted in R[®] 2.15.1 using the *ordinal*, *rms*, and *MuMin* libraries (R Development Core
185 Team 2012).

186

187 **3. Results**

188

189 Geographic range size, habitat specialization, body size, and annual precipitation were the
190 strongest predictors of extinction risk in New Zealand lizards (Tables 1, 2). Collectively,

191 these four variables explained ~65% of the variation in extinction risk. Extinction risk
192 increased with decreasing geographic range size (Fig. 1a) and increasing habitat
193 specialization (Fig. 1b), body size (Fig. 1c), and annual rainfall (Fig. 1d). We also found
194 moderately strong evidence that diurnal species that were exposed to high human population
195 densities were more prone to extinction. Finally, exotic mammalian predators and habitat
196 affinities had relatively weak effects. Lizards that occupied at least one predator-free offshore
197 island and that were terrestrial, or both terrestrial and arboreal, were less likely to be
198 threatened (see Table 2 for relative variable importance weights).

199
200 Excluding species that were assigned a conservation ranking on the basis of their geographic
201 range size (i.e., range-restricted species, and species with only one location; n = 24 species)
202 changed model rankings and relative importance weights, but did not qualitatively change our
203 conclusions (Tables B1 and B2). The most notable difference when range-restricted species
204 were removed from our analysis was that the effect of annual precipitation was weaker,
205 whereas habitat loss had a much stronger effect. Extinction risk increased with increasing
206 habitat loss, but this relationship was non-linear (Table B2).

207
208 We then used our highest ranked model based on all species to predict the extinction risk of
209 eight species of New Zealand lizards that were not assigned a conservation ranking due to
210 insufficient data on threats and population trends. This exercise demonstrated that four of
211 these data-deficient species could be *threatened*, whereas three could be *at risk* (Table 3). Our
212 model also revealed that seven species that are currently listed as *not threatened* could be *at*
213 *risk*, whereas five species that are *at risk* could be *threatened* (Table 4).

214

215 4. Discussion

216

217 Anthropogenic activities are the predominant driver of the modern extinction crisis, but not
218 all species respond equally to these threats (Bennett and Owens 1997; Cardillo et al., 2004).
219 Indeed, our results clearly demonstrate that imperilled New Zealand lizards are a highly non-
220 random subset of the New Zealand fauna with respect to their intrinsic biological traits. In
221 particular, habitat specialists with large body sizes and small geographic ranges are more
222 likely to be at risk of extinction.

223

224 Our findings regarding intrinsic biological traits accord with the results of previous studies
225 on a wide array of vertebrate taxa (Duncan et al., 2002; Jones et al., 2003; Fisher and Owens
226 2004; Olden et al., 2007; Sodhi et al., 2008; Davidson et al., 2009; Siliceo and Díaz 2010;
227 Murray et al., 2011). Compared to generalists, specialists should be less capable of dealing
228 with novel environmental challenges (e.g., habitat loss, climate change) because they are
229 often unable to persist outside of their narrow range of preferred habitats (Reed and Shine
230 2002; Fisher et al., 2003; Fisher and Owens 2004; Murray et al., 2011). Large-bodied species
231 may also be particularly vulnerable to anthropogenic threats, as they typically possess
232 characteristics that make them slow to recover from rapid environmental perturbations
233 (Owens and Bennett 2000; Reed and Shine 2002). Fossil and extinct reptile species on islands
234 have larger body sizes than their extant relatives (Case and Bolger 1991; Case et al., 1992,
235 1998), and in New Zealand, two reptile species have gone extinct (one gecko and one skink),
236 and both have been the largest representatives of their family on the archipelago (Bauer and
237 Russell 1986; Worthy 1987). Additionally, species with small geographic ranges are typically
238 at greater risk of extinction because they have small population sizes, rendering them
239 particularly susceptible to demographic stochasticity, inbreeding, and localized threats and
240 catastrophes (Allendorf and Luikart 2007).

241 New Zealand is home to a wide array of exotic mammals that prey on lizards and previous
242 studies have implicated exotic mammals in lizard declines (Whitaker 1973; Towns and
243 Daugherty 1994; Hitchmough et al., 2010). Our finding that large lizards were more
244 vulnerable to extinction may therefore reflect the inability of large-bodied species to
245 overcome high rates of predation by exotic mammals (e.g., Polynesian rats *Rattus exulans*:
246 Whitaker 1973). In New Zealand specifically, smaller lizards can escape predation while
247 inactive or torpid by choosing retreat sites that are too narrow for small predators such as
248 mice and weasels to enter. In contrast, larger lizards that overlap in body diameter with the
249 smaller mammalian predators are extremely vulnerable to predation while immobile in
250 retreats. Most of the largest New Zealand lizards now have distributions that have contracted
251 to islands where mammals are absent, having been extirpated over the majority of their
252 former ranges. Our analyses revealed some support for the notion that lizards that occupy at
253 least one predator-free offshore island were less prone to extinction, but counter to previous
254 studies, we did not find that nocturnal and ground-dwelling species that overlap with the
255 small mammal niche were currently disproportionately at risk (Towns and Daugherty 1994;
256 Hitchmough et al., 2010). In fact, after controlling for additional confounding traits, we found
257 that diurnal and arboreal species were more prone to extinction. Future studies should seek to
258 clarify the mechanism responsible for the relationship between body size and extinction risk
259 by investigating more causal intrinsic variables (e.g., abundance, population size and growth
260 rate) and more direct measures of threats imposed by exotic species (e.g., range overlap or
261 predator abundance) (Fisher et al., 2003; Murray et al., 2011).

262

263 The fact that habitat specialization, body size, and geographic range size were such strong
264 predictors of extinction risk suggests that species' intrinsic traits mediate the impacts of
265 extrinsic threats imposed by human activities. However, variables describing direct human

266 impacts (e.g., habitat loss, human population density) were of secondary importance
267 compared to intrinsic biological traits in our analyses. One plausible explanation for this
268 finding is that populations of threatened species may have already been extirpated from the
269 most disturbed habitats (Cardillo et al., 2004). For example, several species of New Zealand
270 lizards in the *at risk* category have very small but stable ranges confined to predator-free
271 offshore islands following extinction over the majority of their pre-human ranges (Worthy
272 and Holdaway 2002). Unfortunately, we lack detailed data on the distributions of New
273 Zealand lizards prior to European settlement, and thus we were not able to disentangle the
274 effects of current and historic threats. Conversely, temporal lags between disturbance and
275 ensuing population declines may obscure the relationship between measures of human impact
276 and extinction risk (Davies et al., 2006).

277
278 We also found strong evidence that species that experienced high levels of annual
279 precipitation across their ranges were more vulnerable to extinction. Importantly, this finding
280 is not simply a result of geographic biases in the origins of *at risk* and *threatened* species
281 (Fig. 2), or due to the fact that many species with restricted ranges occur on the wet west
282 coast (correlation between geographic range size and precipitation = -0.18). Instead,
283 contemporary precipitation patterns may serve as a proxy for historical land-use change.
284 Lowland habitat modification in wetter regions has been both more recent and more
285 uniformly severe than in the drier rain-shadow regions east of the main mountain ranges.
286 Alternatively, the observed relationship between rainfall and extinction risk may be due to
287 different predator dynamics in wet and dry forests. Podocarp-broadleaf forests, which
288 typically dominate wetter regions of the country, support consistently high predator numbers,
289 whereas mast seeding in dry beech forests creates more intermittent predation pressure. These
290 differences in predation pressure have resulted in more severe declines in a number of New

291 Zealand bird species in podocarp-broadleaf forests (Gaze 1985; Elliott 1996; Kearvell et al.,
292 2002). We suggest a similar difference in predator impacts may be a driver of extinction
293 vulnerability in the lizard fauna. Regardless of the precise mechanism underlying the
294 relationship between rainfall and extinction risk in New Zealand lizards, this finding
295 demonstrates the need to consider environmental characteristics in order to identify spatial
296 biases in the probability of extinction.

297
298 Our results not only reveal novel insights into the factors that lead to a high risk of extinction
299 in New Zealand lizards, but also provide a cost-effective framework for making quantitative
300 predictions regarding the likelihood of future population declines. For example, our model
301 predicted that nearly all of the species that were ranked as data-deficient (Hitchmough et al.,
302 2010) are either *at risk* or *threatened*, suggesting that these species require urgent
303 conservation assessment. Additionally, our model identified 12 species that could be at
304 greater risk than their current statuses suggest. These species may be prone to extinction, but
305 understudied or not declining rapidly enough to capture the attention of researchers (Reed
306 and Shine 2002). Thus, our analysis can help focus future research and conservation efforts
307 by prioritizing species that deviate from model expectations.

308

309 4.1. Conclusions

310 Our finding that habitat specialization, body size, and geographic range size were the most
311 important biological correlates of extinction risk in New Zealand lizards accords with the
312 results of previous studies conducted on a wide range of vertebrate taxa (Duncan et al., 2002;
313 Fisher and Owens 2004; Olden et al., 2007; Davidson et al., 2009; Murray et al., 2011),
314 suggesting that the intrinsic traits that render species vulnerable to extinction are largely
315 consistent across different taxonomic groups. These traits may therefore serve as useful

proxies for extinction risk in the absence of species-specific data on population trends. However, our analyses also revealed that species that occupied areas with high levels of annual rainfall and were exposed to exotic predators and high human population densities were at greater risk of extinction. Thus, future studies of extinction risk will need to simultaneously consider both intrinsic traits and extrinsic threats in order to accurately predict (and thus prevent) future population declines. Integrated approaches that account for both types of threats will become increasingly important as novel selection pressures imposed by habitat loss, climate change, and species introductions further create spatial heterogeneity in extinction risk.

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Commented [RT1]: Pimm 1988 not properly alined
 Anderson 2011 has lower case 'a' in name: Hutchings, J.a.
 R reference: should be R Development Core Team

482 **Table 1. Top-ranked models of extinction risk among New Zealand lizards.**

Model	df	LL	Δ BIC	wBIC	R ²
Range+Rain ² +Size ² +Specialization	8	-50.52	0	0.21	0.65
Range+Rain ² +Size ²	7	-53.18	0.86	0.14	0.61
Humans+Range+Rain ² +Size ² +Specialization	9	-49.13	1.68	0.09	0.66
Range+Size ² +Specialization	6	-55.98	1.98	0.08	0.58
Activity+Range+Rain ² +Size ² +Specialization	9	-49.34	2.11	0.07	0.66
Range+Size ²	5	-58.51	2.58	0.06	0.54
Activity+Humans+Range+Rain ² +Size ² +Specialization	10	-47.45	2.79	0.05	0.68
Activity+Range+Rain ² +Size ²	8	-52.47	3.89	0.03	0.62

483
484 Shown are the degrees of freedom (df), the log likelihood (LL), the difference in the Bayesian
485 Information Criterion (BIC) between each model and the highest ranked model (Δ BIC), the
486 model weights (wBIC), and Nagelkerke's R² for models with Δ BIC $\leq$ 4. Superscript numbers
487 refer to quadratic fits. Range = geographic range size (ln-transformed); Rain = annual
488 precipitation; Size = body size; Specialization = habitat specialization; Humans = mean
489 human population density (ln-transformed); Activity: diurnal versus nocturnal activity.
490

491 **Table 2. Drivers of extinction risk among New Zealand lizards.**

Variable	Estimate	SE	Lower CI	Upper CI	Importance
Range	-1.06	0.26	-1.56	-0.55	1.00
Size	12.75	3.26	6.26	19.23	1.00
Size ²	-8.85	2.80	-14.42	-3.28	-
Rain	17.26	8.40	0.56	33.97	0.76
Rain ²	11.92	6.94	-1.90	25.74	-
Specialization	-0.19	0.09	-0.36	-0.02	0.69
Activity: nocturnal	-0.87	0.59	-2.05	0.31	0.26
Humans	0.29	0.21	-0.14	0.71	0.23
Presence on mammal-free island	-0.19	0.57	-1.32	0.94	0.09
Habitat use: terrestrial	-1.55	0.84	-3.23	0.12	0.08
Habitat use: terrestrial-arboreal	-0.69	1.04	-2.76	1.38	-

492
493 Shown are model-averaged coefficients and their unconditional standard errors and 95%
494 confidence intervals across the models comprising > 95% of wBIC. Also shown is the
495 relative importance weight for each variable. Superscript numbers refer to quadratic fits.
496 Range = geographic range size (ln-transformed); Rain = annual precipitation; Size = body
497 size; Specialization = habitat specialization; Humans = mean human population density (ln-
498 transformed); Activity = diurnal versus nocturnal activity; Habitat use = arboreal, terrestrial,
499 or terrestrial-arboreal; Presence on mammal-free island = at least one population present on a
500 mammal-free offshore island.

501

502 **Table 3. Predicted conservation statuses of eight New Zealand lizards that were not**
 503 **evaluated by Hitchmough et al., (2010) due to insufficient data on threats and**
 504 **population trends. Predictions were based on the highest ranked model of extinction**
 505 **risk shown in Table 1.**

Taxa	Predicted conservation status
<i>Mokopirirakau aff. granulatus 'Cupola'</i>	Threatened
<i>Mokopirirakau aff. granulatus 'Okarito'</i>	Threatened
<i>Oligosoma aff. inconspicuum 'Okuru'</i>	Threatened
<i>Oligosoma pikitanga</i>	Threatened
<i>Oligosoma toka</i>	At Risk
<i>Oligosoma 'Whirinaki'</i>	At Risk
<i>Toropuku aff. stephensi 'Coromandel'</i>	At Risk
<i>Oligosoma levidensum</i>	Not Threatened

506

507 **Table 4. New Zealand lizards that are predicted to have a higher risk of extinction on**
508 **the basis of their geographic distributions and intrinsic characteristics. Predictions were**
509 **based on the highest ranked model of extinction risk shown in Table 1.**

Taxa	Observed threat status	Predicted threat status
<i>Mokopirirakau aff. granulatus</i> 'southern North Island'	Not threatened	At risk
<i>Oligosoma aff. polychroma</i> Clade 2	Not threatened	At risk
<i>Oligosoma aff. polychroma</i> Clade 4	Not threatened	At risk
<i>Oligosoma notosaurus</i>	Not threatened	At risk
<i>Oligosoma repens</i>	Not threatened	At risk
<i>Woodworthia aff. maculata</i> 'Central Otago'	Not threatened	At risk
<i>Woodworthia aff. maculata</i> 'Cromwell'	Not threatened	At risk
<i>Dactylocnemis aff. pacificus</i> 'Three Kings'	At risk	Threatened
<i>Oligosoma acrinasum</i>	At risk	Threatened
<i>Oligosoma fallai</i>	At risk	Threatened
<i>Oligosoma macgregori</i>	At risk	Threatened
<i>Oligosoma oliveri</i>	At risk	Threatened

510

511

512 **Figure legends**

513

514 Fig. 1. Relationships between extinction risk and geographic range size (a), habitat
515 specialization (residuals of range size vs. number of habitat types used) (b), body size (c), and
516 annual precipitation (d) within each species' range (mean $\pm$ SE) for 87 lizard species from
517 New Zealand.

518

519 Fig. 2. Geographic distribution of New Zealand lizard richness and mean annual precipitation
520 (10 km resolution). (A) Total number of lizard species. (B) Number of *at risk* lizard species.
521 (C) Number of *threatened* lizard species. (D) Mean annual precipitation (1950–2000).

522

523 **Supplementary Material**

524

525 Tables of the ecological traits of New Zealand lizards (Table A1), top-ranked models (Table
526 B1) and important correlates (Table B2) of extinction risk after removing species assigned a
527 conservation ranking on the basis of their geographic range size. The authors are solely
528 responsible for the content and functionality of these materials. Queries (other than absence
529 of material) should be directed to the corresponding author.