

Diversity, invasive species and extinctions in insular ecosystems

C. Josh Donlan^{1,2,*} and Chris Wilcox³

¹Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, New York 14853, USA;

²Advanced Conservation Strategies, P.O. Box 1444, Driggs, Idaho 83422 USA; and ³CSIRO Marine and Atmospheric Research, Hobart, Tasmania 7001, Australia

Summary

1. Species invasions are a primary driver of species additions and deletions in ecosystems. Understanding the intricacies of invasions and their consequences is central to ecology and biodiversity conservation. Extinctions are rarely random and often are influenced by a suite of factors.

2. We explored abiotic and biotic factors that correlate with and help to provide proximate explanations for insular extinctions driven by invasive predators on islands off western Mexico.

3. A number of factors that were hypothesized a priori to explain the observed extinction patterns performed better than island size alone. Alternative prey available to invasive predators was negatively correlated with extinction, with twice the number of alternative prey species present on extinction-free islands compared to islands with extinctions. Carrying capacity estimates of extant populations were 27 times that of extinct populations.

4. An aggregate model that included alternative prey, carrying capacity, and seasonal precipitation was the best performing model. Those factors, which are supported by theory and empirical evidence, are informative to conservation decision-makers.

5. *Synthesis and applications.* Islands with small native mammals and no, or few, alternative prey species available to invasive predators should be prioritized for eradication. By focusing regionally on a specific threat, we provide a framework to practitioners that aids in prioritizing invasive predator eradications to halt insular extinctions.

Key-words: conservation prioritization, Baja California, endangered species, cats, *Felis catus*, Gulf of California, introduced species, *Peromyscus*, rats, *Rattus*, small mammals

Introduction

Understanding the causes and impacts of species additions and deletions in ecosystems is a central focus of ecology and conservation biology. The composition of local biotic communities arises via a series of successful invasions from a larger species pool, and subsequent interactions with resident species such as predators, competitors, and prey (Ricklefs & Schluter 1993; Terborgh *et al.* 2001). A suite of factors, including life history and geographical range, affect the dynamics of species invasions and extinctions; while some are well documented, many remain unknown and elusive (McKinney 1997; Fisher & Owens 2004). Invasions often cause species declines and extinction, particularly in insular ecosystems (Atkinson 1989; Towns, Atkinson & Daugherty 2006). However, invasions and extinctions are rarely random,

and are usually caused by multiple factors and their interactions (Terborgh *et al.* 2001; Roemer, Donlan & Courchamp 2002). Nonetheless, an emerging generality of anthropogenic global change is the replacement of native species by invasive species followed by extensive biodiversity impoverishment (Lockwood & McKinney 2001).

Comparative methods are important tools in conservation biology, and the techniques are particularly useful for searching for mechanisms that underlie patterns of extinction risk (Terborgh 1974; Wilson & Willis 1975). Comparative methods also often hope to inform on-the-ground conservation planning and interventions, yet this goal is arguably more difficult to achieve for at least three reasons.

First, most comparative studies seeking factors underlying extinction risk only explore intrinsic biological traits such as body size, life-history traits, or habitat specialization (Fisher & Owens 2004). Few investigate the role of extrinsic factors such as anthropogenic forces or interactions with the environment

*Correspondence author. E-mail: jdonlan@advancedconservation.org

and other species (but see Blackburn & Gaston 2002; Fisher, Blomberg & Owens 2003). Invasive species and habitat destruction, two primary threats to biodiversity, commonly trigger novel, complex interactions within species assemblages, often resulting in population declines or extinctions (Norbury 2001; Terborgh *et al.* 2001; Roemer *et al.* 2002).

Second, many studies combine correlation analyses across multiple species with phylogenetic independent contrasts to test hypotheses with respect to changes in ecological factors (Fisher & Owens 2004). Contrasting species with independent phylogenies is important to control for similarities that might be caused by phylogeny (e.g. body size). However, the appropriateness of using phylogenetic comparative methods to explore extinction risk is actively debated (Cardillo, Mace & Purvis 2005; Putland 2005). Some researchers have argued that the approach gives priority to phylogeny over ecology, and the unit of analyses is evolutionary events within a clade rather than the unit of extinction (Westoby, Leishman & Lord 1995; Sullivan *et al.* 2006). In contrast, the distribution of extinction risk is phylogenetically non-random for many taxa, and failing to account for such factors can arguably lead to pseudoreplication (McKinney 1997; Purvis *et al.* 2000).

Third, irrespective of the methods employed, the majority of studies exploring extinction risk have been broad in scope, covering large taxonomic groups or using worldwide data sets and pooling data on different extinction risks across suites of locales and species (Fisher & Owens 2004; Sullivan *et al.* 2006). Since current extinction threats are taxon- or context-specific (Owens & Bennett 2000), such analyses may be of limited utility for conservation planning or in elucidating the natural history of extinctions. While global models are vital for exploring general patterns, given the idiosyncratic nature of extinctions, regional models focusing on specific taxa and/or specific extinction drivers may be the most instructive in informing on-the-ground conservation interventions (Fisher & Owens 2004). Working at the appropriate scale to maximize practical use presents an analytical conundrum because regional or threat-specific data sets are often necessarily small, and thus employing phylogenetic independent contrasts is difficult. All of the issues raised above call for additional and complementary approaches to phylogenetic-independent contrasts to help provide useful risk assessment tools to decision-makers, whose goal is to manage a suite of species (or populations) in a focal community.

Regional extinction studies on islands are particularly informative. Of the threatened mammal and bird species listed by the World Conservation Union, 43% are insular (Aguirre-Muñoz *et al.* 2008). Invasive species are the primary driver of extinction and ecosystem change on islands (Townes *et al.* 2006). Invasive predators, such as cats *Felis catus* and rats *Rattus* spp., are present on over 80% of the world's islands and new introductions still occur (Atkinson 1985; Pitman, Ballance & Bost 2005). However, invasive mammals can now be routinely removed from islands; more than 800 successful eradications have taken place over the past four decades (Donlan 2008; Donlan & Wilcox 2008). Prioritizing islands for invasive mammal eradication should thus be an important

focus for conservation science. For example, assuming that a certain amount of resources are available to remove feral cats from an island archipelago, based on the available data, which islands should be targeted to maximize the probability of preventing extinctions?

Here, we use the islands off western Mexico, known for their endemism and biodiversity, to explore patterns of small mammal extinctions and how intrinsic and extrinsic factors interact in ways that might predispose populations to extinction by invasive predators. Feral cats and rats have recently caused a number of extirpations and extinctions on some of these islands (Alvarez-Castañeda & Patton 1999; Alvarez-Castañeda & Ortega-Rubio 2003; Donlan *et al.* 2005; Knowlton *et al.* 2007). Yet, on other islands in the region with invasive predators, biodiversity loss has not occurred. Using theory and empirical evidence, we test eight a priori hypotheses that may have contributed to insular extinctions (Table 1). We use three complementary analytical approaches with a limited data set. This data-poor scenario is representative of most conservation planning exercises. We explore geographical (i.e. habitat heterogeneity and productivity), autecological (i.e. carrying capacity and population growth rate), and synecological (i.e. presence of predators and alternative prey) factors that potentially correlate with and, thereby, help to provide proximate explanations for extinctions driven by invasive predators.

Materials and methods

Using an island biodiversity data base for the region (Donlan *et al.* 2000), we collated biotic and abiotic information for all the islands off the Pacific coast of Baja California ($n = 23$) and in the Gulf of California ($n > 135$) where feral cats and rats are present or have recently been removed after extinctions occurred (Fig. 1). We recorded the extant ($n = 58$) and extinct ($n = 9$) native, nonvolant mammals occurring on the 25 islands with invasive predators. Two carnivores (ringtail *Bassariscus astutus* and coyote *Canis latrans*) were excluded since predation by cats or rats is not a threat (these species are included in the native predation index below).

Taxa included in the analysis were from the following genera (number of populations): *Ammospermophilus* (2), *Chaetodipus* (16), *Dipodomys* (2), *Lepus* (5), *Neotoma* (13), *Notiosorex* (1), *Peromyscus* (25), *Sylvilagus* (2), and *Thomomys* (1). The biodiversity and extinctions on the islands are well documented, with species losses attributed to the impacts of cats and/or rats (Alvarez-Castañeda & Patton 1999; Alvarez-Castañeda & Cortes-Calva 2002; Alvarez-Castañeda & Ortega-Rubio 2003; Vázquez-Domínguez, Ceballos & Cruzado 2004; Donlan *et al.* 2005; Espinosa-Gayosso & Álvarez-Castañeda 2006; Knowlton *et al.* 2007). On Meija Island, *Peromyscus guardia* was recently observed (A. Samaniego, personal communication, 2005). However, it is unclear whether the individuals observed are from the same population that was last collected in 1973 and declared extinct after substantial trapping efforts (Alvarez-Castañeda & Ortega-Rubio 2003), or a new population that has immigrated from one of the two islands nearby (~570 m). Introduction by fishermen during camping activities is also a possibility. Given the historical trapping effort, the small size of the island (3.3 km²), and the reality of stow-away introductions (Hafner, Riddle & Alvarez-Castaneda 2001), we assumed the population is newly arrived.

Table 1. Geographical, autecological, and synecological proposed proxies, variables, and their potential contribution to extinction risk of small mammals on islands where invasive predators are present

Proposed proxy (variable) [+ or – correlation with population decline/extinction risk]	Possible mechanism	Support
Geographical		
Maximum elevation (habitat heterogeneity) [–]	Spatial structure promotes population persistence, including within predator–prey systems	1–5
Rainfall (<i>in situ</i> primary productivity) [–/+]	Low or variable productivity results in proneness to demographic perturbations or stochasticity, or the reverse trend via the <i>paradox of enrichment</i>	7–10
Perimeter–area ratio (allochthonous input) [–/+]	Depending on the subsidy magnitude and prey preference, donor-controlled resources could stabilize or destabilize food web interactions or predatory–prey interactions	11–14
Autecological		
K_{\max} (carrying capacity) [–]	Small populations are prone to demographic perturbations and stochasticity	1, 15–17
r_{\max} (population growth rate) [–]	Populations with low intrinsic growth rates may lack the ability to recover from disturbances	18–20
σ_r (variance in population growth rate) [+]	Populations with greater temporal variation are more prone to extinction	15, 16, 18, 21
Synecological		
Mammal and lizard richness (alternative prey) [+/-]	Alternative prey could stabilize strong predator–prey interactions or destabilize them via apparent competition	2, 22–25
Snake and carnivore richness (presence of predation pressure) [–]	Many islands lack predators; thus, prey lack anti-predator defences, making them more vulnerable to predation	26, 27, 28

References: 1-MacArthur & Wilson 1967; 2-Holt 1977; 3-Boecklen 1986; 4-Ricklefs & Lovette 1999; 5-Ellner et al. 2001; 6-Rosenzweig 1971; 7-O'Conner 1991; 8-Abrams & Roth 1994; 9-O'Conner 1991; 10-Braithwaite & Muller 1997; 11-Bustamante et al. 1991; 12-Huxel & McCann 1998; 13-Sabo & Power 2002; 14-Polis et al. 2004; 15-Leigh 1981; 16-Brown 1995; 17-Fisher & Owens 2004; 18-Pimm 1991; 19-Owens & Bennett 2000; 20-Bodmer et al. 1997; 21-Diamond 1984; 22-Elton 1927; 23-Holt et al. 1994; 24-Hanski et al. 2001; 25-Roemer et al. 2002; 26-Stone et al. 1994; 27-Bowen & Van Vuren 1997 28-Buckley & Jetz 2007

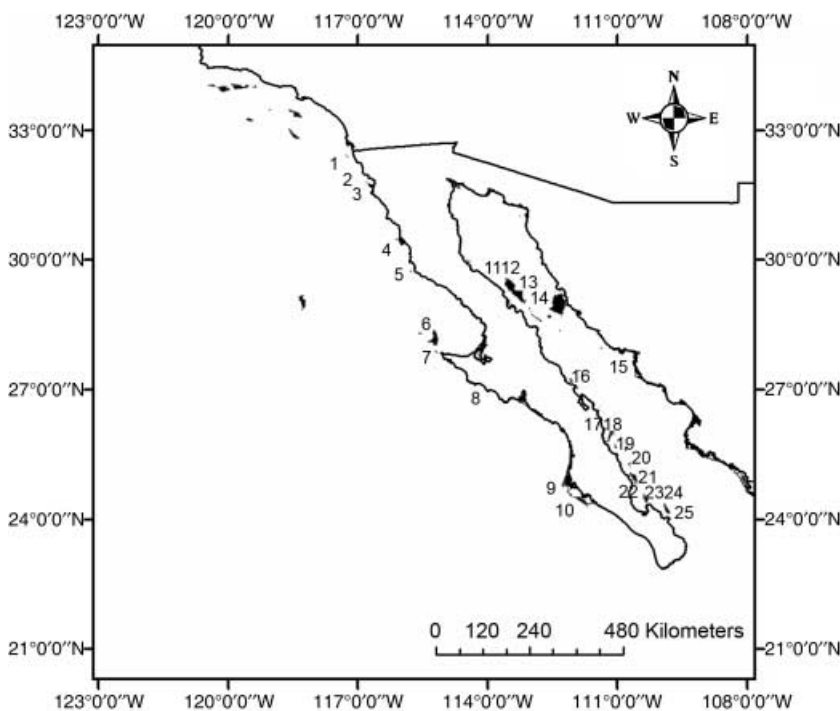


Fig. 1. The islands of western Mexico that have (or recently had) feral cat and/or invasive rat populations and native non-volant small mammals. Baja California: 1 Coronado North, 2 Todos Santos South, 3 Todos Santos North, 4 San Martin, 5 San Geronimo, 6 Cedros, 7 Natividad, 8 San Roque, 9 Magdalena, 10 Santa Margarita, Gulf of Mexico: 11 Granito, 12 Meija, 13 Angel de la Guarda, 14 Estanque, 15 San Pedro Nolasco, 16 San Marcos, 17 Coronados, 18 Carmen, 19 Monserrate, 20 Santa Catalina, 21 San Jose, 22 San Francisco, 23 Partida, 24 Espiritu Santo, 25 Cerralvo.

Island area (range: 0.6–951 km²), perimeter (range: 3.5–278 km), and maximum altitude (range: 15–1318 m above sea level) were calculated from a geospatial data base (Donlan *et al.* 2000) and the literature (e.g. Case, Cody & Ezcurra 2002). Perimeter–area ratio

(PA ratio) is a demonstrated proxy for the amount of allochthonous resource input from the marine environment to island ecosystems in the region (Polis & Hurd 1996). Climatic parameters were calculated from long-term weather data sets from the islands directly or from

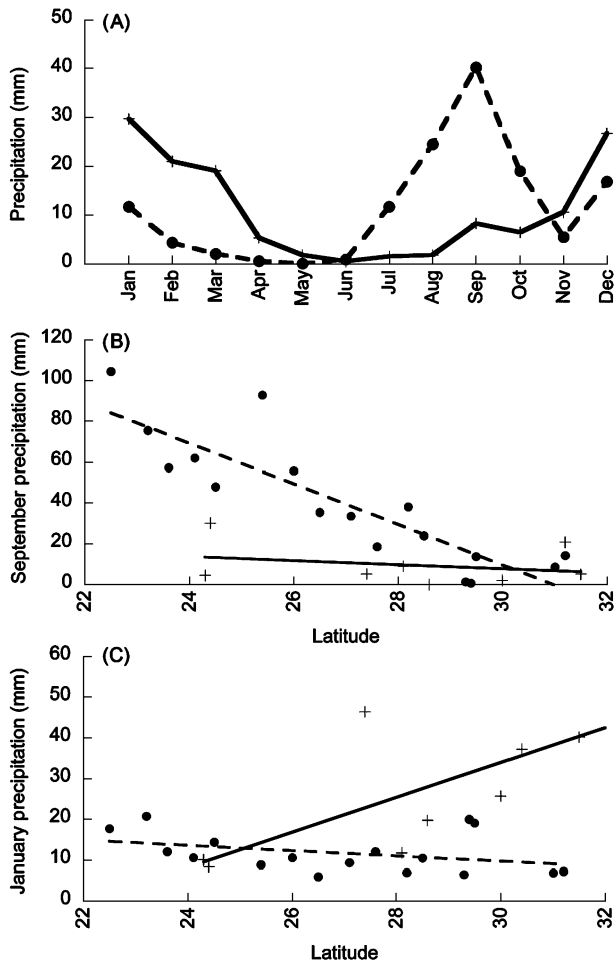


Fig. 2. Precipitation on the islands off western Mexico. (A) Mean monthly rainfall for the Gulf of California (dotted line) and off the Pacific side of Baja California (solid line). (B) Mean September and (C) January rainfall for the Gulf of California and Baja California. Data are based on long-term monthly rainfall records averaging 23 years (range: 2–54 years).

a nearby station on the adjacent mainland (Hastings & Humphrey 1969). The islands are dominated by two climatic regimes: a monsoonal pattern moving north from the tropics and a Mediterranean pattern moving south. To capture those patterns, means and the coefficients of variation were calculated for annual, January, and September rainfall; the latter 2 months represent bi-modal peaks for precipitation in the region (Fig. 2).

Adult body mass was recorded directly ($n = 46$) or estimated from closely-related species/subspecies ($n = 21$) from the literature (Lackey 1991; Alvarez-Castañeda & Patton 1999; Wilson & Ruff 1999). Autecological parameters were estimated using allometric relationships. The potential maximum rate of increase (r_{\max}) was estimated from the equation $r_m = 1.375 W^{-0.315}$, where W is the estimated mean mass and r_m is the maximum instantaneous, intrinsic rate of increase over a year (Sinclair 1996). The standard deviation of instantaneous rate of change (σ) was estimated from the equation $\sigma = 0.805 W^{-0.316}$ (Sinclair 1996). Population density (number km^{-2}) was estimated from mass, based on an < 100 kg herbivorous mammal-specific allometric relationship [$\log(\text{density}) = 1.38(\log W^{-0.75})$] (Silva & Downing 1995). Carrying capacity (K_{\max}) was estimated by multiplying estimated population density by island area.

Our index for alternative prey available to invasive predators included all additional nonvolant, native mammal and lizard taxa. This is an underestimate for two reasons. First, both cats and rats feed on terrestrial and intertidal invertebrates (Reed & Bowen 2001; Towns *et al.* 2006). Second, both predators are known to prey on seabirds and their eggs when available, and land birds to a lesser extent (Keitt *et al.* 2002; Towns *et al.* 2006). Neither birds nor invertebrates were included due to incomplete data. However, tenebrionid beetle and breeding land bird diversity correlate with island area in the region (Case *et al.* 2002) and, therefore, we expect their diversity to correlate with our index.

The number of native mammalian carnivores and snake species known to feed on small mammals was used as an index of predation pressure. Data on the densities of predators was not available; thus, we used species richness as a proxy for predation strength (Buckley & Jetz 2007). Raptor diversity was not included due to incomplete data; however, it too correlates with island area in the region (Case *et al.* 2002). Ringtails and coyotes are present on four islands; known prey items include invertebrates, small mammals, and lizards (Rose & Polis 1998; Rodriguez-Estrella, Moreno & Tam 2000). Snake diet was based on island-specific data and/or inferred based on closely related populations or taxa (Grismer 2002). Our index is conservative in the sense that only snakes that prey regularly or solely on small mammals were included (i.e. *Crotalus*, *Lichanura*, *Masticophis*, *Pituophis*, and *Trimorphodon*).

Certain variables (K_{\max} , PA ratio, and $\text{CV}_{\text{annual rain}}$) were log-transformed to meet the criteria necessary for statistical analyses. All abiotic and biotic factors (Table 1) were standardized [(observation-mean)/standard deviation] to allow for comparisons. We combined two statistical approaches for inference (Stephens *et al.* 2005). First, we used one-way ANOVA tests allowing both F and P values to inform our a priori hypotheses regarding parameters that influence extinction. Abiotic and biotic parameters were the independent variables. Our binomial response variable was extinction probability, with populations considered to be replicates. Partial Bonferroni-corrected P values were adjusted for correlated variables, and are reported with a family wide α -level of 0.05 (Sankoh, Huque & Dubey 1997).

Second, we assessed the a priori hypothesis using logistic regression, exploring a range of functional forms for each hypothesis. Abiotic and biotic parameters were the independent variables; extinction probability was the dependent variable. The best performing models for each a priori hypothesis were selected based on Akaike's Information Criterion values (AIC, Burnham & Anderson 2002). Pooling the parameters from the best-performing models, we then explored all possible sets of the aggregate models, and selected the best-performing global model based on AIC values. Our a priori approach, together with exploring all possible model subsets within a specified set of models, controls for the possibility of spurious results due to multi-collinearity (Graham 2003).

While from ecological and conservation perspectives, populations are the unit of extinction and the motivation for this analysis, using population as the replicate could be potentially viewed as pseudoreplication from two perspectives. First, geographical and synecological parameters are a function of both the target population and the island. Second, due to the regional focus and thus small sample size, we were not able to control for the possibility of phylogenetic non-independence among species. Thus, autecological parameters could potentially be non-independent. To explore those potential biases, we repeated the univariate analyses twice: once with island as the replicate using the entire data set, and again restricting the data to the genus *Peromyscus*, collapsing 26 *Peromyscus* populations

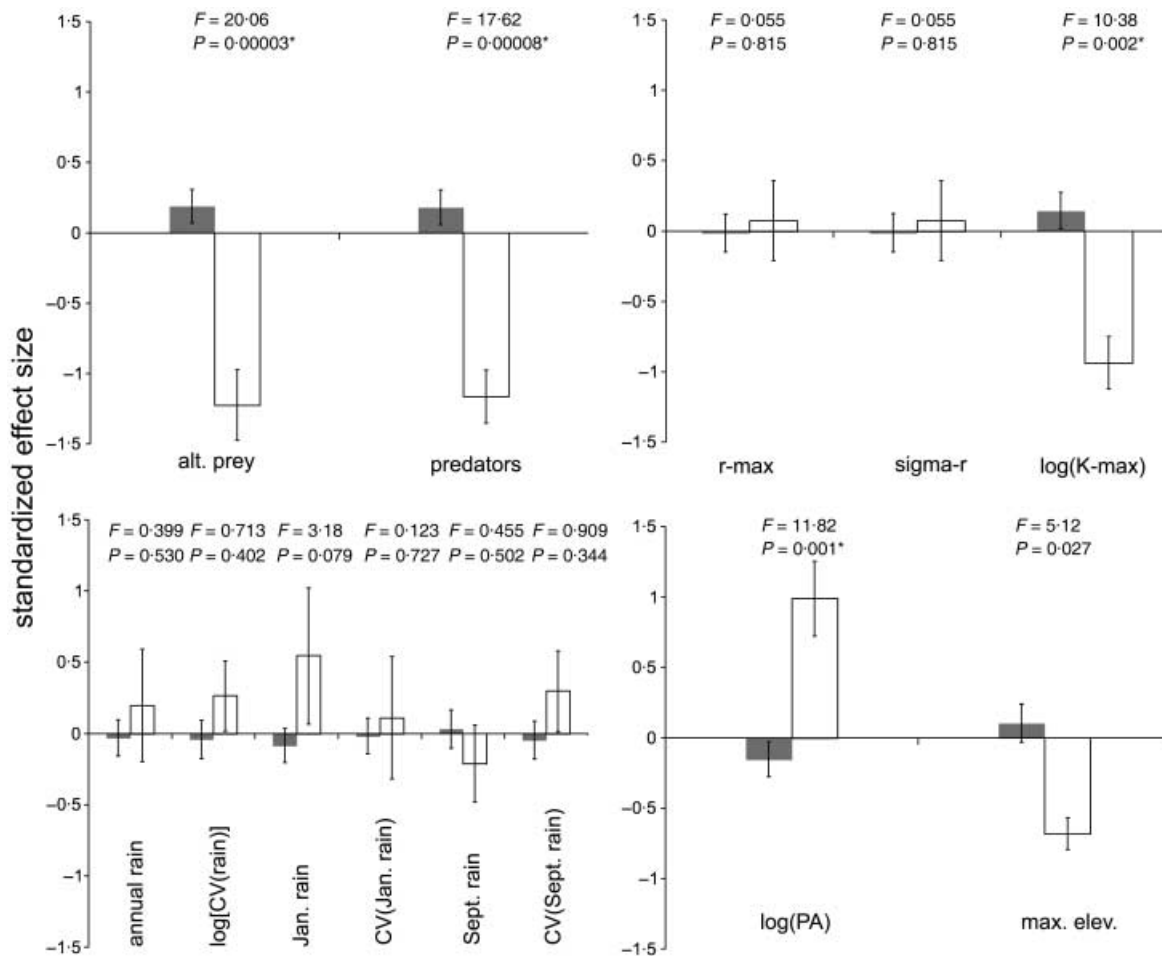


Fig. 3. Differences in synecological, autecological, and geographical traits between extant (grey) and extinct (white) insular populations in western Mexico [mean (SE); $n = 67$ populations]. Asterisks (*) indicate significant differences with a family-wide Bonferroni-corrected α level of 0.05.

to five independent groups according to their known mainland phylogenetic affinity (Hafner *et al.* 2001; Lawlor *et al.* 2002). The *Peromyscus*-specific analysis provides some insight with regard to the potential evolutionary role of the autecological parameters on extinction.

Lastly, since island size is often the focus of island biogeography and extinction studies, and that many of our a priori factors were estimated by and correlate with island area, we tested the performance of the logistic regression models with and without the inclusion of island area. Analyses were conducted in the statistical programs SPSS and R (SPSS 1999; R Development Core Team 2005).

Results

With the univariate analysis, alternative prey explained the most variance between extant and extinct populations, followed by native predators, perimeter–area ratio, and carrying capacity (Fig. 3). Alternative prey was negatively correlated with extinction, with extinction-free islands having on average over twice the alternative prey than islands with extinctions (non-standardized means: 10.4 vs. 4.3; one-way

ANOVA with island as the replicate: $F_{1,23} = 6.64$, $P = 0.017$). Alternative prey also had the lowest AIC value of the a priori models (Table 2). Native predators were three times greater on extinction-free islands (non-transformed means: 2.88 vs. 0.89; one-way ANOVA with island as the replicate: $F_{1,23} = 7.00$, $P = 0.014$). Carrying capacity estimates of extant populations were 27 times that of extinct populations (Fig. 3; non-standardized means: 5.2×10^4 vs. 1.9×10^3). Of autecological parameters, carrying capacity had the lowest AIC value (Table 2). There were no differences in r_{\max} or σ_r (Fig. 3). Perimeter–area ratio had the lowest AIC of the a priori geographical parameters, and was positively correlated with extinction (Fig. 3; Table 2; non-transformed means: 2.02 vs. 3.44; 1-way ANOVA: $F_{1,23} = 4.62$, $P = 0.042$). Extinctions occurred on islands with lower perimeter–area ratios compared to islands where extinctions did not occur. Despite the small sample size ($n = 7$), the *Peromyscus*-specific analysis on autecological variables revealed similar patterns compared to the analysis that included the entire small mammal community, but with marginal or no statistical significance (Table 3, Fig. 3).

Table 2. Comparison of models for probability of small mammal extinctions from invasive predators. Alternative prey, carrying capacity, and January rain made up the best-performing aggregate model relative to the single-parameter a priori models (see Table 1). For synecological, autecological, and geographical parameters, the best-performing model was selected from all possible models. Δ AIC is the difference between AIC values for each model and the lowest AIC value. A lower AIC value indicates a better fitting model; W is the model's Akaike weight, the relative probability that the model is the best fit to the data tested

Proposed factor(s)	Parameter(s)	Best Model – Parameter(s)	AIC	Δ AIC	W
<i>Synecological + Autecological + Geographical</i>	All parameters	Alternative prey + $\log K_{\max}$ + January rain	39.07	0.00	0.68
<i>Synecological</i>					
Alternative prey	Mammal and lizard richness	Mammal and lizard richness	41.02	1.95	0.26
Native predation/history	Mammal and snake predators				
<i>Autecological</i>					
Carrying capacity	$\log K_{\max}$		46.49	7.42	0.02
Population growth rate	r_{\max}	$\log K_{\max}$			
Variance in population growth rate	$\sigma_{r-\max}$				
<i>Geographical</i>					
Island area	$\log \text{km}^2$	$\log \text{km}^2$	45.03	5.96	0.03
Allochthonous input	$\log \text{PA ratio}$	$\log \text{PA ratio}$	47.11	8.04	0.01
Habitat heterogeneity	Maximum elevation	Maximum elevation	49.45	10.38	< 0.01
<i>In situ</i> primary productivity	Mean and CV [annual rain, September rain, January rain]	January rain	54.36	15.29	< 0.01

Table 3. Insular *Peromyscus* populations ($n = 25$) collapsed to mainland phylogenetic affinity groups ($n = 5$). Means of autecological parameters for each group are shown, along with means of extinct and extinct populations collapsed to group

Phylogenetic grouping (mainland affinity)	No. of populations (extinct)	$\log K_{\max}$	r_{\max}	$\sigma_{r-\max}$
<i>Peromyscus boylii</i>	1 (0)	3.2	4.2	2.5
<i>Peromyscus eremicus</i>	11 (3)	4.1	4.3	2.6
<i>Peromyscus fraterculus</i>	2 (0)	4.3	4.3	2.5
<i>Peromyscus maniculatus</i>	10 (1)	3.4	4.6	2.7
<i>Peromyscus merriami</i>	1 (1)	3.2	4.4	2.6
Phylogenetic independent extant mean	4	3.9	4.3	2.5
Phylogenetic independent extinct mean	3	2.8	4.6	2.6
$F_{1,5}$		5.71	0.605	0.606
P value		0.062	0.47	0.47

Pooling across the best-performing a priori single parameter models, the best-performing aggregate model included three parameters: alternative prey, carrying capacity and January rain (Table 2). The three-parameter model was nearly 20 times more likely to explain variation in extinctions among small mammal populations than island area (evidence ratio = $W_{\text{alt prey} + K_{\max} + \text{Jan. rain}} / W_{\text{island area}}$, Burnham & Anderson 2002). The best-performing aggregate model did not include island area. As a single parameter, island area performed best compared to other geographical parameters (Table 2). Island area was different on islands with and without extinctions (non-transformed mean: 4.8 vs. 146.7 km²; one-way ANOVA on log area: $F_{1,23} = 6.098$, $P = 0.021$).

Discussion

Over the last 500 years, feral cats and invasive rats are likely to have been responsible for more documented vertebrate extinctions worldwide than any other agent (Atkinson 1989; Towns *et al.* 2006; Aguirre-Muñoz *et al.* 2008; Jones *et al.*

2008). Cats are present on 24 of the 25 islands in this study (or were recently removed, Tershy *et al.* 2002), and are responsible for eight of the observed extinctions (see references in Methods). Rats, present on five islands, are known to compete with and suppress insular rodent populations elsewhere (Harris & Macdonald 2007). They are presumed to be responsible for the additional extinction and may have contributed to others. Our results suggest that the interplay of autecological, synecological, and geographical traits may predispose small mammals to extinction via feral cat predation.

SYNECOLOGICAL FACTORS

Alternative prey was consistently the most powerful explanatory variable between extant and extinct populations. Feral cats are generalist and opportunistic predators, with small mammals commonly making up a large percentage of their diet (Bloomer & Bester 1990; Molsher, Newsome & Dickman 1999). Cats are also known to prey on seabirds

and lizards, particularly when mammals are in low abundance or absent (Bloomer & Bester 1990; Keitt *et al.* 2002). With high prey densities, prey-switching in generalist predators can lead to type III functional responses (Hanski, Hansson & Henttonen 1991). In Australia, cats commonly show evidence of a type III functional response to their preferred prey species (i.e. rabbits), with prey consumption following primary prey abundance and prey switching when that prey declines (Catling 1988; Reed & Bowen 2001). As originally hypothesized by Elton (1927), in a community with diverse prey, this predator functional response can have stabilizing effects on prey abundance (Hanski *et al.* 2001). Alternatively in less diverse communities, a generalist predator could feasibly destabilize prey populations and increase the extinction probability of the preferred prey species.

Long-term empirical studies on rodent predator–prey dynamics in other systems support the hypothesis of a context-dependent community response from predators. In Fennoscandia and arctic Canada, specialist predators show a delayed numerical response to changes in rodent prey populations, which results in unstable prey population dynamics due to delayed density-dependent mortality of rodents (Hanski *et al.* 2001). In contrast, generalist predators in the same high-latitude ecosystems stabilize (i.e. inhibit population oscillations) rodent demography (Erlinge *et al.* 1984; Reid, Krebs & Kenney 1995; Hanski *et al.* 2001). Similarly, systems such as islands with low prey diversity, could necessarily limit prey switching for generalist predators such as feral cats, which in turn could lead to extinction of the preferred prey. Our results are consistent with the hypothesis that similar dynamics are occurring on the islands of western Mexico.

AUTECOLOGICAL FACTORS

Low mean abundance, which often correlates with extinction, is a function of intrinsic traits (i.e. survival and reproduction) interacting with extrinsic abiotic and biotic factors. Our carrying capacity estimate probably errs toward its upper bound because it assumes populations are saturated in the habitat, and the estimate is based on an intrinsic trait and a single-bounded abiotic factor: maximum available habitat (i.e. island area). In contrast to others (Owens & Bennett 2000; Duncan, Blackburn & Worthy 2002), we found no evidence that slow life-history attributes (i.e. r_{\max} and σ_r) correlate with extinction by invasive predators. While theory predicts that species with slow life histories should be more vulnerable to exploitative forces (Pimm 1991), results of empirical studies have been mixed (Fisher & Owens 2004).

For autecological traits, population size (and percent change) may be the best predictor of extinction risk (O'Grady *et al.* 2004); however, it is often unavailable. While imprecise, carrying capacity estimated by body size and available habitat (data that is commonly available) may be a useful proxy of population size to help predict extinction vulnerability by invasive mammals. When combined with alternative prey, it

was more informative than using island area alone and provides insights into possible mechanisms. In contrast, area is multi-factorial and a proxy for a suite of correlated factors (MacArthur & Wilson 1967; Ricklefs & Lovette 1999). Further, island area does not always correlate linearly with ecological factors. For example, populations of *Peromyscus* are often found at high densities on very small islands (Stapp & Polis 2003).

GEOGRAPHICAL FACTORS

In western Mexico, we suspect primary productivity via precipitation influences the probability of extinction by invasive predators in complex ways by interacting with island-specific factors. While the entire arid region is heavily influenced by rainfall, precipitation differs between the islands in the Gulf of California and off the Pacific side of Baja California. In the Gulf of California, September rainfall from tropical storms decreases moving northward. The Pacific islands receive the majority of their rainfall during the winter, with a decreasing trend moving southward away from the Mediterranean climate of California (Fig. 2). The role of January rain in invasive predator-driven extinctions in western Mexico is equivocal. While the inclusion of January rain in the aggregate model is consistent with a *paradox of enrichment* hypothesis (Rosenzweig 1971), it is unclear whether this effect is general, or alternatively, heavily influenced by two extinctions that have occurred on northern islands with greater January rainfall compared to the rest of the region. When those two (two of nine) extinctions are removed from the analysis, January rain is not included in the aggregate model.

Precipitation is known to heavily influence island dynamics in the region, particularly high rainfall events and subsequent prolonged droughts associated with the El Niño Southern Oscillation (ENSO, Polis *et al.* 1997; Donlan, Tershy & Croll 2002). While the details of how introduced predation and precipitation interact at the landscape scale are unclear, empirical studies with insular *Peromyscus* in the region suggest the interaction may be important (Stapp & Polis 2003).

Of the nine extinctions, *Peromyscus* spp. were the most frequent (5 out of 25 populations), followed by woodrats (*Neotoma* spp., 3) and pocket mice (*Chaetodipus baileyi*, 1). With the exception of one population, all *Peromyscus* extinctions have occurred on islands where it was the only native mammal present. Insular *Peromyscus* populations are dynamic, with drastic fluctuations driven by ENSO-related rainfall events (Stapp & Polis 2003). Populations show precipitous declines with a return to arid conditions following ENSO rains, and often become restricted to near-shore habitats due to a reliance on littoral resources (Stapp & Polis 2003). During prolonged droughts, the large numerical responses of *Peromyscus* to bottom–up forcing, coupled with a reliance on allochthonous resources, may make them more vulnerable to novel top–down forces (Rosemond, Mulholland & Elwood 1993).

Feral cats, and other predators, often are known to rely heavily on near-shore habitats for both terrestrial and littoral

prey (Tidemann, Yorkston & Russack 1994; Rose & Polis 1998, C.J.D. personal observation). Significant allochthonous inputs from the marine environment to island ecosystems have been documented (Polis *et al.* 2004). Subsidy effects in predator–prey systems are predicted to be positive or negative on a target consumer depending on the preference of allochthonous versus autochthonous sources and the level of allochthonous input (Huxel & McCann 1998). Both positive effects driven by a consumer's functional response and negative effects driven by a consumer's numerical response have been reported in other ecosystems (see references in Table 1). While the results of our study are consistent with a negative effect (Fig. 3), which has also been hypothesized elsewhere (Power *et al.* 2004), empirical research is needed to determine if marine subsidies commonly increase invasive predation pressure on native, island species.

INFORMING CONSERVATION INTERVENTIONS

Information that is both relatively accessible and instructive to conservation planning is in high demand. While some useful information may be universal, most is likely to end up being geographically or situationally dependent (Donlan *et al.* 2005; Greene 2005). Models that require a minimum amount of data will be more useful, since the majority of conservation planning scenarios are data-poor (Doak & Mills 1994).

Over the past four decades, the eradication of invasive mammals has become one of society's most powerful conservation tools to prevent extinctions and restore ecosystems (Veitch & Clout 2002; Donlan *et al.* 2003). The accumulation of pre-eradication impact and post-eradication recovery studies provide some support for the alleged biodiversity benefits of invasive mammal eradications (Keitt & Tershy 2003; Donlan & Heneman 2007). Consequently, there is increasing interest in prioritizing islands for invasive mammal eradication to maximize conservation return on investment. Biological and geographical information that ranks island scenarios where invasive mammal-driven extinctions are likely would be extraordinarily useful in prioritizing islands for eradication.

For predicting interactions between invasive predators and native prey, empirical data such as population abundance and predator density are preferable over carrying capacity estimated by body size and predator species richness. The former, however, are more often than not unavailable. For the islands off western Mexico and perhaps other archipelagos, alternative prey and carrying capacity are two factors that could help to guide the prioritization of invasive predator eradication campaigns. Islands with small, native mammals and no, or few, alternative prey species available to invasive predators should be prioritized for eradication. In particular, islands with such community structure and low estimated carrying capacity of native prey should be high conservation priorities. Our analysis demonstrates that synecological and autecological parameters are more informative in predicting extinction risk than island area alone. Influences of precipitation appear more complex, which highlights the challenge of elucidating relationships that balance the search for mechanism and

utility to conservation decision-making. The methodological approach used here could be used as a template for other archipelagos in guiding conservation programmes.

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