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Notes and Comments

Biogeographic and Ecological Regulation of Disease: Prevalence of Sin Nombre Virus in Island Mice Is Related to Island Area, Precipitation, and Predator Richness

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abstract: The relative roles of top-down and bottom-up forces in affecting disease prevalence in wild hosts is important for understanding disease dynamics and human disease risk. We found that the prevalence of Sin Nombre virus (SNV), the agent of a severe disease in humans (hantavirus pulmonary syndrome), in island deer mice from the eight California Channel Islands was greater with increased precipitation (a measure of productivity), greater island area, and fewer species of rodent predators. In finding a strong signal of the ecological forces affecting SNV prevalence, our work highlights the need for future work to understand the relative importance of average rodent density, population fluctuations, behavior, and specialist predators as they affect SNV prevalence. In addition to illustrating the importance of both bottom-up and top-down limitation of disease prevalence, our results suggest that predator richness may have important bearing on the risk of exposure to animal-borne diseases that affect humans.

Keywords: California Channel Islands, disease ecology, habitat area, hantavirus, predators, Sin Nombre virus.

Introduction

With increasing global emergence of infectious diseases (e.g., Jones et al. 2008), understanding the dynamics of pathogen prevalence in host populations is critical for mitigating the transmission of infectious diseases from wildlife hosts to humans (i.e., zoonoses). Although it is appreciated that bottom-up limitation of host density by resources or limited habitat area may affect prevalence by reducing host abundance (Ostfeld et al. 1996; Yates et al. 2002), recent theory suggests that an increase in predators can also lead to a reduction in disease prevalence among hosts if predators reduce host density and predation is independent of host infection (Packer et al. 2003; Ostfeld and Holt 2004; but see also Holt and Roy 2007). Although rarely examined in the context of zoonotic disease, more diverse communities of predators may also more effectively reduce prey abundance, thereby reducing disease prevalence in prey (Keesing et al. 2006). Understanding the role of resources and predators in affecting prevalence is important because available habitat area (Vitousek et al. 1997), primary productivity (Vitousek et al. 1997), and predator abundance and diversity (Crooks and Soule 1999) are being dramatically altered by contemporary land use and global change, but little is known about how these combined characteristics affect the prevalence of infectious diseases (Langlois et al. 2001; Lehmer et al. 2008; Dizney and Ruedas 2009). Efforts to understand the importance of area, productivity, and predators are further complicated because boundaries in ecological systems are rarely discrete, and it is often difficult to determine the actual area available to organisms, the resources available for organism use, or the predator species incident on that area.

Islands are classic models for biogeographic study that provide an empirically tractable opportunity to understand the relative importance of predators, primary productivity, and biogeographic characteristics in affecting disease prevalence in wildlife hosts. In insular systems, predator communities are often completely known, and primary productivity, habitat area, perimeter, and elevation can be objectively quantified to predict their effect on prey abundance (e.g., Buckley and Jetz 2007).

Here, we use a compilation of data to examine whether the richness of top predator species, annual precipitation (strongly tied to primary production in the study area; Williams et al. 2005), and biogeographic characteristics

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Table 1: Pearson correlations between Sin Nombre virus (SNV) prevalence in *Peromyscus maniculatus* and island characteristics

Characteristic	SNV	Area	Perimeter	Elevation	Annual precipitation	PPSR
SNV prevalence	...					
Area (km^2)	.83**	...				
Perimeter (km)	.72**	.96***	...			
Elevation (m)	.65*	.92***	.97***	...		
Annual precipitation (cm)	.90***	.59	.46	.41	...	
PPSR	.62*	.90***	.91***	.89***	.39	...
Primary and secondary predator species richness	.72**	.91***	.88***	.88***	.62*	.84***

Note: Complete descriptions of data and data sources are in the appendix in the online edition of the *American Naturalist*. PPSR = primary predator species richness.

* $P \leq .1$.

** $P \leq .05$.

*** $P \leq .01$.

(island area, perimeter, and elevation) are related to the prevalence of a highly virulent strain of hantavirus (Sin Nombre virus) in deer mice (*Peromyscus maniculatus*) on the California Channel Islands. Sin Nombre virus (SNV) causes chronic infections in deer mice (Kuenzi et al. 2005) that are thought to have minimal effects on adult deer mouse mortality in the wild, although young mice may experience higher mortality due to infection (Douglass et al. 2001). SNV is the etiologic agent of hantavirus pulmonary syndrome in humans, one of the most virulent zoonotic diseases in North America, and prevalence in *P. maniculatus* is thought to be indicative of human disease risk (Yates et al. 2002). As SNV prevalence in *P. maniculatus* on the Channel Islands is among the highest recorded anywhere in the world (Graham and Chomel 1997; Jay et al. 1997; Orrock and Allan 2008) and a rich array of biogeographic studies have been conducted in this system (e.g., Power 1972; Weissman and Rentz 1976; Moody 2000), the Channel Islands provide an ideal natural laboratory in which to explore the influences of top-down and bottom-up forces on the prevalence of an important emerging infectious disease in wild hosts.

Methods

The Channel Islands include eight islands located off the coast of southern California: San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, San Nicolas, Santa Catalina, and San Clemente. Data on SNV prevalence in rodents on the Channel Islands have been collected by several researchers (Graham and Chomel 1997; Jay et al. 1997; Orrock and Allan 2008). For our analyses, we use data on antibody prevalence collected by Jay et al. (1997) because they sampled all eight islands in 1994, whereas other available studies did not sample all of the islands (see the appendix in the online edition of the *American Naturalist* for details on SNV prevalence data). Data describing island area, perimeter, elevation, precipitation, and predator communities were obtained from published and unpublished sources (see the appendix for a complete description and listing of data).

Several rodent predator species are found on most of the islands (Collins et al. 1979; Schoenherr et al. 1999). From this pool of predator species, we retained a subset of primary predators based on whether predators have been documented to affect mouse populations or whether predator effects on mouse populations are likely based on predator activity patterns (i.e., nocturnal vs. diurnal) and predator diet (details can be found in the appendix).

Although interactions among rodent species may also be important in determining the dynamics of SNV prevalence (Mills 2005; Peixoto and Abramson 2006; Dizney and Ruedas 2009; Suzán et al. 2009), rodent communities on the Channel Islands are composed of very few species. Deer mice are the sole small mammal species on three islands, two islands have deer mice plus restricted occurrence of one other species, and three islands have deer mice and one or two other species (Collins et al. 1979; Schoenherr et al. 1999; Schwemm and Coonan 2001). Deer mice are generally the most abundant rodent species on all of the islands. The general lack of interspecific competition on islands may contribute to the high densities of deer mice and high SNV prevalence observed on the islands. Because of the paucity of other small mammals on the islands, we did not examine the richness of competitor species in our model comparison (moreover, prevalence of SNV was not correlated with the richness of other small mammal species in our study; $r = -0.03$, $P = .94$).

We used a model-comparison approach (Burnham and Anderson 2002; Johnson and Omland 2004) to evaluate the importance of island biogeographic variables (e.g., island area, perimeter, maximum elevation) and ecological variables (e.g., precipitation, predator richness) in determining SNV prevalence (table 1). Because island area, perimeter, and elevation were all highly correlated (i.e., all $r \geq 0.92$; table 1), we used only island area in our model. Area was selected because it is often readily determined from remote data (and thus useful for prediction) and because area was more strongly related to SNV prevalence via simple correlation than elevation and perimeter (table 1). We chose to use island area rather than utilize a data-factoring approach (e.g., factors created by subjecting independent variables to principal components analysis) because the use of island area facilitates comparison of our study to studies of other insular systems. Importantly, ancillary analyses conducted with factored data yield identical results (i.e., significant relationships are detected with factors that load heavily for the same variables that are significant in the analysis using raw data).

We included variables for consideration in our final regression model only if there was a significant simple correlation with SNV prevalence at $\alpha = 0.05$ (table 1). Models were created by evaluating the three best candidate models for models with one, two, or three independent variables via ordinary least squares linear regression and multiple linear regression. Because of the limited number of islands in our data set, we did not develop candidate models with more than three explanatory variables; we use the Akaike Information Criterion ($\mathrm{AIC_c}$) for model comparison because it incorporates small sample sizes (Johnson and Omland 2004). We considered models within 4 $\mathrm{AIC_c}$ units of the best model to be competing models (Burnham and Anderson 2002). We applied the arcsine–square root transformation to the dependent variable (proportion of mice with antibodies for SNV). Examination of residuals suggested that all relationships were linear (see fig. 1) and normally distributed. To evaluate the potential effect of multicollinearity, we evaluated variance inflation factors and the condition index (Quinn and Keough 2002). Analyses were conducted with R 2.10.1 (R Development Core Team 2009).

Results

Several biogeographic and ecological variables were significantly correlated with prevalence of SNV (table 1). Of models with only one explanatory variable, there was strongest support for precipitation (table 2): as annual precipitation increased, the proportion of *Peromyscis maniculatus* with SNV also increased (table 1). Of the two-variable models, there was strongest support for the model with precipitation and island area, with less support for models containing other combinations of variables (i.e., no other models were within 4 $\mathrm{AIC_c}$ units; table 2). One three-variable model emerged as providing a superior fit (table 2); the next-best model differed by 12.07 $\mathrm{AIC_c}$ units: SNV prevalence in island rodents was a function of island area, annual precipitation, and the richness of rodent predator species (table 2; fig. 1). Prevalence increased with

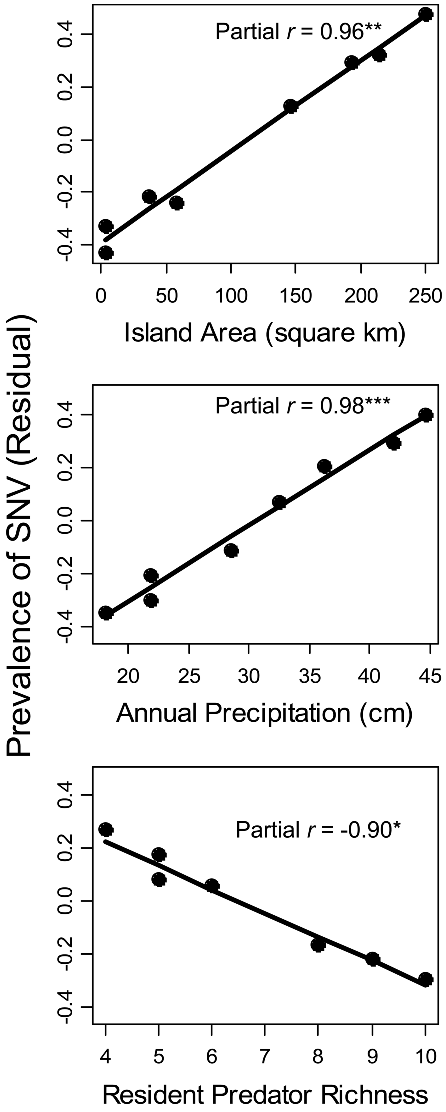

Figure 1: Prevalence of Sin Nombre virus (SNV) antibodies in deer mice (*Peromyscus maniculatus*) on the eight California Channel Islands as a function of island area, annual precipitation, and the number of primary and secondary rodent predator species on the island. Proportion of SNV-positive mice was arcsine–square root transformed before analysis. Plots are partial-regression plots to indicate the unique relationship between SNV prevalence and each of the independent variables while accounting for covariation with the other independent variables; asterisks indicate the significance of partial correlation statistics: a single asterisk indicates $P \leq .05$, two asterisks indicate $P \leq .01$, and three asterisks indicate $P \leq .001$.

Table 2: Summary of models examining the proportion of *Peromyscus maniculatus* with antibodies to Sin Nombre virus (SNV) on the California Channel Islands

	Model parameters				
Independent variables	Adjusted R^2	$\mathrm{AIC_c}$	F_{df}	P	Estimate (±SE)
One-variable model	.79	5.21	$27.09_{1,6}$	.002	
Annual precipitation					.036 ± .007
Two-variable model	.93	4.39	$46.53_{2,5}$	<.001	
Annual precipitation					.026 ± .005
Area					.0018 ± .0005
Three-variable model	.98	9.91	$133.90_{3,4}$	<.001	
Annual precipitation					.029 ± .003
Area					.0034 ± .0004
Primary and secondary predator richness					−.09 ± .022

Note: Models differ in having one, two, or three independent variables. For each number of independent variables, models with the lowest Akaike Information Criterion ($\mathrm{AIC_c}$) values are shown (no other competing models exhibited difference in $\mathrm{AIC_c}$ less than 4 units from the best model). Among the best models, each additional variable explains a significant fraction of the variation in SNV prevalence (likelihood ratio test, df = 1, both $P \leq .001$).

island area (fig. 1; partial regression: $t = 7.27$, $P < .01$), increased with annual precipitation (fig. 1; partial regression: $t = 11.11$, $P < .001$), and decreased as the number of rodent predator species increased (fig. 1; partial regression: $t = -4.09$, $P < .02$). The largest variance inflation factor between independent variables (6.07) and the largest condition index (19.07) were less than the values of 10 and 30, respectively, that indicate collinearity (Quinn and Keough 2002); these values were largely driven by the significant relationship between island area and predator richness (table 1), as would be expected by island biogeography theory (MacArthur and Wilson 1967). In addition to island area, the richness of rodent predators was significantly related to perimeter and elevation (table 1). Importantly, significant collinearity would generate large standard errors around parameter estimates, which were not observed (table 2), and predator richness still explained a significant fraction of variation in SNV prevalence, once the effects of precipitation and area were considered (fig. 1).

Discussion

Island productivity, physical characteristics, and predator richness have been found to be important in affecting the density of insular vertebrates (Buckley and Jetz 2007); our work suggests that these bottom-up and top-down constraints on deer mouse populations may have direct implications for understanding the prevalence of SNV, the agent of a highly virulent zoonotic disease. The strong relationship between SNV prevalence and annual precipitation, island area, and predator richness (fig. 1) likely arises because of the effect that these factors have on both the size and the variability of deer mouse populations. Although additional factors, such as climate, small-mammal community composition (Suzán et al. 2009), and demographic structure, may affect prevalence of SNV (Mills 2005), numerous studies have now demonstrated a positive, though often temporally delayed, relationship between mouse population density and seroprevalence for SNV (Mills et al. 1999; Yates et al. 2002; Madhav et al. 2007; Suzán et al. 2009). This evidence suggests that deer mouse density is an important predictor of SNV prevalence in mice and human cases of hantavirus pulmonary syndrome (Yates et al. 2002). High variability of deer mouse populations on some of the Channel Islands (Drost and Fellers 1991) may also influence transmission dynamics by creating years during which host density is below the basic reproductive rate of the pathogen, R_0 (Anderson and May 1990). The importance of population variability is underscored by recent models that show how high stochastic variability in rodent abundance may cause SNV prevalence to decline to very low levels for extended periods of time (Allen et al. 2006).

Annual precipitation was the best single predictor of SNV prevalence (table 2). Annual precipitation may directly affect rodent populations because it is strongly correlated with increased primary productivity in California (Williams et al. 2005), and the abundance of insular mice has been shown to be related to increased precipitation (Schwemm and Coonan 2001; Stapp and Polis 2003*a*).

Although island area was strongly related to SNV prevalence, it is not possible to ascribe unique effects to area because island area, perimeter, and elevation are highly correlated (table 1). However, there are several mechanisms by which area, perimeter, and elevation might affect SNV. The positive influence of island area on SNV prevalence may be due to increased absolute abundance of rodents, as the total number of mice on an island is likely to be a function of the total terrestrial habitat available, and studies in mainland habitat have shown that SNV prevalence increases with the amount of deer mouse habitat (Langlois et al. 2001). Island area, elevation, and perimeter may all contribute to increased SNV prevalence by reducing fluctuations in deer mouse populations, as larger islands with greater elevational range are likely to contain a higher diversity of habitats. The potential for island area to affect habitat diversity is supported by previous studies of vegetation on the Channel Islands, which suggest that habitat heterogeneity increases with island area (Westman 1983); island perimeter is also correlated with topographic diversity (Westman 1983). Habitat diversity may be important because some habitats may serve as refuges that buffer mouse populations from periods of decline due to harsh climatic events or provide safety from predation (e.g., habitats dominated by *Coreopsis gigantea* on Santa Barbara Island; Schwemm and Coonan 2001). Island area and perimeter may also contribute to increased abundance of island deer mice, and thus potentially increased prevalence of SNV, because island geometry determines the portion of the island available for allochthonous oceanic inputs that have been found to subsidize insular deer mouse populations (Stapp and Polis 2003*b*), although the islands studied by Stapp and Polis (2003*b*) were generally much smaller than the Channel Islands. Importantly, our data are ultimately limited in their ability to discern the independent effects of area, perimeter, and elevation, as well as being limited in their ability to test the mechanisms by which island characteristics affect SNV prevalence. Threfore, we stress that disentangling the unique roles of area, elevation, and perimeter in affecting the dynamics of SNV and rodent populations will require a strong experimental approach, observational data sets with many more islands, or both.

Our finding that SNV prevalence is also related to predator richness (fig. 1) has implications for the “are predators good for your health?” hypothesis, which suggests that top predators may reduce human risk of exposure to zoonoses by regulating prey populations that serve as hosts for infectious diseases (Packer et al. 2003; Ostfeld and Holt 2004). Two mechanisms, which are not mutually exclusive, may contribute to the observation that predator diversity is associated with reduced SNV prevalence, once the effects of island area and precipitation are incorporated. First, more diverse predator communities may also more effectively maintain low average densities of deer mice. The effectiveness of direct regulation of prey populations by their predators has been shown to increase with predator diversity in terrestrial (Schmitz 2007) as well as insular systems (Buckley and Jetz 2007). Second, because SNV is often transmitted among hosts via aggressive interactions between individuals (Mills et al. 1999), more diverse suites of predators may reduce transmission rates by altering the behavior of their prey (Keesing et al. 2006; Dizney and Ruedas 2009).

Our data also highlight several important points that may often go overlooked. First, strong effects of island biogeographic variables on insular communities may obscure relationships within insular communities. For example, both predator richness and SNV prevalence are related to area (table 1), and there is a significant positive correlation between SNV and predator richness (table 1). Only after the effect of area is accounted for in the multiple-regression model does the unique (and negative) relationship between SNV and predators become apparent (fig. 1). A second, related point is that the types of predators in the predator community, also likely shaped by island biogeographic characteristics, may contribute to the dynamics of SNV prevalence. In our study, small islands contain less diverse rodent predator communities (table 1), generally composed of avian predators (i.e., owls), that may drive cyclic dynamics in rodent populations (Drost and Fellers 1991). On these smaller islands, mouse populations are characterized by both high densities and sharp declines to very low densities. This increased variance could increase the likelihood of years when rodent densities fall below the threshold needed to consistently maintain high rates of SNV prevalence. In these cases, SNV may be reduced or eliminated from small islands with specialist predators (e.g., Anacapa and Santa Barbara Islands), although the richness of the predator community is relatively low on these islands.

In finding a relationship between predator richness and SNV prevalence (fig. 1), our results suggest that the conservation of predators and biological diversity may have benefits to human health via the control of infectious-disease prevalence in wildlife. An additional pragmatic implication of our findings is that habitat- and climate-based data may be useful for predicting SNV prevalence, as precipitation and area had strong, clear relationships with SNV (table 2; fig. 1). For example, the area- and productivity-dependent characteristics important in our study have also been found to affect the abundance of other insular vertebrates (Buckley and Jetz 2007), suggesting that the link between island characteristics and predator communities may be useful for understanding disease prevalence in other insular systems. In the context of the Channel Islands, our results suggest that the ongoing reintroduction of the island fox, a dominant predator that was nearly extirpated on several islands (Coonan et al. 2005), may have the benefit of reducing human risk of exposure to SNV. In addition, the potential importance of specialist predators in driving cyclic variation in deer mouse populations may also be critical for SNV prevalence on smaller islands (Drost and Fellers 1991) that have not historically supported foxes. More generally, the strong influence of productivity on SNV prevalence suggests that changes in terrestrial habitat productivity (i.e., via nutrient enrichment, irrigation, or changes in future precipitation regimes) may lead to changes in the prevalence of SNV. Although more work is necessary to understand the importance of within-island variation (Graham and Chomel 1997), the contribution of cyclic rodent dynamics (Drost and Fellers 1991), and the role of particular predators in affecting SNV prevalence (Holt and Roy 2007), the patterns that we observe suggest that conservation efforts aimed at preserving biodiversity may have the added benefit of potentially reducing human exposure to zoonotic disease.

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Jumping mouse (*Jaculus hudsonius* Baird.). From "Hibernation of the Jumping Mouse" by Sanborn Tenney (*American Naturalist*, 1872, 6:330-332).

Appendix from J. L. Orrock et al., "Biogeographic and Ecological Regulation of Disease: Prevalence of Sin Nombre Virus in Island Mice Is Related to Island Area, Precipitation, and Predator Richness"

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Methodological Details

Additional Details Regarding Sin Nombre Virus Prevalence Data

The data from Jay et al. (1997) represent average values collected from a single location on each island, and substantial variation in SNV prevalence can occur among different habitats on at least two of the islands where spatial sampling has been conducted (Graham and Chomel 1997). Nonetheless, the values reported in Jay et al. (1997) provide meaningful information on the variation among islands, as use of mean SNV prevalence calculated from two studies conducted at similar times (Graham and Chomel 1997; Jay et al. 1997) did not change our results. Data collected from a subset of the islands also suggest that patterns of SNV prevalence are stable among islands over time, as mean SNV prevalence from Jay et al. (1997) was significantly correlated ($r = 0.97$, df $= 3$, $P = .03$) with islandwide averages from four islands in 2007 (Orrock and Allan 2008).

Data from Jay et al. (1997) were collected primarily near human habitations on some of the islands because the sampling objective was to estimate human exposure risk. We view this as particularly relevant to our goal of understanding how ecological factors affect the likelihood of human exposure to SNV.

Estimation of Island Area, Elevation, and Annual Rainfall

Data for island area, perimeter, and elevation were derived from the U.S. National Oceanic and Atmospheric Administration (NOAA)/National Geodetic Survey (http://www.ngs.noaa.gov/). Annual precipitation for each island was estimated by compiling data from published sources (Westman 1983; Miller 1985; Drost and Fellers 1991; Levine et al. 2008) as well as by tabulation of unpublished weather station data for all of the islands (NOAA National Climatic Data Center; http://www.ncdc.noaa.gov/oa/ncdc.html). The precipitation values for the islands are calculated long-term averages. On average, precipitation data covered 26.5 years of observation for individual islands (a total of 212 years used for calculations), with an average of 480 observations of monthly total precipitation for each island (including incomplete years). Estimates derived via regression against the best complete long-term reference data sets (94 years of data from Santa Cruz Island Main Ranch and Los Angeles International Airport) were used to account for gaps in the available records for individual islands. This approach to estimating long-term precipitation patterns produces results that are significantly related to average values calculated using available island-specific data ($r^2 = 0.97$, $F_{1,6} = 227.7$, $P < .001$), but it has the added advantage of leveraging long-term data to provide a more complete picture of historical precipitation trends. All data used in analyses are presented in table A1.

Table A1. Summary of data used in multiple-regression models

	Island							
Characteristic	SBI	ANA	SMI	SNI	CLE	CAT	SRI	SCI
Island area (km^2)[a]	2.58	2.77	37.18	57.46	146.06	193.15	213.72	249.63
Island perimeter (km)[a]	10.21	21.13	43.34	44.47	99.67	107.67	86.14	124.29
Annual precipitation (cm)[b]	21.76	28.45	36.25	21.79	18.01	32.41	41.96	44.58
Elevation (m)[a]	193.9	284.5	254.8	277.0	600.0	649.0	482.4	740.4
Proportion SNV prevalence[c]	0	0	.179	0	.029	.143	.58	.714
Primary predator species	2	2	2	4	4	5	4	6
Primary and secondary predator species	4	5	5	5	6	10	8	9

Note: Islands are listed from smallest to largest by area: SBI = Santa Barbara Island; ANA = Anacapa Island; SMI = San Miguel Island; SNI = San Nicolas Island; CLE = San Clemente Island; CAT = Santa Catalina Island; SRI = Santa Rosa Island; SCI = Santa Cruz Island.

[a] National Geodetic survey data.

[b] C. A. Drost, unpublished data (based on data from NOAA [http://www.ngs.noaa.gov/] and the U.S. National Park Service).

[c] Jay et al. (1997).

Criteria Used to Calculate the Richness of Rodent Predator Species

In general, we considered predator species to be important if other work has documented that these predators can have an influence on deer mouse populations (either on the mainland or on the Channel Islands). We designated as primary predators those species that are widespread, common, year-round residents on an island and include mice as a significant portion of their diet. Secondary predators were those species that occur regularly on a particular island (either year-round or seasonally) but are restricted in distribution, occur in low numbers, or prey on mice only occasionally on the islands. Predators are summarized in table A2, and a description of each predator species is detailed below.

Table A2. Rodent predators found on the Channel Islands and used in the calculation of predator species richness

	Island							
	SBI	ANA	SMI	SNI	CLE	CAT	SRI	SCI
Island fox (*Urocyon littoralis*)			1	1	1	1	1	1
Western spotted skunk (*Spilogale gracilis*)							2	1
Feral cat (*Felis catus*)				1	1	1		
Black rat (*Rattus rattus*)		2						
Barn owl (*Tyto alba*)	1	1	1	1	1	1	1	1
Burrowing owl (*Athene cunicularia*)	2	2	2	2	2	2	2	2
Short-eared owl (*Asio flammeus*)	2							
Saw-whet owl (*Aegolius acadicus*)						2		2
American kestrel (*Falco sparverius*)	1	1		1	1	2	1	1
Red-tailed hawk (*Buteo jamaicensis*)		2	2			2	2	2
Northern harrier (*Circus cyaneus*)			2		2		2	
Western rattlesnake (*Crotalus oreganus*)						1		
Gopher snake (*Pituophis catenifer*)						1	1	1
Racer (*Coluber constrictor*)								1
Common kingsnake (*Lampropeltis getula*)						2		

Note: Islands are listed from smallest to largest by area: SBI = Santa Barbara Island; ANA = Anacapa Island; SMI = San Miguel Island; SNI = San Nicolas Island; CLE = San Clemente Island; CAT = Santa Catalina Island; SRI = Santa Rosa Island; SCI = Santa Cruz Island. Primary rodent predators are indicated by 1 and secondary rodent predators by 2 (see text).

Mammalian Rodent Predators

Field studies indicate that mice are commonly consumed by island foxes *Urocyon littoralis* (Crooks and Van Vuren 1995; Schwemm and Coonan 2001; Phillips et al. 2007), and they also suggest that the decline and loss of foxes on one island resulted in an increase in mouse abundance (Schwemm and Coonan 2001). The spotted skunk (*Spilogale gracilis*) is found on Santa Cruz and Santa Rosa islands (Schoenherr et al. 1999). It consumes a wide variety of invertebrate and small vertebrate prey, with deer mice being one of the most common prey items (Crooks and Van Vuren 1995). Spotted skunks on Santa Cruz Island increased in abundance between 1992 and 1998 (Crooks and Van Vuren 2000), so we considered skunks to be primary rodent predators on Santa Cruz during the time when disease prevalence data were collected. On the other hand, skunks were rare on Santa Rosa Island during this time, so we listed the spotted skunk as a secondary predator on Santa Rosa. Feral cats (*Felis catus*) are widespread on San Nicolas, San Clemente (Laughrin 1980; Phillips et al. 2007), and Santa Catalina (McChesney and Tershy 1998; Guttilla 2007). We considered cats primary predators because they are known to prey heavily on rodents on the islands (Phillips et al. 2007). Feral cats were formerly present on Santa Barbara Island, but they were removed more than a decade before the collection of the SNV data used in our study (McChesney and Tershy 1998).

Black rats (*Rattus rattus*) may opportunistically prey on smaller rats and mice. Rats have been found on Anacapa Island, San Miguel Island, Santa Catalina Island, and San Clemente Island (Collins 1979; McChesney and Tershy 1998). Rats were included as predators only on Anacapa island, where their abundance became so great that an islandwide rat eradication program was initiated in 2002 (Pergams et al. 2000). On the other three islands, rat distribution is likely limited to areas along the coastal margin where rats can find cover and forage in intertidal regions.

Avian Rodent Predators

Red-tailed hawks (*Buteo jamaicensis*) are uncommon residents on most of the larger islands and on Anacapa. We list this species as a secondary predator because it occurs in low numbers, has a generalized diet, and forages during the day, where there is little opportunity to capture mice. Northern harriers (*Circus cyaneus*) are frequent winter visitors to Santa Rosa and San Clemente and have recently established resident populations on San Miguel Island (Collins and Jones, forthcoming). Although harriers are rodent predators, we list them as secondary predators on these islands because of their relatively low abundance. American kestrels are common residents on several islands (Collins and Jones, forthcoming), and mice may make up the majority of their prey during at least part of the year (Heintzelman 1964). Surveys show that kestrels are abundant on San Clemente Island (Jorgensen and Ferguson 1984), San Nicolas Island (C. A. Drost, unpublished data), and Santa Barbara Island (C. A. Drost, unpublished data). As a result, we considered them to be primary predators on all islands except Santa Catalina, where they are uncommon and therefore classified as secondary rodent predators.

Barn owls (*Tyto alba*) are resident, breeding species on all of the Channel Islands (Collins and Jones, forthcoming). Prey pellets examined from San Miguel, San Nicolas, Santa Barbara, and Santa Rosa islands indicate that barn owls on the islands feed largely or entirely on mice (C. A. Drost, unpublished data). Burrowing owls are winter residents on most of the islands, but a breeding resident population is present on Santa Catalina Island, and burrowing owls have bred irregularly on other islands (Collins and Jones, forthcoming). Burrowing owls are generalist predators, consuming arthropods, small mammals, birds, reptiles, and amphibians (Jaksić and Marti 1981). Examination of island burrowing owl prey pellets also indicates both invertebrate and small mammal prey (C. A. Drost, unpublished data). Because of their generalized diet, local distribution, and relatively low abundance, burrowing owls were considered secondary predators on islands where they occur.

Saw-whet owls (*Aegolius acadicus*) are known only from Santa Cruz and Santa Catalina islands (Collins and Jones, forthcoming). Although this species primarily consumes small mammals (Earhart and Johnson 1970), we list it as a secondary predator because of its low numbers, restricted distribution, and primary habitation of forested habitats that are relatively rare on most of the Channel Islands. Short-eared owls (*Asio flammeus*) are rare winter visitors to the Channel Islands, and their diet consists largely of rodents (Earhart and Johnson 1970). We include this species as a secondary predator on Santa Barbara Island because they have been recorded on that island during periods of high rodent abundance (Drost and McCluskey 1992).

Reptilian Rodent Predators

Gopher snakes (*Pituophis catenifer*) occur on Santa Catalina, Santa Cruz, and Santa Rosa islands (Schoenherr et al. 1999). They are widespread on all three islands, although they are rare on Santa Rosa. Racers (*Coluber constrictor*) are found on Santa Cruz Island, where they are widely distributed and fairly common. Western rattlesnakes are found on Santa Catalina Island and are fairly common on that island (Backlin et al. 2005). The common kingsnake is found only on Santa Catalina Island, where it is fairly common (Backlin et al. 2005). Because this snake consumes a variety of prey species, we list it as a secondary predator.

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