Mesopredator release and avifaunal extinctions in a fragmented system

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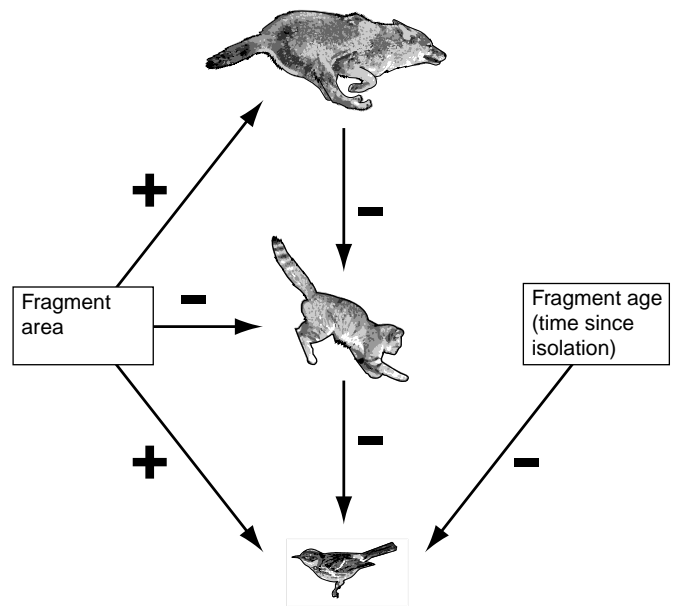* *Department of Biology, University of California, Santa Cruz, California 95064, USA*

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Figure 1 Model of the combined effects of trophic cascades and island biogeographical processes on top predators (for example, coyote), meso-predators (domestic cat) and prey (scrub-breeding birds) in a fragmented system. Direction of the interaction is indicated with a plus or minus.

Mammalian carnivores are particularly vulnerable to extinction in fragmented landscapes[1], and their disappearance may lead to increased numbers of smaller carnivores that are principle predators of birds and other small vertebrates. Such 'mesopredator release'[2] has been implicated in the decline and extinction of prey species[2–6]. Because experimental manipulation of carnivores is logistically, financially and ethically problematic[6,7], however, few studies have evaluated how trophic cascades generated by the decline of dominant predators combine with other fragmentation effects to influence species diversity in terrestrial systems. Although the mesopredator release hypothesis has received only limited critical evaluation[8] and remains controversial[9], it has become the basis for conservation programmes justifying the protection of carnivores[6]. Here we describe a study that exploits spatial and temporal variation in the distribution and abundance of an apex predator, the coyote, in a landscape fragmented by development. It appears that the decline and disappearance of the coyote, in conjunction with the effects of habitat fragmentation, affect the distribution and abundance of smaller carnivores and the persistence of their avian prey.

In coastal southern California, intensive urbanization over the past century has destroyed most of the native sage-scrub habitat, leaving undeveloped steep-sided canyons as habitat islands in an urban sea. The mesopredator release hypothesis[2] was proposed as a possible mechanism to explain the rapid disappearance of scrub-breeding birds from this system. It predicted that the decline of the most common large predator (coyote) would result in the ecological release of native (striped skunk, raccoon, grey fox) and exotic (domestic cat, opossum) mesopredators, and that increased predation by these effective predators[5,10–12] would result in higher mortality and local extinction rates of scrub-breeding birds.

To test these predictions, we surveyed coyotes, mesopredators and scrub-breeding birds in 28 urban habitat fragments (see Methods). Coyote populations have declined or disappeared from some fragments; backward elimination multiple regression (BEMR) analyses (Table 1a) indicated that fragment size was a positive predictor of mean coyote abundance (averaged over quarterly sampling sessions). As predicted, the relationship between coyote and mesopredator abundance among fragments was consistently negative (Table 2). Total mesopredator abundance, summed over all mesopredator species, was higher in fragments with fewer coyotes; coyote abundance had the strongest negative relationship with grey fox, cat and opossum abundance (Table 2). BEMR analyses indicated that coyote abundance was the strongest predictor of total mesopredator, fox and opossum abundance after accounting for the potentially confounding effects of fragment area, age and isolation (Table 1b). The most important predictor of cat abundance was the inverse of fragment area, as would be expected because smaller fragments have proportionally more urban edge and therefore greater access by housecats bordering the fragment.

Simply the presence or absence of coyotes in a fragment also influenced mesopredator abundance. Mean total mesopredator abundance was more than twice as high in fragments that coyotes never visited during the course of the study (mean, 1.17; s.d., 0.299) than in fragments where coyotes were detected at least once (mean, 0.52; s.d., 0.436). Coyote presence had the strongest negative effect on domestic cat, opossum and raccoon abundance (Table 2). BEMR indicated that coyote presence or absence was an important predictor of total mesopredator, domestic cat, opossum and raccoon abundance after accounting for fragment area, age and isolation (Table 1c); the negative effect of fragment area was retained in the final regression models for total mesopredator, grey fox and domestic cat abundance.

In accordance with the mesopredator release hypothesis, the direction of the correlation between the number of native scrub-specialist bird species persisting in fragments (see Methods) and mesopredator abundance was consistently negative (Table 2). Bird species diversity decreased with total mesopredator abundance; bird diversity had the strongest inverse correlation with grey fox, domestic cat, opossum and raccoon abundance (Table 2). BEMR revealed that the positive effect of fragment area and the negative effect of fragment age were the strongest determinants of bird diversity in this system (Table 1d). However, the negative effects of total mesopredator, cat and raccoon abundance on bird diversity persisted even after accounting for age and area effects.

According to the mesopredator release hypothesis, the top predator should have an indirect and positive effect on bird species diversity[13]. As predicted, scrub bird diversity was higher in fragments where coyotes were either present or more abundant (Table 2). Both coyote presence or absence and coyote abundance remained significant predictors of bird diversity even after accounting for the strong effects of fragment area and age on bird populations (Table 1d).

Coyote abundance also varied across time in some fragments, permitting a more direct test of the causal mechanisms underlying the correlational patterns observed in the regression analyses; temporal variability was masked in the above analyses by using mean abundances averaged across quarterly sampling sessions in each fragment. In the 13 fragments that coyotes visited only temporarily during the study, mean abundance of total mesopredators in quarters without coyotes was higher than in quarters with coyotes (Wilcoxon matched pairs test: $Z = 3.110$, $P = 0.002$); this pattern of temporal avoidance was significant for foxes ($Z = 2.667$, $P = 0.008$), cats ($Z = 2.353$, $P = 0.019$) and skunks ($Z = 2.045$,

$P = 0.041$), and was not significant for opossums ($Z = 1.334$, $P = 0.182$) or raccoons ($Z = 1.007$, $P = 0.314$). Indeed, temporal variance in total mesopredator visitation rate was significantly higher in the 13 fragments in which coyotes came and went compared to the 15 fragments in which coyotes were either constantly present or absent ($t = 2.18$, $P = 0.038$). Finally, within each of the five fragments surveyed for two years, total mesopredator visitation rate increased when coyote visitations declined (Table 3); this temporal avoidance between coyote and mesopredators was largely driven by coyote–cat interactions.

Mesopredators not only temporally avoided coyotes within fragments, but also avoided sites in fragments where coyotes were most active. In the 11 fragments where mesopredators were detected and where coyotes were present in every quarterly sampling session, coyotes and mesopredators visited the same track station on the same night significantly less than expected based on random visitations of both taxa (contingency $X^2 = 12.39$, $P < 0.001$). This pattern was evident for foxes ($X^2 = 4.572$, $P = 0.032$ in 8 fragments with foxes) and opossums ($X^2 = 2.96$, $P = 0.086$ in 9 fragments), but was not significant for cats ($X^2 = 0.856$, $P = 0.355$ in 11 fragments), skunks ($X^2 = 1.74$, $P = 0.187$ in 7 fragments) or raccoons ($X^2 = 0.900$, $P = 0.343$ in 4 fragments).

The interactions between coyotes, cats and birds probably have the strongest impact on the decline and extinction of scrub-breeding birds. Coyotes kill domestic cats in these habitat fragments. Cat remains were found in most fragments with coyotes, and 21% of 219

Table 1 BEMR models of effects of trophic interactions and biogeographical variables

	Whole model			
	R^2	P	Parameter estimate	P
(a) Dependent variable: coyote abundance*				
Coyote abundance	0.111	0.046		
Area			0.381	0.046
(b) Dependent variables: mesopredator abundance†				
Total mesopredator abundance	0.314	0.002		
Coyote abundance			−0.560	0.002
Grey fox abundance	0.356	<0.001		
Coyote abundance			−0.596	<0.001
Domestic cat abundance	0.316	0.002		
Area			−0.562	0.002
Opossum abundance	0.373	<0.001		
Coyote abundance			−0.611	<0.001
Skunk abundance				
n.s.‡				
Raccoon abundance				
n.s.				
(c) Dependent variables: mesopredator abundance§				
Total mesopredator abundance	0.266	0.021		
Coyote presence/absence			−0.349	0.063
Area			−0.290	0.119
Grey fox abundance	0.083	0.137		
Area			−0.288	0.137
Domestic cat abundance	0.475	<0.001		
Coyote presence/absence			−0.418	0.011
Area			−0.438	0.008
Opossum abundance	0.285	0.003		
Coyote presence/absence			−0.533	0.003
Skunk abundance				
n.s.				
Raccoon abundance	0.122	0.068		
Coyote presence/absence			−0.350	0.068
(d) Dependent variable: bird diversity‖				
Bird diversity	0.886	<0.001		
Coyote presence/absence			0.464	<0.001
Area			0.511	<0.001
Age			−0.388	<0.001
Bird diversity	0.757	<0.001		
Coyote abundance			0.234	0.042
Area			0.558	<0.001
Age			−0.531	<0.001
Bird diversity	0.741	<0.001		
Total mesopredator abundance			−0.199	0.101
Area			0.569	<0.001
Age			−0.486	<0.001
Bird diversity	0.745	<0.001		
Domestic cat abundance			−0.235	0.082
Area			0.516	<0.001
Age			−0.480	<0.001
Bird diversity	0.762	<0.001		
Raccoon abundance			−0.241	0.031
Area			0.592	<0.001
Age			−0.478	<0.001
Bird diversity¶	0.739	<0.001		
Area			0.648	<0.001
Age			−0.558	<0.001

At successive steps in the backward elimination procedure, the least significant independent variable was removed from the model if the significance of the parameter estimate >0.15 (refs 18, 19). This process was continued until no variables met this criteria. Tolerance values indicated that no set of independent variables violated multicollinearity assumptions[19]. The resulting final models are presented above, with the independent variables retained in the final model in italics. Path analyses conducted on these data yielded similar results as the multiple regression analyses.
* Independent variables: fragment area, fragment age and fragment isolation.
† Independent variables: coyote abundance, fragment area, fragment age and fragment isolation.
§ Independent variables: coyote presence/absence, fragment area, fragment age and fragment isolation.
‖ Independent variables: coyote presence/absence, coyote abundance or mesopredator abundance, and fragment area, age and isolation.
‡ No independent variables were retained in the final model.
¶ Skunk, fox and opossum abundance were not retained in final models that included area and age effects.

coyote scats collected in these sites contained cat remains. Moreover, 25% of radio-collared cats were killed by coyotes (K.C., manuscript in preparation). Perhaps the strongest effect of coyotes on cats, however, is indirect. Seventy-one per cent of 636 respondents to questionnaires distributed to residents bordering the fragments realized that coyotes were a threat to cats, 42% of all cat owners in areas with coyotes reported that coyotes had attacked or killed their cats and, most importantly, 46% of cat owners restricted their cat's outdoor activity when they believed coyotes were in the fragment.

Unlike wild predators, domestic cats are recreational hunters maintained far above carrying capacity by nutritional subsidies from their owners; they continue to kill prey species even when populations of that species are low[11]. Thirty-two per cent of residents bordering the San Diego fragments owned cats, and on average each cat owner owned 1.7 cats. Seventy-seven per cent of cat owners let their cats outdoors, and 84% of outdoor cats brought back kills to the residence. Thus, approximately 35 hunting, outdoor cats surround a moderately sized fragment (~20 ha) bordered by 100 residences. In comparison, each fragment may support only one or two pairs of native predators such as foxes or coyotes. Cat owners reported that each outdoor cat that hunted returned on average 24 rodents, 15 birds and 17 lizards to the residence each year. Using these data, we estimate that cats surrounding a moderately sized fragment (~100 residences) return about 840 rodents, 525 birds and 595 lizards to residences per year. These approximations are probably underestimates, assuming that cats do not bring back all prey that they kill[14]. Identification of 68 prey items returned by cats bordering the fragments indicated that 67% of 26 rodents, 95% of 21 birds and 100% of 11 lizards were native species.

This level of bird predation appears to be unsustainable. Existing population sizes of some birds do not exceed 10 individuals in small to moderately sized fragments[15], so even modest increases in predation pressure from mesopredators, in conjunction with other fragmentation effects, may quickly drive native prey species, especially rare ones, to extinction. Extinctions of scrub-breeding birds are frequent and rapid; at least 75 local extinctions may have occurred in these fragments over the past century[15].

Our results indicate that the disappearance of a dominant carnivore results in elevated numbers and activity of mesopredators that exert strong predation pressure on native prey species. This conclusion is strengthened by changes in mesopredator activity in accord with temporal changes in coyote presence within fragments, as well as direct evidence of coyote predation on mesopredators and mesopredator predation on birds. We conclude that these trophic interactions combine with fragmentation effects to help structure this ecological community (Fig. 1). □

Methods

Biogeographical variables. We used fragment area, age and isolation as island biogeographical descriptors of the 28 urban habitat fragments[2]. The total area of each fragment was taken from digitized images of scaled aerial photographs taken in 1995 (range: 2–102 ha). Fragment age was defined as the number of years since isolation of the fragment by urban development (range: 11–95 yr). Fragment isolation was measured as the distance to the closest fragment of equal or larger size (range: 40–2,865 m). Biogeographical variables were log-transformed for analyses.

Carnivore surveys. From September 1995 through to August 1997, we conducted carnivore surveys in 28 habitat fragments originally studied in ref. 2. Relative abundance for each species was determined by establishing track detection stations at 250-m intervals along transects in each fragment, and conducting track surveys for five consecutive days in the autumn, winter, spring and summer for one year. In five fragments where coyote presence varied during the first year of surveys, we extended surveys for a second year to monitor further the effects of variation in abundance within sites. The presence of each species was verified using scat and remotely triggered camera surveys. Abundance in each quarter was expressed as the total number of visits to track stations for each species divided by the total sampling effort[16,17]; track indices were log-transformed for analyses. For each species, we averaged track indices across quarterly sampling sessions to derive a mean abundance per fragment for the duration of the study. In addition to calculating abundance for each species individually, we summed the relative abundance of mesopredators in each fragment to derive one metric for the total abundance of all small carnivores.

Bird surveys. We determined the number of scrub bird species in each fragment by point count and transect surveys, conducted in each fragment at least three different times by at least two different teams of trained observers from April 4 to June 9 1997 between sunrise and 10:30. Eight-minute point counts were conducted at stations established in or near native habitat at ~250-m intervals along the long axis of each fragment. For transect surveys, we walked slowly along the entire fragment and recorded all species detected (mean time spent per transect survey in each fragment, 107 min). We then combined the species occurrences generated by both the point count and transect surveys to calculate the number of scrub bird species at each site. We considered only those species that specialize on chaparral and coastal sage scrub habitat and rarely breed in developed sites: California quail, wrentit, spotted towhee, Bewick's wren, California thrasher, greater roadrunner, cactus wren and California gnatcatcher. Bird diversity was square-root transformed for analyses.

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Table 2 Trophic interactions

	Coyote abundance r†	Coyote presence/ absence t‡	Bird diversity r§
Total mesopredator abundance	−0.569***	−2.463**	−0.539***
Fox abundance	−0.597***	−1.090	−0.361*
Domestic cat abundance	−0.375**	−3.344***	−0.635***
Opossum abundance	−0.611***	−3.220***	−0.464**
Skunk abundance	−0.105	0.362	−0.112
Raccoon abundance	−0.264	−1.908*	−0.487***
Bird diversity	0.452**	5.580***	

† Pearson correlations between mean coyote abundance (averaged across quarterly sampling sessions) and mean abundance of mesopredator species (averaged across quarterly sampling sessions) or number of scrub-breeding bird species in each of the 28 habitat fragments.
‡ *t*-test of mean abundance of mesopredator species or bird species diversity as function of coyote presence or absence in each fragment.
§ Pearson correlations between number of scrub-breeding bird species per fragment and mean mesopredator abundance.
*$P < 0.10$, **$P < 0.05$, ***$P < 0.01$.

Table 3 Temporal avoidance of coyotes by mesopredators

Coyote abundance versus:	Total mesopredator abundance	Domestic cat abundance	Fox abundance	Skunk abundance	Opossum abundance	Raccoon abundance
Fragment	r†	r	r	r	r	r
Baja	−0.785**	−0.667*	−0.577**	−4.401	−0.502	−0.328
Laurel	−0.769**	−0.814**	−0.426	−0.694*	−0.521	0.338
Spruce	−0.740**	−0.846***	−0.559	−0.272	−0.582	−0.198
Washington	−0.679*	−0.709**	−0.639	−0.424	−0.122	−0.773**
Titus	−0.723*	−0.424	−0.695*	−0.253	−0.581	0.193

† Pearson correlations between quarterly mesopredator and coyote abundance within five habitat fragments surveyed over two years.
*$P < 0.10$, **$P < 0.05$, ***$P < 0.01$.

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Linking a genetic defect to its cellular phenotype in a cardiac arrhythmia

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Advances in genetics and molecular biology have provided an extensive body of information on the structure and function of the elementary building blocks of living systems. Genetic defects in membrane ion channels can disrupt the delicate balance of dynamic interactions between the ion channels and the cellular environment, leading to altered cell function[1–3]. As ion-channel defects are typically studied in isolated expression systems, away from the cellular environment where they function physiologically, a connection between molecular findings and the physiology and pathophysiology of the cell is rarely established. Here we describe a single-channel-based Markovian modelling approach that bridges this gap. We achieve this by determining the cellular arrhythmogenic consequences of a mutation in the cardiac sodium channel that can lead to a clinical arrhythmogenic disorder (the long-QT syndrome) and sudden cardiac death.

Several distinct genetic mutations in the *SCN5A* gene give rise to a congenital form of the long-QT syndrome and have been mapped to the α-subunit of the cardiac sodium channel (LQT3)[4]. The most severe is the ΔKPQ mutation, a three-amino-acid deletion of Lys 1505, Pro 1506 and Gln 1507 in the highly conserved portion of the III–IV linker, which is responsible for fast inactivation[5]. Clinically, the ΔKPQ mutation is associated with substantial prolongation of the Q–T interval on the electrocardiogram, which may precede syncope and sudden cardiac death.

To evaluate the electrophysiological consequences of the ΔKPQ defect at the level of the cardiac action potential, we constructed Markov models of the wild-type and ΔKPQ mutant channels based on experimental data[5–7]. The models were then integrated into the Luo–Rudy theoretical model of the cardiac ventricular action potential[8–10].

The Markovian models for the wild-type and ΔKPQ sodium channel are shown in Fig. 1. The wild-type channel model (Fig. 1a) includes three closed states (C3, C2 and C1), a conducting open state (O), and fast and slow inactivation states (IF and IS, respectively). The mutant channel model (Fig. 1b) contains two possible modes of gating, a 'background (dispersed) mode' and a 'burst mode'. The background mode includes the above six states (Fig. 1b); it is similar to the wild-type model except for alterations in the voltage dependence of activation, inactivation and recovery from inactivation (Box 1). Most (>99%) of the mutant channels reside in the background mode states. The models were incorporated into the Luo–Rudy model (Fig. 1c) for action potential simulations.

Box 1 Simulation methods

The general approach to modelling the action potential is the same as that described for the Luo–Rudy model[8–10] except that the I_{Na} transmembrane current is reformulated from the single-channel kinetics. We use the general approach of refs 20 and 21. All kinetic parameters were normalized to 37 °C with a Q_{10} of 3 (ref. 19).

All the simulations were encoded in C/C++. Simulations were implemented (double precision) on a Sun Workstation Ultra 1. A time step of 0.005 ms was used during the stimulus and the action potential upstroke. At all other times, a 0.01-ms time step was used.

Transition rates

Wild-type channel (ms^{-1});

C3 → C2	$\alpha 11 = 3.802/(0.1027 \times \exp(-v/17.0) + 0.20 \times \exp(v/150))$
C2 → C1	$\alpha 12 = (3.802/(0.1027 \times \exp(-v/15.0) + 0.23 \times \exp(-v/150)))$
C1 → O	$\alpha 13 = 3.802/(0.1027 \times \exp(-v/12.0) + 0.250 \times \exp(-v/150))$
C2 → C3	$\beta 11 = 0.1917 \times \exp(-v/20.3)$
C1 → C2	$\beta 12 = 0.20 \times \exp(-(v-5)/20.3)$
O → C1	$\beta 13 = 0.22 \times \exp(-(v-10)/20.3)$
O → IF	$\alpha 2 = (9.178 \times \exp(v/29.68))$
IF → O	$\beta 2 = ((\alpha 13 \times \alpha 2 \times \alpha 3)/(\beta 13 \times \beta 3))$
IF → C1	$\alpha 3 = (3.7933^{-9} \times \exp(-v/5.2))$
C1 → IF	$\beta 3 = (0.0084 + 0.00002 \times v)$
IF → IS	$\alpha 4 = \alpha 2/100$
IS → IF	$\beta 4 = \alpha 3$

ΔKPQ mutant channel* (ms^{-1}):

xC3 → xC2	
	$\alpha 11 = 1.25 \times (3.082/(0.1027 \times \exp(-v/17.0) + 0.20 \times \exp(-v/150)))$
xC2 → xC1	
	$\alpha 12 = 1.25 \times (3.082/(0.1027 \times \exp(-v/15.0) + 0.23 \times \exp(-v/150)))$
xC1 → xO	
	$\alpha 13 = 1.25 \times (3.082/(0.1027 \times \exp(-v/12.0) + 0.250 \times \exp(-v/150)))$
xC2 → xC3	$\beta 11 = 0.1917 \times \exp(-v/20.3)$
xC1 → xC2	$\beta 12 = 0.20 \times \exp(-(v-5)/20.3)$
xO → xC1	$\beta 13 = 0.22 \times \exp(-(v-10)/20.3)$
O → IF	$\alpha 2 = (9.178 \times \exp(v/100))$
IF → O	$\beta 2 = ((\alpha 13 \times \alpha 2 \times \alpha 3)/(\beta 13 \times \beta 3))$
IF → UC1	$\alpha 3 = 20 \times (3.7933^{-9} \times \exp(-v/5.2))$
UC1 → IF	$\beta 3 = 2 \times (0.0084 + 0.00002 \times v)$
IF → IS	$\alpha 4 = \alpha 2/100$
IS → IF	$\beta 4 = \alpha 3$

* x represents U or L, as transition rates in the background or burst modes are the same.

Transition rates between modes are background to burst, $\mu 1 = 2 \times 10^{-6}$ ms^{-1}; burst to background, $\mu 2 = 1 \times 10^{-4}$ ms^{-1}.