Carnivore distributions across chaparral habitats exposed to wildfire and rural housing in southern California

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Abstract.　Chaparral and coastal sage scrub habitats in southern California support biologically diverse plant and animal communities. However, native plant and animal species within these shrubland systems are increasingly exposed to human-caused wildfires and an expansion of the human–wildland interface. Few data exist to evaluate the effects of fire and anthropogenic pressures on plant and animal communities found in these environments. This is particularly true for carnivore communities. To address this knowledge gap, we collected detection–non-detection data with motion-sensor cameras and track plots to measure carnivore occupancy patterns following a large, human-caused wildfire (1134 km^2) in eastern San Diego County, California, USA, in 2003. Our focal species set included coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*) and striped skunk (*Mephitis mephitis*). We evaluated the influence on species occupancies of the burned environment (burn edge, burn interior and unburned areas), proximity of rural homes, distance to riparian area and elevation. Gray fox occupancies were the highest overall, followed by striped skunk, coyote and bobcat. The three species considered as habitat and foraging generalists (gray fox, coyote, striped skunk) were common in all conditions. Occupancy patterns were consistent through time for all species except coyote, whose occupancies increased through time. In addition, environmental and anthropogenic variables had weak effects on all four species, and these responses were species-specific. Our results helped to describe a carnivore community exposed to frequent fire and rural human residences, and provide baseline data to inform fire management policy and wildlife management strategies in similar fire-prone ecosystems.

Additional keywords: chaparral, human–wildland interface, occupancy.

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Introduction

Chaparral and coastal sage scrub habitats support a diverse array of organisms and a high number of endemic species (Dobson *et al.* 1997). However, these shrubland habitats are exposed to increasing frequencies of wildfire due to rapid human population growth and the expansion of the wildland–urban interface (Keeley *et al.* 1999; Keeley and Fotheringham 2001; Syphard *et al.* 2009). These anthropogenic pressures have contributed to habitat loss, fragmentation and fire-mediated exotic invasions, which have degraded the native biological diversity of southern California (D'Antonio and Vitousek 1992; Keeley *et al.* 2003; Crooks *et al.* 2004; Diffendorfer *et al.* 2007). Information on how different taxa respond to increasing rates of wildfire and other anthropogenic pressures will

help inform management decision making and policy in chaparral habitats.

In the shrublands of southern California, several decades of research has been carried out on plant, bird and small mammal responses to habitat loss, fragmentation and fire (Keeley and Zedler 1978; Soulé *et al.* 1988; Sauvajot *et al.* 1998; Crooks *et al.* 2004; Diffendorfer *et al.* 2012). Studies in areas between Los Angeles and San Diego have evaluated the influence of urban edges and habitat fragmentation on the native carnivore community, which includes coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*) and striped skunk (*Mephitis mephitis*) (Crooks and Soulé 1999; Fedriani *et al.* 2001; Riley *et al.* 2003; Markovchick-Nicholls *et al.* 2008), yet we know very little about their response to wildfire

in these areas (Lawrence 1966; Fisher and Wilkinson 2005). In fact, only a few studies worldwide have described carnivore responses to fire. Prior research has documented foraging patterns in grizzly bears (*Ursus arctos horribilis*) (Blanchard and Knight 1990), gray wolves (*Canis lupus*) (Ballard *et al.* 2000) and Florida panthers (*Puma concolor coryi*) (Dees *et al.* 2001), and habitat use in black bears (*Ursus americanus*) (Cunningham *et al.* 2003). Only two published studies of which we are aware have examined the response to fire by carnivore species that occur in southern California (Cunningham *et al.* 2006; Borchert 2012). As wildfire frequency is correlated with human population density in southern California (Keeley and Fotheringham 2001), it is important that we address this knowledge gap on carnivores and integrate the information into future management decisions.

From 25 October to 2 November 2003, the Cedar fire burned 1134 km^2 (28 0278 acres) of chaparral, coastal sage scrub and pine forest, making it the largest recorded fire in California's history (CDF 2003); though the 2007 wildfires were comparable in scope. In many areas, the Cedar fire burned to the edge of suburban residential areas and into rural housing areas. Although fire severity varied across the burned landscape, little aboveground vegetation remained, except in protected patches in drainages and near rock outcrops. Studies of vegetation in the Cedar fire (Keeley *et al.* 2008; Diffendorfer *et al.* 2012) reported a range of fire severity, but most areas were entirely denuded of shrub cover with the exception of sites near riparian areas or rock outcroppings, which had more shrub cover than open areas. Fire severity had a small effect on post-fire vegetation dynamics (Keeley *et al.* 2008) and vegetation cover in burned locations varied according to rainfall (Diffendorfer *et al.* 2012). Herbaceous vegetation cover peaked in the spring of 2005 following rainfall but then declined through time as shrub cover increased from 2004 to 2006. Small mammals – the prey base for many carnivores – were present in burned locations but their relative abundances differed between burned and unburned plots, primarily due to the absence or low abundances of species associated with shrub cover. In general, small mammal abundances increased on burned plots between 2004 and 2007 (Diffendorfer *et al.* 2012).

Following the fire, we examined carnivore distributions in relation to environmental and anthropogenic variables in areas within the Cedar fire perimeter and nearby unburned areas. Specifically, our intent was to evaluate spatial and temporal patterns of four behaviourally diverse carnivore species that are common in chaparral shrublands: coyote, a highly mobile, habitat and foraging generalist (Kamler and Gipson 2000; Grinder and Krausman 2001); gray fox, a foraging generalist that prefers dense habitats (Fuller 1978; Hockman and Chapman 1983); striped skunk, a habitat and foraging generalist (Dijak and Thompson 2000; Ng *et al.* 2004) and bobcat, a cryptic, obligate predator that prefers dense habitats (Litvaitis *et al.* 1986; Delibes *et al.* 1997).

Our primary objectives were to (1) document occupancy patterns of four medium-sized carnivore species that are native to chaparral shrublands and (2) evaluate whether occupancies changed through time across sites that varied in their combination of exposure to burn status, rural human residences and other environmental attributes. In our study, rural homes were typified

as suburban dwellings with small areas of cleared land. Agriculture around homes was not present, given the high topographic relief, boulders and arid conditions. Post-fire patterns could be caused by species' responses to unburned habitat (preference or avoidance) and their ability to disperse into burned areas, assuming they either died or fled during or soon after the fire. We examined the following specific hypotheses based on behavioural attributes for each species: (1) coyote would be common across all sites, regardless of burn status, rural homes and environmental factors, because of their high vagility and their generalist foraging patterns; (2) striped skunk occupancies would be low in the burn interior because of their lower vagility than coyotes, but they would exhibit high occupancies across all other areas because of their generalist foraging patterns; (3) gray fox occupancies would be low in the burn interior because they also have lower vagility than coyotes, but their occupancies would be high in unburned areas where dense cover exists and moderate in burned edges, and these patterns would be unrelated to rural homes and environmental factors because of their generalist foraging patterns and (4) bobcat occupancies would be high in unburned areas where dense cover is available, and they would avoid areas in close proximity to rural homes.

Materials and methods

Study area

From January 2006 to June 2007, we used motion-sensor cameras and track plots to conduct detection–non-detection surveys in the Cleveland National Forest and Cuyamaca Rancho State Park in eastern San Diego County, California, USA (Fig. 1). All sites were located in chaparral habitat composed primarily of burned or unburned stands of *Adenostoma fasciculatum*, *Artemisia californica* and *Arctostaphylos* spp. The climate is arid with an average rainfall of 400 mm per year and average minimum and maximum temperature range of 10.1–24.8°C (50.2–76.6°F) (Western Regional Climate Center 2011).

Sampling design

We selected 31 sites spaced ≥2 km apart and spanning areas that varied in their burn status, distance from the fire perimeter, proximity to rural homes, elevation and distance to riparian area. We classified sites based on their burn status as follows: (1) *burn edge*, areas that burned in the Cedar fire and were <4 km from the fire perimeter (11 sites); (2) *burn interior*, areas that burned in the Cedar fire and were >4 km from the fire perimeter (10 sites) and (3) *unburned*, areas that did not burn in the Cedar fire and had not burned in >20 years (10 sites) (Fig. 1). We used burn status as a measure of habitat, based on the assumption that burn status would alter vegetation structure and density in a manner that affects carnivore movement, visibility and protective cover. Burned sites consisted of dense stands of mature chaparral shrubs (high protective cover, low visibility and limited movement), and unburned sites were composed of seedlings and resprouting shrubs, which provided less habitat structure and density (less protective cover, higher visibility and greater ease of movement) (see Fig. S1 of the Supplementary material for representative site photographs). Sites were also categorised by their proximity to rural homes as follows: (1) *low-density rural*, sites with <5 houses within a 1-km radius (18 sites) and
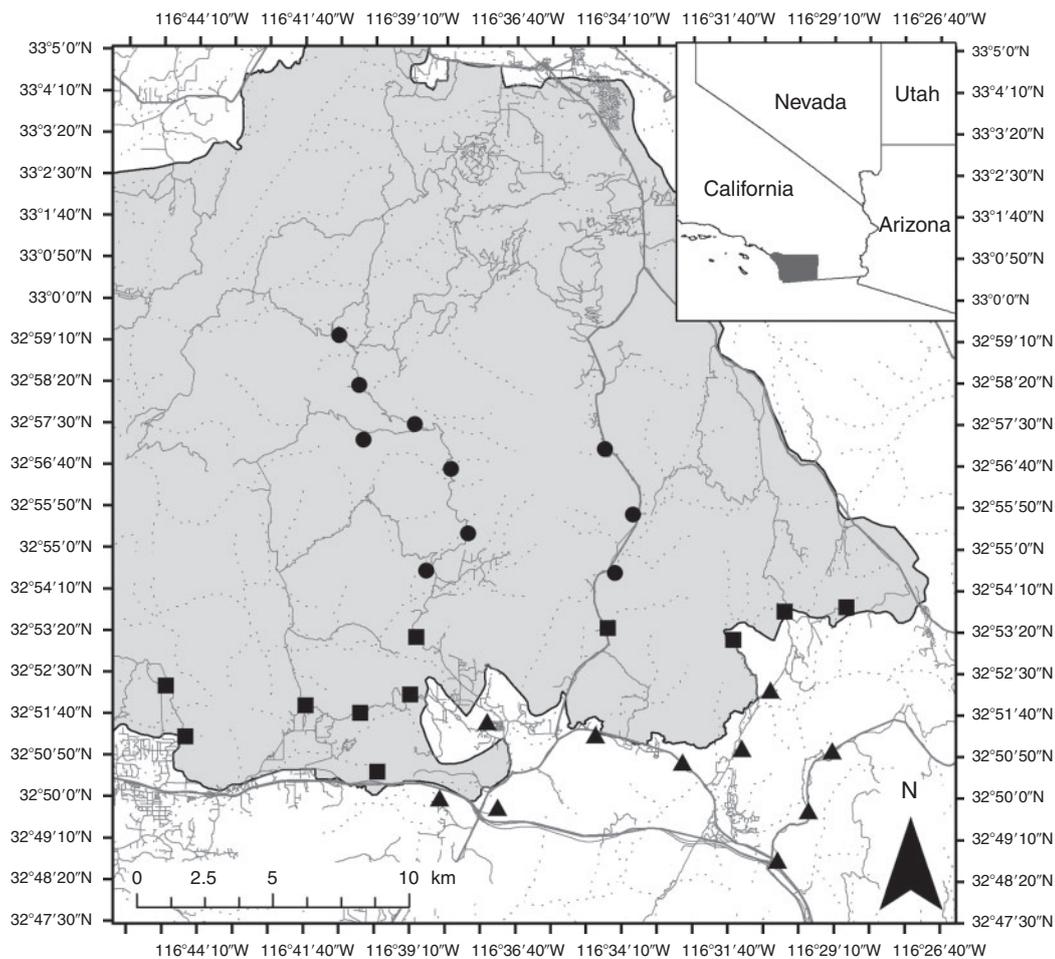
Fig. 1. Focal study area in chaparral habitats in east-central San Diego County, California, USA. Detection–non-detection surveys were implemented at sites inside the Cedar fire perimeter (grey area), including sites within areas classified as burn edge (squares) and burn interior (circles), and nearby unburned areas (triangles). Sites were located >200 m from paved roads (thick black lines) and low-use (<10 vehicles per day) and unpaved roads (thin black lines), and at variable distances from riparian areas (stippled lines). Despite the availability of roads, site selection was limited due to public accessibility, permissions from local agencies and closures from fire hazards. The inset shows the location of the Cedar fire and our focal study site in San Diego County, California.

(2) *moderate-density rural*, sites with >10 houses within a 1-km radius (13 sites). Sites ranged in distance to riparian area (0–1.4 km) and elevation (765–1577 m). In general, lower elevation chaparral habitats were dominated by the typical local chaparral shrub species and higher elevation habitats consisted of these species plus a mix of oak shrubs (*Quercus* spp.) and conifers. All sites were located in the south-eastern section of the Cedar fire. Sites were limited to public lands where agencies allowed us to work and where we had road access, and to areas that were not closed because of post-fire hazards. All sites were located >200 m from paved or rarely used roads (<10 vehicles per day) in areas where the potential for human disturbance at a camera station or track plot was minimal.

Each site contained three sampling stations consisting of one motion-activated, infrared camera (Game-Vu, Nature Vision, Baxter, Minnesota, USA) and two track plots. All sampling stations were spaced 100 m from each other. At camera stations, one camera was set ~20 cm from the ground with the focal area

fixed on a scent post 2 m from the camera. Track plots consisted of a 1-m² area of smoothed gypsum powder with a scent post in the middle (Linhart and Knowlton 1975; Crooks 2002). Scent posts for both camera stations and track plots consisted of a 30-cm metal tent stake wrapped with a pipe cleaner around the top portion that was coated with a scent lure suitable for multiple North American carnivore species (Carman's Pro's Choice, Sterling Fur and Tool Co., Ohio).

We surveyed each site for 6 nights three times per year (five times total) during the winter (January 2006, 2007), spring (May–June 2006, 2007) and autumn (August–September 2006). We visited sites every 3 days (2 nights) to record camera images and tracks to the species level, ensure cameras were operating properly (e.g. check battery power), smooth gypsum powder at track plots and reapply scent lure. We surveyed one-third of all burn edge, burn interior and unburned sites during each 6-night survey. Thus, it required 18 nights to survey all 31 sites each season. We considered each 6-night survey the primary

sampling period that consisted of three, 2-night secondary sampling occasions.

Data analysis

We analysed detection-non-detection data with single-species, multi-season occupancy models (MacKenzie *et al.* 2006). This technique provides unbiased estimates of species occupancies by accounting for detection probability and allows parameters to vary as a function of environmental variables, site characteristics and time. Multi-season occupancy models estimate the probability a species is present at a site during the first primary sampling period (occupancy, $\hat{\psi}_1$), the probability a species will be detected at a site given it is present ($\hat{p}$) and the probability of local colonisation ($\hat{\gamma}$) and extinction ($\hat{\varepsilon}$) through time (MacKenzie *et al.* 2006). We examined each parameter in relation to variables we hypothesised would influence species occupancy patterns. We evaluated the influence of three environmental variables (burn status, distance to riparian area, elevation) and one anthropogenic variable (rural homes) on species occupancy. We also included models where the occupancy parameter was held constant (i.e. uninfluenced by any of our environmental or anthropogenic variables). We examined whether species occupancies were constant or changing through time by including the primary sampling period as a potential covariate affecting local colonisation and extinction. Last, we examined whether species detection probabilities were constant or were affected by environmental conditions (burn status) or rural homes. We also accounted for the possibility that detection probability may change within a primary sampling period (i.e. a 6-night period) by including secondary sampling occasions as a potential covariate influencing detection probability. Overall, our *a priori* model set included 128 candidate models we hypothesised may explain carnivore occupancies and changes in occupancies through time (i.e. post-fire recovery) (see Table S1 of the Supplementary material). We examined the fit of each model for each species using the UNMARKED package in R (R Development Core Team 2010; Chandler *et al.* 2011). We compared support for models using Akaike's Information Criterion (AIC), delta AIC (ΔAIC), and AIC weights (AIC *w*) (Burnham and Anderson 2002; R Development Core Team 2010). We present model-averaged estimates of each parameter value for models where ΔAIC ≤ 4 (Burnham and Anderson 2002).

Prior to our analysis, we examined whether our continuous independent variables (elevation, riparian area) were correlated and did not find a strong relationship ($r = -0.21$). We used McNemar's test of symmetry (Agresti 1990) to test for sampling bias among the track plots and the cameras at each site. This comparison revealed that track plots and the camera at each site were not independent samples ($P > 0.05$ for all pairwise comparisons) and thus it was appropriate to pool data from the three scent stations at each site during each secondary sampling occasion. Interestingly, coyotes were detected more often at each track plot (61 detections at track plot 1 and 56 detections at track plot 2) than at cameras (39 detections) (track plot 1 *v.* camera, $\chi^2 = 5.13$, $P = 0.024$; (track plot 2 *v.* camera, $\chi^2 = 3.32$, $P = 0.068$), whereas bobcats showed the opposite pattern (6 detections at track plot 1, 4 detections at track plot 2, 23 camera detections) ($\chi^2 = 8.83$, $P = 0.003$; $\chi^2 = 15.43$,

$P = <0.001$). These results support previously observed patterns for these species using similar data collection strategies (Windberg 1996; Harris and Knowlton 2001).

Results

We conducted surveys on 451 of 465 (97%) possible sampling occasions (31 sites × five primary sampling periods × three secondary occasions). On the other 14 occasions, inclement weather or other logistical constraints prevented us from visiting a site.

Overall, we detected gray fox most often, followed by coyote, striped skunk and bobcat (Table 1). Raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), mule deer (*Odocoileus hemionus*), rabbit (*Sylvilagus* spp.), domestic dogs and cats, and a variety of rodents, birds and lizards were also detected occasionally, but were not considered in this analysis because of the low number of detections. Estimated detection probability was highest for gray fox, followed by coyote, striped skunk and bobcat. For gray fox and striped skunk, detection probability was generally constant across space and time (Table 2). Coyote detection probability was influenced primarily by proximity to rural homes (cumulative AIC $w = 0.31$) and burn status (cumulative AIC $w = 0.24$). Bobcats followed a similar pattern, with their detection probability influenced primarily by burn status (cumulative AIC $w = 0.15$) and proximity to rural homes (cumulative AIC $w = 0.14$) (Tables 1, 2).

Model selection procedures indicated constant levels of occupancy per species with some influences of environmental conditions. For all species but bobcat, models that included constant occupancies across sites were well supported (i.e. ΔAIC <2 and high AIC *w*) (Table 2) given the data and the candidate model set, a pattern that indicates these generalist species are common in this post-fire environment. However, we observed substantial differences in occupancy across species. Gray fox had the highest occupancy, followed by striped skunk, coyote and possibly bobcat, although inferences for this species are limited because of a low number of detections (Fig. 2, grey horizontal bands). Though the generalist species were common in this landscape, all four species were influenced to some degree by anthropogenic and environmental conditions (Table 2). In general, burn status had the most substantial influence (based on cumulative AIC *w*) on gray fox and striped skunk occupancies. Model-averaged estimates of gray fox occupancies were slightly higher in the burn interior that in the burn edge and unburned areas (Fig. 2a). This pattern does not support our hypothesis of high gray fox occupancy in the burn edge and unburned areas. In contrast, our hypothesis regarding striped skunk response to the fire was partially supported. Striped skunk occupancy was higher in areas within the burn edge (Fig. 2b) than in the burned interior and unburned areas. Though proximity to rural homes, elevation, and distance to riparian areas received support in our model-selection procedures, model-averaged occupancy estimates (±s.e.) for these species did not show any strong patterns.

Burn status appeared in well-supported models for coyote and bobcat, but model-averaged estimates of occupancies (±s.e.) for these species were similar across burn status types. Of the variables we considered, only proximity to rural homes had an apparent effect on coyote occupancy. Coyote occupancy was higher in areas that had few or no rural homes (<5 homes

within 1 km) compared with areas with moderate levels of rural homes (>10 homes within 1 km). However, this effect was weak, and it was only apparent in the burn interior (Fig. 2c). Estimated occupancies of bobcat were weakly associated with elevation (Fig. 2d). However, the overall low number of detections for bobcats limits our ability to make inferences. We attribute our low sample sizes for bobcat primarily to the difficulty of collecting data for cryptic carnivores at scent stations or their overall low abundance in our focal study area (Conner *et al.* 1983).

Observed gray fox, striped skunk and bobcat occupancy patterns were consistent across our five sampling periods

Table 1. Total number of detections per species and model-averaged estimates of detection probability ($\hat{p}$) and standard error (s.e.) using the covariate that received the most overall support (based on cumulative Akaike Information Criterion (AIC) weights) per species

Species	Detections	Variable influencing $\hat{p}$	$\hat{p}$	s.e.
Gray fox	215	Constant	0.55	0.04
Coyote	129	Burn(unburned)	0.51	0.06
		Burn(edge)	0.54	0.05
		Burn(interior)	0.38	0.16
Striped skunk	44	Constant	0.22	0.06
Bobcat	30	Residential(moderate)	0.07	0.03
		Residential(low)	0.11	0.04

(Table 2). For these three species, models where the local colonisation and extinction parameters were held constant were well supported. The lack of response by these species suggests that despite changes in vegetation structure and potential prey in the burned areas (Diffendorfer *et al.* 2012), these species were not responding to changes in the post-fire environment during the period we studied. In contrast, coyote occupancy patterns did change through time, as shown by the number of well-supported models where primary sampling period is associated with local colonisation and extinction (Table 2). Estimates of local colonisation and extinction indicate coyote occupancy patterns fluctuated across primary sampling periods, particularly within the first two to three sampling periods (Fig. 3). Our data indicate that despite coyote being only weakly associated with the environmental and anthropogenic variables, their overall occupancy patterns (regardless of site attributes) increased through time (Fig. 4). Whether this pattern represents coyotes recolonising the region (burned and unburned) after the fire and settling into new territories or another mechanism is uncertain, but our data indicate a peak in coyote occupancy across all environmental and anthropogenic conditions approximately 34 months after the Cedar fire.

Discussion

Despite the vast size of the area burned by the Cedar fire and its effects on habitat structure, carnivore occupancy was generally

Table 2. Model selection output for models where ΔAIC ≤ 2

The occupancy parameter ($\hat{\psi}$) could be associated with rural residences (two levels), burn status (three levels), riparian area (0–1.5 km) or elevation (700–1600 m). The colonisation ($\hat{\gamma}$) and extinction ($\hat{\varepsilon}$) parameters could be constant (1) or changing through time (primary sampling periods). Detection probability ($\hat{p}$) could be either constant (1), or associated with rural residences (two levels), burn status (three levels) or secondary sampling occasions

Species	$\hat{\psi}$	$\hat{\gamma}$	$\hat{\varepsilon}$	$\hat{p}$	Number of parameters	AIC	ΔAIC	AIC w
Coyote	1	primary	primary	burn	12	489.82	0.00	0.13
	residential + burn + riparian + elevation	primary	primary	residential	16	490.20	0.39	0.11
	residential + burn + riparian + elevation	1	1	residential	10	490.85	1.03	0.08
	residential	primary	primary	burn	13	490.90	1.08	0.08
	residential + burn + riparian	primary	primary	residential	15	491.58	1.76	0.06
	elevation	primary	primary	burn	13	491.70	1.88	0.05
	riparian	primary	primary	burn	13	491.82	2.00	0.05
Gray fox	1	1	1	1	4	592.68	0.00	0.12
	burn	1	1	1	6	593.69	1.01	0.07
	residential	1	1	1	5	594.45	1.77	0.05
	1	1	1	residential	5	594.59	1.90	0.05
	elevation	1	1	1	5	594.67	1.99	0.04
	riparian	1	1	1	5	594.68	2.00	0.04
Bobcat	riparian + elevation + burn	1	1	residential	9	212.12	0.00	0.15
	residential + riparian	1	1	burn	8	213.22	1.10	0.08
	residential + elevation	1	1	burn	8	213.89	1.77	0.06
	burn + elevation	1	1	secondary	9	213.89	1.78	0.06
Striped skunk	burn	1	1	1	6	282.37	0.00	0.11
	1	1	1	1	4	283.31	0.94	0.07
	burn + riparian	1	1	1	7	283.97	1.60	0.05
	burn + elevation	1	1	1	7	284.03	1.66	0.05
	burn	1	1	residential	7	284.19	1.82	0.04
	riparian	1	1	1	5	284.27	1.90	0.04
	residential + burn	1	1	1	7	284.30	1.93	0.04
	elevation	1	1	1	5	284.33	1.96	0.04
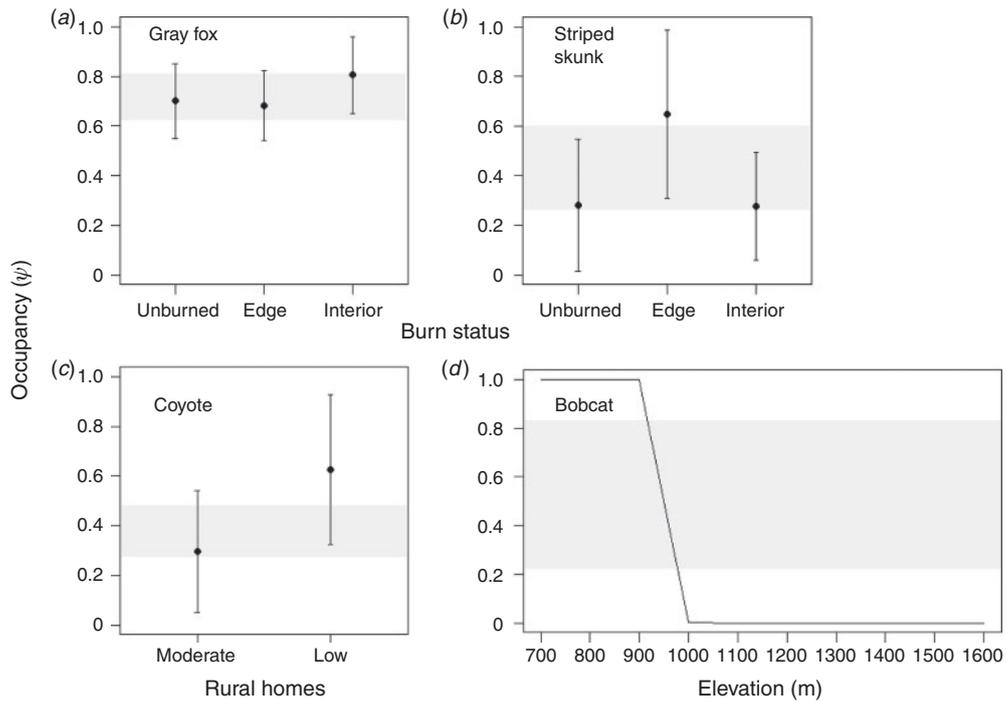
Fig. 2. Model-averaged occupancy estimates (±s.e.) (models with ΔAIC $\leq$4) for (*a*) gray fox, (*b*) striped skunk, (*c*) coyote and (*d*) bobcat. Estimated occupancy (±s.e.) with the occupancy parameter held constant (i.e. no covariates) are shown in grey bands, which can be used to compare overall occupancy rates across species. Estimates from the most influential covariate for each species are shown with black points and standard errors. For coyote, the effect of rural homes was only apparent in the burn interior. Estimated standard errors for bobcat were close to zero and are not shown.
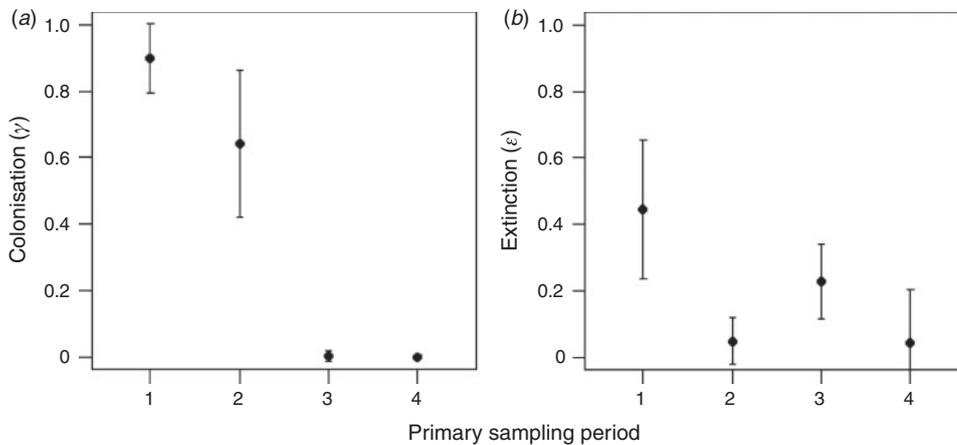
Fig. 3. Changes in coyote occupancy through time (primary sampling period). Estimated patterns of local (*a*) colonisation and (*b*) extinction (±s.e.) for a model where occupancy was constant across space because of the low influence of anthropogenic or environmental variables on this generalist species. Coyote was the only species whose occupancy changed through time.

constant across space and fire effects were mild, on par with rural housing effects, proximity to riparian areas and elevation gradients. Observed species-specific effects, though weak, do provide baseline information that documents how three generalist carnivores and one specialist carnivore respond to the post-fire environment. These results address a gap in our

understanding of carnivore ecology in chaparral habitats of southern California.

Burn status

Burn status appeared in well-supported models in all species, but the effects were most apparent in gray fox, striped skunk
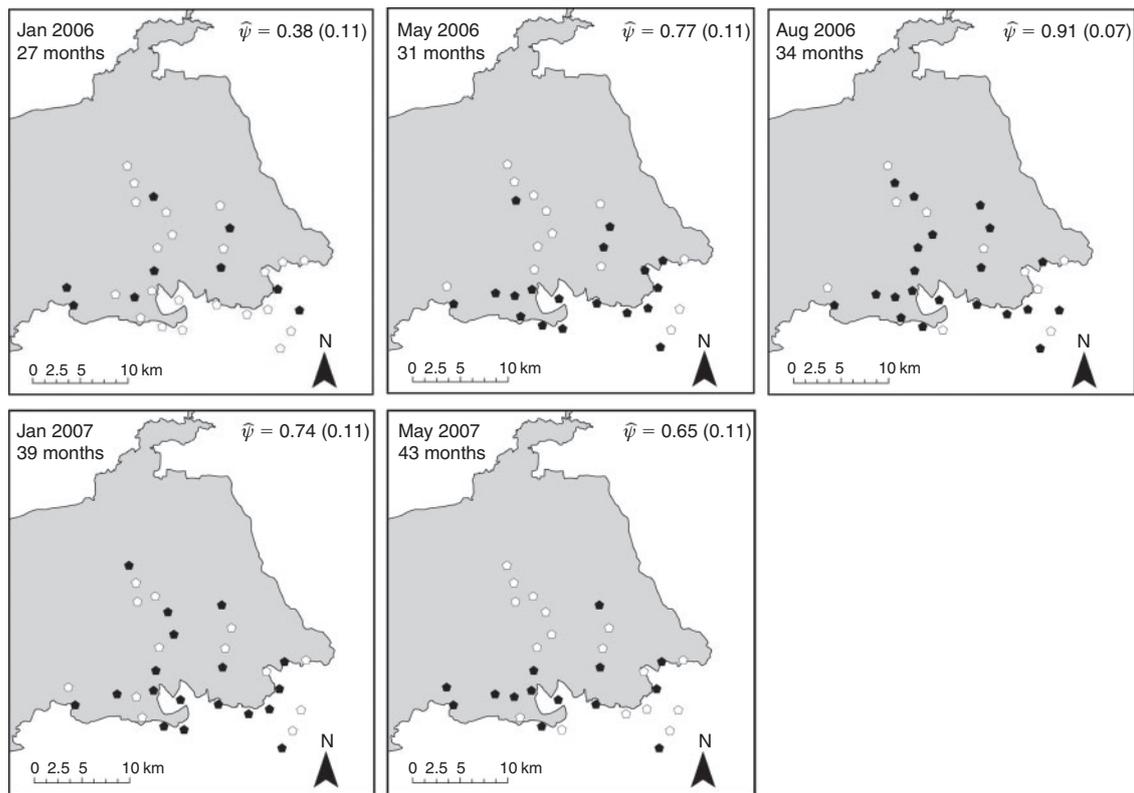
Fig. 4.   Model-averaged estimates of coyote occupancy ($\hat{\psi}$) (s.e.) over 27–43 months following the Cedar fire in San Diego County, California (grey area). Black pentagons represent sites where a coyote was detected and white pentagons represent sites where a coyote was not detected during each primary sampling period.

and to a lesser extent, coyote. Slightly higher gray fox occupancy in the burn interior was contrary to our expectation, and could be explained by several possible mechanisms. First, gray fox may have found refuge during the Cedar fire in unburned patches or rocky crevices that did not require recolonisation. Alternatively, gray fox occupancy may have declined during and immediately following the Cedar fire, but our sampling methods failed to detect these changes beginning 27 months after the fire. Though we do not have data to distinguish between these alternatives, slightly higher gray fox occupancy in the burn interior suggests that the early successional stages of recovery in this area provided a suitable and available niche for these species to exploit, possibly due to high prey availability (Blanchard and Knight 1990; Dees *et al.* 2001; Cunningham *et al.* 2003). An independent study of the small mammal community following the Cedar fire indicated that several potential prey species, including the California pocket mouse (*Chaetodipus* spp.) and cactus mouse (*Peromyscus eremicus*), had high population growth rates in the burn interior (Diffendorfer *et al.* 2012). Thus, high population growth rates of potential prey species may help explain observed gray fox occupancy patterns in the burn interior. High prey availability in the burn interior may have also influenced coyote, which were weakly associated with the burn interior, particularly in areas where rural homes were rare or nonexistent (Fig. 2*c*). High striped skunk

occupancies in the burn edge environment support our expectations for this generalist species. It is possible this stage of successional recovery or this edge habitat provided suitable conditions for striped skunk but not for other species to occur at high rates. The burn edge may have allowed striped skunk to move freely between burned and unburned habitats, potentially seeking food sources in the burned area, but resting or bedding down in the more densely vegetated unburned habitats (Blanchard and Knight 1990). However, despite observed differences to the burned environment, the lack of temporal dynamics in species occupancy (except in coyote) indicate any changes likely took place at a slower rate than we could detect or occurred before the start of our study.

Rural housing

Despite the appearance of rural housing in well-supported models of all focal species, only coyote showed any evidence of a difference in occupancy between areas classified as containing moderate and low densities of rural homes. This result seemingly contrasts with several studies that have reported that coyotes are tolerant of, or even prefer, residential areas (Fedriani *et al.* 2001; Grinder and Krausman 2001; Riley *et al.* 2003). However, our study was in rural areas where even our classification of moderate human residences is far less than the urban areas considered in prior studies in southern California. The lack

of a strong response by co-occurring carnivores indicates that the current level of rural human residences in our focal study does not have a strong limiting effect on species occupancies, except in coyote.

Elevation and riparian areas

Model output indicated elevation and distance to riparian areas affected species occupancies, but these effects were weak. We expected occupancy patterns to vary across these gradients, particularly in gray fox and bobcat (because of their previously described preference for dense cover, Fuller 1978; Fritzell 1987; Farias 2005), which were typically more common at high elevations and near riparian areas. However, only bobcat occupancies were associated with elevation, and followed a trend in the opposite direction of our expectation.

Overall, our results agree with the classification of these species as habitat and foraging generalists that occur at variable rates across this landscape. This first baseline study indicates our focal set of carnivore species seems to be resilient to fire and can quickly begin utilising successional habitat. However, coyote exhibited a unique response to the post-fire environment that may provide additional insights into patterns of carnivore recolonisation. In general, coyote occupancy increased across the study area in a manner that was not directly attributable to the variables we considered. This pattern could indicate that both burned areas and unburned areas adjacent to the fire (<10 km from fire perimeter) may have experienced an overall decline in the coyote population, or that coyotes dispersed from this region following the fire and slowly recolonised and established new territories (Harrison 1992). Alternatively, this could present a sampling bias, in which the scent lure provided an attractant to coyotes, which was then frequently visited for scent-marking and territoriality purposes (Allen *et al.* 1999). If so, then high occupancy rates could represent a learned response in which coyotes were cautious to investigate scent stations during the first sampling period, but they started to investigate these novel visual (track plot, camera) or olfactory stimuli (scent lure) through time (Windberg 1996; Harris and Knowlton 2001). To test for this possibility, we conducted a *post hoc* test to determine whether detection probability increased through time. We did this by reanalysing the coyote data, but we included models in our model set in which detection probability could vary by primary sampling period (model set increased from 128 to 144 models). Using this test, we found no support for models with primary sampling period influencing the detection probability parameter (ΔAIC >4). Thus, we consider observed coyote occupancy an ecological response rather than a methodological bias.

Carnivore interactions

We did not explicitly test competitive interactions within our focal set of carnivores. However, species-specific responses to burn status and rural housing support patterns of spatial partitioning that have been previously documented in this carnivore community (Fedriani *et al.* 2000; Neale and Sacks 2001; Farias 2005). For example, gray fox occurred at slightly higher rates in the burn interior than any of the other focal species. This response may be related to habitat and foraging opportunities, but might also be related to avoidance of coyotes and bobcats (competitively dominant to gray fox), or exploitation of habitat and foraging opportunities not exploited by these two species (Henke and Bryant 1999; Neale and Sacks 2001; Farias 2005). Although we do not have data to test these hypotheses, observed differences among species suggests competitive avoidance or displacement may be a factor influencing carnivore spatial patterns. Further detailed investigations of carnivore interactions through behavioural tracking of radio-collared individuals would help to clarify the mechanisms associated with observed spatial patterns.

In conclusion, our study revealed that four carnivores are common in the post-fire environment, at least in a period of time 27–43 months after the Cedar fire. We attribute this pattern to behavioural plasticity among generalist carnivores, which probably allows them to adjust to variable conditions in the burned environment. This pattern was particularly evident in gray fox, striped skunk and possibly bobcat. We encourage future researchers to investigate coyote (and other carnivores capable of moving large distances) to evaluate the mechanisms behind spatial and temporal changes in occupancy in the post-fire environment.

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