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Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California

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ABSTRACT

Human-driven declines of apex predators can trigger widespread impacts throughout ecological communities. Reduced apex predator occupancy or activity can release mesopredators from intraguild competition, with unknown repercussions on the ecological community. As exurban development continues to expand worldwide, it is important to document how mesopredators are impacted by the combined influences of apex predators and humans. We used motion-detecting camera traps to examine spatial and temporal patterns of meso- and apex predator occupancy and activity in a fragmented landscape in California. We hypothesized that both spatial and temporal partitioning among the carnivore guild would be affected by varied levels of human influence. We found that higher residential development reduced puma occupancy but was not related to the occupancy of mesopredators. Bobcats, grey foxes, and Virginia opossums were detected more often at sites occupied by pumas, whereas coyotes and raccoons were detected less often. The detection probabilities of smaller mesopredators were related to coyotes, a dominant mesopredator, but the magnitude and direction of these correlations differed depending upon puma occupancy. We also found that species altered their activities temporally in locations with higher human use, with pumas, bobcats and coyotes reducing diurnal activities and increasing nocturnal ones. These activity shifts were reflected in reduced temporal partitioning between intraguild competitors, with unknown effects on species interactions and repercussions to the prey community. Our results suggest that human development and activity alters predator community structure through both direct and indirect pathways. Therefore effective carnivore conservation requires an understanding of how mesopredators respond to varying levels of apex predator and anthropogenic influences.

1. Introduction

Anthropogenic-driven extirpation of apex predators from ecosystems across the globe has had led to large changes in community structure and dynamics in diverse ecosystems (Estes et al., 2011). Such changes to the predator guild can greatly alter ecological networks by releasing mesopredators from intraguild predation and competition, thus initiating trophic cascades that propagate throughout food webs (Levi and Wilmers, 2012; Noss et al., 1996; Pace et al., 1999; Polis and Holt, 1992). The combined extirpation of apex predators and release of mesopredators has been identified as a possible cause for the decline or extinction of songbirds and small mammals, because they are disproportionately preyed upon by mesopredators (Crooks and Soulé, 1999; Johnson et al., 2007; Ritchie and Johnson, 2009).

Habitat fragmentation due to human development can lead to the extirpation of top predators (Gehrt et al., 2010; Šálek et al., 2014) and irreversibly alter ecosystem stability (Hansen et al., 2005). Exurban development (0.06–2.5 houses/hectare) is the fastest growing form of land use change in the United States, and building low-density developments adjacent to wildlands results in habitat fragmentation, increased human wildlife contact and conflict, and homogenization of ecological communities (Hansen et al., 2005; McKinney, 2006). The spread of human development or activity into nearby open space disrupts both sensitive species (e.g. apex predators) and entire communities by altering predator interactions and their traditional ecological roles. These changes do not always progress linearly with increasing levels of development; instead abrupt shifts in community composition may occur with gradual increases in exurban development (Hansen et al., 2005). Because exurban development now encompass more than five times as much land as do suburban and urban development, it is crucial that we understand how low-density human pressures alter the composition and interactions of nearby predator

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communities in order to balance conservation and development needs (Bateman and Fleming, 2012).

While apex predators limit mesopredators through competition and predation, they also affect mesopredator survival and reproduction through indirect, trait-mediated effects (Ritchie and Johnson, 2009). Natural selection favors adaptations such as behavioral avoidance through spatiotemporal partitioning, which reduce costly interactions between mesopredators and dominant competitors (Gehrt and Clark, 2003; Wang and Fisher, 2012; Wilson et al., 2010). Within the predator guild, however, apex predators can also benefit smaller predators by suppressing larger-bodied mesopredators (Berger and Conner, 2008; Elmhagen et al., 2010). Levi and Wilmers (2012) demonstrated an "intraguild cascade" in which the apex predator, gray wolves (*Canis lupus*), suppressed the mesopredator, coyotes (*Canis latrans*), and thereby released the smaller red foxes (*Vulpes vulpes*). In addition, carrion provided by apex predators can serve as an important food source for smaller predators (Allen et al., 2015a; Ruth and Murphy, 2009; Selva et al., 2005; Wilmers and Getz, 2005). Therefore, the relationship between dominant and smaller predators may reflect a complex balance of risk-avoidance and energetic needs, all of which may be influenced by anthropogenic subsidies and disturbances and direct predation.

We used camera traps to simultaneously examine how the combined influences of bottom-up exurban development and top-down apex predator pressures affected mammalian mesopredator communities in the Santa Cruz Mountains of California. Native carnivores in the region include pumas (*Puma concolor*, an apex predator), coyotes (a dominant mesopredator and an emerging apex predator in many urbanizing regions), bobcats (*Lynx rufus*; a dominant mesopredator), and subordinate mammalian mesopredators (e.g., grey foxes, *Urocyon cinereoargentus,* striped skunks, *Mephitis mephitis*, Virginia opossum, *Didelphus virginianus*, and raccoons, *Procyon lotor*). We placed motion-detecting digital cameras along a gradient of human development to test whether spatial and temporal niche partitioning of the local predator community shifted across disparate levels of human influence.

Based on results from previous studies of human impacts on predators, we expected the predator community to respond to the combined influences of higher ordered predators and development and formulated the following hypotheses. (1) Predator responses to anthropogenic pressures would vary by species: Puma occupancy would decline as human development and activity increased due to their particular sensitivity to anthropogenic influences (Crooks, 2002; Wilmers et al., 2013). Exurban development would not reduce the occupancy probabilities of bobcats, coyotes and grey foxes because we expected these versatile predators to adapt to low levels of development, especially when access to nearby open spaces are available (Goad et al., 2014; Riley, 2006). However, we expected detection levels of bobcats to decline with higher development, because this species is less likely to use developed areas (Riley, 2006). In contrast, we expected occupancy probabilities for synanthropic species, such as raccoons and striped skunks, and domestic species (e.g., domestic cats, *Felis catus*) to increase with development (Bateman and Fleming, 2012; McKinney, 2006). (2) Predator interactions would be altered with increasing anthropogenic development: Dominant mesopredators (i.e. coyotes and bobcats), which have greater niche overlap with pumas, would be deterred by higher puma occupancy and activity whereas subordinate mesopredators would be released by this suppression of their competitors (Levi and Wilmers, 2012). In areas where puma occupancies declined, we expected coyotes would act as an emergent apex predator and negatively affect the occupancy and detection of smaller mesopredators (Gehrt and Prange, 2007; Levi and Wilmers, 2012; Pace et al., 1999). (3) Subordinate predators would exhibit temporal avoidance of dominant ones to reduce risk of intraguild predation and competition (Palomares and Caro, 1999; Polis and Holt, 1992). However, we expected areas with higher human activity would reduce temporal niche partitioning by restricting wildlife activities during diurnal hours (George and Crooks, 2006; Reed and Merenlender, 2008).

2. Methods

2.1. Study Site

Our study occurred in the southern Santa Cruz Mountains in west-central California, an area encompassed within Santa Cruz, Santa Clara and San Mateo counties (Fig. 1). This region has a legacy of preserving large tracts of open space, with 24% of the surrounding San Francisco Bay Area held in some form of public land trust or conservation easement (Rissman and Merenlender, 2008). The Santa Cruz Mountains includes diverse habitats ranging from intact wildlands to urban regions, providing a gradient of environmental conditions to study the impacts of development on interspecific interactions. Significant portions of public land are available for a wide variety of recreational activities, including biking, hiking, and dog walking. There are also many large private landholdings, some of which are managed for resource extraction activities, but are not open to the public for recreation. Our study area abuts the urban municipalities of Santa Cruz and the South Bay Area and contains several small suburban and exurban mountain communities. A major highway bisects our study region, and numerous arterial (>35 mph), neighborhood (<35 mpg) and unpaved roads also mark the landscape.

The Santa Cruz Mountains experiences a dry season from May to October and a wet season from November to April. Small to large-sized mammalian carnivores that occur in the Santa Cruz Mountains include: pumas, bobcats, coyotes, grey foxes, red foxes, raccoons, striped skunks, Virginia opossums (hereafter opossums), western spotted skunks (*Spilogale gracilis*), American badgers (*Taxidea taxus*), and two domestic species, cats and dogs (*Canis lupus familiaris*).

2.2. Camera trap survey

Between May 2011 and June 2013 we placed cameras (Bushnell Trophy Cam; Bushnell Corp., Overland Park, KS, USA) at 50 locations throughout the study site (Fig. 1) to monitor animal activity across a gradient of human development from undeveloped to exurban neighborhoods. We measured human development from building structures identified from high-resolution satellite imagery. We digitized structures manually in exurban landscapes and used address points to locate houses in suburban and urban areas to create a development layer in ArcGIS (v. 10.0, ESRI 2010, Redlands, CA). We used ArcGIS to randomly select 50 camera locations across a stratified development gradient of approximately 0–2 houses per hectare. We further restricted potential camera locations to within 100 meters from a road or trail for access purposes and at least 1 km away from the next closest camera.

We traveled to each randomly generated location and placed a camera along the closest trail or road to maximize native carnivore detection (Gompper et al., 2006). Most trails we selected were used by vehicles on an infrequent to regular basis. When recreational trails were not available, we placed the camera on a well-defined game trail wide enough for people to walk on. We programmed the cameras to take three photographs when triggered with a one-minute delay between successive image sets. We excluded data collected by cameras when they were heavily obscured by fallen or growing vegetation or when interference by humans or animals significantly altered the camera angle or field of visibility. We