Spring 2023

Combining Camera Trap and Fitness App Data Demonstrates that Mammals Change Behavior Near High-Use Bike Trails on Mount Tamalpais, Ca

Erin Rose Lacour
San Jose State University

Recommended Citation
Lacour, Erin Rose, "Combining Camera Trap and Fitness App Data Demonstrates that Mammals Change Behavior Near High-Use Bike Trails on Mount Tamalpais, Ca" (2023). *Master's Theses*. 5406.
DOI: https://doi.org/10.31979/etd.pvae-42n8
https://scholarworks.sjsu.edu/etd_theses/5406

COMBINING CAMERA TRAP AND FITNESS APP DATA DEMONSTRATES THAT MAMMALS CHANGE BEHAVIOR NEAR HIGH-USE BIKE TRAILS ON MOUNT TAMALPAIS, CA

A Thesis

Presented to

The Faculty of the Department of Environmental Studies

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Erin Rose Lacour

May 2023

The Designated Thesis Committee Approves the Thesis Titled

COMBINING CAMERA TRAP AND FITNESS APP DATA DEMONSTRATES THAT MAMMALS CHANGE BEHAVIOR NEAR HIGH-USE BIKE TRAILS ON MOUNT TAMALPAIS, CA

by

Erin Rose Lacour

APPROVED FOR THE DEPARTMENT OF ENVIRONMENTAL STUDIES

SAN JOSÉ STATE UNIVERSITY

May 2023

Lynne Trulio, Ph.D.	Department of Environmental Studies
Rachel O'Malley, Ph.D.	Department of Environmental Studies
Sulekha Anand, Ph.D.	Department of Biological Sciences

ABSTRACT

COMBINING CAMERA TRAP AND FITNESS APP DATA DEMONSTRATES THAT MAMMALS CHANGE BEHAVIOR NEAR HIGH-USE BIKE TRAILS ON MOUNT TAMALPAIS, CA

by Erin Rose Lacour

Anthropogenic disturbance that results in habitat loss is the leading cause of the current extinction crisis. To mitigate loss of habitat, protected lands are dedicated to preserving ecosystems, but such areas often allow outdoor recreational activities. Research has shown negative impacts on a range of species from outdoor recreational activities, and there is little information about potential impacts of mountain biking on wildlife. Mountain biking and hiking tracking data from the social fitness app Strava Metro and data from a camera trap project in Marin County, CA, were analyzed to assess how mammal species' spatial distribution, temporal activity, and richness respond to distance from trails and different levels of mountain biking and hiking. While Strava Metro data provided an index of trail use versus actual numbers, this data was valuable for comparing more trafficked verses less used trails. This research found that three diurnal/crepuscular species and one nocturnal/crepuscular species were attracted to trails but changed their behavior to use trails more often at night. Most of the mammals observed were found less frequently on high-use bike trials compared to low-use. The fact that most mammal species avoided high bike-use trails altogether or during the day indicates this type of use is impacting mammals. Managers should consider how to maintain non-bike and non-recreation zones within open spaces to support mammal species and biodiversity.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the tremendous support of the mentors and peers who have journeyed through this project alongside me. First to my advisor Dr. Lynne Trulio for her knowledge, passion, and encouragement. To my committee members, Dr. Rachel O'Malley and Dr. Sulekha Anand for their advice and aid in the design and statistical analysis.

Secondly to the entire team at One Tam who first introduced me to the Marin Wildlife Watch and who have inspired me to pursue my masters and continue working in wildlife biology. To my One Tam mentors Rosa Schneider and Dr. Lisette Arellano, to Lizzy Edson and Dr. Sue Townsend for the help and advice in working with camera trap data, to my SPT and GGNRA colleagues Suzanne Whelan, Rachel Townsend, and Katie Smith. To my Marin County Parks family Serena Hubert, Michelle Huppert, Dana Lui, Jacob Martin, and Oliver Chesley. And to all the staff, volunteers, and interns who helped catalogue all the camera trap photos.

Lastly, I would not have been able to complete this program without the support, love, and encouragement from my fiancé Gaurav Thayil. And to my parents Maurice and Donna Lacour for instilling my love of the outdoors and supporting my goals.

TABLE OF CONTENTS

List of Tables viii

List of Figures ix

List of Abbreviations x

Introduction 1

Background 4
    Biodiversity Loss and Protected Lands 4
    Types of Outdoor Recreation Impacts on Wildlife 5
    Short and Long-term Effects of Recreation on Mammals 12
    Recreation Impacts on Mammals in the San Francisco Bay Area 14
    Using Strava Metro to Study Recreational Use Patterns 16

Problem Statement 18

Objective 20
    Research Questions 20

Methods 21
    Study Area 21
    Camera Site Methodology 23
    Camera Data Selection 24
    Site Characteristics 25
    Mammal and Recreation Variables 27
        Spatial Distribution 27
        Diversity 28
        Temporal Activity 28
        Mountain Biking and Hiking Rates 29
    Variable Assessment and Preliminary Analysis 29
        Subregion 30
        Habitat 30
        Season 30
    Statistical Analysis 31
        Visitation Frequency by Species 31
        Species Richness 32
        Percent Daytime Activity 32

Results 33
    Camera Distance from Trail 34
        Species Richness 34
        Visitation Frequency 34

    Percent Daytime Activity 35
  Mountain Biking and Hiking 38
    Species Richness 38
    Visitation Frequency 39

Discussion 42
  Recommendations 48
    Future Research 48
    Management Recommendations 48

References 50

Appendices

  Appendix A - Species and Status 57
  Appendix B - Seasonal Distributions by Distance Category 58
  Appendix C - Best-fit Generalized Linear Model Comparisons 59

LIST OF TABLES

Table 1. Land Agencies and their Recreation Policies within the Study Area 26

Table 2. Description of Variables 28

Table 3. Number of Close-distance Cameras Within Each Recreation Level 29

Table 4. Number of Camera Detections for Each Species 33

Table 5. Mean Visitation Frequency and Mean Percent Daytime Activity for Each Distance Category 36

Table 6. Results from Best-fit Models for Visitation Frequency in Response to Distance from Trail 37

Table 7. Results from PDA in Response to Camera Distance 39

Table 8. Results for Species VF in Response to Hiking Level on Close-Distance Cameras 41

Table 9. Results for Species VF in Response to Level of Mountain Biking on Close-Distance Cameras 41

Table 10. Taxonomy and Conservation Status of Species in Study Area 57

Table 11. Model Comparison for Response of Species Richness to Distance from Trail 59

Table 12. Model Comparison for Response of Species VF to Distance from Trail 59

Table 13. Model Comparison for Response of Species Richness to Hiking Level 60

Table 14. Model Comparison for Response of Species Richness to Mountain Biking Level 61

Table 15. Model Comparison for Response of Species VF to Hiking Level 61

Table 16. Model Comparison for Response of Species VF Mountain Biking Level 63

LIST OF FIGURES

Figure 1. Map of Study Area on the Northern Side of Mount Tamalpais, Marin County, CA 22

Figure 2. Total Number of Cameras in Each Habitat 30

Figure 3. Number of Individual Cameras Visited by Each Species by Distance Category 34

Figure 4. Mean Species Richness by Distance Category 35

Figure 5. Mean Species Visitation Frequency by Distance Category 38

Figure 6. Mean Species PDA by Distance Category 40

Figure 7. Trends in Visitation Frequencies by Season 58

LIST OF ABBREVIATIONS

GGNRA – Golden Gate Recreation Area
MCP – Marin County Parks
MMWD - Marin Municipal Water District
SPT – Samuel P. Taylor State Park
MWW – Marin Wildlife Watch
VF – Visitation Frequency
PDA – Percent Daytime Activity

Introduction

Protected lands are set aside for a number of reasons including to conserve natural resources from anthropogenic disturbance and to provide outdoor experiences for the public. Often, these two goals are combined, requiring land managers to make decisions that balance the protection of ecosystems and the recreational desires of visitors who support parks and open spaces. Recreationists are attracted to protected lands with high wildlife and plant diversity and visit these areas to foster connections with nature and escape urban centers (Mitrovich et al., 2020). Even though park visitors enjoy nature and support conservation, outdoor recreation activities often pose a threat to natural resources, decreasing the effect protected lands have on mitigating human disturbance.

In a systemic review of academic literature on recreation impacts on wildlife around the world, Larson et al. (2016) found most impacts to be negative. They categorized these impacts into changes in wildlife abundance, reproductive rate, survival rate, behavior, and physiology. These negative impacts are relevant because, as Balmford et al. (2015) show, protected areas receive roughly 8 billion visitations per year, of which 3.3 billion are in North America alone. These billions of park visitors participate in a variety of recreational activities, such as hiking, hunting, mountain biking, rock climbing, horseback riding, and wildlife viewing, all of which can contribute to the kinds of negative impacts to wildlife described by Larson et al. (2016). For land managers, it is important to monitor and mitigate as many negative impacts recreational activities may have on wildlife populations and other natural resources as possible.

Outdoor recreation harms wildlife species in a variety of ways. Some examples of how people may disturb wildlife while recreating include noise pollution, the spread of pathogens and non-native species, nesting bird failure, trampling of native fauna, loss of wildlife habitat, wildlife shifting their activity times to night, avoidance of human-use areas, and pollution (Marzano & Dandy, 2012). Impacts on animals that visitors may witness include fleeing when people get too close (flushing) or cautious behavior (Larson et al., 2016). Most recreation impacts on animals, however, are not obvious to park visitors, such as nesting or reproductive failure (Thompson, 2015), increased stress (Barja et al., 2011), shifting the time of day they are most active (Wang et al., 2015), and disruption to foraging time and location (Cassirer et al., 1992; Larson et al., 2016).

It is important for land managers to find out how their park visitors may be affecting local animal populations. Mammal communities are indicators of ecosystem health (Cheyne et al., 2016), and are a useful group for monitoring changes in community-level dynamics. A wide range of methods can be used to study recreation influences on mammals, including observing flushing distance (Cassirer et al., 1992), scat detection and analysis (Reed & Merenlender, 2011), capture and tagging (Cassirer et al., 1992), and camera traps (Reilly et al., 2017; Wang et al., 2015). Of these, motion-activated camera traps are increasingly reliable for collecting data on species abundance, diversity, distribution, and temporal activities (Burton et al., 2015; O'Brien et al., 2010). Wildlife cameras can detect many cryptic mammal species, are non-invasive, and they can reveal wildlife activity across a landscape (Burton et al., 2015; O'Brien et al., 2010). An increasing number of land agencies are adopting their own camera projects to monitor resident mammals (Burton et al., 2015).

One example is the Marin Wildlife Watch (MWW) in the San Francisco Bay Area in northern California. While the goal of the MWW is to develop baseline information on mammals on Mount Tamalpais and monitor trends in biodiversity, the data can also be used to assess the impacts of trail users on mammal species.

Impacts of recreational activities vary by the type of recreational use and the species (Kays et al., 2017; Reilly et al., 2017). While extensive literature documents the effects of trail walkers on wildlife (Coppes et al., 2017; Kays et al., 2017), there is very little published information on the effects of mountain biking. Camera trap studies can be used in densely populated areas such as the San Francisco Bay Area to discover if and how park visitors are affecting mammals. With pressure on land managers to accommodate recreation and increase trail usage while conserving natural resources (Townsend et al., 2020), wildlife camera data must be included as part of land management decisions and conservation policies.

Background

Biodiversity Loss and Protected Lands

Anthropogenic disturbance that results in habitat loss is considered the leading cause of the current extinction crisis (Brauer & Beheregaray, 2020; Newbold et al., 2015). To help mitigate habitat loss and degradation and protect species from human disturbance, significant areas have been set aside and preserved. Anthropogenic disturbance on wildlife that these areas aim to mitigate include habitat destruction, reproductive failure, increased stress, increased human-wildlife confrontations, and reduced species richness (Newbold et al., 2015).

Protected lands are an important conservation tool to mitigate the effects of anthropogenic disturbance on wildlife and other natural resources (Jones et al., 2018; Rodrigues et al., 2004). As of 2020, protected areas occupy about 17% of the Earth's terrestrial surface (International Union for Conservation of Nature, 2021), but only 38% of the Earth's biodiversity hotspots are within protected regions (Myers et al., 2000). Furthermore, most public protected lands in the United States are open to the public for access and recreational use (White et al., 2014).

In the United States, visitation to protected areas and participation in outdoor recreation have increased sharply in the past 10 years (Balmford et al., 2015; Clark et al., 2019). This increase is likely due to greater accessibility, promotion of protected areas through social media, human population increase, and economic expansion (U.S Department of the Interior, 2019). In addition to visiting protected lands, development contiguous to these open spaces to support the recreation industry is also expanding (Wittemyer et al., 2008). Housing and infrastructure around protected areas contributes increased parkland visitation, increases habitat fragmentation between open spaces, and reduces the value of these lands as a conservation tool (Wittemyer et al., 2008). The increasing pressure of human disturbance in and around protected areas degrades habitat and reduces the ability of protected lands to sustain ecosystems (Angulo et al., 2016).

Types of Outdoor Recreation Impacts on Wildlife

The outdoors is important for people's mental and physical health (Mitrovich et al., 2020) and creates connections between humans and nature (Deringer et al., 2020). These connections and appreciations for the environment improve social and economic support for protected lands and their managers (Deringer et al., 2020). For example, in a park visitor survey in Orange County, California, Marzano and Dandy (2012) found that recreationists prioritized enjoying nature over fitness at a 2:1 ratio as their reason for visiting the park. The authors also found that most visitors were interested in conservation, and those who lived adjacent to the protected area felt more connected to the land (Marzano & Dandy, 2012). Protected lands open to the public also benefit the U.S. economy, bringing about $350-500 billion into the economy in North America as of 2015, of which only $10 billion is spent on land management (Balmford et al., 2015).

The number of people participating in outdoor recreation is on the rise (Bowker et al., 2012; Larson et al., 2016; Lawson, 2022). Participation in mountain biking alone rose 22% in the United States between 2006 and 2015 (Wisdom et al., 2018) and has increased dramatically since the start of the COVID-19 pandemic (Newcomb, 2020). Growing participation in outdoor recreation is cause for concern due to disturbances recreation causes on protected lands (Larson et al., 2016). In a meta-analysis of recreational impacts on wildlife, the authors found frequent negative relationships between wildlife and recreation around the globe, including changes in abundance, reproductive rate, survival rate, behavior, and physiology (Larson et al., 2016).

Outdoor recreational activities take many forms, and, despite an extensive body of literature, the way some of these activities affect wildlife is still unclear. Common recreational activities include consumptive recreation, such as hunting or fishing, and non-consumptive recreation such as motorized (off-road vehicles and snow mobiles) and non-motorized activities (hiking, mountain biking, or horseback riding). Even though most literature has identified negative impacts of recreation on wildlife (Coppes et al., 2017; Larson et al., 2016; Marzano & Dandy, 2012; Taylor & Knight, 2003), the findings are not consistent. This inconsistency is due to a range of variables that affect species reactions and the data collected including habitat, species, research methodology and type of recreation.

In 2010, Ordeñana et al. examined how a combination of infrastructure bordering protected areas and non-motorized recreation affected native mammalian carnivores in public lands within Southern California. They used existing camera trap studies on public lands and conducted a meta-analysis to examine carnivore activity near these urban edges. They found that coyote (*Canis latrans*) and raccoon (*Procyon lotor*) occurrence increased with proximity to urban areas but decreased for bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), and puma (*Puma concolor*). In the Santa Cruz Mountains of the San Francisco Bay Area, Wang et al. (2015) found that carnivore occurrence decreased with proximity to urban borders including coyote detections which were less likely at camera sites closer to housing (Wang et al., 2015).

Most research on recreation in protected areas focuses on hiking or general trail use impacts (Larson et al., 2016), and most researchers study impacts on birds (Marzano & Dandy, 2012). Thompson (2015) looked at trail impacts on bird density in Eastern North American forests and found density decreased with increased human trail use compared with non-trail areas, especially for ground-nesting birds.

Many studies on ungulate responses to hiking have found avoidance of high-use trails. In Germany, Coppes et al. (2017) used GPS telemetry to look at the red deer's (*Cervus elaphus*) spatial and temporal relationships with trails in a protected forest that had a spatial zonation scheme, or designated zones. These zones were designated areas with no trails or recreational access, set up for the red deer and other wildlife to occupy undisturbed. They found that red deer avoided trails, especially during the day when more people are hiking, and that the zone scheme was a predictor for where the red deer were most active, since they were most active in non-trail zones (Coppes et al., 2017).

Using motion-activated camera traps along trails and roads in the Italian Alps, Oberosler et al. (2017) also found a negative association between red deer and human presence on trails, as well as increased nocturnality. They also observed these effects in roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*), badger (*Meles meles*), and brown bear (*Ursus arctos*), while red fox (*Vulpes vulpes*) and marten (*Martes sp.*) were more tolerant of human activity.

Like Coppes et al. (2017) and Oberosler et al. (2017), Taylor and Knight (2003) also found negative relationships between ungulates and hiking. Taylor and Knight (2003) used visual observations to compare black-tailed mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), and bison (*Bison bison*) response and fleeing distances from both hikers and bikers in Utah. They found that all three ungulates had similar alert responses to hikers and bikers, and all three fled an oncoming hiker or biker when they were within 100 m of a trail (Taylor & Knight, 2003).

In contrast, George and Crooks (2006) found that mule deer had no significant relationship with trail use in a Southern Californian nature reserve. This contrasting finding of ungulate response to hikers could result from different environmental factors, unique species characteristics, or from differing sampling methods. Instead of the telemetry or visual observation methods that Coppes et al. (2017) and Taylor and Knight (2003) used, George and Crooks (2006) utilized camera traps to study the relationship between different types of trail recreation and the spatial and temporal activity of native mammals. George and Crooks (2006) also found that both bobcats and coyotes were sensitive to trails with more human use and were more nocturnal in those areas. This observation was reported by Wang et al. (2015), which used similar camera trapping methods.

Like George and Crooks (2006), Kays et al.'s (2017) camera trap research on hunting and hiking found no significant relationship between hiking and mule deer and white-tailed deer (*Odocoileus virginianus*) frequency and occupancy. The same was true for most of the mammals Kays et al. (2017) studied, except for coyotes and bobcats, which shared a positive relationship with trails. These results are in opposition to the findings of Wang et al. (2015)

who also used camera traps to look at mammal spatial and temporal activity in relation to trail use in California. Kays et al. (2017) discovered that a lack of continuous habitat was a stronger negative covariate for species distribution than either hiking or hunting and concluded that the recreation impact in their study area at the time was non-critical.

Reed and Merenlender (2008) used a combination of scat detection and scat DNA analysis to study the difference in mammalian carnivore density in protected lands with recreation and without recreation in the northern San Francisco Bay Area. They found a five-fold decline in species density between recreation and non-recreation sites (Reed & Merenlender, 2008). These results oppose other studies that found no or only moderate negative relationships between recreation and carnivores (Kays et al., 2017; Reilly et al., 2017). The stark contrast between Kays et al. (2017) and Reed and Merenlender (2008) could be because Kays et al. (2017) did not compare their sites to areas without human recreation as Reed and Merenlender (2008) did.

A notable study that also took place in the San Francisco Bay Area was conducted by Reilly et al. (2017). Reilly et al. (2017) used camera traps in protected lands across the Bay Area to look for relationships between recreation and mammalian spatial and temporal activity. Like Reed and Merenlender (2008), Reilly et al. (2017) also compared recreation sites with non-recreation sites but found no statistically significant relationships between hikers and carnivore occurrence. Reilly et al. believe their results opposed those of Reed and Merenlender (2008) because of differing methodology. Reed and Merenlender used scat detection to determine carnivore density, but scat in protected lands that allow recreation may be disturbed or consumed by domestic dogs, reducing detectability (Reilly et al., 2017; Townsend et al., 2020).

In a small San Diego preserve, Larson et al. (2020) took advantage of a trail closure to assess mammal occupancy before and after the trail opened, using camera traps along the treatment trail and camera traps at nearby trails that remained open as a control. Their analysis found that both bobcat and coyote occupancy decreased after the trail re-opened to hikers and bikers, with bobcats most impacted (Larson et al., 2020). This study was limited by a short time span and small sample size, but their results were consistent with findings of negative associations between mammal occurrence and trail activity (George & Crooks, 2006; Reed & Merenlender, 2008, 2011) while contrasting studies that found no significant relationship between wildlife and trail use (Reilly et al., 2017).

Compared to all other forms of trail recreation, there is even less research on how mountain biking affects native mammals. Like with dog-walking, managers generally assume it harms wildlife and they may institute no-biking rules and policies to protect wildlife, prevent soil erosion, protect trail integrity, and avoid collisions with other trail users (Taylor & Knight, 2003). Biking is presumed to be harmful to wildlife because it is fast, quiet, and unpredictable (George & Crooks, 2006; Taylor & Knight, 2003). Other experts believe mountain biking does not cause as much fear in wildlife as hikers because of the loss of "human form" (Papouchis et al., 2001). When riding a bicycle or any other vehicle, the "human form" or human shape that wildlife recognize is lost, causing them to not see people in the shapes of humans riding bikes and therefore not be as fearful (Papouchis et al., 2001).

The results of Taylor and Knight's (2003) observational experiment contradict managers' assumptions of negative mountain biking impacts on wildlife. In examining both hiking and mountain biking flush responses in ungulates, they found that there was no significant difference in distance of alertness, flush distance travelled, or distance from trail when fleeing for all three ungulate species (Taylor & Knight, 2003). Even though there was no difference in responses to biking and hiking, all three species were negatively impacted by both activities, and fled oncoming people when within 100-meter of a trail. These results contradict a similar study that also took place in Utah, but focused on bighorn sheep (*Ovis canadensis nelsoni*) (Papouchis et al., 2001). Papouchis et al. (2001) found that hikers caused more sheep to flee, followed by motorized vehicles and then bicycles. These different observations on ungulate response to hikers and bikers could be from unique sensitivity levels of the specific species or from differences in the methodologies used (Taylor & Knight, 2003).

Scholten et al. (2018) studied ungulate response to mountain biking on trails of red deer in Norway. Combining scat counts and camera traps, they found that red deer avoided mountain biking trails in a 40 m avoidance zone. Their methods, however, did not compare mountain biking to other uses of the trails, and so, like Taylor and Knight's (2003) 100 m flush zone for ungulates, Scholten et al.'s (2018) 40 m avoidance zone may only be applicable for general trail use.

George and Crooks (2006) and Reilly et al. (2017) also included mountain biking in their California camera trap studies examining multiple types of recreation on mammals. Reilly et al. (2017) found no significant relationships between biking and wildlife behavior, but

George and Crooks (2006) did find impacts for bobcats and coyotes. However, because both studies used similar methods to look at all forms of trail use, and multiple species shared the same response with different recreation activities, the species responses can only be associated with trail use in general. More research is needed specifically on if and how mountain biking negatively impacts mammal presence and behavior.

Short and Long-term Effects of Recreation on Mammals

Because recreation elicits a response in wildlife activity, it is important to understand how recreation impacts species and their interactions with ecosystems. Recreation has both short and long-term effects on mammals, as well as other taxa. Short-term impacts include fleeing an area (Cassirer et al., 1992; Larsen et al., 2016; Moranzo & Dandy, 2012), loss of cover from predators (Gaynor et al., 2018), and interruptions in foraging, hunting, or caring for young (Taylor & Knight, 2003). Though these impacts may seem brief at the time of disturbance, repetition of short-term responses to trail disturbance has cascading effects.

Repeated interruptions in foraging and hunting for food caused by fleeing from approaching hikers or increased alertness in high-human activity areas leads to increased energy loss and less time spent finding food (Cassirer et al., 1992; Larson et al., 2016; Marzano & Dandy, 2012; Taylor & Knight, 2003). Fleeing an approaching park visitor uses energy, which has to be made up through increased hunting; this is difficult to accomplish if wildlife are repeatedly interrupted when searching for food.

Frequent fleeing not only impacts feeding behavior and energy expenditure, but also makes wildlife and their offspring more vulnerable to predation and can cause reproductive failure (Marzano & Dandy, 2012; Taylor & Knight, 2003). Phillips and Alldredge (2000) used telemetry to study reproductive success of elk (*C. elaphus*) in response to direct human disturbance in Colorado. A treatment group included researchers that would mimic recreational hiking and record the responses, and the control group was free of human disturbance. The calf per mother proportion in the treatment group declined over the course of the study while the proportion in the control population remained the same, suggesting a negative relationship between hiking disturbance and reproductive success.

An increase in stress levels is a likely physiological effect of recreation on wildlife. Stress induced by human activity and other non-natural factors has negative implications on fitness and reproductive success (Taylor & Knight, 2003). Studying the actual chemical levels of stress an animal is experiencing in response to a specific event is difficult and remains a gap in research. Barja et al. (2011) determined stress levels of European pine martens (*Martes martes*) by testing cortisol levels in their scat. They found heightened levels of cortisol during the spring compared to other seasons but interpreted this as a symptom of the breeding season. Cortisol levels were especially high in females who are feeding and caring for young in the spring and were also high in males who are competing for mates and territory. However, to use this method when studying specific disturbances, a way to determine the cause of stress would be required.

Temporal shifts and increased nocturnality of wildlife around areas of high human activity cause changes in predator-prey dynamics and trophic-level interactions, which affect fitness of prey species and prey animal reproductive success (Gaynor et al., 2018; Taylor & Knight, 2003). By becoming more nocturnal, more mammals are active at the same time, causing an overlap in activity not observed in remote areas further from people and development (Gaynor et al., 2018). By overlapping activity times, predators must directly compete for food in the same space at the same time. When prey and predator activity times overlap, prey species may spend more time hiding than foraging or completing other actions that promote fitness. These changes in species interactions, combined with increased stress and interruptions in foraging, limit mammals' activity time and chance to improve fitness.

Spatial shifts such as avoidance of trails and areas of high human disturbance remove available suitable habitat (Coppes et al., 2017; Papouchis et al., 2001; Taylor & Knight, 2003; Wang et al., 2015). By causing some species to avoid areas around trails or other human-activity areas within and adjacent to protected lands, recreation is reducing the amount of suitable habitat for wildlife that the protected land was created to conserve.

Recreation Impacts on Mammals in the San Francisco Bay Area

Several studies have examined the relationships between outdoor trail recreation and mammal presence and activity around the San Francisco Bay Area. The Bay Area is densely populated with over 7.7 million people (U.S. Census Bureau, 2019), all within a short drive of an extensive network of national, state, county, municipal and privately owned protected lands open for outdoor recreation. All but two of these studies (see Reed & Merenlender, 2008, 2011) used similar camera trap methodology.

In the Northern Bay Area, Townsend et al. (2020) used camera traps to look at mammal occupancy in a protected area before and after it opened to the public and allowed recreation. This study did not compare specific recreation activities to occupancy. Also, trail use already occurred in the study area despite it being closed to the public, and although trail use spiked after the park opened, human activity dropped back down over the course of the post-opening year. Aside from puma and wild turkey (*Meleagris gallopavo*), most species occupancy either did not change significantly or returned to their pre-opening number (Townsend et al., 2020). As also found by Reilly et al. (2017), coyote, bobcat, and gray fox trail use appeared neutral to human presence; however, mule deer and gray squirrels (S*ciurus* g*riseus*) decreased their trail use after opening. A longer-term version of this study in an area that was previously human-free would be valuable in determining impacts of recreation on mammals.

The largest study of recreation on wildlife in the Bay Area was conducted by Reilly et al., (2017) which, unlike Reed and Merenlender (2008, 2011) and Wang et al. (2015), found almost no significant relationships between mammals and trail use. Reilly et al. (2017) found only increased nocturnality around high human use trails for coyote and mule deer, and slightly more for striped skunk (*Mephitis mephitis*), while Wang et al. (2015) found increased nocturnality in human use areas for bobcats in addition to coyote. Reilly at al. (2017) also found no differences in types of recreation except for pumas and opossums which were negatively associated with domestic dogs.

All five of these studies took place in the San Francisco Bay Area and only one included mountain biking impacts in their analysis. There were also no consistent patterns in the findings across all species and recreation types, leaving the unanswered question of how recreation impacts wildlife abundance and which forms of recreation elicit the greatest behavioral response. Researchers agree that more information is needed about how mountain biking and other recreation activities disrupt mammal community interactions (George & Crooks, 2006; Scholten et al., 2018; Taylor & Knight, 2003). These data gaps are especially crucial to fill in the San Francisco Bay Area because of its high volume of recreationists and sensitivity of its biologically diverse protected lands.

Using Strava Metro to Study Recreational Use Patterns

Strava is a popular social fitness app that collects and aggregates its member's geospatial and activity data into a global heat map through its platform, Strava Metro. Strava Metro's global heatmap is composed of over 13 trillion data points, showing various levels of running, biking, and other outdoor activities on roads and trails around the world (Robb, 2017). For the goal of improving infrastructure management to benefit bicyclists and pedestrians, Strava partners with urban and transportation organizations, and provides free use of their heat map data to local governments (Strava Metro, 2020). To protect user's privacy, only the data of users who have opted to share their activities through the app are represented in Strava Metro and all data from deleted accounts is removed (Strava Metro, 2020). Activity data are also aggregated into multiples of five to prevent tracking of individuals, and Strava Metros' data plan follows the California Consumer Privacy Act.

Research has found Strava's user data to be a good predictor of true trends in bicycling and running/walking activities. In 2016, the Centers for Disease Control found a strong correlation between Strava's user data and the Census's American Community Survey bicycling and pedestrian commuter numbers across 2,049 census blocks (Whitfield et al., 2016). Unlike trail counters which show recreation use at a single point, Strava Metro's global heat map shows how people bike or run across a landscape as well as changes over time. To increase accuracy, Strava data can be combined with bicyclist or pedestrian counters to strengthen Strava's predictability factor in a given area and along nearby trails that do not have counters (Strava Metro, 2020).

Strava Metro's global heatmap data has been used in research to understand pedestrian and biking commuter patterns and recreational biking behavior in response to various environmental and road factors (Lee & Sener, 2021; Sun et al., 2017). It has not yet been used to look at relationships between recreational use in protected lands and natural resources and may prove a valuable data source to land managers, especially when combined with trail counters.

Problem Statement

Wildlife around the world is negatively impacted by anthropogenic activities that result in habitat loss, degradation, and fragmentation. To limit habitat damage, protected areas, such as open space parklands, have been set aside to preserve areas and habitat (Balmford et al., 2015). However, recreational uses are often allowed in preserves. Visitations to protected lands and participation in mountain biking are increasing (Clark et al., 2019; Wisdom et al., 2018) while habitat and space for wildlife to occupy without human disturbances is decreasing (Coppes et al., 2017). Visitation of protected lands and participation in outdoor recreation by humans also disturbs wildlife (Larson et al., 2016). Recreational impacts can cause wildlife to experience stress and changes in behavior, habitat use, spatial distribution, and predator-prey dynamics.

Multiple studies have found changes in wildlife behavior and activity in reaction to outdoor recreation (Kays et al., 2017; Reed & Merenlender, 2008; Wang et al., 2015). Most studies examine the impacts of multi-use trails or sites on wildlife. Some studies have tried to assess the response of wildlife to specific recreation activities but with little success (Oberosler et al., 2017; Reed & Merenlender 2008, 2011; Reilly et al., 2017). To detect recreational impacts on wildlife, land managers need data on specific recreational activities and species-level responses.

Mountain biking is a popular form of recreation in Marin County, and little research to-date describes the impacts of mountain biking on wildlife in protected lands. Mount Tamalpais, in the densely populated San Francisco Bay Area, is an ideal location to study the impact of mountain biking on wildlife. This site is accessible to the over 7 million people who live there (U.S. Census Bureau, 2019). The California coast is a biodiversity hotspot, with this study site alone hosting over 250 animal species and 750 native plant species (Edson et al., 2016). Mount Tamalpais has an extensive wildlife camera system designed to collect data on mammals. Utilizing this camera array to study how individual mammals respond to trail use will inform land managers on if mountain biking and other recreational use of their lands adversely affects mammals. This knowledge is crucial in making land management decisions that accommodate both accessible recreation and wildlife conservation.

Objective

The objective of this project is to assess whether mountain biking affects mammal visitation frequency (VF), temporal behavior, and species richness in protected lands on Mount Tamalpais in the San Francisco Bay Area differently than hiking. To carry out this objective, I explored two sets of secondary data. For species behavior and richness, I analyzed existing data from the MWW, where motion-activated cameras captured images continuously between 2014 and 2017 along the Lagunitas Creek Watershed on the northern side of Mount Tamalpais in Marin County. For recreation activity, I used data from Strava Metro's global heat map, which provides the daily number of mountain biking and hiking trips on trails within the same study area. Using these data sets, I looked for relationships between species' daily VF, temporal activity, and richness and the following conditions: distance of camera to nearest trail, and level of biking and hiking along the nearest trail. The results of this project will inform land management decisions regarding wildlife management, recreational policies, and planning.

Research Questions

RQ1: How does species richness change in response to distance from trail?

RQ2: How does spatial distribution change in response to distance from trail for each species?

RQ3: How does temporal behavior change in response to distance from trail for each species?

RQ4: How does species richness change in response to the level of mountain biking and hiking on camera sites close to trails?

RQ5: How does spatial distribution change in response to the level of mountain biking and hiking on camera sites close to trails?

Methods

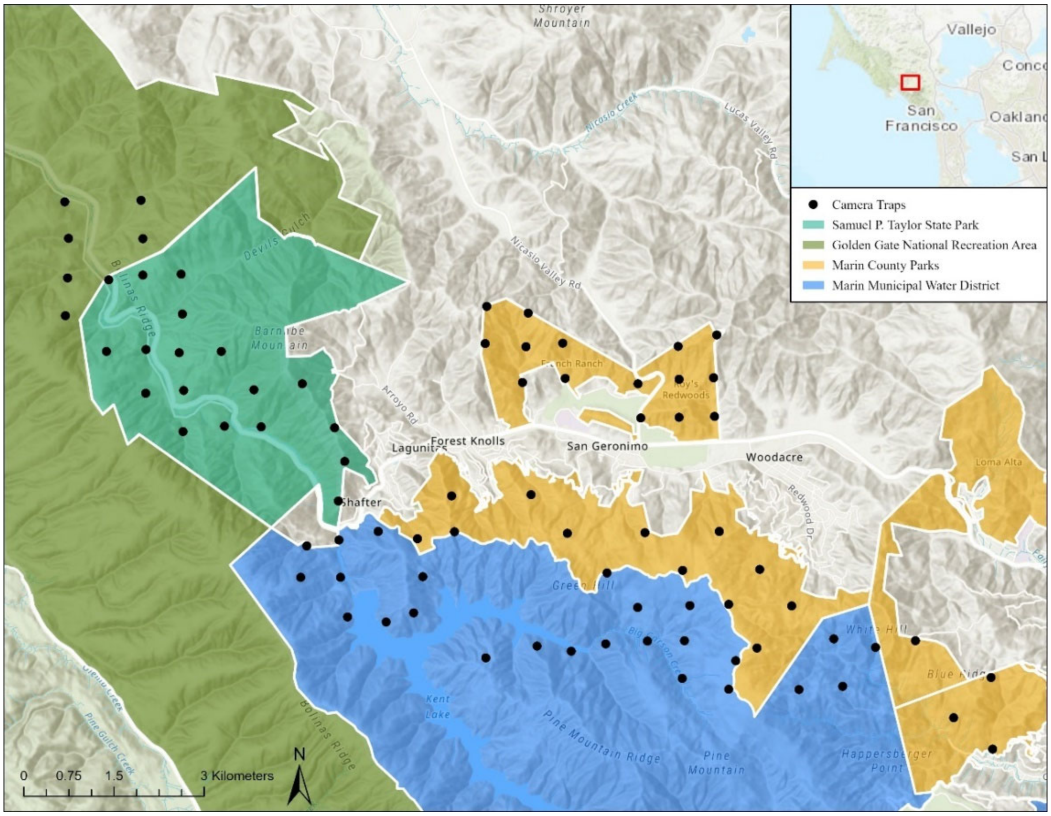
Study Area

The Mount Tamalpais region is an internationally recognized biodiversity hotspot that contains multiple endemic and special status species (Edson et al., 2016). A full list of mammals detected by the MWW's cameras between 2014 and 2017 can be found in Table 10 in Appendix A. This region is located within the San Francisco Bay Area. Due to its proximity to a major urban center, this area experiences high traffic of park visitors year-round, with over 15 million annual visits to the Golden Gate National Recreation Area (National Park Service, 2020), and 107,508 annual visits to Samuel P. Taylor State Park (SPT) (California State Parks, 2017). Aside from being a popular recreation area, Mount Tamalpais is bordered by development and housing. It also experiences high biking traffic and is considered the birthplace of modern mountain biking (Breeze & Vendetti, 2014). The land agencies of Mount Tamalpais provide accessible non-motorized recreation opportunities throughout the study site, including hiking, dog-walking, mountain biking, and horse-back riding. Due to the combination of high biodiversity and high levels of human use, this area is an ideal site to study the impacts of outdoor recreation on natural resources. The elevation of the specific study site ranges from 23 m to 462 m a.s.l. Habitats within the study area include grasslands, conifer forest, chapparal, riparian, oak-bay woodland, and mixed forest. Some features of the study area also include campsites, facilities with paved roads, and a network of trails and fire roads. In addition, a major boulevard and a few small towns lie within and around the study site.

In September 2014, One Tam initiated the MWW to fill knowledge gaps about the mammal community on Mount Tamalpais by monitoring species occupancy and biodiversity trend. One Tam is a partnership between four public agencies who own land within the study site. These agencies include the Golden Gate National Recreation Area (GGNRA) of the National Park Service, SPT of California State Parks, Marin County Parks (MCP), and the Marin Municipal Water District (MMWD). The study site is a 32 km^2 area on the northern side of Mount Tamalpais in Marin County, California (Figure 1). The MWW is still ongoing as of 2023.

Figure 1

Map of Study Area on the Northern Side of Mount Tamalpais, Marin County, CA



Note. All 80 camera sites are represented with points, and the four land jurisdictions are represented with different colors. The northern cameras of Marin County Parks are separated by a boulevard and towns.

Camera Site Methodology

This study used camera data collected between Spring of 2016 and Summer of 2017 by the MWW. These data were collected by staff, interns, and volunteers of the One Tam partnership. The camera site locations of the MWW were randomized by generating a grid with 0.5 km^2 cells. One hundred twenty-eight cameras were placed within 100 m of the center of each cell so that the cameras are 0.5 km away from each other and are equally distributed across the landscape. The 100 m radius from the center of each cell was designed to accommodate for unique topography and to maximize animal detection by finding a trail or clearing for the camera to face.

This camera trap methodology is modeled after the protocol described by the Tropical Ecology Assessment and Monitoring (TEAM) Network, and was selected because of its ability to monitor wildlife across a landscape, obtain occupancy data, and monitor biodiversity trends in real time (TEAM Network, 2011). These sampling and data collection methods have proved useful in multiple studies on recreation impacts on wildlife and are described by Nichols et al. (2008), O'Brien et al. (2010), and TEAM Network (2011).

Bushnell TrophyCams (model #119636c) were used for the MWW. Upon camera setup, GPS coordinates, cardinal direction, elevation, and habitat category (open, closed, or mixed) were recorded. Depending on the site, cameras were either strapped to a tree or a wooden stake, and their height varied depending on slope. However, they were positioned to capture animals of about 0.5 m tall at 2 m distance from the camera (Townsend, 2018). Cameras located on trails or visible from trails were secured in a lockbox with a python lock to prevent theft. Data were collected four times each year every 3-month season (more often in the beginning during the pilot months) by collecting and replacing SD cards, recording camera settings and any changes made on data sheets, and other upkeep required to keep the cameras running. Standard settings across all cameras were three images per event (when camera was triggered), six mega-pixel photos, five second intervals, and timestamp on. Sensitivity level varied depending on site characteristics, but high sensitivity was used and lowered for cameras frequently triggered by vegetation or other false triggers (Townsend, 2018).

The time span of the raw camera data set received from One Tam is three years, September 2014 through August 2017. In these three years, a total of about 4 million images were collected in 89,835 trap nights and 1,333,300 unique camera events (Townsend, 2018). Photos were backed up on the servers and hard drives of the four agencies, and were cataloged through Microsoft Excel, Wild I.D., and Wildlife Insights. Cataloging platforms changed over time to accommodate the data set as it grew and to improve data management. The original photographs were cataloged by staff and volunteers from the One Tam partnership.

Camera Data Selection

Data from the MWW was granted by the One Tam partnership by requesting access for research through their steering committee and is available to others upon approval of application. Data available for each camera location included GPS coordinates, cardinal direction, elevation, and habitat category. Before the start of this study, the image data from each camera were already collected and analyzed for baseline information, occupancy, and wildlife picture index. This data was analyzed by the principal investigator and the data manager for the MWW and presented to the One Tam land agencies in an unpublished report. The baseline information collected included which species were detected by the cameras, the number of detections for each species, the occupancy of each species per land jurisdiction, and the trend in biodiversity between 2014 and 2017.

While the MWW array included 128 cameras, only a subset of 80 cameras active between March of 2016 and August of 2017 were used to address the research questions in this study. Recreation activity data from Strava Metro were only available from 2016 onwards, limiting the time frame of the original data set to just 2016 and 2017, and omitting cameras that were removed from the study area before 2016. Additionally, other cameras were removed from the study if they were not active for at least two seasons, or if they were closer to a street, campground, or private road than an open space trail. Between March of 2016 and August of 2017, these 80 camera traps collected data for 36,804 trapnights.

Site Characteristics

Camera sites were characterized by land jurisdiction, habitat, season, and distance from trail. All four land agencies within the study area are connected except for a portion of the MCP area, which is separated by Sir Francis Drake Blvd and a few small towns (Figure 1). Each land agency has a diversity of the same habitat types and enforces similar management practices (Table 1). In each park, mountain bikers are allowed on at least some trails. Dog rules differ between agencies, with SPT forbidding dogs from trails yet allowing dogs in their campgrounds, and MMWD only allowing dogs on leash. However, preliminary analysis and photos taken by the cameras show that park visitors do not always follow these rules, and therefore no section of the study area is completely free of mountain bikers or dogs. Dogs

Table 1

Land Agencies and their Recreation Policies within the Study Area

	GGNRA	SPT	MMWD	MCP
Area (km^2)	2	5.5	7.25	17.25
Camera sites	6	18	25	31
Hiking	Yes	Yes	Yes	Yes
Mountain Biking	On designated trails only	On designated trails only	On designated trails only	On designated trails only
Horseback Riding	On designated trails only	On designated trails only	On designated trails only	On designated trails only
Other	Dogs, cattle grazing	No dogs on trails, camping	On-leash dogs on designated trails only	On and off-leash dogs on designated trails only

were not included in this study because there are not enough trail-facing cameras to do analysis on dog visitation and trail activity, and there was no other reliable source of dog data. Both on and off-leash dogs are present throughout the study area, and likely on every trail despite trail-specific dog rules.

Spatial and temporal data from the camera traps were calculated for each season between March of 2016 and August of 2017. Each season was three months with spring being from March through May, summer from June through August, fall from September through November, and winter from December through February. There was one fall and one winter season, and two seasons each of spring and summer.

Habitat types were identified using the Marin County Fine Scale Vegetation Map in ArcGIS Pro (version 2.7.2). Except for a few smaller and rare species, most mammals in this study are known to occupy multiple habitats and may therefore not show a preference for habitat in the context of this study. Over half of the 80 cameras reside in conifer forest, which include coast redwood, Douglas fir, and dwarf sergeant cypress forest. Some habitat types only contain a few cameras, which is not enough for a reliable comparison between habitats.

Distances between cameras and both their closest trail were calculated in ArcGIS Pro. These distances were then divided into three categories: close, medium and far. Close-distance cameras were less than 30 m from trails and the most exposed to human disturbance. Medium-distance cameras were between 30 and 100 m from trails, and far-distance cameras were over 100 m from trails and assumed to not be impacted by direct human disturbance. Of the 80 cameras, 29 were located close to trails, 23 were a medium distance from trails and 28 were far from trails. These distance categories are similar to those selected by Kays et al. (2017), Mols et al. (2022), and Reilly et al. (2017).

Mammal and Recreation Variables

Table 2 provides a full description of each variable. Response variables included spatial and temporal definitions for each species in each season, and the diversity of species. Predictor variables described the distance from trails and amount of different recreation types on trails.

Spatial Distribution

In order to measure each species' spatial preference, seasonal visitation frequency (VF) was calculated for each species, which is the number of camera trap events divided by the number of trapnights (24-hour period the camera was active) within the season, divided by 100. VF is also referred to by other authors as rate of detection, relative activity, and relative abundance index (George & Crooks, 2006; Kays et al., 2017; Oberosler et al., 2017). VF was calculated for each species on each camera during all six seasons.

Table 2

Description of Variables

Variable	Definition	Analysis Tools	Source
Response			
Visitation Frequency	# detections / (Trapnights / 100)	R; GZLM	MWW; One Tam
Species Richness	sum of unique mammal species	R; GZLM	MWW; One Tam
Percent Daytime Activity	# of daytime detections / # total detections	R; GZLM	MWW; One Tam
Predictors			
Distance from trail	Distance (m) of camera site from nearest trail	ArcGIS Pro; Near Tool	MCP, SPT, and One Tam
Mountain Biking Level	Mean biking trips on trails nearest cameras	ArcGIS Pro; Microsoft Excel	Strava Metro
Hiking Level	Mean hiking/running trips on trails nearest cameras	ArcGIS Pro; Microsoft Excel	Strava Metro
Nuisance			
Season	3-month seasons	R	
Habitat	Habitat type of each camera site	ArcGIS Pro	Marin County Fine Scale Vegetation Map; One Tam
Subregion	Land jurisdiction of each camera site	ArcGIS Pro	One Tam

Diversity

Species richness was calculated as the sum of unique mammal species found on each camera during each season and used to represent mammal diversity.

Temporal Activity

To measure temporal activity of each species, the percentage of daytime activity (PDA) was calculated as the number of daytime camera detections divided by the total number of detections for each species on each camera during each season. Daytime camera visitations were defined as occurring between 06:00 and 17:59 (PST), and nighttime visitation occurred between 18:00 and 05:59 (PST) for all seasons. Thus, PDA represents the proportion of camera visitations that occurred diurnally.

Mountain Biking and Hiking Rates

Bicycling and hiking count data were obtained from Strava Metro through the County of Marin. This data does not require institutional review board (IRB) approval because the data set does not included data from users who have either deleted or made their accounts private, and all data “has been aggregated and deidentified, consistent with the European Union’s GDPR and the California Consumer Privacy Act (CCPA)” (Lee & Sener, 2019; Strava Metro, 2020). Daily average rates of biking and hiking activities were calculated in Microsoft Excel (Version 2209) as the number of occurrences on a trail divided by the number of days in the season. These rates were then categorized into either high-use or low-use trails for mountain biking and hiking to compare the three response variables between recreation activities. The high-low thresholds were chosen based on a visual inspection of natural breaks within the distribution of mountain biking and hiking activities on close-distance cameras (Table 3). This methodology was also used by George and Crooks (2006).

Table 3
Number of Close-distance Cameras Within Each Recreation Level

	Low use	High use
Bike	20	9
Hike	14	15

Variable Assessment and Preliminary Analysis

During preliminary analysis, three potential variables were inspected to determine if they had any significant relationships of the three response variables (VF, species richness, and PDA) on potentially important variables. These variables were subregion (the land agency each camera site was in), habitat, and season.

Subregion

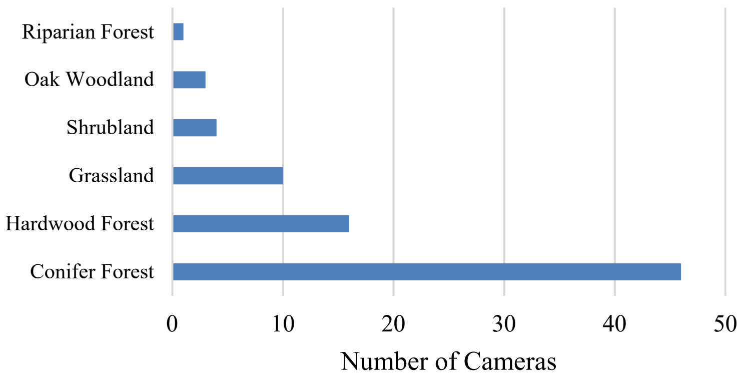
Through linear regression, subregion did not affect any response variables and so was omitted from further analysis.

Habitat

The proportion of habitat types in which cameras were located is described in Figure 2. The most common habitat type was conifer forest followed by hardwood forest. Because camera sites did not evenly represent each habitat and most species in this study is known to occupy multiple habitat types, this research was conducted to examine species in this overall mix of habitats.

Figure 2

Total Number of Cameras in Each Habitat



Note. N = 80 cameras

Season

Visual inspection comparing the VF for each species between seasons showed that VF for each camera distance had a similar trend in each season (Figure 7 in Appendix B). In each, the "trend" or amount of VF for each distance category is about the same for each season. The same was true when comparing PDA of each species between seasons.

Since the response variables were collected seasonally, season was used as a covariate when comparing species responses to camera distances. When comparing species response variables to recreation activities on trails, only data from close-distance cameras were compared. Due to the smaller camera site sample size, season was omitted as a covariate by taking the average of each species response variable across all six seasons.

Statistical Analysis

As expected with camera trap and ecological count data, all data were inflated with zeros and low values and none of the variables were normally distributed. I used R Studio version 4.1.1 to run generalized linear models (GZLMs) using packages *stats, MASS,* and *countreg* to test all hypotheses (R Core Team, 2021; Venables & Ripley, 2002; Zeileis & Kleiber, 2022). With a choice of family links to account for distributions, GZLMs are a robust alternative to linear regression models when working with non-normal distributions. They have more power when identifying statistically significant P-values, can handle zero and low-value inflation, and work with count, rate, and proportion response variables (Crawley, 2012; Ngo, 2016). Because different species may respond to the same disturbances differently and populate an area in different frequencies, the severity of zero-inflation differs between each species. Therefore, different models that handle these types of inflations differently were compared to find the best fit model for each species. The results for all model comparison tests are found in Appendix C.

Visitation Frequency by Species

GZLM models with a Poisson distribution were used to look for relationships between species VF and both distance from trail and levels of mountain biking and hiking. These models included Poisson, quasi-Poisson, negative binomial, zero-inflation, and hurdle models. For each species, these models were compared and the one that scored the lowest Akaike information criterion (AIC) was selected as the best fit model for that species.

Species Richness

A model comparison based on AIC value was also used to look for relationships between SR and camera distance and recreation levels. The compared models were Poisson, quasi-Poisson, and negative binomial generalized linear models. Hurdle and zero-inflated models were not included because none of the cameras had zero mammal detections.

Percent Daytime Activity

For PDA in response to distance from trail and recreation level, GZLMs with either a binomial or quasi-binomial link were used. These tests are designed to handle proportions as the response variable (Crawley, 2012). The binomial family link assumes equi-dispersion, so in the case of overdispersion, or if the dispersion parameter was greater than one, a quasi-binomial link was used instead.

Results

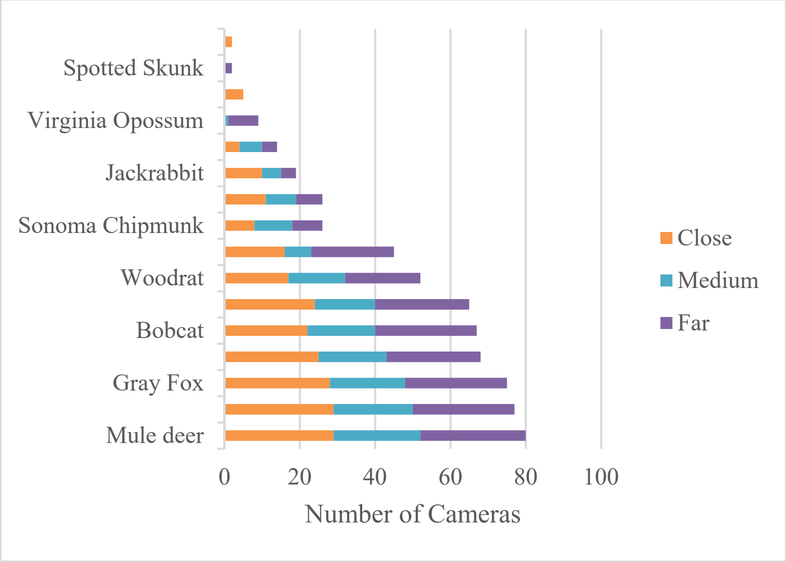
Out of the 36,804 trapnights, mule deer, gray squirrel, and gray fox were captured on cameras most often (Table 4). Out of the 16 mammal species, 12 were detected on cameras from all three trail distance categories at least once (Figure 3). The other four species were detected rarely and did not have enough observations for statistical analysis. These species included puma, American badger, Virginia opossum, and spotted skunk.

Table 4
Number of Camera Detections for Each Species

Species	Detections
Mule deer	11564
Gray Squirrel	2136
Gray Fox	1208
Raccoon	864
Jackrabbit	599
Woodrat	459
Coyote	375
Bobcat	332
Brush Rabbit	276
Striped Skunk	186
Sonoma Chipmunk	95
Fox Squirrel	45
Virginia Opossum	16
Puma	9
Spotted Skunk	8
Badger	2
Total	**18174**

Figure 3

Number of Individual Cameras Visited by Each Species by Distance Category



Camera Distance from Trail

Species Richness

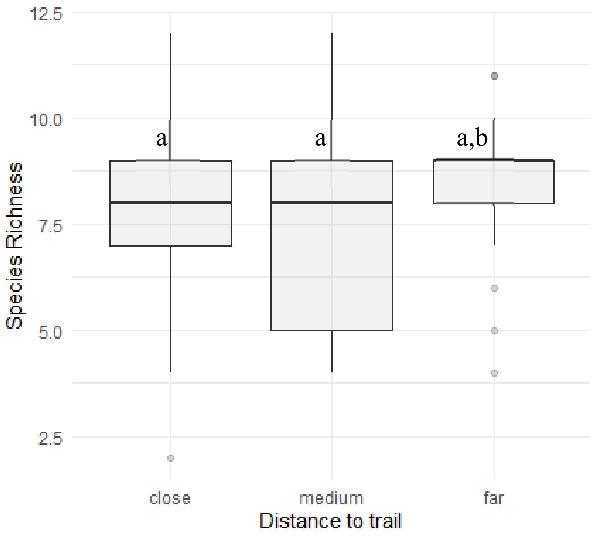
The average species richness and SE across all six seasons was 7.93 ± 0.42, 7.30 ± 0.48, and 8.39 ± 0.31 for close, medium, and far-distance cameras, respectively. Regarding distance from trail, average species richness differed between far and medium-distance cameras, with greater richness on far-distance cameras (z(442) = 3.02, p = 0.0072). Species richness recorded on close and far-distance cameras did not differ (Figure 4).

Visitation Frequency

Analysis of VF for camera site distance from trail showed that mule deer, gray fox, and jackrabbit were found significantly more often on cameras close to trails compared to medium and far-distance cameras (Table 5; Table 6). This pattern was similar for bobcat (Figure 5). Sonoma chipmunk VF was significantly greater for close-distance cameras

Figure 4

Mean Species Richness by Distance Category



Note. Boxes marked with the same lowercase letter are not significantly different from each other, while boxes marked with different letters are significantly different (GZLM; P < 0.05).

compared to medium-distance cameras but not far-distance cameras. Woodrats and fox squirrels were captured more frequently on medium-distance cameras while striped skunks were captured less frequently on medium-distance cameras compared to the other two distances. Gray squirrels frequented camera traps far from trails more than close and medium-distance cameras. Species that showed no difference in VF between trail distances were coyote, brush rabbit, and raccoon.

Percent Daytime Activity

While mule deer, bobcat and jackrabbits were, overall, found most often on cameras close to trails, the PDA (compared to all activity) showed that these three species, which are primarily diurnal or crepuscular, were found on cameras closest to trails during the day only

Table 5

Mean Visitation Frequency and Mean Percent Daytime Activity for Each Distance Category

	Mean Visitation Frequency (±SE)			Mean % daytime activity (±SE)		
Species	**Close**	**Medium**	**Far**	**Close**	**Medium**	**Far**
Diurnal & Crepuscular						
Mule deer	60.86 ± 12.43	28.54 ± 8.20	14.50 ± 3.73	0.28 ± 0.032	0.44 ± 0.052	0.51 ± 0.031
Coyote	1.46 ± 0.21	1.086 ± 0.19	1.15 ± 0.14	0.44 ± 0.063	0.50 ± 0.068	0.58 ± 0.050
Bobcat	1.37 ± 0.19	0.70 ± 0.094	0.83 ± 0.088	0.34 ± 0.055	0.41 ± 0.067	0.57 ± 0.060
Sonoma Chipmunk	0.13 ± 0.034	0.51 ± 0.17	0.290 ± 0.084	0.99 ± 0.010	0.94 ± 0.039	0.99 ± 0.009
Gray Squirrel	5.48 ± 0.99	5.84 ± 1.59	8.54 ± 2.31	0.96 ± 0.013	0.91 ± 0.061	0.97 ± 0.006
Fox Squirrel	0.063 ± 0.037	0.29 ± 0.19	0.032 ± 0.016	0.80 ± 0.20	1.0 ± 0.0050	0.80 ± 20
Jackrabbit	4.27 ± 1.74	0.72 ± 0.62	0.047 ± 0.028	0.25 ± 0.089	0.57 ± 0.207	0.24 ± 0.245
Brush Rabbit	0.67 ± 0.22	0.63 ± 0.25	1.12 ± 0.91	0.33 ± 0.135	0.46 ± 0.112	0.42 ± 0.17
Nocturnal						
Gray Fox[a]	6.99 ± 1.45	2.32 ± 0.72	1.82 ± 0.25	0.09 ± 0.021	0.2 ± 0.058	0.17 ± 0.022
Raccoon	2.70 ± 0.45	2.025 ± 0.47	2.55 ± 0.39	0.04 ± 0.011	0.14 ± 0.063	0.08 ± 0.016
Woodrat	0.74 ± 0.24	2.58 ± 0.96	0.71 ± 0.18	0.06 ± 0.059	0.01 ± 0.005	0.02 ± 0.013
Striped Skunk	0.68 ± 0.27	0.23 ± 0.060	0.64 ± 0.12	0.07 ± 0.062	0	0.07 ± 0.025
Spotted Skunk	0	0	0.055 ± 0.029	NA	NA	0
Virginia Opossum	0	0.009 ± 0.009	0.10 ± 0.034	NA	0	0
Puma	0.067 ± 0.024	0	0	0	NA	NA
Badger	0.019 ± 0.014	0	0	0	NA	NA

Note. For VF, 0 means there were no camera detections. For PDA, 0 means that all camera visitations occurred at night and NA means there were no camera visitations. The lower the PDA below 50%, the less likely animals were to be photographed during the day and, thus, were more active at night. The greater the PDA above 50%, the more likely the species was to be photographed during the day. [a]Gray foxes are both nocturnal and crepuscular.

Table 6

Results from Best-fit Models for Visitation Frequency in Response to Distance from Trail

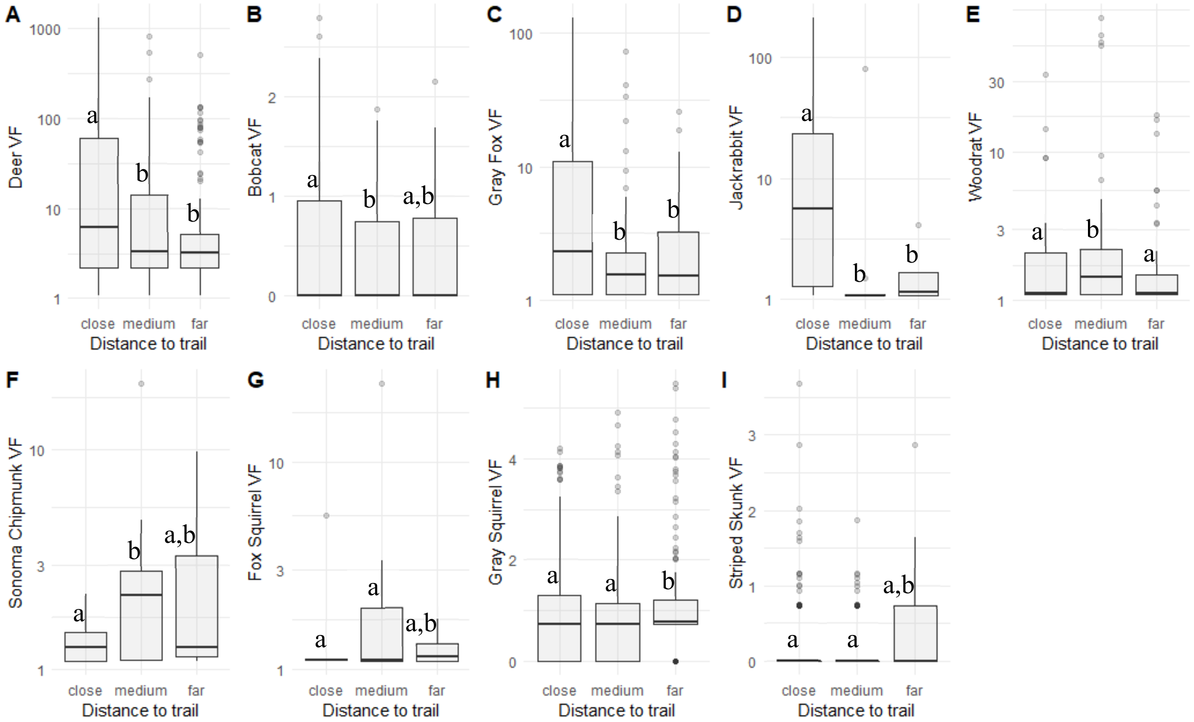
	Test statistic			**P value**		
Species (test stat)	Close-Far	Close-Medium	Far-Medium	Close-Far	Close-Medium	Far-Medium
Mule deer (z)	9.68	7.60	-1.50	<0.0001**	<0.0001**	0.2928
Coyote (t)	0.076	0.820	0.532	1.0	0.69	0.86
Bobcat (z)	2.12	2.42	0.42	0.085	0.042*	0.91
Gray Fox (z)	9.20	7.16	-1.97	<0.0001**	<0.0001**	0.12
Woodrat (z)	0.082	-4.89	-4.91	0.996	<0.0001**	<0.0001**
Sonoma Chipmunk (z)	-1.88	-2.49	-0.47	0.14	0.034*	0.88
Jackrabbit (z)	4.82	3.94	-2.24	<0.0001**	0.0002**	0.065
Brush Rabbit (z)	-0.48	0.50	0.82	0.88	0.87	0.69
Raccoon (z)	0.53	1.87	1.54	0.86	0.15	0.28
Gray Squirrel (z)	-6.24	-0.90	4.25	<0.0001**	0.64	0.0001**
Fox Squirrel (z)	0.89	-2.01	-2.38	0.64	0.11	0.046*
Striped Skunk (z)	0.22	1.86	2.45	0.97	0.15	0.038*

Note. Whether the test statistic is a t-value or z-value, depending on the best-fit model, is indicated in the species column. Season was added as a covariate. Spotted skunk, opossum, puma, and badger did not have enough observations for statistical analysis. **p < .05, ** p < .01

28%, 34% and 25% of the daytime, respectively (Table 5). Thus, these species were avoiding near-trail spaces during the day and using them mostly at night (Table 7; Figure 6). Mule deer also showed significantly more nocturnal activity on medium-distance cameras compared to far-distance cameras. Jackrabbit was significantly more diurnal on medium-distance cameras, with similar PDA on close and far-distance cameras. Though primarily a nocturnal and crepuscular species, gray fox temporal behavior matched those of mule deer, bobcat, and jackrabbit with significantly more nocturnal detections on close-distance cameras compared to medium and far-distance sites. Camera detections for the four rare species, Virginia opossum, puma, American badger, and spotted skunk, were all at night.

Figure 5

Mean Species Visitation Frequency by Distance Category



Note. Boxplots of species visitation frequencies per camera distance for all species with significant results. Plots A – D are for species that were more common close to trails, plots E – G were more common on medium-distance cameras, and species for plots H and I preferred sites far from trails. The y-axis is log10 scaled for improved visualization. Boxes marked with the same lowercase letter are not significantly different from each other, while boxes marked with different letters are significantly different (GZLM; $P < 0.05$).

Mountain Biking and Hiking

Species Richness

Species richness did not differ between trails with high mountain biking levels versus those with low levels ($z(27) = 0.48$, $p = 0.63$). Species richness was also not significant between camera sites with high or low levels of hiking ($z(27) = 0.53$, $p = 0.60$).

Table 7

Results from PDA in Response to Camera Distance

Species	Z value			P value		
	Close-Far	Close-Medium	Far-Medium	Close-Far	Close-Medium	Far-Medium
Diurnal & Crepuscular						
Mule deer[a]	-8.64	-1.54	6.02	<.0001**	0.27	<.0001*
Coyote	-1.78	-1.08	0.45	0.18	0.53	0.90
Bobcat	-2.67	-1.70	0.68	0.021**	0.21	0.77
Sonoma Chipmunk[a]	0.39	0.82	1.25	0.92	0.69	0.43
Gray Squirrel	-0.084	0.13	0.24	1.0	0.99	0.97
Fox Squirrel	0.72	-1.14	-1.69	0.75	0.49	0.21
Jackrabbit[a]	-0.84	-6.59	-1.22	0.68	<0.001**	0.44
Brush Rabbit[a]	0.42	-0.74	-1.03	0.91	0.74	0.56
Nocturnal						
Gray Fox[a]	-5.67	-3.56	1.65	<0.0001**	0.0011**	0.22
Raccoon	0.039	-2.067	-2.12	1.0	0.097	0.087
Woodrat	-0.79	1.26	1.88	0.71	0.42	0.15
Striped Skunk	-1.13	0.008	0.008	0.50	1.0	1.0

Note. [a]Tested with a quasi-binomial family link instead of binomial due to overdispersion. Spotted skunk, opossum, puma, and badger did not occur on enough cameras for statistical analysis. Season was added as a covariate. ** $p < .01$

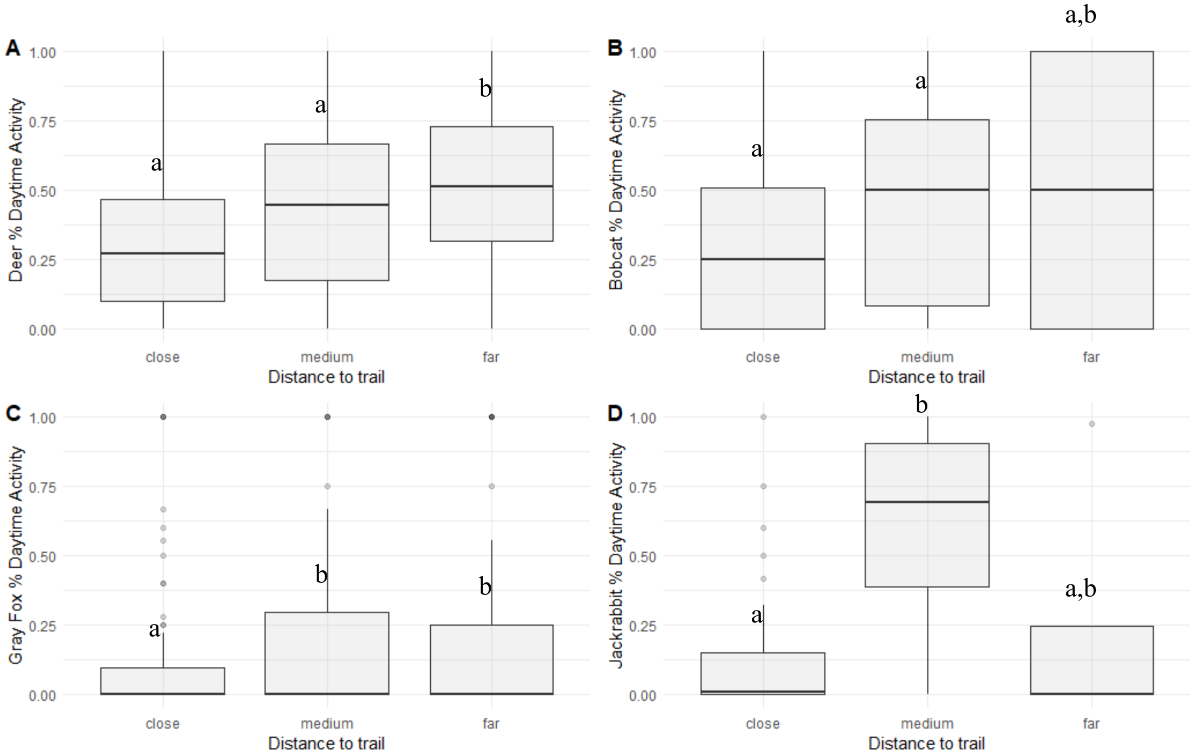
Visitation Frequency

Analysis of cameras close to trails showed that woodrat, gray squirrel, and striped skunk VF was significantly higher near trails with high levels of hiking over trails with low-hiking levels (Table 8). While not statistically significant, mean VF for mule deer, gray fox, and jackrabbit were noticeably higher on cameras near trails with high-hiking levels than low-hiking levels.

The opposite pattern was found for levels of biking on trails near close-distance cameras. Mule deer, gray fox, jackrabbit, brush rabbit, and striped skunk were found more often near trails with low levels of biking versus high-biking trails (Table 9). No species were detected significantly more frequently on cameras near high-biking trails than low-biking trails.

Figure 6

Mean Species PDA by Distance Category



Note. A-Mule deer, B-bobcat, and C-gray fox were all more nocturnal on close-distance cameras and more diurnal on far-distance cameras. D-Jackrabbit had more diurnal camera visitations on medium-distance cameras. Significance is denoted with letters above each box. Boxes marked with the same lowercase letter are not significantly different from each other, while boxes marked with different letters are significantly different (GZLM; $P < 0.05$).

Table 8

Results for Species VF in Response to Hiking Level on Close-Distance Cameras

Species	High hike use mean (±SE)	Low hike use mean (±SE)	Z value	P value
Mule deer	65.32 ± 37.42	49.38 ± 24.21	-0.49	0.624
Coyote (t)	1.61 ± 0.39	1.26 ± 0.36	-0.638	0.529
Bobcat	1.33 ± 0.32	1.27 ± 0.32	0.395	0.693
Grey fox	7.94 ± 4.18	5.28 ± 3.39	-0.342	0.733
Woodrat	1.1 ± 0.44	0.38 ± 0.16	-4.249	2.148e-5**
Sonoma Chipmunk	0.23 ± 0.08	0.04 ± 0.04	-16.626	0.894
Jackrabbit	6.11 ± 5.53	1.55 ± 1.37	-0.996	0.319
Brush Rabbit	1.01 ± 0.59	0.21 ± 0.12	-1.760	0.0783
Raccoon	2.23 ± 0.58	3.03 ± 1.65	0.452	0.652
Gray Squirrel	7.68 ± 3.32	2.96 ± 1.51	-7.267	3.669e-13**
Fox squirrel	0.10 ± 0.60	0.042 ± 0.030	-0.59	0.55
Striped skunk	0.77 ± 0.52	0.46 ± 0.26	-3.073	0.00212**
Spotted skunk	0	0	NA	NA
Virginia Opossum	0	0	NA	NA
Puma	0.09 ± 0.04	0.04 ± 0.04	NA	NA
Badger	0.03 ± 0.02	0	NA	NA

Note. Coyote hurdle model produced a t-value, all other species results include z-values. ** p < .01

Table 9

Results for Species VF in Response to Level of Mountain Biking on Close-Distance Cameras

Species	High bike use mean (SE)	Low bike use mean (SE)	Z value	P value
Mule deer	14.32 ± 7.83	77.11 ± 31.36	7.168	<0.001**
Coyote	1.52 ± 0.33	1.41 ± 0.35	0.322 (t)	0.75
Bobcat	1.61 ± 0.49	1.16 ± 0.24	-0.465	0.642
Grey fox	5.23 ± 2.27	7.29 ± 3.78	3.475	0.000511**
Woodrat	0.78 ± 0.47	0.74 ± 0.30	-2.261	0.7706
Sonoma Chipmunk	0.25 ± 0.11	0.089 ± 0.046	-0.921	0.357
Jackrabbit	0.65 ± 0.33	5.37 ± 4.22	1.975	0.0483*
Brush Rabbit	0.39 ± 0.33	0.73 ± 0.44	2.128	0.0334*
Raccoon	2.029 ± 0.73	2.88 ± 1.18	0.630	.0529
Gray Squirrel	6.52 ± 4.49	4.90 ± 1.93	-0.438	0.662
Fox Squirrel	0.17 ± 0.15	0.030 ± 0.021	0.15	0.88
Striped skunk	0.17 ± 0.10	0.83 ± 0.42	2.004	0.0450*
Spotted skunk	0	0	NA	NA
Virginia Opossum	0	0	NA	NA
Puma	0.086 ± 0.063	0.053 ± 0.032	NA	NA
Badger	0	0.025 ± 0.018	NA	NA

Note. Coyote hurdle model produced a t-value, all other species results include z-values. *p< .05, ** p < .01

Discussion

This study investigated the relationship between recreation and the spatial and temporal distribution of common mammals in the San Francisco Bay Area. It showed that species differed in their responses to trail proximity and amount of mountain biking and hiking on trails. Unlike other research regarding natural resources management, this study incorporated data from a social fitness app. Additionally, most research on mammal responses to recreation combines all trail activities; this study provided data specifically on bike versus hike impacts to mammals. Finally, most research focuses on large species and carnivores such as deer and coyote, while little is known about trail impacts on smaller species, such as skunks and rodents.

On Mount Tamalpais, mule deer, bobcats, gray foxes, and jackrabbits all showed a statistically significant preference for camera sites close to trails. They select to travel on or near man-made trails more often than habitat not adjacent to trails. In similar camera trap studies, Kays et al. (2017) and Bandak et al. (2020) found a positive relationship between bobcats and trail proximity. In addition, research on road and trail use by mammals has documented the importance of trails as least-cost corridors for travel, foraging, and territory marking for larger species, especially carnivores (Hill et al., 2021). No other studies in nearby ecoregions included jackrabbits in their analysis on recreation impacts.

While also detected on close-distance cameras, Sonoma chipmunks, fox squirrels, and woodrats were more commonly found on medium-distance camera sites while gray squirrels, striped skunks, and brush rabbits frequented far-distance cameras sites most often. Some rodents such as squirrels and chipmunks habituate to humans in both rural and urban parks

(Williams, 2002). The fact that these species are not frequenting close-distance sites suggests Mount Tamalpais does not have issues with visitors feeding squirrels and chipmunks that other parks experience (Williams, 2002). Given that bobcats and other predators were preferencing close-distance camera sites, these smaller mammals may be avoiding close-distance sites to avoid predators.

Species that had no significant difference in presence between the three trail-distance categories were coyotes, brush rabbits, and raccoons, all three of which are common in urban areas. Two studies in the eastern US, however, found coyotes prefer sites on trails (Bandak et al., 2020; Kays et al., 2017). This difference could be due to other environmental, community-level, or land management factors not present on Mount Tamalpais, that cause coyotes to favor trails in those regions.

In addition to being detected on close-distance cameras more often, deer, bobcats, and jackrabbits, which are primarily diurnal or crepuscular species, were using close-distance sites mostly at night compared to medium and far-distance sites. Though mostly nocturnal and crepuscular, gray foxes were also using close-distance sites more at night than farther sites. Thus, these four species were changing their behavior to avoid trails during the day, which is when most people are hiking and biking. Temporal shifts in response to trail distance and proximity to human activity have been documented in numerous other studies (Bandak et al., 2020; Coppes et al., 2017; George & Crooks, 2006; Lewis et al., 2021; Uetrecht, 2021; Wang et al., 2015). Bandak et al. (2020) saw shifts toward nocturnality in deer, bobcats, and red foxes in New York. Wang et al. (2015), studying mammals in the nearby Santa Cruz Mountains, on the other hand, did not see a temporal shift by gray foxes between cameras sites with high and low human presence. This may be because they focused more on distance from development than specifically trails.

Other species, such as the diurnal Sonoma chipmunks, gray squirrels, and fox squirrels were very abundant at all three camera locations during the day. As noted earlier, their ability to habituate to humans may make them more tolerant to trail disturbance (Martin & Réale, 2008; Williams, 2002). Or perhaps as prey species, their ability to hide from predators and humans gives them enough protection to not warrant shifting to nocturnality when more predators are active. The nocturnal species—woodrats, striped skunks, and raccoons—were active at all locations mostly at night. Nocturnal species do not encounter humans as often, and it is expected that they would not alter their behavior near trails which have less human use at night.

The buffers used to define trail distance categories in this study (< 30 m, ≥ 30 m and < 100 m, and ≥ 100 m) are like the trail-distance categories used in other camera trap studies and help define the buffer of human disturbance around trails for different species. Bobcats were both more common during the night and visited sites within 30 m of trails most often compared to far-distance sites. Bandak et al. (2020) and Kays et al. (2017) found the same pattern with bobcats on their on-trail cameras compared to their 150 m and 200 m far-distance cameras, respectively. Given this, managers can assume at least a 100 m buffer of disturbance around trails during the daytime for bobcats on Mount Tamalpais. This same buffer applies for the other species either avoiding close-distance sites, or using those sites more at nighttime than sites farther from trails.

A key objective of this research was to ascertain whether mountain biking, as a recreational activity, might be affecting the spatial and temporal distributions of mammals, and whether these distributions are different for hiking. Analysis of mountain bike data from Strava Metro—which provides an index of activity levels—indicated that mule deer, gray foxes, jackrabbits, brush rabbits, and striped skunks all preferred trail sites with a lower level of mountain bikers compared to trails with greater numbers of mountain bikers. Similar species responses were seen by Taylor and Knight (2003) and Scholten et al. (2018) who found deer and brush rabbit activity drop in areas with mountain biking. Lewis et al. (2021) combined their mountain biking and hiking data and found brush rabbit occupancy was also less on trails with more biking, but found deer, gray fox, and striped skunk occupancies were not impacted by combined recreation in Colorado.

Species in this study that showed no camera site preference regarding mountain biker activity were coyotes, raccoons, woodrats, and bobcats. George and Crooks (2006) and Reilly et al. (2017) were unable to find any relationships between these species and mountain biking, except for bobcat which was negatively associated with level of mountain biking for George and Crooks (2006). In fact, a larger-scale study of recreation impacts on mammals throughout the Bay Area, including near Mount Tamalpais, found zero relationships between species and all trail activity (Reilly et al., 2017). This may be attributed to different statistical approaches, the use of occupancy versus VF for spatial analysis, and shorter camera deployments (Reilly et al., 2017). Some species—Sonoma chipmunk, gray squirrel, and fox squirrel—appeared more often near high-bike trails compared to low-bike ones, but this effect was not significant nor seen in past research.

Research has shown mammals to flush from bikers or avoid trails with mountain biking (Scholten et al., 2018; Taylor & Knight, 2003). Literature suggests mountain biking is stressful to wildlife because it is fast and unpredictable and species perceive mountain biking in the same way as motorized recreation (George & Crooks, 2006; Naidoo & Burton, 2020; Taylor & Knight, 2003). Most hiking and mountain biking occur during the day, so nocturnal species such as grey foxes and striped skunks who encounter park visitors less frequently may avoid high-bike trails for other reasons. These could include impacts of biking on trails such as the quality of trail, soil erosion, vegetation, loss of canopy cover, and trail width (Marzano & Dandy, 2012; Taylor & Knight, 2003).

With respect to high and low levels of hiking, most species showed a response opposite to that of mountain biking. Woodrats, gray squirrels, and striped skunks preferred close-distance sites with more hikers than sites near trails with less hiking. Though not statistically significant, deer, gray foxes, jackrabbits, and brush rabbits showed a similar pattern. As with mountain biking, coyotes, bobcats, and raccoons in addition to fox squirrels were neutral to the level of hiking at close-distance sites. However, as noted earlier, many species were using the trails more at night than during the day when people were present. Why some species preferred trails more heavily used by hikers is not clear. Past research has not found this trend of preferring trails with greater levels of hiking activity, but a lot of research including in the Bay Area have found species occupancy and frequency to not differ between combined hiking and biking activity for brush rabbits, deer, gray foxes, striped skunks, and other species (George & Crooks, 2006; Larson et al., 2020; Lewis et al., 2021; Reilly et al., 2017)

The four rare species that did not have enough detections for analysis were puma, badger, spotted skunk, and Virginia opossum. The few photos taken of pumas and badgers were all at night and only on man-made trails. Pumas occurred on three trails with low-bike activity and two trails with high-bike activity, and badgers only occurred on trails with low-bike activity. Of the five puma camera trap events, only one occurred on a low-hike trail. Both badger camera events occurred on high-hike trails. The few spotted skunk photos taken were only on far-distance cameras, which is expected given the cryptic nature of this rare species. Finally, Virginia opossums, commonly found in urban areas, were only seen on far and medium-distance cameras away from human activity.

Species richness was highest on cameras farthest from trail disturbance, and second highest on cameras close to trails. On average, far-distance cameras had about one more mammal species than medium-distance cameras, and about half a species more than close-distance cameras. One more species on far-distance cameras could indicate a biological significance in species richness on cameras without trail disturbance. Species richness may have been higher on close-distance cameras than medium-distance cameras because many species were shown to prioritize trails, especially at night. These species may be utilizing trails when park visitors are absent, and then retreating to areas far from trails during the day, with medium-distance areas acting as a transition zone between far and close areas. When looking at just cameras close to trails, the average species richness was about the same regardless of the level of mountain biking or hiking on the nearest trail.

Recommendations

Future Research

This study used existing datasets which limited the type of analysis and number of camera sites. Future research on trail impacts in the Mount Tamalpais region or similar study areas would benefit from focused methodology, such as cameras set equidistant from trails. Strava Metro is a great resource for recreational data, but having more trail-facing cameras or trail counters than were available in this study can determine direct data on trail use and can show how reliably Strava user data predicts trail activity in the given study area.

Deer and rabbits serve as high frequency indicator species (Cheyne et al., 2016; Hanley, 1996). These indicator species displayed an ecologically important preference for low-use over high-use mountain biking areas and an increase in nocturnality closer to trails. However, future research can help narrow down other variables at play such as trail quality and width. Another gap in research is defining species-specific response buffers to recreation disturbance for mammals. Finally, acoustic detectors could be paired with trail-facing cameras to see if mammals respond to the loudness of hikers more or less than mountain bikers and other recreation activities.

Management Recommendations

Based on the findings of this study and similar literature, land managers should consider trophic-level interaction impacts caused from temporal shift. In this study, many mammals were not as responsive to recreation at camera sites of 100 m or more. Within 30 m of trails that had a higher level of mountain biking, species occurred less frequently, and diurnal species were more nocturnal than at far-distance camera sites. Until species-specific response buffers are defined, managers should consider a general buffer of 100 m around high-use trails as compromised habitat taken out of use during daytime hours. Finally, this study showed that trails are an important resource for medium and large-sized mammals, and considerations for wildlife use of trails should be given in trail and recreation management.

References

Angulo, E., Boulay, R., Ruano, F., Tinaut, A., & Cerdá, X. (2016). Anthropogenic impacts in protected areas: Assessing the efficiency of conservation efforts using Mediterranean ant communities. *PeerJ*, *4*, Article e2773. https://doi.org/10.7717/peerj.2773

Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M., & Manica, A. (2015). Walk on the wild side: Estimating the global magnitude of visits to protected areas. *PLOS Biology*, *13*(2), Article e1002074. https://doi.org/10.1371/journal.pbio.1002074

Bandak, S., Sarno, R., Peterson, M., Farkas, D., & Grigione, M. (2020). Active humans, inactive carnivores, and hiking trails within a suburban preserve. *Suburban Sustainability*, *6*(1), Article 1. https://doi.org/10.5038/2164-0866.6.1.1032

Barja, I., Silván, G., Martínez-Fernández, L., & Illera, J. C. (2011). Physiological stress responses, fecal marking behavior, and reproduction in wild European pine martens (Martes martes). *Journal of Chemical Ecology*, *37*(3), 253–259. http://dx.doi.org.libaccess.sjlibrary.org/10.1007/s10886-011-9928-1

Bowker, J. M., Askew, A. E., Cordell, H. K., Betz, C. J., Zarnoch, S. J., & Seymour, L. (2012). *Outdoor recreation participation in the United States - Projections to 2060: A technical document supporting the Forest Service 2010 RPA assessment* (Gen. Tech. Rep. SRS-160). U.S. Department of Agriculture Forest Service, Southern Research Station. https://doi.org/10.2737/SRS-GTR-160

Brauer, C. J., & Beheregaray, L. B. (2020). Recent and rapid anthropogenic habitat fragmentation increases extinction risk for freshwater biodiversity. *Evolutionary Applications*, *13*(10), 2857–2869. https://doi.org/10.1111/eva.13128

Breeze, J., & Vendetti, M. (2014, January 7). *Mountain biking history.* Marin Museum of Bicycling. https://mmbhof.org/mtn-bike-hall-of-fame/history/

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685. https://doi.org/10.1111/1365-2664.12432

California State Parks. (2017). *Statistical report: 2016-17 fiscal year*. Planning, Recreation and Support Section Marketing and Business Development Office. https://www.parks.ca.gov/pages/795/files/16-17%20Statistical%20Report%20FINAL%20for%20web.pdf

Cassirer, E. F., Freddy, D. J., & Ables, E. D. (1992). Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin (1973-2006)*, *20*(4), 375–381. https://www.jstor.org/stable/3783054?seq=1

Cheyne, S. M., Sastramidjaja, W. J., Muhalir, Rayadin, Y., & Macdonald, D. W. (2016). Mammalian communities as indicators of disturbance across Indonesian Borneo. *Global Ecology and Conservation*, *7*, 157–173. https://doi.org/10.1016/j.gecco.2016.06.002

Clark, M., Wilkins, E. J., Dagan, D. T., Powell, R., Sharp, R. L., & Hillis, V. (2019). Bringing forecasting into the future: Using Google to predict visitation in U.S. national parks. *Journal of Environmental Management*, *243*, 88–94. https://doi.org/10.1016/j.jenvman.2019.05.006

Coppes, J., Burghardt, F., Hagen, R., Suchant, R., & Braunisch, V. (2017). Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). *PLoS One*, *12*(5), Article e0175134. https://doi.org/10.1371/journal.pone.0175134

Crawley, M. J. (2012). *The R book*. Wiley.

Deringer, S. A., Hanley, A. W., Hodges, J. S., & Griffin, L. K. (2020). Improving ecological behavior in outdoor recreation through mindfulness interventions: A mixed methods inquiry. *Journal of Outdoor Recreation, Education and Leadership*, *12*(2), 149–164. https://doi.org/10.18666/JOREL-2020-V12-I2-9802

Edson, E., Farrell, S., Fish, A., Gardali, T., Klein, J., Kuhn, W., Merkle, W., O'Herron, M., & Williams, A. (2016). *Measuring the health of a mountain: A report on Mount Tamalpais natural resources*. One Tam. https://www.onetam.org/media/pdfs/peak-health-white-paper-2016.pdf

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

George, S. L., & Crooks, K. R. (2006). Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, *133*(1), 107–117. https://doi.org/10.1016/j.biocon.2006.05.024

Hanley, T. A. (1996). Potential role of deer (Cervidae) as ecological indicators of forest management. *Forest Ecology and Management*, *88*(1), 199–204. https://doi.org/10.1016/S0378-1127(96)03803-0

Hill, J. E., DeVault, T. L., & Belant, J. L. (2021). A review of ecological factors promoting road use by mammals. *Mammal Review*, *51*(2), 214–227. https://doi.org/10.1111/mam.12222

International Union for Conservation of Nature. (2021). *Protected planet report 2020*. Retrieved November 8, 2022, from https://livereport.protectedplanet.net

Jones, K. R., Venter, O., Fuller, R. A., Allan, J. R., Maxwell, S. L., Negret, P. J., & Watson, J. E. M. (2018). One-third of global protected land is under intense human pressure. *Science*, *360*(6390), 788–791. https://doi.org/10.1126/science.aap9565

Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas? *Journal of Applied Ecology*, *54*(1), 242–252. https://doi.org/10.1111/1365-2664.12700

Larson, C. L., Reed, S. E., & Crooks, K. R. (2020). Increased hiking and mountain biking are associated with declines in urban mammal activity. *California Fish and Wildlife Journal Special Issue*, *2020*, 52–61. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=178952&inline

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS One*, *11*(12), Article e0167259. https://doi.org/10.1371/journal.pone.0167259

Lawson, M. (2022, September 16). *Economic impact of National Parks*. Headwaters Economics. https://headwaterseconomics.org/public-lands/protected-lands/economic-impact-of-national-parks/

Lee, K., & Sener, I. N. (2021). Strava Metro data for bicycle monitoring: A literature review. *Transport Reviews*, *41*(1), 27–47. https://doi.org/10.1080/01441647.2020.1798558

Lee, K., & Sener, I. N. (2019). Understanding Potential Exposure of Bicyclists on Roadways to Traffic-Related Air Pollution: Findings from El Paso, Texas, Using Strava Metro Data. *International Journal of Environmental Research and Public Health*, *16*(3), 371. https://doi.org/10.3390/ijerph16030371

Lewis, J. S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A. R., VandeWoude, S., & Crooks, K. R. (2021). Human activity influences wildlife populations and activity patterns: Implications for spatial and temporal refuges. *Ecosphere*, *12*(5), Article e03487. https://doi.org/10.1002/ecs2.3487

Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, Tamias striatus. *Animal Behaviour*, *75*(1), 309–318. https://doi.org/10.1016/j.anbehav.2007.05.026

Marzano, M., & Dandy, N. (2012). Recreationist behaviour in forests and the disturbance of wildlife. *Biodiversity and Conservation*, *21*(11), 2967–2986. https://doi.org/10.1007/s10531-012-0350-y

Mitrovich, M., Larson, C. L., Bar, K., Beck, M., & Unger, R. (2020). Balancing conservation and recreation. *California Fish and Wildlife Journal Special Issue*, *2020*, 11–27. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=178948&inline

Mols, B., Lambers, E., Cromsigt, J. P. G. M., Kuijper, D. P. J., & Smit, C. (2022). Recreation and hunting differentially affect deer behaviour and sapling performance. *Oikos*, *2022*(1), Article e08488. https://doi.org/10.1111/oik.08448

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–859. https://doi.org/10.1038/35002501

Naidoo, R., & Burton, A. C. (2020). Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. *Conservation Science and Practice*, *2*(10), Article e271. https://doi.org/10.1111/csp2.271

National Park Service. (2020). *Welcome to visitor use statistics*. NPS Stats. https://irma.nps.gov/STATS/

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., & Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Newcomb, T. (2020). Amid cycling surge, sport of mountain biking is seeing increased sales and trail usage. *Forbes.* https://www.forbes.com/sites/timnewcomb/2020/07/13/amidst-cycling-surge-sport-of-mountain-biking-seeing-increased-sales-trail-usage/

Ngo, T. H. D. (2016). *Generalized linear models for non-normal data* (Paper No. 8380-2016). SAS Global.

Nichols, J. D., Bailey, L. L., O'Connell, A. F., Talancy, N. W., Grant, E. H. C., Gilbert, A. T., Annand, E. M., Husband, T. P., & Hines, J. E. (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, *45*(5), 1321–1329.

Oberosler, V., Groff, C., Iemma, A., Pedrini, P., & Rovero, F. (2017). The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mammalian Biology*, *87*, 50–61. https://doi.org/10.1016/j.mambio.2017.05.005

O'Brien, T. G., Baillie, J. E. M., Krueger, L., & Cuke, M. (2010). The wildlife picture index: Monitoring top trophic levels. *Animal Conservation*, *13*(4), 335–343. https://doi.org/10.1111/j.1469-1795.2010.00357.x

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., Haas, C. D., Harris, S., Hathaway, S. A., Turschak, G. M., Miles, A. K., & Van Vuren, D. H. (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy*, *91*(6), 1322–1331. https://doi.org/10.1644/09-MAMM-A-312.1

Papouchis, C. M., Singer, F. J., & Sloan, W. B. (2001). Responses of desert bighorn sheep to increased human recreation. *The Journal of Wildlife Management*, *65*(3), 573–582. https://doi.org/10.2307/3803110

Phillips, G. E., & Alldredge, A. W. (2000). Reproductive success of elk following disturbance by humans during calving season. *The Journal of Wildlife Management*, *64*(2), 521–530. https://doi.org/10.2307/3803250

R Core Team. (2021). *R: A language and environment for statistical computing*. R foundation for Statistical Computing. https://www.R-project.org/

Reed, S. E., & Merenlender, A. M. (2008). Quiet, nonconsumptive recreation reduces protected area effectiveness: Quiet recreation in protected areas. *Conservation Letters*, *1*(3), 146–154. https://doi.org/10.1111/j.1755-263X.2008.00019.x

Reed, S. E., & Merenlender, A. M. (2011). Effects of management of domestic dogs and recreation on carnivores in protected areas in Northern California: Managing dogs in protected areas. *Conservation Biology*, *25*(3), 504–513. https://doi.org/10.1111/j.1523-1739.2010.01641.x

Reilly, M. L., Tobler, M. W., Sonderegger, D. L., & Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biological Conservation*, *207*, 117–126. https://doi.org/10.1016/j.biocon.2016.11.003

Robb, D. (2017, November 1). *Building the global heatmap.* Strava-Engineering. https://medium.com/strava-engineering/the-global-heatmap-now-6x-hotter-23fc01d301de

Rodrigues, A. S. L, Akcakaya, H. R., Andelman, S. J., Bakarr, M. I., Boitani, L, & Brooks, T. M. (2004). Global gap analysis: Priority regions for expanding the global protected-area network. *BioScience*, *54*(12), 1092–1100.

Scholten, J., Moe, S. R., & Hegland, S. J. (2018). Red deer (*Cervus elaphus*) avoid mountain biking trails. *European Journal of Wildlife Research*, *64*(1), Article 8. https://doi.org/10.1007/s10344-018-1169-y

Strava Metro. (2020). *Frequently asked questions*. https://metro.strava.com/faq

Sun, Y., Du, Y., Wang, Y., & Zhuang, L. (2017). Examining associations of environmental characteristics with recreational cycling behaviour by street-level Strava data.

International Journal of Environmental Research and Public Health, *14*(6), Article 644. https://doi.org/10.3390/ijerph14060644

Taylor, A. R., & Knight, R. L. (2003). Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications*, *13*(4), 951–963.

TEAM Network. (2011). *Terrestrial vertebrate protocol implementation manual* (v. 3.1). Tropical Ecology, Assessment and Monitoring Network.

Thompson, B. (2015). Recreational trails reduce the density of ground-dwelling birds in protected areas. *Environmental Management*, *55*(5), 1181–1190. https://doi.org/10.1007/s00267-015-0458-4

Townsend, S. E. (2018). *The Marin wildlife picture index project: Diversity, occupancy and trends in biodiversity Fall 2014 – Summer 2017*. One Tam.

Townsend, S. E., Hammerich, S., & Halbur, M. (2020). Wildlife occupancy and trail use before and after a park opens to the public. *California Fish and Wildlife Journal Special Issue*, *2020*, 74–94. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=178955&inline

Uetrecht, M. R. (2021). *Mammals respond differently to human recreation* [Master's thesis, University of California, Los Angeles]. UCLA eScholarship. https://escholarship.org/uc/item/4vd2b852

U.S. Census Bureau. (2019). *U.S. Census Bureau quickfacts: San Francisco County, California*. https://www.census.gov/quickfacts/sanfranciscocountycalifornia

U.S. Department of the Interior. (2019). *National parks visitation.* Office of Congressional and Legislative Affairs. https://www.doi.gov/ocl/national-parks-visitation

Venables, W. N. & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation*, *190*, 23–33. https://doi.org/10.1016/j.biocon.2015.05.007

White, E. M., Bowker, J. M., Askew, A. E., Langner, L. L., Arnold, J. R., & English, B. K. (2014). *Federal outdoor recreation trends: Effects on economic opportunities*. U.S. Forest Service. https://www.fs.fed.us/research/docs/outdoor-recreation/ficor_2014_rec_trends_economic_opportunities.pdf

Whitfield, G. P., Ussery, E., Riordan, B., & Wendel, A. (2016). Association between user-generated commuting data and population-representative active commuting surveillance data—Four Cities, 2014–2015. *Morbidity and Mortality Weekly Report, 65*(36), 959-962. https://doi.org/10.15585/mmwr.mm6536a4

Williams, D. (2002). Conspicuous consumption. *National Parks*, *76*(3/4), 40-42.

Wisdom, M. J., Preisler, H. K., Naylor, L. M., Anthony, R. G., Johnson, B. K., & Rowland, M. M. (2018). Elk responses to trail-based recreation on public forests. *Forest Ecology and Management, 411*, 223–233. https://doi.org/10.1016/j.foreco.2018.01.032

Wittemyer, G., Elsen, P., Bean, W. T., Burton, A. C. O., & Brashares, J. S. (2008). Accelerated human population growth at protected area edges. *Science*, *321*(5885), 123–126. https://doi.org/10.1126/science.1158900

Zeileis, A., & Kleiber, C. (2022). *_countreg: Count Data Regression_. R package version 0.2-1*. R-Forge. https://R-Forge.R-project.org/projects/countreg/

Appendix A

Species and Status

Table 10

Taxonomy and Conservation Status of Species in Study Area

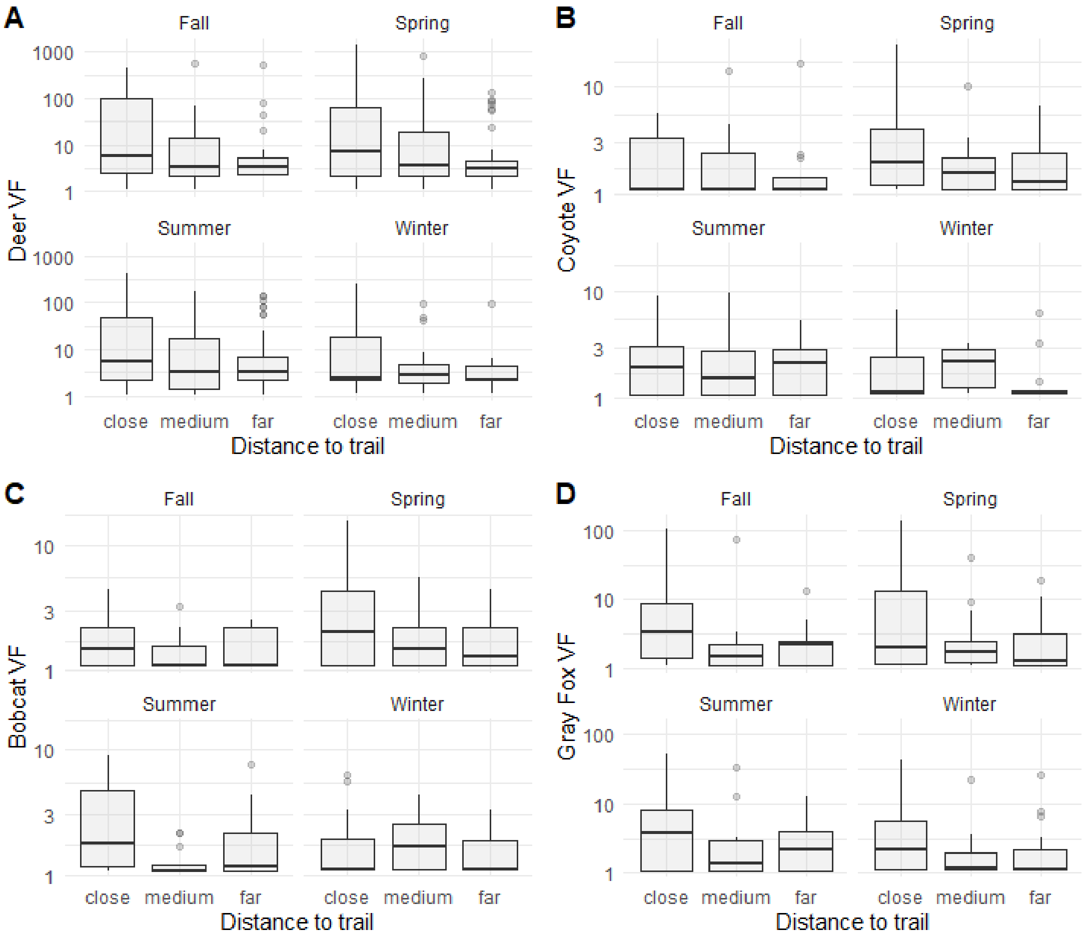
Taxon	Common Name	Species	Conservation Status
Marsupilia	Virginia opossum	*Didelphis virginiana*	Non-native
Carnivora	Grey fox	*Urocyon cinereoargenteus*	No status
Carnivora	Coyote	*Canis lattrans*	No status
Carnivora	Striped skunk	*Mephitus mephitus*	No status
Carnivora	Western spotted skunk	*Spilogale gracilis*	No status
Carnivora	American badger	*Taxidea taxus*	Species of special concern
Carnivora	Bobcat	*Lynx rufus*	No status
Carnivora	Puma	*Puma concolor*	Specially protected species
Procyonidea	Raccoon	*Procyon lotor*	No status
Artiodactyla	Black-tailed mule deer	*Odocoileus hemionus*	No status
Rodentia	Dusky-footed woodrat	*Neotoma fuscipes*	No status
Rodentia	Sonoma chipmunk	*Tamias sonomae*	Endemic
Rodentia	Gray squirrel	*Sciurus griseus*	No status
Rodentia	Fox squirrel	*Sciurus niger*	Non-native
Lagomorpha	Black-tailed jackrabbit	*Lepus californicus*	No status
Lagomorpha	Brush rabbit	*Sylvilagus bachmani*	No status

Appendix B

Seasonal Distributions by Distance Category

Figure 7

Trends in Visitation Frequencies by Season



Note. A) Visitation frequency of mule deer on close, medium, and far cameras has same trend in each season, with greater mule deer VF medians and distributions on close cameras, followed by medium and far cameras. B) Visitation frequency of coyote on close, medium, and far cameras has same trend in each season, with similar VF distributions in each season. C) Visitation frequency of bobcat on close, medium, and far cameras has a similar trend in each season except for winter, with higher VF on close cameras in fall, spring, and summer. Winter has a higher mean VF on medium cameras. D) Visitation frequency of gray fox on close, medium, and far cameras has a similar trend in each season, with higher VF on close cameras then medium or far cameras.

Appendix C

Best-fit Generalized Linear Model Comparisons

Table 11

Model Comparison for Response of Species Richness to Distance from Trail

Variable	Model	Log(Lhood)	ΔAIC	W	Res. dev
Species Richness	Poisson	-980.653	0	0.72	518.32
	Negative-Binomial	-980.584	1.93	0.28	506.31
	Quasi-Poisson	NA	NA	NA	518.32

Note. Dispersion parameter was equal to one, indicating no overdispersion and confirming Poisson as the best fit model. Residual df = 442.

Table 12

Model Comparison for Response of Species VF to Distance from Trail

Species	Model	Log (Lhood)	ΔAIC	W	Res. dev
Mule Deer	Negative binomial	-6626.013	0	1	2245
	Zero-inflated (Poisson)	-17619.824	22011.62	<0.001	36177
	Hurdle-Poisson	-17624.866	22021.70	<0.001	36177
	Poisson	-18754.923	24255.70	<0.001	36177
	Quasi-Poisson	NA	NA	NA	36177
Coyote	Hurdle-Poisson	-568.487	0	0.971	661.22
	Zero-inflated (Poisson)	-572.029	7.08	0.028	661.22
	Poisson	-588.126	13.16	<0.001	661.22
	Quasi-Poisson	NA	NA	NA	661.22
	Negative binomial	-2367.385	3573.80	<0.001	1764.6
Bobcat	Zero-inflated (neg bin)	-507.458	0	0.9987	1775.3
	Poisson	-527.140	11.00	0.0013	582.69
	Quasi-Poisson	NA	NA	NA	582.69
	Hurdle-Poisson	-526.290	35.42	<0.001	582.69
	Negative binomial	-2220.399	3399.64	<0.001	1775.3
Gray Fox	Zero-inflated (Poisson)	-1765.563	0	1	3357.7
	Hurdle-Poisson	-1773.166	15.21	<0.001	3357.7
	Poisson	-2018.775	480.30	<0.001	3357.7
	Quasi-Poisson	NA	NA	NA	3357.7
	Negative binomial	-3537.626	3520.13	<0.001	1780.2
Woodrat	Zero-inflated (Poisson)	-843.107	0	1	1831.6
	Hurdle-Poisson	-850.520	14.83	<0.001	1831.6
	Poisson	-1073.883	435.33	<0.001	1831.6
	Quasi-Poisson	NA	NA	NA	1831.6
	Negative binomial	-2044.662	2379.11	<0.001	1225.6

Species	Model	Log (Lhood)	ΔAIC	W	Res. dev
Sonoma Chipmunk	Zero-inflated (Poisson)	-222.113	0	0.220	391.57
	Hurdle-Poisson	-224.594	4.96	0.018	391.57
	Poisson	-261.683	53.02	<0.001	391.57
	Quasi-Poisson	NA	NA	NA	391.57
	Negative binomial	-980.663	1493.10	<0.001	752.21
Jackrabbit	Zero-inflated (Poisson)	-726.599	0	0.73	3224.1
	Hurdle-Poisson	-727.610	2.02	0.27	3224.1
	Negative binomial	-996.749	516.30	<0.001	437.1
	Poisson	-1675.651	1871.98	<0.001	3224.1
	Quasi-Poisson	NA	NA	NA	3224.1
Brush Rabbit	Zero-inflated (neg bin)	-264.377	0	1	622.27
	Hurdle-Poisson	-436.777	396.56	<0.001	1636.16
	Poisson	-890.272	1223.43	<0.001	1636.16
	Quasi-Poisson	NA	NA	NA	1636.16
	Negative Binomial	-1127.156	1699.32	<0.001	622.27
Raccoon	Zero-inflated (Poisson)	-1147.797	0	<0.001	1909.5
	Hurdle-Poisson	-1169.760	43.93	<0.001	1909.5
	Poisson	-1286.274	250.83	<0.001	1909.5
	Quasi-Poisson	NA	NA	NA	1909.5
	Negative binomial	-3408.337	4497.08	<0.001	1808.1
Gray Squirrel	Zero-inflated (Poisson)	-3676.163	0	1	7713.6
	Hurdle-Poisson	-3687.893	23.46	<0.001	7713.6
	Poisson	-4252.866	1127.29	<0.001	7713.6
	Quasi-Poisson	NA	NA	NA	7713.6
	Negative binomial	-4332.564	1288.80	<0.001	1884.6
Striped Skunk	Zero-inflated (neg bin)	-311.022	0	1	1106.38
	Hurdle-Poisson	-342.958	61.63	<0.001	653.82
	Poisson	-440.325	230.24	<0.001	653.82
	Quasi-Poisson	NA	NA	NA	653.82
	Negative binomial	-1474.739	2301.19	<0.001	1106.38
Fox Squirrel	Zero-inflated (Poisson)	-111.30	0	0.75	287.42
	Hurdle-Poisson	-112.397	2.19	0.25	287.42
	Poisson	-166.37	97.60	<0.001	287.42
	Quasi-Poisson	NA	NA	NA	287.42
	Negative binomial	-439.68	646.29	<0.001	282.23

Note. Comparing GZLM models Poisson, quasi-Poisson, negative binomial, hurdle (Poisson), and either zero-inflated with a Poisson or negative binomial link depending on which was more compatible with the data. Quasi-Poisson models do not generate a log(likelihood) or AIC, so if Poisson was rated best fit but theta was > 1.10 indicating overdispersion, quasi-Poisson was chosen. Residual df = 442

Table 13

Model Comparison for Response of Species Richness to Hiking Level

	Model	Log(Lhood)	ΔAIC	W	Res. dev
Species Richness	Poisson*	-66.037	0	0.73	19.555
	Quasi-Poisson				19.555
	Negative-Binomial	-66.037	2.5	0.27	19.554

Note. Dispersion parameter was equal to one, indicating no overdispersion and confirming Poisson as the best fit model. Residual df = 27.

Table 14

Model Comparison for Response of Species Richness to Mountain Biking Level

	Model	Log(Lhood)	ΔAIC	W	Res. dev
Species Richness	Poisson*	-66.062	0	0.73	19.604
	Quasi-Poisson				19.604
	Negative-Binomial	-66.062	2.5	0.27	19.604

Note. Dispersion parameter was equal to one, indicating no overdispersion and confirming Poisson as the best fit model. Residual df = 27.

Table 15

Model Comparison for Response of Species VF to Hiking Level

Species	Model	Log(Lhood)	ΔAIC	W	Res. dev
Mule Deer	Negative binomial	-1013.043	0	1	227.2
	Poisson	-8497.545	14966.51	<0.001	16837.9
	Quasi-Poisson				16867.9
Coyote	Quasi-Poisson				
	Poisson	-114.213	0	1	135.84
	Negative binomial	-475.526	725.12	<0.001	171.37
Bobcat	Zero-inflated (neg bin)	-74.395	0	1	200.5
	Zero-inflated (Poisson)	-83.841	15.95	<0.001	125.3
	Hurdle-Poisson	-83.947	16.16	<0.001	125.3
	Poisson	-100.566	44.19	<0.001	125.3
	Quasi-Poisson		770.05		125.3
	Negative binomial	-432.245		<0.001	200.5
Gray Fox	Zero-inflated (neg bin)	-114.698	0	1	209.58
	Negative binomial	-687.737	1140.43	<0.001	209.58
	Hurdle-Poisson	-988.325	1744.31	<0.001	1917.14
	Zero-inflated (Poisson)	-988.325	1744.31	<0.001	1917.14
	Poisson	-1011.859	1786.17	<0.001	1917.14
	Quasi-Poisson				1917.14
Woodrat	Zero-inflated (neg bin)	-56.839	0	1	172.25
	Zero-inflated (Poisson)	-73.736	30.85	<0.001	169.25
	Hurdle-Poisson	-74.665	32.71	<0.001	169.25
	Poisson	-110.507	99.19	<0.001	169.25
	Quasi-Poisson				169.25
	Negative binomial	-358.957	598.59	<0.001	172.25
Sonoma Chipmunk	Zero-inflated (Poisson)	-24.488	0	0.43	35.244
	Hurdle-Poisson	-24.817	0.66	0.31	35.244
	Poisson	-27.896	1.61	0.10	35.244
	Quasi-Poisson				35.244
	Zero-inflated (neg bin)	-24.488	2.94	0.16	122.643
	Negative binomial	-159.151	266.62	<0.001	122.643
Jackrabbit	Zero-inflated (neg bin)	-57.931	0	1	115.85
	Negative binomial	-349.166	576.82	<0.001	115.85
	Zero-inflated (Poisson)	-600.901	1083.00	<0.001	2253.61
	Hurdle-Poisson	-600.901	1083.00	<0.001	2253.61
	Poisson	-1146.526	2169.04	<0.001	2253.61
	Quasi-Poisson				2253.61

Species	Model	Log(Lhood)	ΔAIC	W	Res. dev
Brush Rabbit	Zero-inflated (neg bin)	-47.122	0	1	131.03
	Zero-inflated (Poisson)	-86.291	75.39	<0.001	224.3
	Hurdle-Poisson	-86.541	75.89	<0.001	224.3
	Poisson	-129.454	156.52	<0.001	224.3
	Quasi-Poison				224.43
	Negative Binomial	-286.015	472.14	<0.001	131.03
Raccoon	Zero-inflated (neg bin)	-97.156	0	1	200.19
	Zero-inflated (Poisson)	-253.513	309.77	<0.001	452.92
	Hurdle-Poisson	-253.520	309.79	<0.001	452.92
	Poisson	-275.068	347.68	<0.001	452.92
	Quasi-Poisson				452.92
	Negative binomial	-585.995	972.03	<0.001	200.19
Gray Squirrel	Zero-inflated (Poisson)	-575.545	0	0.5	1173.15
	Hurdle-Poisson	-575.545	0	0.5	1173.15
	Poisson	-634.391	112.49	<0.001	1173.15
	Quasi-Poisson				1173.15
	Negative binomial	-639.338	124.88	<0.001	202.49
Striped Skunk	Zero-inflated (Poisson)	-114.597	0	0.57	242.50
	Hurdle-Poisson	-114.871	0.55	0.43	242.50
	Poisson	-143.658	52.92	<0.001	242.50
	Quasi-Poisson				242.50
	Negative binomial	-346.536	461.17	<0.001	161.67
Fox Squirrel	Zero-inflated (Poisson)	-18.028	0	0.39	38.64
	Hurdle-Poisson	-18.37	0.68	0.28	38.64
	Zero-inflated (neg bin)	-17.17	1.23	0.34	66.14
	Poisson	-24.37	7.47	0.005	38.64
	Quasi-Poisson				38.64
	Negative binomial	-106.56	174.36	<0.001	66.14

Note. Comparison of GZLM models Poisson, quasi-Poisson, negative binomial, hurdle (Poisson), and zero-inflated with either a Poisson or negative binomial link depending on which was more compatible with the species data. Quasi-Poisson models do not generate a log(likelihood) or AIC, so if Poisson was rated best fit but theta was > 1.10 indicating overdispersion, quasi-Poisson was chosen. Mule deer and coyote VF's were not zero-inflated so hurdle and zero-inflated models were not included in those comparisons. Residual df = 27.

Table 16

Model Comparison for Response of Species VF Mountain Biking Level

Species	Model	Log(Lhood)	ΔAIC	W	Res. dev
Mule Deer	Negative binomial	-995.449	0	1	221.9
	Poisson	-7463.634	12933.87	<0.001	14770.1
	Quasi-Poisson				14770.1
Coyote	Quasi-Poisson				138.11
	Poisson	-115.347	0	1	138.11
	Negative binomial	-475.382	722.57	<0.001	171.30
Bobcat	Zero-inflated (neg bin)	-74.149	0	1	200.33
	Zero-inflated (Poisson)	-83.804	16.37	<0.001	126.24
	Hurdle-Poisson	-83.886	16.53	<0.001	126.24
	Poisson	-101.038	45.63	<0.001	126.24
	Quasi-Poisson		771.76		126.24
	Negative binomial	-462.855		<0.001	200.33
Gray Fox	Negative binomial	-682.719	0	1	208.04
	Hurdle-Poisson	-970.065	577.40	<0.001	1855.31
	Zero-inflated (Poisson)	-970.065	577.40	<0.001	1855.31
	Poisson	-980.943	593.95	<0.001	1855.31
	Quasi-Poisson				1855.31
Woodrat	Zero-inflated (neg bin)	-62.028	0	1	171.53
	Zero-inflated (Poisson)	-100.171	73.34	<0.001	201.24
	Hurdle-Poisson	-100.336	73.67	<0.001	201.24
	Poisson	-126.500	120.80	<0.001	201.24
	Quasi-Poisson				201.24
	Negative binomial	-370.395	611.08	<0.001	171.53
Sonoma Chipmunk	Zero-inflated (Poisson)	-26.336	0	0.430	39.925
	Hurdle-Poisson	-26.552	0.43	0.347	39.925
	Poisson	-30.237	2.60	0.064	39.925
	Quasi-Poisson				39.925
	Zero-inflated (neg bin)	-26.336	2.94	0.158	123.561
	Negative binomial	-168.072	280.76	<0.001	123.561
Jackrabbit	Zero-inflated (neg bin)	-57.287	0	1	116.2
	Negative binomial	-344.602	568.98	<0.001	116.2
	Hurdle-Poisson	-627.853	1138.19	<0.001	2167.7
	Zero-inflated (Poisson)	-627.858	1138.20	<0.001	2167.7
	Poisson	-1103.573	2084.42	<0.001	2167.7
	Quasi-Poisson				2167.7
Brush Rabbit	Zero-inflated (neg bin)	-47.114	0	1	130.95
	Zero-inflated (Poisson)	-86.283	75.40	<0.001	228.92
	Hurdle-Poisson	-86.329	75.49	<0.001	228.92
	Poisson	-131.697	161.02	<0.001	228.92
	Quasi-Poison				228.92
	Negative Binomial	-283.767	467.66	<0.001	130.95
Raccoon	Zero-inflated (neg bin)	-97.108	0	1	199.99
	Zero-inflated (Poisson)	-251.517	305.88	<0.001	446.96
	Hurdle-Poisson	-251.521	305.89	<0.001	446.96
	Poisson	-272.089	341.81	<0.001	446.96
	Quasi-Poisson				446.96
	Negative binomial	-583.912	967.86	<0.001	199.99

Species	Model	Log(Lhood)	ΔAIC	W	Res. dev
Gray Squirrel	Zero-inflated (neg bin)	-107.062	0	1	202.91
	Zero-inflated (Poisson)	-598.780	980.49	<0.001	1230.48
	Hurdle-Poisson	-598.780	980.49	<0.001	1230.48
	Negative binomial	-641.771	1063.77	<0.001	202.91
	Poisson	-663.058	1103.84	<0.001	1230.48
	Quasi-Poisson				1230.48
Striped Skunk	Zero-inflated (neg bin)	-54.700	0	1	160.57
	Zero-inflated (Poisson)	-114.683	117.03	<0.001	223.29
	Hurdle-Poisson	-114.791	117.24	<0.001	223.29
	Poisson	-134.052	150.56	<0.001	223.29
	Quasi-Poisson				223.29
	Negative binomial	-337.340	559.63	<0.001	160.57
Fox Squirrel	Zero-inflated (Poisson)	-17.65	0	0.38	34.23
	Hurdle-Poisson	-18.01	0.71	0.26	34.23
	Zero-inflated (neg bin)	-16.78	1.19	0.33	68.671
	Poisson	-22.16	3.82	0.03	34.23
	Quasi-Poisson				34.23
	Negative binomial	-103.13	168.25	<0.001	68.671

Note. Comparison of GZLM models Poisson, quasi-Poisson, negative binomial, hurdle (Poisson), and zero-inflated with either a Poisson or negative binomial link depending on which was more compatible with the species data. Quasi-Poisson models do not generate a log(likelihood) or AIC, so if Poisson was rated best fit but theta was > 1.10 indicating overdispersion, quasi-Poisson was chosen. Mule deer and coyote VF's were not zero-inflated so hurdle and zero-inflated models were not included in those comparisons. Residual df = 27.