TREE SQUIRRELS AND FISHERS IN NORTHERN CALIFORNIA: THE EFFECTS OF MASTING HARDWOODS ON STAND USE

By

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ABSTRACT

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In western North America, tree squirrels such as western gray (*Sciurus griseus*) and Douglas squirrels (*Tamiasciurus douglasii*) are potentially important prey for fishers (*Pekania pennanti*). Western gray squirrels in particular may be highly ranked due to their large body size. Masting trees including black oak (*Quercus kelloggii*) and tanoak (*Notholithocarpus densiflorus*) produce an important food source for tree squirrels; therefore, forest stands containing these trees may be useful to foraging fishers. I hypothesized that; 1) the abundance of western gray and Douglas squirrels in a stand is influenced by the mast production capacity of that stand, and 2) fisher stand use is influenced by the tree squirrel abundance in a stand. I deployed remote cameras for 44 weeks in 2017 in 85 forest stands dominated by compositions of conifer, or co-dominant with conifers and tanoak or black oak in the northern Sierra Nevada Mountains of California. I predicted that; 1) forest stands with the greatest capacity for mast production would have the highest probability of occupancy and detection of tree squirrels; 2) stands with the highest occupancy and detection of tree squirrels would have the highest probability of fisher occupancy and detection, and 3) fisher stand use and detection would be conditional on the western gray squirrel occupancy status of that stand. I tested the effects of stand type and other covariates on tree squirrel and fisher occupancy and detection using single-species occupancy models, and tested the effect of gray squirrel presence on fisher occupancy and detection probability using two-species co-occurrence models. Douglas squirrels occupied most sites (psi = 0.96-1.0) irrespective of stand type. Gray squirrels and fishers had highest rates of occupancy (psi = 0.86, $\Psi = 0.93$) and detection ($p = 0.28$, $p = 0.13$) in tanoak co-dominant stands. Fisher stand use patterns suggested both conditional and unconditional occupancy with western gray squirrels, and model-averaged occupancy estimates were highest in tanoak co-dominant stands regardless of whether gray squirrels were present (psi = 0.95) or absent (psi = 0.97). The results of this study indicate that habitats containing masting trees such tanoak may support greater numbers of western gray squirrels than other habitats, and retention of these trees across the landscape may improve foraging habitat for fishers.

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INTRODUCTION

Habitat selection is an important aspect of behavioral ecology, landscape management, and species conservation. Definitions and analytical techniques, however, vary widely (Garshelis 2000, Lele et al. 2013). Morris (2003) outlined a broadly applicable and useful definition of habitat selection as: “the process whereby individuals preferentially use, or occupy, a non-random set of available habitats”. The inclusion of “non-random” is significant because it implies that animals use habitats in some way that can be predicted or explained. Researchers have long agreed that animals select particular habitats to increase fitness (Fretwell and Lucas 1969, Holt 1985, Morris 1988, Pullium 1988). Different factors influence whether a particular habitat will have positive or negative effects on fitness, including the presence/absence of predators and competing species (Hallett et al. 1983, DeCesare et al. 2013, Buxton and Sperry 2017, Bylak 2018), landscape attributes and characteristics (Newbold and MacMahon 2014, Abouelezz et al. 2018, Fourcade et al. 2018), and habitat fragmentation or alteration caused by human development (Ordeñana et al. 2010, Erb et al. 2012, Pearse et al. 2017) or natural disturbances (Jones et al. 2001, Kortmann et al. 2018). All of these mechanisms can impact habitat selection in various ways depending on the spatial and temporal scale at which selection is occurring (Mayor et al. 2009, McGarigal et al. 2016). Habitat selection by predatory species, such as carnivores, is additionally influenced by the availability and distribution of prey (Castillo et al. 2012, Bled et al. 2015, Wolff et al. 2015). The bestinformed predictions about carnivore habitat use should therefore include some measure of prey availability.

Herbivorous and granivorous species, which are commonly consumed by carnivores, are tied to food resources that do not move independently on the landscape but are stationary when available. Stationary food resources create a “spatial anchor” (Sih 2005), or an association to particular habitat conditions that provide the resources need to optimize fitness. Carnivores may frequent those habitat patches of high resource value to their prey to increase hunting success, an idea sometimes referred to as the prey-habitat hypothesis (Mitchell and Lima 2002). This habitat selection strategy has largely been studied in mammalian carnivores that tend to target only one or a few prey species, such as lynx (*Lynx canadensis*) and wolves (*Canis lupus*) (Simmons-Legaard et al. 2013, Kittle et al. 2017, Roffler et al. 2018). This selection approach, however, may also be employed by generalist carnivores with a more diverse prey base, particularly if certain prey species are metabolically more efficient to hunt and kill and have differential availability across the landscape. Researchers and manager need to better understand the relationship between prey abundance and predator habitat use. Understanding which habitat metrics affect prey availability is critically important for the proper management of carnivores, especially those those that face potential population declines due to anthropogenic or natural disturbance. Here I test hypotheses concerning factors that drive prey habitat use for fishers (*Pekania pennanti*) in North America.

The fisher is a mid-sized mammalian carnivore in the family *Mustelidae* whose range extends throughout forests of Canada and the northern U.S. (Powell 1993). The fisher’s current range in North America has contracted considerably post-European settlement, and currently in the western U.S., fishers exist in fragmented populations in areas of Montana, Idaho, Oregon, Washington, and California (Lofroth et al. 2010). Reintroduction efforts have occurred in British Columbia, Washington, Oregon, and California to re-establish fisher populations in historically inhabited regions on the West Coast (Weir 1995, Aubry and Lewis 2003, Callas and Figura 2008, USDI National Parks Service 2008). In their western range, fishers are generally found in low- to mid-elevation coastal and interior mountainous forests containing medium-to large-sized, primarily conifer trees with varying amounts of hardwoods (Grinnell et al. 1937, Hagmeier 1956, Buskirk and Zielinksi 2003, Davis et al. 2007, Spencer et al. 2011).

Extensive habitat suitability modeling has been conducted for fishers across western North America (Raley et al. 2012). Variables commonly shared by these different models include canopy cover, tree diameter at breast height (DBH), and the presence of hardwood tree species (Powell 1993, Carroll et al. 1999, Carroll et al. 2001, Weir and Harestad 2003, Zielinski et al. 2004(a), Zielinski et al. 2006). Habitat suitability models predicted, and field data confirmed, that suitable fisher habitats have a minimum average canopy cover of 60 to 75%, a minimum average tree DBH of 28 to 38 cm, and multi-storied or structurally diverse canopies (Allen 1983, Thomasma et al. 1991, Davis et al. 2007, Zielinski et al. 2010, Facka 2016). Researchers agree that the presence of hardwoods is an integral component of suitable fisher habitat throughout their range (Buskirk and Powell 1994, Powell and Zielinski 1994, Weir and Harestad 2003, Zielinski et al. 2004b, Purcell et al. 2009). Fisher occurrence is positively associated with the proportion of hardwoods in a landscape (Carroll et al. 1999, Davis et al. 2007). A proportion of 24 to 50% hardwoods is considered suitable for fishers, above which habitat quality begins to decline (Allen 1983, Thomasma 1991, Zielinski et al. 2010). Fishers use tree cavities for denning and resting (Powell 1993, Weir et al. 2012), and often select cavities in hardwood species for these purposes (Mazzoni 2002, Zielinski et al. 2004a, Lofroth 2010, Raley et al. 2012, Thompson et al. 2015). Hardwoods may also be significant to fishers because they are an important habitat component for many of their preferred prey species.

The fisher is an opportunistic predator that most commonly consumes mammalian prey (Stevens 1968, Powell 1977, Brown and Will 1979, Grenfell and Fasenfest 1979, Arthur et al. 1989). When attainable, large-bodied carrion, such as from ungulates, is a preferred food source because it requires only the energy of searching for the carcass and provides large amounts of digestible energy for consumption (Clem 1977, Kelly 1977, Powell 1979, 1981, 1993). The metabolized efficiency of prey items is dependent on the amount of energy expended in the search and handling of that prey and the amount of energy gained from consuming that prey (Charnov and Orians 2006). Prey items that provide a greater amount of energy gained than that expended in foraging are “ranked” higher than organisms that provide less acquired energy, require greater energy expenditure to find and capture, or some combination of the two (Charnov 1976, Pyke et al. 1977). Thus, when items such as carrion are not available, fishers will forage for lower-ranked prey that are small enough to efficiently kill, but large enough to replace the calories lost while searching and handling.

Throughout a large portion of the fisher's range, snowshoe hares (*Lepus americanus*) are a key component of fisher diets (DeVos 1951, Brander and Brooks 1973, Clem 1975, Powell 1978, 1979). Porcupine (*Erethizon dorsatum*), animals that fishers are specialized to hunt and kill (Powell 1979: 1981,1993, Powell et al. 2017), are also common prey for fishers where their populations overlap. Snowshoe hares and porcupines are absent or occur at very low densities in some parts of the fisher's range, particularly in California (Collins 1998, Appel et al. 2017). In the absence of snowshoe hares and porcupines, fishers in California must select prey items from a different suite of available species.

Diet analysis conducted on fisher populations in western North America found that while fishers will consume prey of diverse taxa, including birds, reptiles, insects, and fungi, fishers consistently show a strong selection for small mammalian prey (Zielinski et al. 1999, Zielinski and Duncan 2004, LoFroth et al. 2010). Sciurids appear to be eaten frequently by fishers in in the western portion of their range (Martin 1994, Zielinski and Duncan 2004, Weir et al. 2005, Golightly et al. 2006, Facka, unpublished data). In the southern Sierra Nevada Mountains of California, western gray squirrel (*Sciurus griseus*, hereafter gray squirrels) occurrence on camera traps overlapped with fisher occurrence on camera traps at all but 2 elevation gradients surveyed, and Douglas squirrel (*Tamiasciurus douglasii*) occurrence mirrored the occurrence of fishers at all 12 elevation gradients surveyed (Sweitzer and Furnas 2016). In the northern Sierra Nevada Mountains, gray and Douglas squirrels were the most commonly identified prey items in scat collected, with gray squirrels being the most frequently identified prey species (A.

Facka, unpublished data). Other smaller-bodied mammals, such as *Peromyscus* and *Neotoma*, that were locally abundant in the same area of the northern Sierra Nevada Mountains (Facka et al., unpublished data), were identified less frequently in the fisher scats surveyed (A. Facka, unpublished data). The results of these studies suggest that fishers are selecting tree squirrels, in the absence of larger, snowshoe hares and porcupines, and over smaller-bodied rodents.

Tree squirrels weigh more and therefore provide a higher metabolized efficiency to fishers compared to smaller mammals such as *Peromyscus* species (Davison et al. 1978, Powell 1979). Assuming a fisher spends equal amounts of energy to capture prey items, squirrels meet daily energy requirements more efficiently than mouse-sized organisms (Powell 1993). Larger prey may also be detected more readily or from farther distances, and therefore may be encountered more frequently than smaller-bodied prey species existing at the similar densities (Ware 1971). Therefore, in the absence of highly ranked food items such as carrion, snowshoe hares, and porcupines, gray and Douglas squirrels may rank as the most important prey species over smaller-bodied prey for fishers in northern California (Charnov 1976, Pyke et al. 1977).

In the Sierra Nevada Mountains, gray and Douglas squirrels are commonly found in conifer, hardwood, and mixed conifer-hardwood forests comprised of medium-to large-sized trees (Verner 1980). Hardwoods appear to be an important habitat component for tree squirrels, as they are for fishers, particularly masting species such as members of the genera *Quercus* and *Notholithocarpus*. These trees produce acorns, a major component of the gray squirrel diet (Stienecker and Browning 1970, Asserson 1974, Gurnell 1983, Foster 1992, Ryan and Carey 1995). While Douglas squirrels specialize in exploiting conifer seeds as food, acorns provide an important secondary food source (Gurnell 1983, Jackson 1983, Carey 1996, Harvey and Polite 2003, Hwang and Larivière 2006). Members of both species also eat hypogeous (truffles) and epigeous (mushrooms) fungi throughout the year (Stienecker and Browning 1970, Maser et al. 1981, Ryan and Carey 1995, Harvey and Polite 2003, Hwang and Larivière 2006). Conifer seeds and acorns are especially important during the fall and winter as they help initiate lipogenesis that will energetically support individuals through the winter months (McKeever 1964, Cross 1969, Asserson 1974, Barnum 1975, Foster 1992). Both gray and Douglas squirrels collect and cache conifer cones and acorns during the summer and fall to provide reliable food sources for winter (Asserson 1974, Harvey and Polite 2003). Gray squirrels use “scatter holes”, which are 3.8 to 5 cm deep containing individual food items that they relocate by smell, while Douglas squirrels gather food items into central locations called middens (Gurnell 1983). Abundance of seed and mast crops can vary seasonally, annually, and among different tree species (Nixon et al. 1975), so stands with diverse food sources provide more stable year-round food supplies (Gurnell 1983).

Black oak (*Quercus kelloggii*) trees contribute the most volume and have the widest distribution and elevational range of any native oak species in California (McDonald 1990). Both black oaks and tanoaks (*Notholithocarpus densiflorus*) are common hardwood masting trees in mixed conifer forests of the Sierra Nevada Mountains (McDonald 1990, Tappeiner et al. 1990). Tanoaks begin rapid production of acorns after 40 years of age, while black oaks do not start producing acorns in large quantities until the trees are 80 to 100 years old (McDonald and Tappeiner 2002). For trees of both species, DBH and crown width increase with age, larger trees have greater mast crop yields, and even-aged stands are fairly common (McDonald 1990, Tappeiner et al. 1990). Black oaks tend to have larger average DBH than tanoaks at similar ages. The average DBH of black oaks between 70 and 275 years old is 40 to 63.5 cm (McDonald 1990), while the average DBH of tanoaks between 40 and 160 years old is 25.5 to 61 cm (Tappeiner et al. 1990).

The fecundity of tanoak has been described as extraordinary (Roy 1957). Individual trees of 46 to 61 cm DBH can produce crops of 3,900 to 4,600 acorns in one season, and a single 76 cm tree was recorded producing a crop of 454 kg of acorns in one masting event (Tappeiner et al. 1990). Black oaks, by comparison, produce far fewer acorns. Trees of 58.5 to 205 cm DBH produce crops of 2 to 64 kg of acorns (McDonald 1990). The periodicity of mast crops in both species can vary widely in California, ranging from 2- to 3-year intervals (Roy 1962). Although no studies have compared directly the benefits of tanoaks versus black oaks for tree squirrels in California, tree species with higher amounts of mast likely support greater numbers of tree squirrels (here and throughout referring only to Douglas and gray squirrels). Density and abundance of *Tamiasciurus* species are most influenced by food resources; as a result, habitats with increased food supplies should support higher densities of squirrels (Sullivan and Sullivan 1982). Additionally, gray squirrels utilize acorns produced by masting trees every month of the year (Stienecker 1977), thus greater availability of acorns should support higher densities of gray squirrels. Tanoaks, even those of small size and of young age, produce greater mast crops than black oaks and, therefore, stands containing tanoaks can potentially support the greatest numbers of tree squirrels due to increased food availability.

Black oaks appear provide a vital habitat component for fishers in the Sierra Nevada Mountains, as they are one of the most commonly selected hardwood trees for denning and resting (Seglund 1995, Mazzoni 2002, Zielinski et al. 2004a, Thompson et al. 2015). In the northern Sierra Nevada Mountains, between 2010 and 2015, 42% of fisher den trees were black oaks (Powell et al. 2016). Black oaks often provide the cavities fishers require for birthing and rearing their kits. Cavities in trees are formed by primary excavators such as woodpeckers (Aubry et al. 2013), or by damage or death to part of the tree, and subsequent decay caused by fungi such as heart rot (Carey 1983, Weir et al. 2012). Cavities may be more abundant in hardwoods than conifers because hardwoods do not require a wound in the tree for fungi to enter and are less resistant to the fungal growth than conifers due to differences in resin and toxic extractive elements (Bunnell et al. 2002, Bunnell 2013). Older trees not only tend to be large but also have had a greater chance for excavation or fungal infection to occur, therefore generating suitable cavities. Black oaks may be predominantly selected as denning trees by fishers in the Sierra Nevada due to their wide range and their larger size than tanoaks (McDonald 1990, Tappeiner et al. 1990).

Fisher populations have been found to respond numerically to changing population sizes of small mammalian prey resulting from fluctuations in the mast production of hardwood trees (Jensen et al. 2012). Given enough canopy closure to support thermoregulation and protection from predators, fishers may use a wider variety of stand types when foraging compared to denning or resting (Raley et al. 2012). Diverse stands containing masting hardwoods may be especially useful for foraging fishers as they may provide access to highly ranked tree squirrel prey.

The main objective of this study was to investigate the interaction between stand type, prey, and predator. Specifically, I sought to understand how food resources influenced tree squirrel and fisher habitat selection in the northern Sierra Nevada Mountains on lands owned and managed for timber production by Sierra Pacific Industries (SPI). Using remote camera data and occupancy modeling, I explored several hypotheses and predictions. I hypothesized that the mast production capacity of a stand influences the abundance of Douglas and gray squirrels in that stand. However, monitoring the abundance of wildlife can be both costly and labor intensive. Currently, live-trapping is the most commonly used method for studying small mammals populations; however, this method often causes physiological harm and stress to animals and can fail to detect animals that are trap shy (Shonfield et al. 2013, Torre et al. 2016). Occupancy molding has recently been used as a common surrogate for abundance, especially when changes in occupancy over time are measured (Steenweg et al. 2017). There is evidence that measured estimates of the occupancy probability of a species reflect abundance (Gaston et al. 2000). Occupancy and abundance can be generalized across spatial scales, and share the same underlying distribution, or a “common currency” with one another (He and Gaston 2003). The occupancy status of a species in an area is specified explicitly by the abundance distribution of that species (Royle et al. 2005). That is to say, the true state of occupancy for a species is occurring because of the heterogenic abundance of a species in a habitat or across different habitats.

I used an occupancy framework to investigate if abundances of Douglas and gray squirrels were influenced by the mast production capacity of a stand. I predicted that the probability of occupancy and detection of squirrels would be highest in forest stands with a tanoak component. Additionally, I hypothesized that fisher stand use is influenced by the tree squirrel abundance in that stand. Again using an occupancy framework, I predicted the probability of occupancy and detection of fishers would be highest in forest stands with a tanoak component. Finally, I hypothesized that fisher stand use and detection is influenced by the tree squirrel occupancy status in that stand. If supported, I predicted that the occupancy and detection probabilities of fishers in a stand would be conditional on the occupancy and detection of squirrels in that stand.

METHODS

Study Area

My research was conducted on SPI's 648 km^2 Stirling Management District. These timber lands were roughly 32 km northeast of Chico, California within Butte, Tehama, and Plumas counties, at elevations ranging from 480 to 1,830 m (Callas and Figura 2008). The northern boundary was near Deer Creek at Highway 32, and the southern and eastern boundaries were near the North Fork Feather River. The district encompassed 5 major watersheds including: Deer Creek, Big Chico Creek, Butte Creek, the West Branch Feather River, and the North Fork Feather River (Callas and Figura 2008) (Figure 1). SPI utilized different timber harvest methods including even-aged (clear-cuts), uneven aged, shelterwood, and seed tree silviculture regeneration systems, in conjunction with pre-commercial and commercial thinning (Sierra Pacific Industries 2018). The average size for a harvest unit was 0.071 km^2 (Sierra Pacific Industries 2019).

Beginning in late 2009 through late 2011, 40 adult fishers (24 females, 16 males) were translocated from source populations in northern California to SPI timberlands in a collaborative effort between the California Department of Fish and Wildlife, the U.S. Fish and Wildlife Service, North Carolina State University, and SPI (Facka 2016, Facka et al. 2016). Released fishers were monitored using radio collars and non-invasive methods for 7 years post-reintroduction to study survival and reproduction,

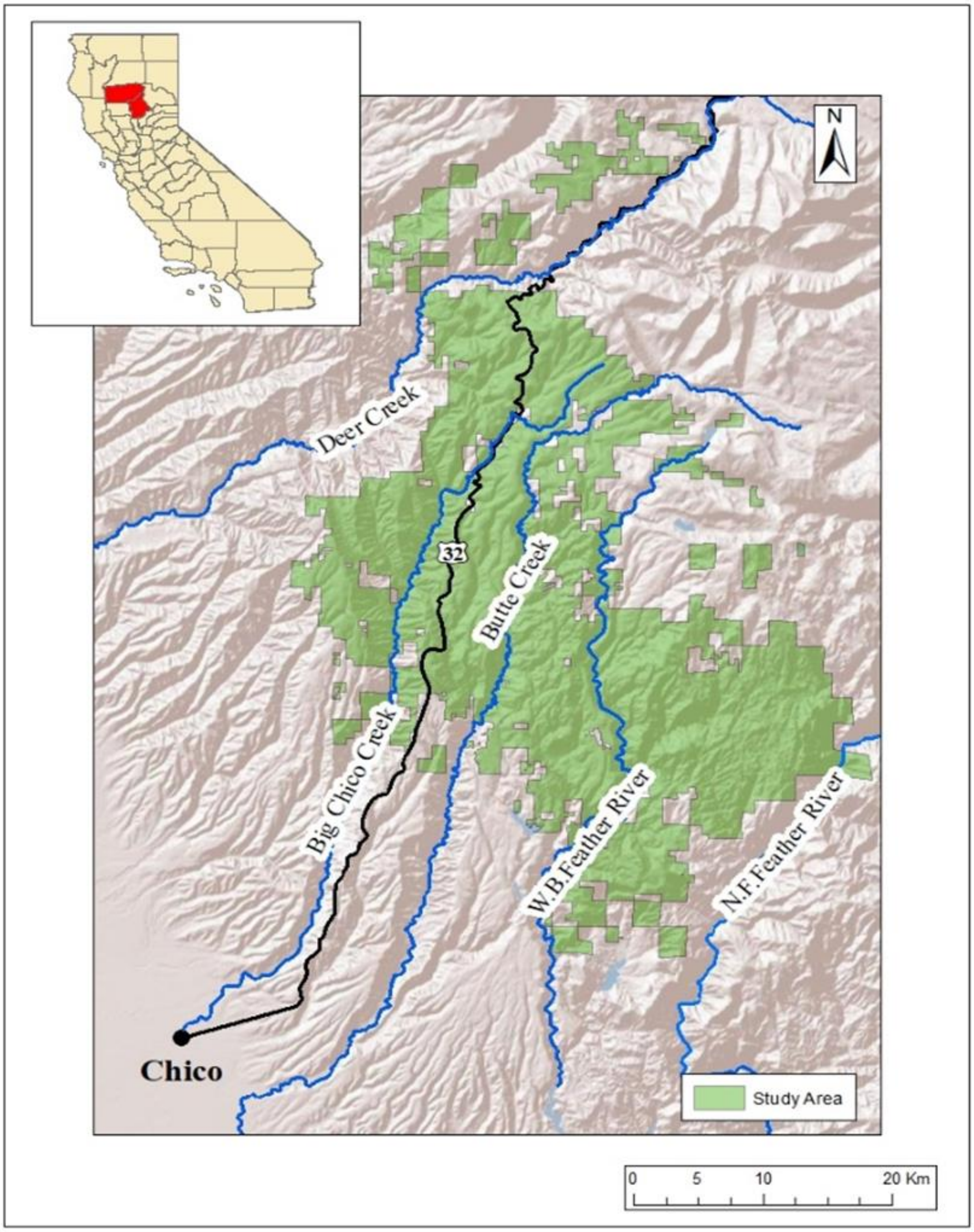

Figure 1. Study area boundary and extent of Sierra Pacific Industries Stirling Management District within Butte, Tehama, and Plumas counties of California, including major watersheds and Highway 32, where stand surveys for tree squirrels and fishers were conducted from January to November 2017.

habitat selection, diet, and effects of intensive forest management (Powell et al. 2016). All individual fishers observed in this study were descendants of the translocated population.

The climate of the study site is temperate, with roughly 85% of precipitation occurring between November and April in the form of rain and snowfall, with low levels of rainfall occurring in other months (Pandey et al. 1999). Between 1992 and 1998, the region averaged roughly 127 cm of rain per year (Department of Water Resources 2013). The study area has tree species typical of mixed conifer/hardwood forests of the Sierra Nevada Mountains at low to medium elevations. The 6 most common tree species include: Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and California black oak. Both tanoak and canyon live oak (*Quercus chrysolepis*) also occur frequently throughout the area and can often form dense stands at the same elevations (Griffin & Critchfield 1972). Due to the historic silviculture practices of the district, stand species composition and age vary across the landscape. Stand types range from single-age pine plantations to multi-aged mixed conifer and hardwood stands, wherein hardwood species composition can be mixed or single-species dominant.

Study Design

I used remote cameras to survey for tree squirrels and fishers using a systematic-random sampling design for 44 weeks from January-November 2017 (Figure 2). Sampling procedures were approved by the Humboldt State University Institutional

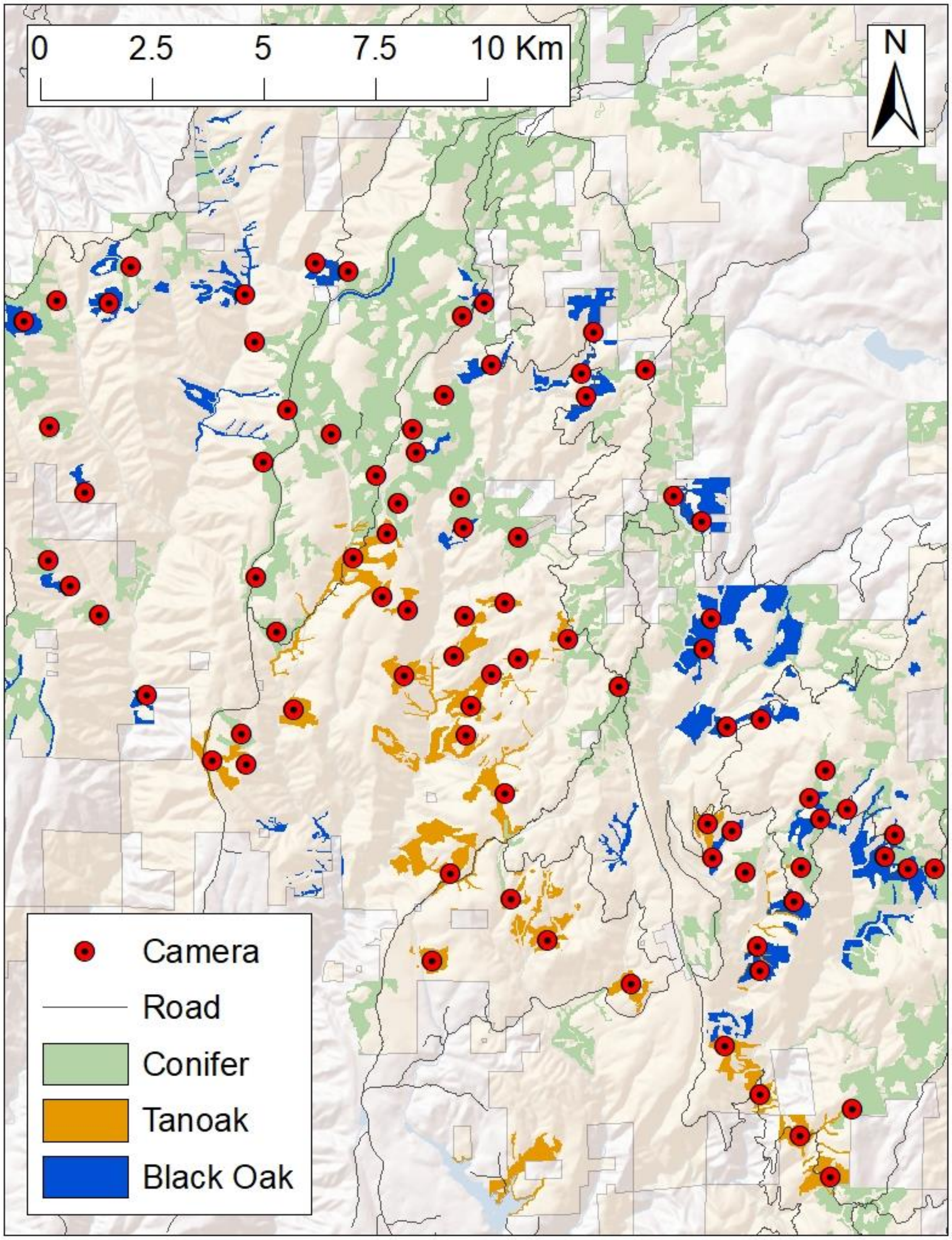

Figure 2. Remote camera sites and distribution of stands surveyed for tree squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017. Camera location circles are not to scale and have been enlarged for visibility.

Animal Care and Use Committee (protocol No. 16/17.W.52-A).

Stand Selection

I defined 3 stand types (conifer, black oak, and tanoak) based on tree species dominance determined using basal area to investigate the influence of variation in potential mast production on tree squirrel and fisher occupancy. I selected 29 stands of each type, for a total of 87 stands (Figure 2). All selected stands had to provide forest conditions found to be important for fishers in previous studies (Allen 1983, Thomasma et al. 1991, Davis et a. 2007). Each stand needed to be composed of 20 to 50% hardwoods, have a minimum average canopy cover of 60%, and be comprised of trees with a minimum average quadratic mean diameter (QMD) of 28cm. Each stand had to have a minimum area of 0.03 km^2, approximately the size of a gray squirrel home range (Cross 1969, Gilman 1986) and roughly twice the size of a Douglas squirrel home range (Koford 1982). Lastly, each stand had to contain a minimum of 1 log per 0.004 km^2. Probability of detection for both gray and Douglas squirrels in the study area were higher when the density of logs was at least 1.5 logs per 0.004 km^2 (Facka et al. unpublished data).

Conifer stands were composed of a diverse assemblage of conifer species and less than a 20% hardwood component. These stands were treated as a control for my hardwood-dominated stands. Black-oak stands were those with a mix of conifer species and a hardwood component comprised of a minimum 20% black oaks. Tanoak stands were those with a mix of conifer species and hardwood component comprised of a minimum 20% tanoak. I chose stands such that cameras were at least 500 m apart to avoid spatial autocorrelation based on the diameter of gray squirrel home ranges (Rovero et al. 2013).

I located stands that met these criteria using ArcMap version 10.4.1 (Esri, Redlands, California), with shapefiles containing forest inventory data collected and provided by SPI. These fine scale data were based on 39,871 plots that were systematically sampled by registered foresters using an angle gauge and variable plot cruising every 5 to 10 years (Facka 2016, Niblett et al. 2017). I prioritized stands that were not largely contiguous with similar forest stand types and that were isolated by different forest stand types whenever possible. The conifer dominant stands were most contiguous, and there were a few large contiguous to semi-contiguous black oak stands (Figure 2). In an attempt to maintain site independence, I only selected contiguous stands that would allow for camera locations to be separated by several roads, large ridges, ravines, or streams. I selected all black oak and tan oak stands first, then when possible selected the nearest conifer stand at least 500 m away in an attempt to pair hardwood stands with control stands. I could not achieve this paired arrangement for every stand, specifically for tanoak stands, which were the most spatially isolated stand type that met the criteria in this study area (Figure 2). I rejected some potentially appropriate stands because they were extremely difficult to reach due to limited road access or potentially dangerous terrain.

Camera and Bait Deployment, Check, and Removal

No stand was perfectly circular or square, rather they tended to be oblong or irregularly shaped (Figure 2).Given the history of silviculture on the study area, the road density was relatively high, although road use-level, quality, and access varied widely across the area. All cameras were placed between 20 to 400 m away from some kind of road, including a paved highway, graded gravel or dirt, high-clearance 4WD, and ATV access only roads.

To place cameras, I hiked as close to the center of the stand as possible. Next, I searched for a microsite that met these additional criteria: 1) a bait tree of at least 20 cm DBH that matched the stand type (e.g., a black oak in a black oak stand etc.); 2) a camera tree 3 to 6 m opposite the bait tree in any direction to attach the camera and to allow for a desirable camera position (e.g., not facing the sun or tall, waving vegetation); 3) a site that had no obvious signs of tree squirrel activity within visible range of the camera or bait tree (e.g., middens, stick nests, or scatter holes) so as not to bias the detection rates of the site higher than those without signs of squirrel activity.

Similar to other studies that have used cameras to survey for small mammals (Eriksson 2016, Sweitzer and Furnas 2016), I used in-shell walnuts and peanut butter as bait to attract tree squirrels. I nailed a ring of metal wire strung with 10 walnuts 1 to 1.5 m above the ground, and smeared roughly 1 cup of smooth peanut butter (Skippy Brand, Hormel Food Corporation, Austin, MN) directly onto the tree above the nail (Figure 3). I placed the camera on the camera tree such that it faced the bait, anywhere from 1 to 2 m

Figure 3. Bait scheme for remote camera stations used to survey for tree squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017.

above the ground. I secured the camera to the tree using either a Python locking cable (MasterLock Company LLC, Oak Creek, WI) or a bungee cord (Kotap). I pointed the camera such that the bait, both sides of the bait tree, and some area of the ground around the base of the bait tree were visible. I attempted to have the base of the tree and ground around it visible to detect animals that did not inspect or take any bait.

I deployed 87 remote cameras over a period of 7.5 weeks starting 25 January 2017 and ending 19 March 2017 (Table 1). The scheme and schedule of deployment was opportunistic. Snow made many of the higher-elevation sites inaccessible during early parts of the year, and some sites were inaccessible because of damage roads or were otherwise impassable. I used 4 different passive remote camera models made by 3 different remote camera manufacturers. I deployed 40 Browning Strike Force Elite HD cameras (Morgan, Utah), 23 Reconyx PC85 Professional cameras (Holeman, Wisconsin), 18 Reconyx PC800 Hyperfire Professional IR cameras (Holeman, Wisconsin), and 6 Bushnell Aggressor cameras (Overland Park, Kansas). I stratified cameras types by stand type such that each stand type had a roughly equal numbers of each camera model (Table 2). I randomly selected which camera model would be placed at each site within each stand type using a random number generator function in Microsoft Excel. I maintained the same settings for each camera throughout the entire study. To try and maximize the detection of small, fast moving animals, I set all cameras to be motion activated at the most sensitive level available, and take 3 or 5 pictures per trigger with no delay. I used 8 GB memory cards (SandDisk Ultra) in all cameras but the Reconyx PC85s, for which I used 2 GB memory cards (Transcend). The date and timestamp of each camera were set

Table 1. Timing of deployment for 87 remote cameras used to survey for tree squirrels and fishers within 3 forest stand types in the northern Sierra Nevada Mountains of California in early 2017.

	Black Oak	**Conifer**	**Tanoak**	**Total**
January	0	5	7	12
February	12	9	16	27
March	17	15	6	38
Total	29[a]	29	29[a]	87[b]

[a] 1 camera malfunctioned and collected no data, 28 sites included in final analysis.

[b] 2 sites excluded; 85 sites included in final analysis.

appropriately before deploying cameras.

I, or volunteers, checked and rebaited cameras 4 times throughout the study. Checking the camera involved collecting the used memory card, and replacing it with a blank, formatted card. Cameras that were moved or pulled off the tree by animals were repositioned to the original aim. When possible, cameras damaged by bears or inclement weather were replaced by Reconyx PC800 cameras (Table 2). Two sites (one black oak, one tanoak) had damaged cameras that were never replaced (Table 2). Peanut butter never remained between station rebaiting, but on rare occasions a few walnuts remained on the wire. Remaining walnuts were added to the new wire before application. On the 5th visit to all stations, the cameras were removed.

Table 2. Deployment scheme for 87 remote cameras deployed to survey for tree squirrels and fishers in 3 forest stand types in the northern Sierra Nevada Mountains of California in 2017[a].

	Black Oak	**Conifer**	**Tanoak**	**Total**
Browning	13	14	13	40
PC85	8[b]	7	8	23
PC800	6	6	6[b]	18
Bushnell	2	2	2	6

[a] 5 cameras were irreparably damaged by a bear or inclement weather throughout the study, these were all replaced by PC800 cameras.

[b] 1 camera malfunctioned and was not replaced.

Photograph Collection and Analysis

I downloaded photographs from memory cards, sorted them by site, and stored them as .jpeg files. All photos were processed through the Reconyx image management program MapView Professional (Reconyx 2010). This program is designed specifically for Reconyx cameras, but can also be used with images taken by cameras of a different manufacturer. Using the software, I produced .csv files containing the data associated with each photograph. Every individual line of the file referenced an individual photograph and included information such as the date, time, and trigger number of photographs taken.

I or one of 6 volunteers viewed each photograph and recorded into the .csv files several different identifiers, including a 4-letter code (first 2 letters of genus and first 2 letters of specific epithet) for all species present, and the number of individuals of each species observed. One difficulty of analyzing camera trap data is determining what constitutes a single detection event, as often one visit to a site by any animal can result in multiple, sometimes even hundreds, of photographs. EACH ONE OF THESE PHOTOGRAPHS IS NOT AN INDEPENDENT VISITATION EVENT, RATHER A SERIES OF PHOTOGRAPHS OF THE SAME SPECIES TAKEN WITHIN A DEFINED TIME PERIOD SHOULD BE CONSIDERED A SINGLE EVENT (OTANI 2002, O’BRIEN ET AL. 2003). RESEARCH USING REMOTE CAMERAS TO SURVEY FOR SMALL MAMMALS IS VERY LIMITED, AND I WAS UNABLE TO FIND PREVIOUS RESEARCH THAT DEFINED AN INDEPENDENT VISITATION EVENT FOR THESE SPECIES. SIMILAR TO MANY REMOTE CAMERA STUDIES ON MEDIUM TO LARGE MAMMALS, I USED 30 MIN BETWEEN A SERIES OF

PHOTOS OF THE SAME SPECIES AS THE LENGTH OF TIME THAT DEFINED A NEW EVENT (KELLY 2003, SILVER ET. AL. 2004, YASUDA 2004, KELLY AND HOLUB 2008). WE RECORDED THE TOTAL NUMBER OF EVENTS AT EACH CAMERA STATION, AS WELL AS OTHER DATA REGARDING CAMERA AIM AND BAIT STATUS FOR EACH PHOTOGRAPH (APPENDICES

Appendix A). Using analysis of variance (ANOVA), I tested for differences in the total number of visitation events between stand types for each of the target species. If there were differences in visitation events between stand types, I then used a post hoc Tukey test to determine which stand type had the most independent visitation events.

The 6 volunteers collectively classified photographs for 26 stations, although the majority of this effort was skewed to a single observer. I classified the photographs for the remaining 59 stations. I also performed a quality check of all volunteer classifications data to ensure accurate species identification; I verified all photos classified as any squirrel species, fisher, or when the species was recorded as unknown. I excluded from analysis all photographs where species identification was not confirmed, usually because only a portion of the animal was visible, or because lighting or other photographic exposure conditions were not optimal. I included all events of identifiable species, even if the camera aim changed somewhat between setting and re-baiting. I considered a camera inoperable when it shut-off due to battery failure, bear disturbance, or very wet conditions. I also considered a camera inoperable when it was moved or removed from the tree by an animal and only the ground or sky was visible. I then used the classification data from the photographs to create detection histories for Douglas squirrels, gray squirrels, and fishers indicating detection/non-detections for each week at each site over a 44-week period.

Additional Environmental Variable

Upon selection of my survey stands, I noticed that some sites contained a few larger diameter hardwood trees that were of a different species than the stand type (e.g., a large tanoak or black oak in a conifer stand, or a large black oak in a tanoak stand etc.), as well as large live oak (*Quercus chrysolepis*) trees. I was interested in testing for the influence of such trees, to address the possibility that stand occupancy by a tree squirrel may be influenced by the presence of a few large masting trees regardless of species type. I used a wedge prism with a basal area factor of 20 such that trees of roughly 28 cm DBH or larger would be counted (G. Pease, HSU Forestry, pers. Comm). I and volunteers counted the number of these trees within a 50m visible distance of each bait tree (Appendix B).

Statistical Analysis

Single-species analysis

I fit single-species occupancy models using the *occu* function in the *unmarked* package in RStudio version 1.1423 (R Development Core Team 2008, RStudio Team 2016) for Douglas squirrels, gray squirrels, and fishers for 85 sites over 44 sampling occasions (1 week = 1 occasion). Two important assumptions when using occupancy models are site independence and a constant occupancy state throughout the survey season (MacKenzie et al. 2006). I accounted for site independence for tree squirrels by spacing stations to reduce detection of the same individuals at multiple cameras. Densities of gray squirrels at 0.25 to 2.8 per 0.01 km^2 (Carraway and Verts 1994) and Douglas squirrels at 0.2 to 0.5 per 0.01 km^2 (Steele 1999) have been documented in the western U.S., and both species have extended periods of breeding and juvenile emergence (Ingles 1947, Asserson, 1974, Linders and Stinson 2007, Koford 1982). Thus, although abundances of squirrels may have varied, I assumed the occupancy status for squirrels in stands remained static over my 44-week study. The temporal and spatial scale of my study did not allow me to meet assumptions of independence and closure for fisher detections. Some dependence between sites can occur for wide ranging species such as fishers when the objective is measuring area used over large spatial scales; in that case, results should be interpreted as a measure of habitat "use" rather than true occupancy (Long and Zielinski 2008, Matthews et al. 2011). I included fisher detection data in my analysis to obtain an index of site use and detection probability, using these metrics as a representation of stand-use.

The utility of occupancy models is their inclusion of imperfect detection, or false absences (MacKenzie and Nichols 2004). In an occupancy model, two stochastic processes are occurring that affect whether a species is detected at a site: a site may be either occupied or un-occupied, and if the site is occupied, there is some probability of detection given the chance of false absences (Cortelezzi et al. 2017). To properly estimate the probability of detection, sites must be surveyed repeatedly. Thus, to determine the probability of a site being occupied, or $\Psi_i = \Pr(Z_i = 1)$, M_i number of sites are surveyed, and there is a binary response Y_{ij} of a species detection (Y = 1) or non-detection (Y = 0) during J_i number of visits to the ith site within a defined season (MacKenzie et al. 2002). A detection probability parameter p accounts for the probability that a species goes undetected ($Y_{ij} = 0$), when it is actually present ($Z_i = 1$). This measure of detection probability is an observational parameter that is dependent on the state parameter, Ψ, which is the true presence/absence state of the site (Kéry and Royle 2016).

Function *unmarked* implements a maximum likelihood hierarchical occupancy model that describes the joint distribution between the observational condition of marginal Ψ state, and the distribution of the Ψ state variable itself (Fiske and Chandler 2017). This is known as a conditional probability distribution, where a joint distribution describes the probabilities of simultaneously observing all unique combinations of X and Y, while the marginal distribution of a variable Y is its distribution averaged over all possible values of X (Kéry and Royle 2016). The model, following Royle and Dorazio (2008), is described as:

$$Z_i \sim \text{Bernoulli}(\Psi) \text{ for } i = 1, 2, \ldots\ldots M$$

$$Y_{ij} \mid Z_i \sim \text{Bernoulli}(Z_i\, p) \text{ for } j = 1,2, \ldots\ldots J$$

Hierarchical modeling allows separate logistic regressions on each component (Ψ and p), which may include covariates or random effects (Rota et al. 2011). The occupancy state can be modeled as a series of variables in a linear model as:

$$\text{logit}(\Psi_i) = x_i \cdot \beta_0 + \beta_1 \ldots \beta_i$$

where x_i is a measured habitat or landscape covariate for site $\acute{i}$, and β is a vector of regression coefficients; the detection process can be modeled as a series of variables in a linear model as:

$$\text{logit}(p_{ij}) = v_{\acute{i}} \cdot \alpha_0 + \alpha_1 \ldots \alpha_{\acute{i}}$$

where v_i is a measured observational-level variable for site $\acute{i}$, and α is a vector of regression coefficients (Fiske and Chandler 2011).

Covariates are used to model the probability of occupancy and detection as a function of site-specific and detection-level variables (MacKenzie et. al 2002), which are variables that influence the state and observational processes that I aimed to describe with my models. For both occupancy and detection, I included both the species and the stand types as categorical variables with 3 levels (“1”, “2”, and “3”) in my models, labeled as “*species*” and “*stand*” respectively.

I used a strict survey site selection process that included several site-level habitat variables; thus, I was able to limit the number of occupancy level covariates. Elevation was one variable I did not account for in site selection. Gray squirrels have different habitat associations in California depending on elevation (Carraway and Verts 1994), and fisher probability of occurrence was highest in forests of the southern Sierra Nevada Mountains at intermediate elevations (1300-2400m, Spencer et al. 2011). The elevation of my sites ranged from 770m to 1159m, so I tested if occupancy varied across these values for all 3 species. I scaled the values for elevation in my analysis by subtracting the mean and dividing by the standard deviation. Scaling of covariate values is done to improve interpretability of coefficients when values for particular variables are large (e.g.

thousands of meters) compared to other variables being tested (Schielzeth 2010). Once values are standardized, a 1-unit change in a scaled covariate value corresponds to a 1-standard deviation change from the mean of the original covariate value (Kéry and Royle 2016). The second covariate I included for occupancy was the additional habitat variable collected at each site counting the number of larger hardwood trees near the camera station opposite the stand type. I labeled these two covariates as "*elev*" and "*hw*" in my analysis.

Detection probability is assumed to be constant across time in occupancy models, unless covariates are used to account for heterogeneity in detection (MacKenzie 2002). The entire survey period was relatively long (44 weeks), such that detection may have varied across the study due to the time of year or season. I tested for time-specific variation in detection probability by including time as a discrete variable with 44 levels ("1", "2", ..."44") in the models analyzed. The presence of bait at a survey station likely created heterogeneity in detection probability as well. I hypothesized that the presence of bait at the station would increase detection of all 3 species. My volunteers and I recorded whether both walnuts and peanut butter were present at a camera station for every photograph, and I used that information to determine for which survey weeks there was bait present ("1") or absent ("0"). I considered bait to be present for a survey occasion if either walnuts or peanut butter were on the bait tree for any length of time within a week. I labeled this covariate as "*bait*" in my analysis.

I used an information theoretic approach for comparing candidate models containing different combinations of covariates. I constructed 22 candidate models using a combination of variables described (method in an effort to weed out unimportant variables or interaction terms through

Table 3. Description of variables used for modeling occupancy (Ψ) and detection (p) of 3 species in 22 single-species occupancy models used to analyze remote camera data from 85 sites in the northern Sierra Nevada Mountains of California in 2017.

Variable	**Type**	**Description**	**Ψ or p**
species	Categorical	Douglas squirrel, gray squirrel, fisher	Ψ and p
stand	Categorical	black oak, conifer, tanoak	Ψ and p
bait	Binary	"1"= present, "0" = absent	p
elev	Continuous	scaled elevation	Ψ
hw	Continuous	count of trees different from stand type	Ψ

). I started with a model where both occupancy and detection probabilities were constant (“.” model in analysis). I then built models with changing variables for detection while holding occupancy constant. I hypothesized that stand type may have had a different effect on the occupancy probability for each species, so in several models I included an interaction term for species and stand type, as well as an additive term, to test if stand type had a similar effect on the occupancy of the 3 species. I then built 4 models with the detection variables species and stand type included one at a time, and together with an additive and an interactive effect. I then built models with changing variables for occupancy while holding detection constant. I then constructed 4 models with occupancy variables species and stand type included the same way as the previous models. I then combined additive and interactive effects of species and stand type on both occupancy and detection simultaneously in 2 models. For the remaining models I included a species and stand type interaction term for both occupancy and detection.

I hypothesized that bait may have had a differential effect on detection probability for each species, so I included an interaction term for species and bait in one model, and another model where I included it as an additive term. I then built 3 models, including occupancy variables elevation and hardwood count as additive effects. I hypothesized that elevation may have had a different effect on occupancy probability for each species, so I included an interaction term for species and elevation in one model. Finally, I made 6 additional models using the combined detection and occupancy terms. I followed this method in an effort to weed out unimportant variables or interaction terms through

Table 3. Description of variables used for modeling occupancy (Ψ) and detection (p) of 3 species in 22 single-species occupancy models used to analyze remote camera data from 85 sites in the northern Sierra Nevada Mountains of California in 2017.

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bait	Binary	“1”= present, “0” = absent	p
elev	Continuous	scaled elevation	Ψ
hw	Continuous	count of trees different from stand type	Ψ

isolation and conjunction within different models.

I tested the fit of my global model using a parametric bootstrap method with a chi-squared statistic (number of simulations = 1,000, MacKenzie and Bailey 2004) via the function *parboot* in RStudio (R Development Core Team 2008, RStudio Team 2016). The p-value reported using this method should not be extreme (i.e., not close to 0 or 1) indicating that a model fit well (Kéry and Royle 2016). Testing the global model for good fit ensures that all subsequent models created using variables from the global model should also fit the data well (Burnham and Anderson 2002).

Delta AIC scores provide a measure of strength of evidence and a scaled ranking of candidate models, and AIC weights represent the approximate probability that model *x* is the best model out of those considered (Anderson et al. 2000). I evaluated the top models based on AIC weights summing to 0.95 (Burnham and Anderson 2002) and selected my top model based on lowest AIC score, a delta AIC of <2.0, and the greatest weight. I did not perform any model averaging as I wanted to understand the relationships between the variables included in the top model and their effects on occupancy and detection probabilities, rather than quantify average parameter estimates across models based on the weight of support for each candidate model (Burnham and Anderson 2002, Slauson et al. 2007). I then checked the goodness of fit of my top model using the same method as for the global model.

Using the parameter estimates generated from the top model, I quantified site-specific occupancy probabilities for each species in all 3 stand types. I averaged site-specific occupancy probabilities across stand types for comparison of stand-type level averages between species. I also quantified time-specific probability of detection for each species at all sites in all 3 stand types. I averaged site-specific detection rates across weeks for each site for comparison of site averages between stand types and species and averaged detection rates across stand types for comparison of stand-type level averages between species. I determined the effect of the covariates included in the top model by calculating the odds-ratio for each parameter estimate using the *exp(coef())* function in RStudio (R Core Development Team 2008, RStudio Team 2016).

Two-species co-occurrence analysis

I fit single-season two-species co-occurrence models using the two-species conditional occupancy estimation available in Program MARK version 9.0 (White and Burnham 1999, Cooch and White 2002) for gray squirrels and fishers over 85 sites with 44 sampling occasions. I explicitly wanted to investigate the relationship between gray squirrels and fishers because they had similar patterns of detection and occupancy in my single-season model, and because gray squirrels may be the most highly ranked tree squirrel species given their relatively large body size. Co-occurrence models use a similar framework to single-species models in that the probability of false absences or missed detections can be quantified via detection probabilities. The utility of this model is that it allows for the testing of several different hypotheses related to conditional occupancy and detection between two species, specifically if the presence of Species B depends on the presence of Species A, if the detection of Species B depends on the presences of Species A, and if the detection of Species B depends on the detection of Species A given A is present (MacKenzie et al. 2017).

Two-species conditional occupancy models in Program MARK use maximum likelihood estimation following the parameterization summarized by Richmond et al. (2010). Under this parametrization, Species A is assumed to be dominant and Species B is assumed to be subordinate. I chose to make gray squirrels the dominant Species A because they are more abundant and widely distributed across the landscape than fishers. I also chose gray squirrels as Species A because I was interested in how gray squirrel occupancy influenced fisher stand use and probability of detection, and making gray squirrels Species A was appropriate for that question given the parameterization of the model.

This model is conditional in that the entire parameterization is based on the occupancy state of Species A. The parameterization can be thought of as a hierarchical tree starting at N_i sites. Here, Species A has the unconditional probability of presence (Ψ^{A}) or absence (1- Ψ^{A}). From there, the probability of Species B being present can be expressed in two ways: (Ψ^{BA}) represents the probability of occupancy for Species B and (1- Ψ^{BA}) represents the probability of absence for Species B conditional on Species A being present, or (Ψ^{Ba}) represents the probability of occupancy or absence (1- Ψ^{Ba}) for Species B conditional on Species A being absent. This can result in 4 different outcomes for occupancy at each station: neither Species A nor B is present; (1- Ψ^{A})(1- Ψ^{Ba}), only Species B is present; (1- Ψ^{A})(Ψ^{Ba}), only Species A is present; (Ψ^{A})(1- Ψ^{BA}), or both species are present; (Ψ^{A})(Ψ^{BA}). This parameterization allows for the calculation of the unconditional probability of occupancy by Species B; however, I already quantified an index of occupancy for fisher in my single-species model, so I did not evaluate the coefficient estimates for this derived parameter.

The lower branches of the tree represent probabilities for detection of Species A and B conditional on the occupancy status of both species. If only Species B is present (Species A absent), it can either be detected (p^B) or not detected (1- p^B). If only Species A is present, it can either be detected (p^A) or not detected (1- p^A). If Species A is present or absent, or if only Species B is present, both species could go undetected (1- p^A)(1- p^B). If both species are present, Species A can be detected (r^A) or not detected (1- r^A). If Species A is not detected, only Species B may be detected (r^{Ba}), or neither species may be detected (1- r^A)(1- r^{Ba}). If Species A is detected, Species B may also be detected (r^{BA}) or only Species A may be detected (r^A)(1- r^{BA}). It is important to note that these probabilities of detection are the probability of detecting at least one individual of a species at a site that may contain multiple species, not simply the probability of detecting an individual species (Richmond et al. 2010).

A species interaction factor (SIF; denoted as Φ), is used to quantify the dependence between the two species (MacKenzie et al. 2006, Richmond et al. 2010). This derived parameter can be calculated as:

$$\Phi \ = \frac{(\Psi^{A})(\ \Psi^{BA})}{(\Psi^{A})(\Psi^{A}\ \Psi^{BA} + \left((1 - \ \Psi^{A})\right)\Psi^{BA})}$$

A value of 1.0 means the two species occur independently and conditional occupancy is not occurring (unconditional occupancy). Under a null hypothesis of independence, a value greater than 1 means that Species B is more likely to occur if Species A is present, and a value less than 1 means that Species B is less likely to occur if Species A is present (Richmond et al. 2010, MacKenzie et al. 2017).

This parameterization, unlike that developed by MacKenzie et al. (2006), can tolerate the inclusion of covariates that may help explain patterns of co-occupancy and detection by two species. Covariates for detection and occupancy can be included using the following multinomial logistic model:

$$\Theta_i^k = \frac{\exp(\mathrm{Y}_i\beta_k)}{1 + \sum_{k=1}^{m-1}\exp(\mathrm{Y}_i\beta_k)} \text{ for k } = 1, 2, \ldots.. \mathrm{m} - 1$$

where Θ_i^k is the probability for occupancy or detection, Y_i is a vector of the covariate value for the íth site, β_k is a vector of the coefficient, and m is the number of discrete occupancy or detection outcomes.

Following Richmond et al. (2010), I only included covariates that I determined to be important from my top single-species model, which included elevation and bait. MARK defaults to scaling covariate data automatically by determining the maximum absolute value of covariates and dividing each covariate by its value, resulting in a scale between -1 and 1 (Cooch and White 2002), thus I did not scale elevation values for this analysis. MARK then back-transforms the scaled values for easy interpretability. To avoid over parameterization of the model, I did not make bait a time-varying covariate as I did in my single-species model. Instead, I totaled the number of weeks bait was present at each site over the entire study, with values ranging from 4 to 25 weeks.

I tested 3 hypotheses regarding the conditional occupancy and detection of gray squirrels and fishers by using different formulations of the two species model and comparing model performance using an information theoretic approach that ranked competing models:

1) I hypothesized that the occupancy of fishers would depend on the occupancy of gray squirrels. I predicted that fishers would be more likely to occur if gray squirrels were present:

$$\Psi^{\mathrm{BA}} \neq \Psi^{\mathrm{Ba}}$$

$$\Psi^{\mathrm{BA}} = \Psi^{\mathrm{Ba}}$$

where the first model is conditional occupancy (labeled "*CO*" in analysis) and the second is unconditional occupancy (labeled "*UO*" in analysis).

2) I hypothesized that the detection of fishers would depend on the occupancy of gray squirrels, and predicted that fishers would be detected more often at a site when occupied by a gray squirrel:

$$p^{\mathrm{B}} \neq r^{\mathrm{BA}} = r^{\mathrm{Ba}}$$

$$p^{\mathrm{B}} = r^{\mathrm{BA}} = r^{\mathrm{Ba}}$$

where the first model is conditional detection type 1 (labeled "*CD1*" in analysis) and the second is unconditional detection (labeled "*UD*" in analysis).

3) I hypothesized that the detection of fishers depended on the detection of gray squirrels when both were present, and predicted that when both animals were present fishers would be detected more often when gray squirrels were detected:

$$r^{\mathrm{BA}} \neq r^{\mathrm{Ba}}$$

$$r^{\mathrm{BA}} = r^{\mathrm{Ba}}$$

where the first model is conditional detection type 2 (labeled "*CD2*" in analysis) and the second is unconditional detection.

I constructed a total of 30 candidate models, each with different combinations of conditional and unconditional occupancy and detection models. Detection histories for gray squirrels and fishers were assigned to 3 groups dependent on stand type. The first 6 models I built included no effect of stand type (labeled "*_nostand*" in analysis) and tested only different combinations of conditional and unconditional occupancy and detection. I then built 6 models that included the stand effect, but no covariates. The final 18 models included the stand effect and different combinations of covariates included with different combinations of conditional and unconditional occupancy and detection. I used this method in an effort to understand if covariates for detection and occupancy influenced the conditional and unconditional occupancy states through isolation and conjunction within different models. In the single-species analysis, I found that gray squirrels and fishers both had similar patterns of occupancy in relation to elevation, and similar patterns of detection in relation to bait, so I included these covariates using a single beta parameter for each as an additive effect on all occupancy and detection beta parameters (labeled as "*elev*" and "*bait*" in my analysis). I also did this in an effort to reduce the number of estimated parameters to avoid issues with extrinsic non-identifiability and over-parameterization. I evaluated and selected the top model(s) based on AICc weights and delta AICc as described previously. I model averaged the occupancy parameter estimates to deal with model selection uncertainty that occurred when selecting the top model.

RESULTS

Camera Stations

I deployed 85 remote cameras over a period of 44 weeks between January and November 2017 for a total of 21,000 camera-nights, including 6,797 nights in black oak stands, 7,196 nights in conifer stands, and 7,007 nights in tanoak stands. I sampled a total of 3,000 camera-weeks (weeks = occasions), with 971 camera-weeks in black oak stands, 1,029 camera-weeks in conifer stands, and 1,001 camera-weeks in tanoak stands. The number of weeks when a camera was inoperable varied only slightly between stand types but ranged widely within stand types (Table 4). The total length of deployment varied by station, but the average was relatively equal across stand types (Table 4).

I collected and classified 508,569 photographs, including 141,128 in black oak stands, 188,615 in conifer stands, and 178,826 in tanoak stands. More photographs were collected than accounted for in these tallies as some unknown number of false trigger images were deleted in error at some stations prior to analysis. Photographs of humans were only captured during station rebaiting and a few sporadic instances of SPI foresters working at a site, totaling 11,049 of photographs. No more than 2 people were ever at a camera station at any given time. Roughly 10% (53,131) of all photographs classified did not include a vertebrate species due to false triggers and triggers that occurred immediately before an animal was observed. The number of photographs classified does

Table 4. Number of weeks cameras were deployed (and inoperable) at 85 remote cameras stations set to survey for tree squirrels and fishers in 3 forest stand types in the northern Sierra Nevada Mountains of California in 2017.

	Black Oak	**Conifer**	**Tanoak**
Minimum	20 (2)	13 (0)	18 (0)
Maximum	43 (24)	44 (31)	44 (26)
Total	971 (261)	1028 (248)	997 (235)
Average	34.7 (9.3)	35.4 (8.6)	35.7 (8.2)
SE	1.3 (1.3)	1.4 (1.4)	1.6 (1.6)

not equal the number of independent visitation events to a camera. The total number of events at my 85 sites was 20,119 of 19 mammalian species (3 classified to genus only) and 3 avian orders (

Appendix C).

The number of visitation events involving non-human vertebrate species varied between stand type, with 5,583 events in black oak stands, 7,076 events in conifer stands, and 7,460 events in tanoak stands. The total number of events where the species ID was unknown was 594, with 184 occurring in black oak stands, 147 in conifer stands, and 263 in tanoak stands. The total number of visitation events for a target species (tree squirrel or fisher) across all stand types was 6,722 (Appendix D), with 1,976 events occurring in black oak stands, 2,459 in conifer stands, and 2,287 in tanoak stands. The total and average number of visitation events for each of the target species varied between stand types (

Table 5). The number of events for gray squirrels ($F_{(2,82)}$=4.445, p=0.015) and fishers ($F_{(2,82)}$=5.342, p=0.007) differed significantly between stand types, but did not differ significantly for Douglas squirrels ($F_{(2,82)}$=0.508, p=0.603). More gray squirrel visitation events occurred in tanoak stands than in conifer stands (p=0.011), and more fisher visitation events occurred in tanoak stands than in black oak stands (p=0.005).

	Black Oak		**Conifer**		**Tanoak**	
	Total	Average	Total	Average	Total	Average
Douglas Squirrel	1673	60(±10.2)	2146	74(±13.28)	1622	57.9(±13.56)
Gray Squirrel	250	8.9(±2.50)	145	5(±1.21)	429	15.3(±3.31)
Fisher	53	1.9(±0.40)	168	5.8(±1.61)	234	8.4(±1.75)

The length of time between rebaiting of sites varied by station but the average was relatively equal across stand types (Table 6). The average number of weeks bait was present at a station was slightly variable between stand types, with 10.8 ± 0.91 weeks on average in black oak stands, 11.1 ± 1.05 in conifer stands, and 9.2 ± 0.91 in tanoak stands

Table 5. The total and average (±SE) number of independent visitation events for 3 target species at 85 remote cameras across 3 forest stand types in the northern Sierra Nevada Mountains of California in 2017.

	Black Oak		**Conifer**		**Tanoak**	
	Total	Average	Total	Average	Total	Average
Douglas Squirrel	1673	60(±10.2)	2146	74(±13.28)	1622	57.9(±13.56)
Gray Squirrel	250	8.9(±2.50)	145	5(±1.21)	429	15.3(±3.31)
Fisher	53	1.9(±0.40)	168	5.8(±1.61)	234	8.4(±1.75)

Table 6. Length of time (in weeks) between rebaiting of 85 remote camera stations set to survey for tree squirrels and fishers in 3 forest stand types in the northern Sierra Nevada Mountains of California in 2017.

	Black Oak	**Conifer**	**Tanoak**
Minimum	5	5	6
Maximum	11	10	14
Average	7.6	7.7	8.1
SE	0.13	0.13	0.14

The minimum number of weeks a station had bait was 4 weeks in black and tanoak stands, and 5 in conifer stands. The maximum number of weeks a station had bait varied from 22-25 in black oak, tanoak, and conifer stands.

Single-Species Occupancy Analysis

The inclusion of time in any of my 22 candidate models indicated that detection probability varied over time for all 3 species, but there was no observable pattern in detection relative to the season or time of year (Figure 4). Thus, I did not include time as a variable in the final candidate models (Table 7). A global model with all possible covariates and their interactions had 25 parameters, and goodness of fit testing showed that the global model fit the data relatively well ($p = 0.854$, Appendix E).

The top 5 models were evaluated as they had a weight that summed to roughly 0.95. All 5 of these models shared identical variables and interaction terms for the detection portion of the model (Table 7). This included an interaction term between species and stand type, and between species and bait. All of the top models also included a species by stand type interaction term in the occupancy portion of the model (Table 7). Occupancy described as null (constant) or without an interaction between stand type and species variables had no support. The number of hardwoods at a camera site different from the stand type did not have an important effect on occupancy. The top model had a cumulative weight of 0.57 and included an additive effect of elevation for occupancy.

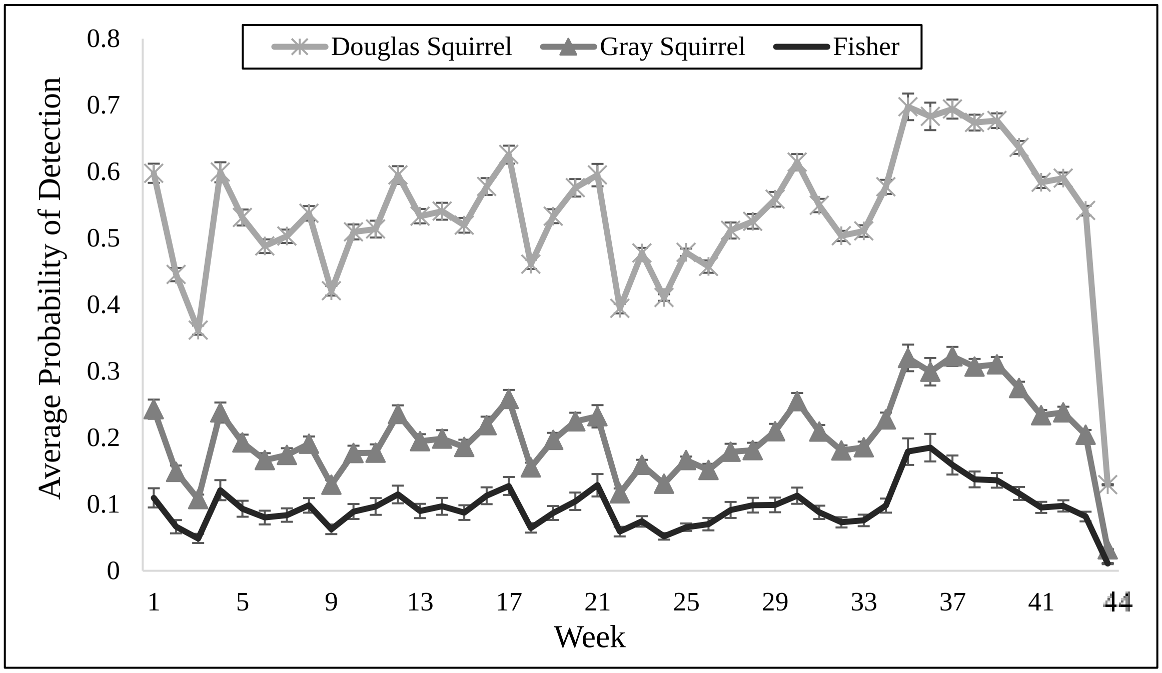

Figure 4. Average weekly detection probabilities, including 95% confidence intervals, for 3 species at 85 sites across 44 weeks, estimated using single-species occupancy analysis from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017.

Table 7. Twenty-two candidate single-species occupancy models constructed to estimate occupancy (psi) and detection probability (p) of tree squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017. Included are the model number of parameters (k), AIC scores, delta AIC scores, and cumulative weights.

Model #	Candidate Model	k	AIC	ΔAIC	Weight
1	psi(species*stand+elev) p(species*stand+bait*species)	22	8224.86	0	0.57
2	psi(species*stand+elev*species) p(species*stand+bait*species)	24	8227.38	2.52	0.73
3	psi(species*stand+elev*species + hw) p(species*stand+bait*species)	25	8228.43	3.56	0.83
4	psi(species*stand) p(species*stand+bait*species)	21	8228.70	3.83	0.91
5	psi(species*stand+hw) p(species*stand+bait*species)	22	8228.82	3.95	0.99
6	psi(species*stand+elev) p(species*stand+bait)	20	8233.41	8.54	1.00
7	psi(species*stand) p(species*stand+bait)	19	8237.37	12.51	1.00
8	psi(species*stand+hw) p(species*stand+bait)	20	8237.46	12.59	1.00
9	psi(species*stand+elev) p(species*stand)	19	8308.68	83.81	1.00
10	psi(species*stand+elev*species) p(species*stand)	21	8311.18	86.32	1.00
11	psi(species*stand) p(species*stand)	18	8312.79	87.92	1.00
12	psi(species*stand+hw) p(species*stand)	19	8312.94	88.08	1.00
13	psi(.) p(species*stand)	10	8324.19	99.32	1.00
14	psi(species+stand) p(species+stand)	10	8365.62	140.76	1.00
15	psi(.) p(species+stand)	6	8384.18	159.32	1.00
16	psi(.) p(species)	4	8394.01	169.14	1.00
17	psi(species+stand) p(.)	6	9759.21	1534.35	1.00
18	psi(species) p(.)	4	9759.77	1534.90	1.00
19	psi(species*stand) p(.)	10	9761.83	1536.97	1.00
20	psi(stand) p(.)	4	9779.71	1554.84	1.00
21	psi(.) p(.)	2	9779.96	1555.09	1.00
22	psi(.) p(stand)	4	9782.52	1557.66	1.00

The remaining 4 models evaluated held considerably less weight and had a delta AIC >2. The top model fit the data relatively well (p = 0.822, Appendix F).

Using the parameter estimates from my top model, I estimated site-specific occupancy for all 3 species in each stand type. I detected Douglas squirrel at every site in black oak and conifer stands, and occupancy was 0.99-1.0 (95% CI: 0-1) in those stands, and was 0.93-0.99 (95% CI: 0.656-0.99) in tanoak stands, where they were detected at all but one camera. Gray squirrel average probability of occupancy was relatively high across all 3 stand types (Figure 5), but minimum and maximum site-occupancy estimates varied between stand types (Appendix G). Site-specific estimates of occupancy overlapped between stand types and confidence intervals were relatively wide (Appendix G). Results for fisher index of occupancy probability were very similar to gray squirrels; overall average occupancy probability was high (Figure 5), but site-specific occupancy probabilities overlapped between stand types and confidence intervals were relatively wide (Appendix H). In general stand level averages had less overlap overall than site-specific estimates (Figure 5). The average occupancy of Douglas squirrels was similar among stand types, while gray squirrels and fishers had less overlap between stand types and showed a slightly higher average for tanoak stands (Figure 5).

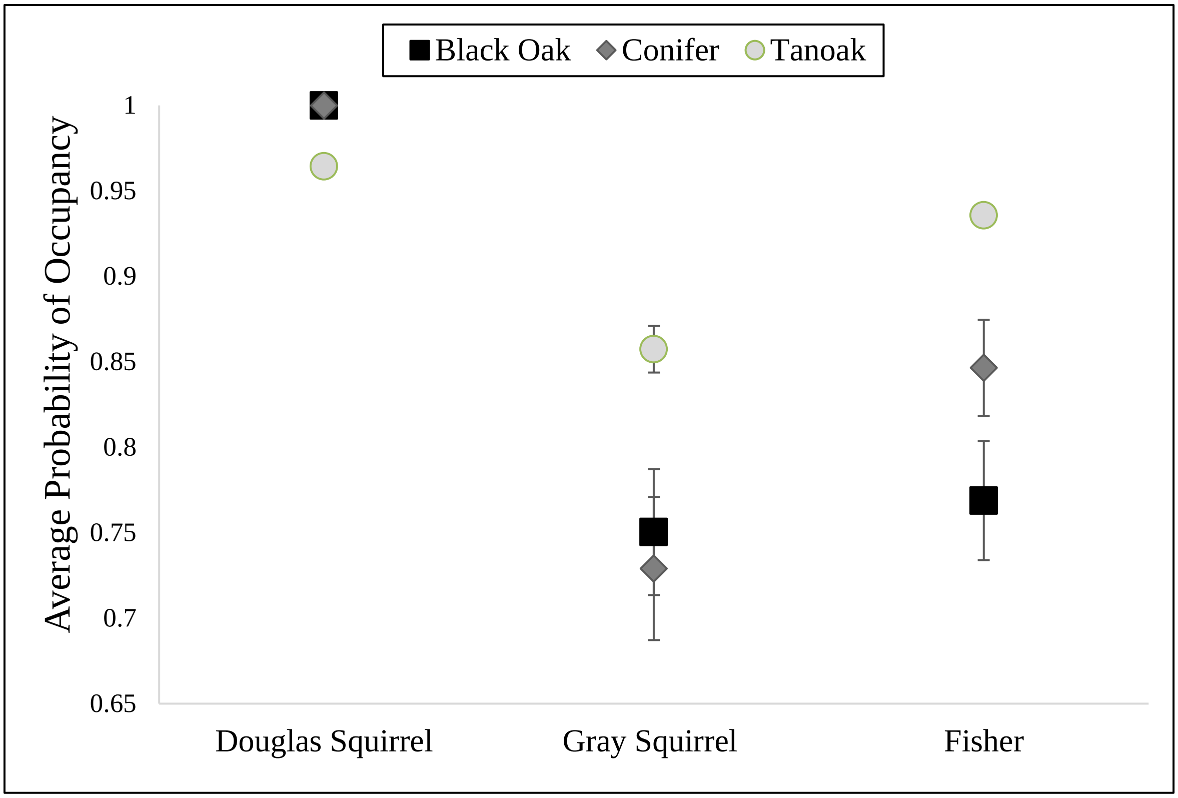

Figure 5. Stand-specific occupancy probabilities (averages, ± 95% confidence intervals) for 3 species at 85 sites, estimated from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017.

The top model included elevation as a descriptor of occupancy for all 3 species (Table 7). Occupancy for gray squirrels and fishers decreased moderately with increasing elevation, while Douglas squirrel occupancy probability was 1.0 at all elevations in black oak and conifer stands and decreased only slightly with increasing elevations in tanoak stands (odds = -0.57, 95% CI = 0.356-0.922, Figure 6). No stand types were skewed towards a higher or lower average or range in elevation compared to the other two. The average and range in elevation of all my sites was 1,161m (770-1559 m), which was very similar to the average and range in elevation for each stand type (black oak = 1,224 m (770 to 1,486 m), conifer = 1,190 m (788 to 1,559 m), tanoak = 1,069 m (818 to 1,283 m), indicating that the pattern of decreased occupancy probability at higher elevations could be observed in all stand types.

Using the parameter estimates from the top model, I estimated weekly probabilities of detection for all 3 species in each stand type. I then averaged those weekly detection probabilities for each of my 85 sites across the entire study period, creating an estimated average site-level detection probability. I also averaged weekly detection rates across stand types to estimate a stand level average for each species (Figure 7).

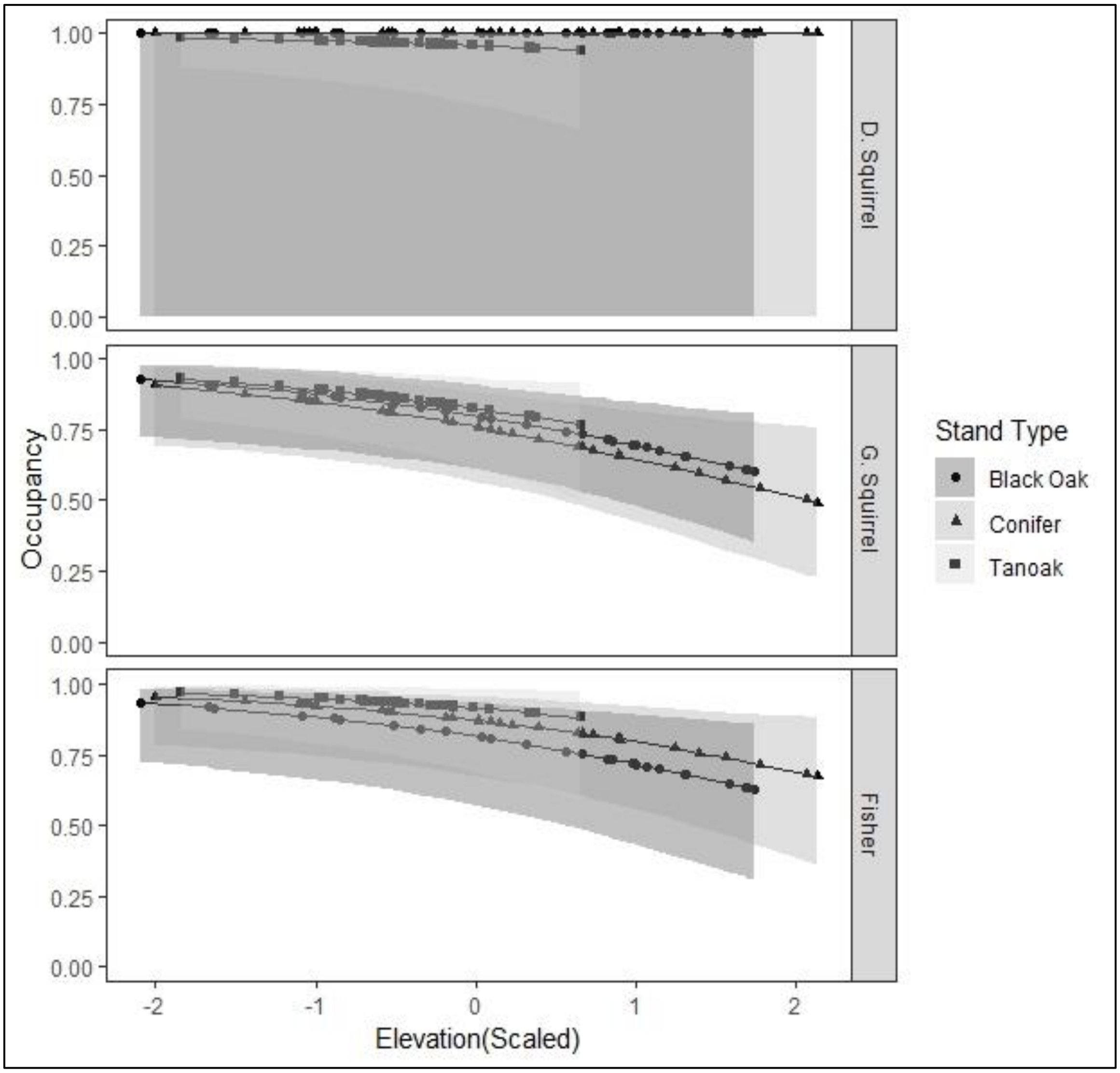

Figure 6. Estimated effect of elevation on the probability of occupancy Douglas squirrels, western gray squirrels, and fishers in 3 forest stand types using remote camera data collected at 85 sites across 3 forest stand types in the northern Sierra Nevada Mountains of California in 2017. Shaded areas are 95% confidence intervals.

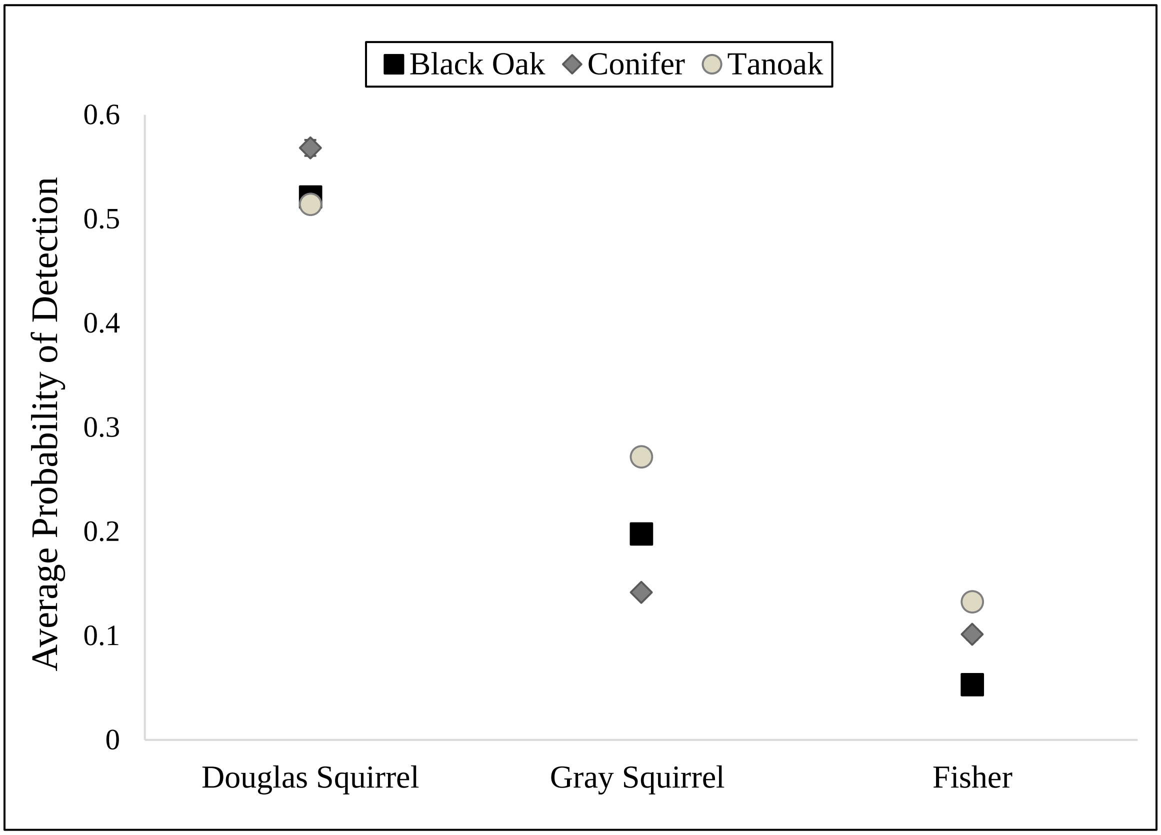

Figure 7. Stand-specific detection probabilities (average ±95% confidence intervals) by stand type for 3 species at 85 sites, estimated from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017.

Douglas squirrel average stand level detection probability was relatively high across all 3 stand types but was highest in conifer stands (Figure 7), and this was also true for average site-level detection probability (Appendix I). Gray squirrel average stand level was highest in tanoak stands, and lowest in conifer stands (Figure 7), and this was also true for site-level average detection probability (Appendix J). Fisher average stand level detection probability was highest in tanoak stands, and lowest in black oak stands (Figure 7), and this was also true for site-level average detection probability (Appendix K). In general stand level averages had less overlap overall than site-specific estimates.

Presence of bait was included in my top model as a descriptor of detection for all 3 species. The interaction term between bait and species in this model suggests that the 3 species were influenced by bait but at different magnitudes. Bait increased the probability of detection for all 3 species; the most for fishers (odds = 2.50, 95% CI = 1.92-3.25), when compared to Douglas and gray squirrels (odds = 0.55, 95% CI = 0.48-0.89, and 0.66, 95% CI = 0.39-0.77, respectively). The probability of detection increased with bait present compared to bait absent for all 3 species in all 3 stand types (Figure 8). Douglas squirrel and gray squirrel average detection probability were influenced by bait similarly across stand types, whereas bait increased the average probability of detection for fishers the most in tanoak stands (Figure 8).

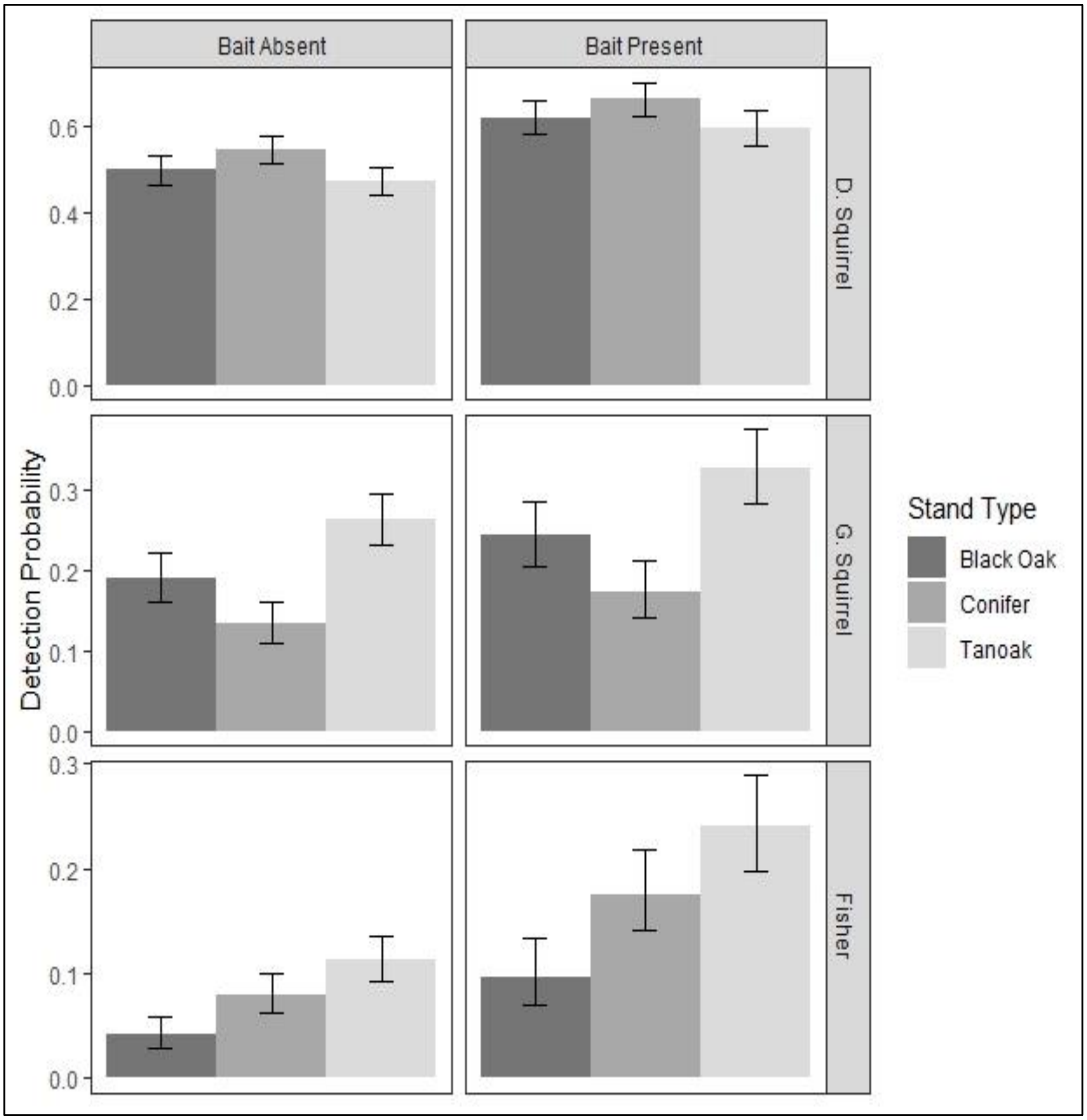

Figure 8. Effect of bait on the probability of detection for Douglas squirrels, western gray squirrels, and fishers in 3 forest stand types using remote camera data collected at 85 sites across 3 forest stand types in the northern Sierra Nevada Mountains of California in 2017.

Two-species Co-occurrence Analysis

I constructed 30 candidate two-species co-occurrence models to test for conditional occupancy and detection between gray squirrels and fishers (Table 8). All 30 models were then ranked via AICc results. The top 4 models were evaluated as they had a weight that summed to roughly 0.95. All 4 of the evaluated models supported un-conditional detection of gray squirrels and fishers, and all but 1 included bait as a descriptor of detection. The top 4 models differed in the occupancy portion of the model; they included unconditional occupancy alone and with the added effect of elevation, as well as conditional occupancy with the added effect of elevation (Table 8).

The top two models had a delta AICc score of less than 2.00, and a weight of 0.48 and 0.40, respectively, meaning there was roughly equal support for each of these two models (Table 8). The top model included unconditional occupancy for gray squirrels and fishers, while the model ranked second included conditional occupancy for gray squirrels and fishers. The top 5 models in my candidate set all included unconditional detection, suggesting that nearly any occupancy model that included unconditional detection rose in the ranks. The inclusion of bait as a covariate for detection also seemed to influence model ranking, as any models including bait coupled with unconditional detection rose in the ranks. Stand type was a predictor of occupancy and detection for gray squirrels and fisher as models without the effect of stand type had no support.

I model averaged the parameter estimates for occupancy probabilities due to the

Table 8. Thirty candidate two-species co-occurrence models constructed to test for conditional occupancy and detection of western gray squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017. Included are the model number of parameters (k), AIC scores, delta AIC scores, and cumulative weights.

Model #	Candidate Model	k	AICc	ΔAICc	Weight
1	(UO + elev) (UD + bait)	17	4204.57	0.00	0.48
2	(CO + elev) (UD + bait)	19	4204.95	0.37	0.88
3	(UO + elev) (UD)	15	4209.31	4.73	0.92
4	(UO) (UD + bait)	16	4209.67	5.09	0.96
5	(CO) (UD + bait)	18	4211.74	7.16	0.97
6	(UO + elev) (CD1)	19	4212.28	7.70	0.98
7	(CO + elev) (UD)	18	4212.45	7.88	0.99
8	(UO) (UD)	15	4214.12	9.54	1.00
9	(CO + elev) (CD1 + bait)	22	4214.44	9.86	1.00
10	(CO) (CD1 + bait)	19	4216.78	12.20	1.00
11	(UO + elev) (CD2)	20	4216.89	12.32	1.00
12	(CO + elev) (CD1)	21	4216.96	12.39	1.00
13	(UO) (CD1 + bait)	19	4217.37	12.80	1.00
14	(UO + elev) (CD2 + bait)	23	4219.09	14.51	1.00
15	(CO) (UD)	18	4219.46	14.88	1.00
16	(UO) (CD1)	18	4220.26	15.68	1.00
17	(CO + elev) (CD2 + bait)	25	4224.02	19.45	1.00
18	(CO + elev) (CD2)	24	4225.98	21.40	1.00
19	(CO) (CD1)	21	4227.84	23.27	1.00
20	(UO) (CD2)	21	4228.97	24.40	1.00

Model #	Candidate Model	k	AICc	ΔAICc	Weight
21	(UO) (CD2 + bait)	21	4230.15	25.57	1.00
22	(CO) (CD2)	24	4236.73	32.15	1.00
23	(UO + elev) (CD1 + bait)	18	4242.00	37.43	1.00
24	(CO)(CD2 + bait)	22	4246.75	42.17	1.00
25	CO.UD_nostand	6	4269.24	64.67	1.00
26	CO.CD2_nostand	7	4270.62	66.05	1.00
27	CO.CD1_nostand	7	4270.62	66.05	1.00
28	UO.UD_nostand	5	4272.51	67.93	1.00
29	UO.CD2_nostand	7	4272.68	68.11	1.00
30	UO.CD1_nostand	6	4272.92	68.34	1.00

UO = unconditional occupancy, $\Psi^{\mathrm{BA}} = \Psi^{\mathrm{Ba}}$
CO = conditional occupancy, $\Psi^{\mathrm{BA}} \neq \Psi^{\mathrm{Ba}}$
CD1 = conditional detection type 1, $p^{\mathrm{B}} \neq r^{\mathrm{BA}} = r^{\mathrm{Ba}}$
CD2 = conditional detection type 2, $r^{\mathrm{BA}} \neq r^{\mathrm{Ba}}$
UD = unconditional detection, $p^{\mathrm{B}} = r^{\mathrm{BA}} = r^{\mathrm{Ba}}$, $r^{\mathrm{BA}} = r^{\mathrm{Ba}}$
elev = elevation in meters
bait = number of weeks with bait present
_nostand = no stand type effect

large amount of model selection uncertainty between the top two models. The model averaged estimates indicated relatively high probability of occupancy for Species A (gray squirrels) in all 3 stand types (Table 9). Species B (fisher) occupancy probabilities were also high in all 3 stand types, and were highest in tanoak stands regardless of the presence of Species A; however, the confidence intervals for all of the averaged parameter estimates were relatively wide, reflecting the limited power of the dataset. The detection data from the 3 stand types revealed a similar pattern for tanoak; this was the only stand type where “neither present” occurred on 0 occasions, and tanoak stands had the greatest number of occasions where both species were present (Table 10).

Similar to the single-species analysis, elevation had a negative effect on occupancy (Odd Ratio = -0.005, ±0.001 SE) and bait had a positive effect on detection (Odds Ration = 1.022, ±0.0081 SE) for both gray squirrels and fishers. The model averaged Species Interaction Factor values estimated were very close to 1.0 in all 3 stand types, indicating there was neither avoidance nor aggregation occurring between gray squirrels and fishers (black oak = 1.0088, 95% CI: 0.9683-1.0493; conifer = 1.0377, 95% CI: 0.9267-1.1486; tanoak = 0.9952, 95% CI: 0.9783-1.012).

Table 9. Model averaged parameter estimates for occupancy probabilities (Psi) of western gray squirrels (Species A) and fishers (Species B) including 95% confidence intervals across 3 forest stand types, estimated using two-species unconditional and conditional co-occurrence models. Abbreviations indicate Species A along (A), Species A and B present together (BA), and Species B present without A (Ba). Estimates come from data collected at 85 remote camera sites in the northern Sierra Nevada Mountains of California in 2017.

	Stand Type		
Parameter	Black Oak	Conifer	Tanoak
Psi(A)	0.83 (0.64-0.93)	0.82 (0.58-0.93)	0.82 (0.59-0.93)
Psi(BA)	0.88 (0.59-0.97)	0.92 (0.65-0.98)	0.95 (0.71-0.99)
Psi(Ba)	0.84 (0.45-0.97)	0.76 (0.28-0.96)	0.97 (0.61-1.00)

Table 10. Number of detection outcomes for western gray squirrels (Species A) and fishers (Species B) across 3 forest stand types using remote camera data collected in the northern Sierra Nevada Mountains of California over a 44-week period in 2017.

Detection Outcome	**Black Oak**	**Conifer**	**Tanoak**
Neither Present	3	4	0
Only A Present	6	1	2
Only B Present	4	4	4
Both Present	15	20	22

DISCUSSION

Generally, the occupancy probabilities for all 3 species were high across all stand types, but patterns of occupancy among stand types varied by species. Douglas squirrel probability of occupancy was at or close to 1.0 for all 3 stand types. Standard error and confidence intervals could not be accurately quantified for black oak and conifer stands due to the high level of detection. In occupancy models, when a species is detected at all (or most) of the sites sampled, the maximum likelihood estimates for the parameters are inflated because occupancy is equal to 1.0 for that species, and therefore the numerical estimate of the Hessian used to compute asymptotic standard error values is in-valid (J. Andrew Royle, personal communication). Gray squirrel occupancy probability was lower than Douglas squirrel overall but still relatively high. While there was some overlap between site occupancy estimates for gray squirrels between stand types, average occupancy was highest in tanoak in stands. The index of the probability of occupancy for fishers was similar to that of gray squirrels; there was overlap in site occupancy estimates, but average occupancy was highest in tanoak stands. My prediction that forest stands with a tanoak component would have the highest probability of occupancy by tree squirrels was supported for gray squirrels, but not for Douglas squirrels. Additionally, my prediction that fisher stand use would be highest in stands with the greatest tree squirrel occupancy was supported for gray squirrels in tanoak stands, but not supported in black oak and conifer stands, or for Douglas squirrels. The findings for occupancy of gray squirrels supports my hypotheses that tree squirrel abundance is influenced by the mast production potential of a stand. My hypothesis that fisher stand use is influenced by tree squirrel abundance was only supported for gray squirrels in tanoak stands. Elevation was an important descriptor of occupancy and site use for gray squirrels and fishers, while Douglas squirrel occupancy was very high regardless of elevation.

Time was not included as a descriptor of detection probability, as the bait variable explained any heterogeneity in detection seen across the study period, except for in week 44. Detection probability was significantly lower in the final week than previous weeks for all 3 species because of the timing of camera removal. The final survey week was only 1 to 3 days long for all survey stations. Patterns in detection probabilities between stand types were evident for all 3 species. Douglas squirrels had high rates of detection overall, with the highest occurring in conifer stands. Average detection probabilities for Douglas squirrels overlapped in black and tanoak stands, suggesting the species of masting hardwood in a stand does not affect detection of Douglas squirrel, contrary to my prediction. Gray squirrels had lower probabilities of detection than Douglas squirrels overall. Detection of gray squirrels varied between stand types, with the highest probability of detection occurring in tanoak stands, followed by black oak stands, which supports my prediction that detection probability of gray squirrels would be highest in tanoak stands. The findings for detection of gray squirrels support my hypothesis that tree squirrel abundance is influenced by mast production capacity. Fishers had the lowest probability of detection overall. Similar to gray squirrels, fisher detection was highest in tanoak stands. However, unlike gray squirrels, fisher probability of detection was lowest in black oak stands, indicating my prediction that fisher patterns of detection between stand types would mirror that of tree squirrels was only supported for gray squirrels in tanoak stands. The findings for detection of fishers partially support my hypothesis that fisher stand use is influenced by tree squirrel abundance. For all 3 species, bait increased the probability of detection in all stand types, with the greatest increase in detection occurring for fishers.

There were no differences in pattern of habitat use to investigate between fishers and Douglas squirrels given the high rates of occupancy and detection for Douglas squirrels in all stand types. Further investigation into the patterns of occupancy and detection between fishers and gray squirrels partially supported my prediction that fisher stand use would be conditional on tree squirrel occupancy. There was relatively equal support for conditional and unconditional models of occupancy between gray squirrels and fishers. Potentially, a model with conditional occupancy ranked highly among unconditional models because of the descriptive power of the detection variables included, as well as the elevation variable for occupancy. Alternatively, conditional occupancy may be occurring between gray squirrels and fisher, but because the majority of the detection outcomes observed across all of the sites was either “Species A Absent” or “Neither Species Present” (Appendix L), I may not have had the power to detect it in this dataset. There is strong evidence to suggest unconditional occupancy is occurring between gray squirrels and fishers, and it is likely that gray squirrels and fishers show similar habitat use patterns for reasons independent of each other. The findings that include both conditional and unconditional occupancy between these two animals does not support yet cannot reject my hypothesis that fishers use stands with the greatest tree squirrel abundance.

Insights into Abundance

Although I did not aim to measure abundance or any index of abundance directly, there is evidence that measured estimates of occupancy and detection probability of a species reflect abundance. There are many possible causes of variation in occupancy and detection probability, all of which researchers attempt to account for in models. It's likely, however, that the most important source of heterogeneity in occupancy and detection probabilities estimated using occupancy models is local abundance (Gaston et al. 2000, Royle and Nichols 2003). Several researchers have used an occupancy framework to estimate species demographics related to abundance (Thorn et al. 2011, Kalle et al. 2014, Clare et al. 2015, Parsons et al. 2017). Similar patterns for both occupancy and detection were evident for each squirrel species, and these metrics together strongly indicate a relationship to abundance.

If occupancy and detection probabilities of Douglas squirrels reflect abundance, the findings of this study suggests that Douglas squirrels are likely highly abundant across the study area, and conifer stands likely support the highest levels of abundance, though only marginally higher than black oak and tanoak stands. Given their relatively small home range size (Koford 1982), Douglas squirrels may also occur in high densities in the study area. Other studies in the West have reported relatively high local abundance and moderately high densities of Douglas squirrels (Waters and Zabel 1998, Carey 2000, Ransome and Sullivan 2002). The territorial behavior of Douglas squirrels may affect the spacing of individuals such that there is some limit on local densities, and those densities will vary with food availability (Steele 1999).

Douglas squirrels are generally conifer cone seed specialists (Steele 1999, Carey 2001), thus it is not surprising that these squirrels would be most abundant in conifer dominant stands. Additionally, all of the established stand types included a mixed conifer element, so the inference that abundance would be relatively high regardless of the presences of masting hardwoods is supported because conifer cones were readily available at all of the sites, regardless of stand type. All of the stands also had a moderately sized minimum average QMD, meaning all sites, regardless of stand type, contained larger trees that could potentially produce more cones, potentially supporting high Douglas squirrel abundance (Buchanan et al. 1990). The occupancy and detection probabilities I estimated for Douglas squirrels support the inference of relatively high local abundance in all stand types.

If occupancy and detection probabilities of gray squirrels reflect local abundance, the findings here suggest that abundance is highest in stands with a higher proportion of masting hardwoods, and tanoak stands have the greatest abundance overall. Low to moderate densities of gray squirrels have been reported in California (Asserson 1974, Gilman 1986), with high densities reported in areas with large amounts of mast producing trees (Ingles 1947), and comparatively low densities in Washington (Vander Haegen et al. 2005). Acorns may become more important than other food sources, such as berries or fungi, during summer and fall in preparation for overwintering (Stienecker and Browning 1970). The hardwood dominant stands in the study area could potentially support a higher abundance of gray squirrels than conifer dominant stands because of the increased number of acorns available. Additionally, hardwoods play a critical role in maintaining fungal diversity (Massicotte et al. 1999). Consequently, hardwood stands may have also provided better access to fungal food resources as they contain a greater proportion of hardwoods compared to conifer stands. Higher acorn abundance, coupled with increased diversity of fungi and availability of conifer seeds, would likely support higher abundances of gray squirrels in hardwood dominant stands.

The presence of hardwoods in mixed conifer forests may also help promote nesting opportunities for gray squirrels (Gregory et al. 2010). Gray squirrels use cavities in oak trees for natal dens almost exclusively when they are available (Cross 1969, Linders 2000). Decay tends to occur earlier in black oak than in other oak species (Hepting et al. 1940), and larger trees tend to be older and therefore more susceptible to cavity formation. The survey stands had a moderate minimum average QMD, meaning there was a high potential of cavity availability in black oak stands. Stands containing a higher proportion of black oaks could potentially support a greater abundance of gray squirrels than conifer dominant stands due to better combined access to food and quality nesting resources.

Insights into Use

The study design did not meet the assumptions of spatial or temporal closure for fishers necessary for estimating true occupancy, therefore direct inference regarding abundance based on detection probabilities cannot be made. Detection probabilities very likely reflect use levels of the immediate area surveyed (Kleist et al. 2007). The clear pattern of detection probability for fishers in different stand types likely reflects the level of use within different stand types. This “use” may be one individual revisiting a site on numerous occasions, multiple individuals using the site, or some combination of the two. The distinction here is not necessarily important as I aimed to show that use patterns between tree squirrels and fishers would be similar in different stand types. The pattern of use observed via detection probabilities suggests highest use-levels by fishers in tanoak stands, followed by conifer stands, with lowest levels of use occurring in black oak stands.

The low level of use by fishers observed in black oak stands was unexpected given the extensive literature supporting the importance of black oaks for fishers in California (Truex et al. 1998, Yaeger 2005, Zielinski et al. 2004a, 2010, Niblett et al. 2015), and given the higher detection rates of gray squirrels in black oak stands compared to conifer stands. The low detection probabilities observed for fishers may reflect the physical use of a stand, not necessarily just the number of revisits. That is to say, detection probability may be linked to the amount of actual movement occurring throughout the period of time a stand was being used.

Individual fishers may move around less in black oak stands because they use these stands most often for their structural component (e.g., cavities, large snags etc.). Cavities are extremely important to denning females, and hardwoods are very often the types of trees selected for natal dens (Paragi 1996, Thompson et al. 2007). Cavities and structures such as broken tops that are often found in larger hardwoods such as black oaks are also used by fishers for resting, both in live trees and standing dead trees (Gess et al. 2013). Fishers may use black oak stands as often as any other stand, but may be more stationary in them, and therefore detected less often. An animal may have memories or a “cognitive map” of cavities or structures that have been used in the past for denning or resting within their home range (Powell 2012), requiring less movement to reach suitable sites within stands when animals are present there. Fishers may have been detected more often in tanoak stands than black oak stands because they move around more in tanoak stands, potentially for foraging, or to alleviate pressures of predation and competition.

There is very little reported in peer reviewed literature regarding basic information about the species associations and ecological functions of tanoak (Cobb et al. 2013). The species is a shade tolerant tree that can form multi-storied canopies with other dominant overstory species (Dillon et al. 2013), and can be a very important component of canopy structure (Cobb et al. 2012). California bay laurel (*Umbellularia californica*), Pacific madrone (*Arbutus menziesii*), and big leaf maples (*Acer macrophyllum*) are some species commonly associated with tanoak in mixed conifer forests, often creating diverse thick under- and mid-story layers (Rizzo et al. 2005). Multi-storied and structurally diverse canopies are thought to have positive effects on many different wildlife species, and the botanical diversity also provides rich food resources for many different taxa.

Tanoak stands can be very productive in terms of fungal diversity and biomass (McFarland and Largent 2001, Bergemann and Garbelotto 2006), and are also pollinated by a diverse community of insects (Wright and Dodd 2013). Fishers in the Sierra Nevada Mountains are opportunistic predators that eat birds, reptiles, insects, and hunt small mammals including moles, mice and rats (Zielinski 1999, Zielinski and Duncan 2004, LoFroth et al. 2010, Facka, unpublished data). The results of this study support high abundance of tree squirrels in tanoak stands, and these stands likely support abundant numbers of other types of fisher prey. Fishers may be moving actively throughout tanoak stands to obtain different prey resources, therefore making them more detectable; and fishers will take larger prey items like gray squirrels when they are encountered. This might explain the high detection rates of fishers in tanoak stands, supporting the hypothesis that fishers use diverse stands while foraging including those with a masting hardwood component.

If tanoaks do support a large and diverse prey base for fishers, there is possibility for conspecific competition in those stands. Fishers tend to exhibit intrasexual territoriality, where male home ranges will overlap extensively with multiple female home ranges, while females’ home ranges tend not to overlap or do only somewhat (Powell 1993). More recent research conducted in northern California has shown that female fishers can have overlapping home ranges, especially amongst closely related individuals, and this may be influenced by abundant food resources (Rennie 2015). If tanoak stands are occurring in areas of home range overlap, individual fishers may actively avoid each other spatially and temporally, possibly resulting in more movement within a stand, and therefore increasing the probability of detection.

Similar to fishers, other carnivores such as gray fox (*Urocyon cinereoargenteus*) and bobcat (*Lynx rufus*) may use tanoak stands in order to access a diverse prey base. Fishers in southern Oregon and northern California were found to occupy the same habitats as gray fox, likely causing interspecific competition observed via increased site turnover by foxes at sites occupied by fishers (Green et al. 2018). If individual gray foxes and fishers are using the same tanoak stands to access prey, fishers may increase their movement to avoid direct competition, and as a result be detected more often. Bobcat, which are a major cause of mortality for fishers in California (Gabriel et al. 2015), may also use tanoak stands to access prey. Fishers may also increase their movement to avoid possible predation by bobcat, and therefore be detected more often in tanoak stands.

Insights into Co-occurrence

The results of this study do not support or refute either unconditional or conditional patterns of occupancy by gray squirrels and fishers, therefore there is some uncertainty around making inferences from these results. It is likely that fishers in the study area used stands regardless of the presence or absence of gray squirrels. In areas where food resources are limited or have a patchy distribution, habitat use may be most strongly influenced by the availability of food in a particular area (Osenberg and

Mittelbach 1996, Pöysä 2000). Due to the opportunistic predatory behavior of fishers in their western range, suitable prey resources are likely available in most habitats. Gray squirrels would be highly ranked when available because of their large body size compared to other prey items, and therefore taken in greater proportion than other prey when locally abundant. In habitats where preferred prey are not locally abundant, given the presence of other suitable resources, lower ranked prey items will be taken (Johnson et al. 2009).

The results of this study suggest that tree squirrels are abundant and therefore available to fishers within different stand types, and past research in this study area has shown that other small mammal species are also locally abundant (Facka et. al, unpublished data). It is reasonable to assume that this area is not food limited for fishers, and that they can obtain suitable prey items regardless of the stand types they utilize, and therefore are not using habitat based on the presence of Douglas or gray squirrels specifically. Fishers may select stands with generally abundant prey resources (e.g., tanoak stands), or select stands for other reasons and forage opportunistically as they move around the landscape. An investigation into the conditional occupancy for fishers and highly ranked prey may result in different patterns in other regions or habitats where species composition, abundance, and density are different from this northern California study area. In particular, patterns of conditional occupancy and detection between fishers and highly ranked prey may be more apparent in regions where food resources are limited.

Patterns of conditional occupancy and detection between gray squirrels and fishers might not have been observed because occupancy may not be the appropriate metric to interpret patterns of habitat use between tree squirrels and fishers. Ecological interactions are extremely complex, and although the inclusion of covariates for occupancy and detection were used to clarify these complexities, a large amount of uncertainty can arise due to sampling design (Cressie et al. 2009). The scale of the sampling scheme in this study may have been too large to observe any real patterns of occupancy or detection. Sampling of additional sites, making sampling occasions shorter (i.e., one day versus one week), or a combination of the two, may have allowed for more observable patterns of occupancy and detection between gray squirrels and fishers (He and Gaston 2000). Ultimately, occupancy analyses do not allow direct observation of abundance and the distribution of abundance cannot be identified using occupancy models (Welsh et al. 2013). Further investigation into the patterns of habitat use for fishers relative to the availability of gray squirrels is needed for a clearer resolution of the relationship between the two species. This could be addressed using direct measures of abundance for gray squirrels, which are more feasible to obtain using non-invasive than mark-recapture methods given the low trap success often observed for this species. For fishers, investigating habitat selection in relation to gray squirrel abundance across the landscape using radio collar data would be a feasible way to address the question of how gray squirrels influence fisher habitat use.

Limitations and Utility

This research had some limitations that could be improved upon for future studies. This study was relatively long at 44 consecutive weeks, but because I only sampled for one year, I have no measure of how occupancy and detection probability may vary over a longer time scale. Inference from the results of camera trap studies, and occupancy studies in general, are much stronger if sampling occurs at the same sites over multiple years, as this can allow for estimates of extinction and colonization of species at each site (O'Connell and Bailey 2011). A measure of the turnover rates for occupied sites between different years for all 3 species may have revealed stronger or weaker patterns of occupancy and detection in different stand types, which may have allowed for a better understanding of how hardwoods influence space use for the 3 species of interest. Additionally, the amount of mast produced by tanoaks and black oaks in California can vary significantly from year to year (Roy 1962), so a multi-year sampling scheme would be required to account for that variation and its effects on tree squirrel occupancy.

Fisher detections may have been relatively low due in part to the bait that was used. In-shell walnuts and peanut butter were chosen to attract tree squirrels primarily, and fishers only secondarily. Nuts and peanut butter are atypical bait types to attract carnivore species, and the effectiveness when compared to other more common bait types, such as chicken, has not been tested. I also did not utilize a scent lure, which is often used when surveying for or trapping fishers. Detections of fishers may have been higher if I had used a different bait and a scent lure. Empirically testing how bait types affect fisher detection probability should be considered in future studies using an atypical bait.

Remote camera studies are extremely useful and relatively easy to implement, but a major limitation in this type of research is species classification in photographs collected. Species with similar morphological features can be difficult to distinguish from one another, creating some level of uncertainty in species identification (Meek et al. 2013). Douglas and gray squirrels can be difficult to distinguish in photographs, especially if part of the animal is not fully in frame. Additionally, small, fast moving animals like squirrels are also more difficult to properly identify using remote cameras than larger animals (Glen et al. 2013), meaning some mis-identification of squirrel species may have occurred. Using expert observers to perform photo classifications may help mitigate these issues. However, classification of similar looking species from remote cameras by a single or few observers may be unreliable, and it is recommended that a minimum of 5 expert observers individually classify all photos to minimize misidentification errors (Hodges 2018). Misclassification rates will likely be higher when non-experts, such as volunteers, are classifying photos (McShea et al. 2016, Swanson et al. 2016). I was the single “expert” observer in my research, and several non-expert volunteers assisted in some photo classification; as a result there was the potential for a low level of error in species identification. Douglas and gray squirrels were generally easy to distinguish in the photographs analyzed, however, so misclassification error was likely very low and would not have affected the detection results. Future studies using remote cameras should consider the limitations of single-observer and volunteer-based classification of photographs, and attempt to include some measure of error for each observer.

Although direct inference from this research is limited, this study provides solid evidence that masting hardwoods are an important habitat component for several wildlife species. Specifically, species such as tanoak that are considered non-merchantable (Kizha et al. 2015) should not be discounted as unimportant for the ecological function of higher order mammals such as carnivores. Relative to forest management, this study indicates that moderate levels of masting hardwoods may be very important. I also presented a relatively inexpensive sampling scheme for surveying squirrels and other small mammals with remote cameras. I collected thousands of photographs of target and non-target species, including medium-to large-sized carnivores, using only in-shell walnuts and peanut butter as (long-lasting) bait. The utility of this sampling scheme could be significant in many studies using remote cameras to survey for a diverse suite of wildlife species.

MANAGEMENT IMPLICATIONS

Managed landscapes in western North America are subject to high levels of disturbance from urbanization, timber harvest, and wildfire. Tree squirrels are not only important prey for fishers in their western range, but also for many other carnivores such as coyotes (*Canis latrans*) (Bekoff and Gese 2003), gray foxes (Cypher 2003), American marten (*Martes americana*) (Powell et al. 2003), and bobcat (Anderson and Lovallo 2003). Habitat management efforts to maintain high densities and abundances of tree squirrels should have positive ecological effects. Land managers in western North America working to conserve fisher populations must understand how changes in the availability or quality of important prey habitat will impact fisher space use. This information can directly inform forest management practices and aid in selection of quality sites for future translocation efforts.

I recommend that land managers of mixed conifer forests in northern California maintain hardwood diversity on the landscape whenever possible to benefit wildlife species. More specifically, larger, older hardwoods that produce mast and provide quality structure for animals should be left standing during timber harvest or other land management activities. Herbicide spraying of commercially undesirable species such as tanoak after timber harvest should be done sparingly and with careful consideration; allowing some stands to maintain younger tanoak trees for regeneration will help ensure the persistence of the species across a landscape susceptible to high levels of disturbance from wildfire and climate change.

Wide-scale, long term monitoring of wildlife with remote cameras is becoming much more common as the technology advances and camera units have become more affordable and efficient, and as analytical tools for these types of data improve. Researchers and land managers that have remote cameras available to them could easily implement long-term monitoring programs using a similar protocol as the one described here, at a relatively low cost. Using inexpensive bait such as nuts and peanut butter, a large diversity of wildlife species could be monitored for changes in detection, occupancy, colonization, extinction, and even abundance, across years in almost any upland habitat.

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PERSONAL COMMUNICATIONS

Pease, George. 2017. Humboldt State University, Department of Forestry. 1 Harpst St. Arcata, CA 95521.

Royle, J. Andrew. 2018. United States Geological Survey, Patuxent Wildlife Research Center. 12100 Beech Forest Rd. Laurel, MD 20708.

APPENDICES

Appendix A. List of variables used, their definition, and possible responses for classification of photographs from remote cameras used to survey for tree squirrel and fisher in the northern Sierra Nevada Mountains of California in 2017. Variables selected were considered a priori to photo classifications.

Variable	Responses and Definition
Bait Tree Centered	Y:Bait tree more or less in center of frame, both sides of tree visible N: One or both side of the bait tree not visible
Ground Visible	Y: Ground around the base of the tree visible N: Ground not visible; ground visible but base of tree not in frame
Peanut Butter	Y: There was visible peanut butter on the bait tree N: There was no visible peanut butter on the bait tree
Walnuts	Y: There were walnuts remaining on the nut ring N: There were no walnuts remaining on the nut ring
Fisher Collar[a]	Y: The fisher in the photograph(s) was collared N: The fisher in the photograph(s) was not collared

[a] This variable only recorded for photographs classified as fisher for the species detected

Appendix B. Explanation of protocol used for counting number of hardwood trees in a stand differing from the dominant hardwood species present in stands surveyed for tree squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017.

1. Stand with your back to the <u>bait</u> tree, facing out towards the stand.
2. Hold the prism a comfortable distance away from the eye with the bottom edge parallel to the ground, sight trees through the prism approximately 1.5 m above the ground.
3. Sweep the prism across your line of sight as you slowly encircle the tree. Count all hardwood trees that are “in” or “borderline” and note the species. Do this until you are back in your starting position. Don’t count trees >50 m away from you.
4. Write the number of each “in” and “borderline” tree for each species in the NOTES section of the station check form when you pull the camera.

In tanoak stand: only count black and/or live oak trees; in black oak stand: only count tanoak and/or live oak trees; in conifer stand, count tanoak, black oak, and/or live oak trees.

“In”, count it

“Borderline”, count it

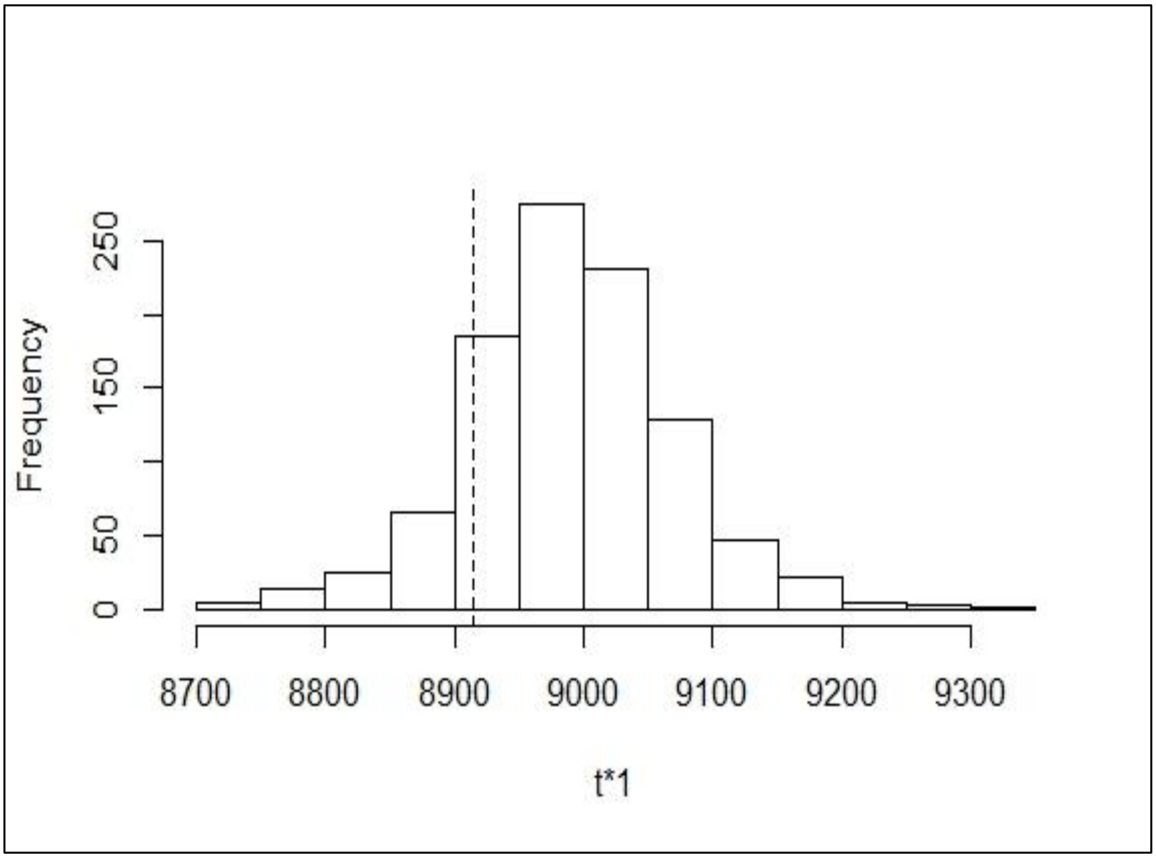
“Out”, don’t count it

Appendix C. List of 21 species (generally in order of number of photos captured, from greatest to least) observed at 85 remote cameras deployed in the northern Sierra Nevada Mountains of California for 44 weeks in 2017.

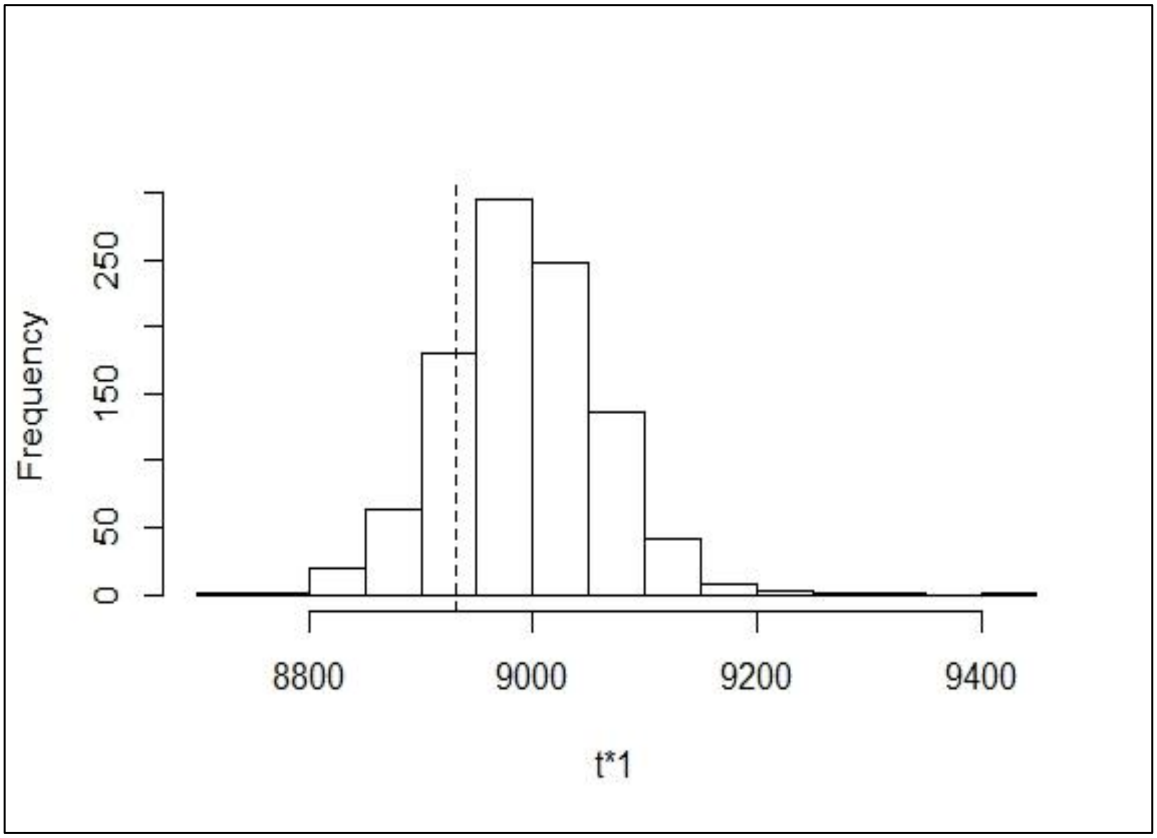
Common Name	**Scientific Name/Order**
Black bear	*Ursus americanus*
Gray fox	*Urocyon cinereoargenteus*
Fisher	*Pekania pennanti*
Black-tailed deer	*Odocoileus hemionus*
Woodrat	*Neotoma spp.*
Deer mouse	*Peromyscus spp.*
Douglas squirrel	*Tamiasciurus douglasii*
Western gray squirrel	*Sciurus griseus*
Humboldt flying squirrel	*Glaucomys oregonensis*
California ground squirrel	*Otospermophilus beecheyi*
Chipmunk	*Tamias spp.*
Ringtail	*Bassariscus astutus*
Raccoon	*Procyon lotor*
Striped skunk	*Mephitis mephitis*
Western spotted skunk	*Spilogale gracilis*
Bobcat	*Lynx rufus*
Mountain lion	*Puma concolor*
Domestic dog	*Canis lupus familiaris*
Song bird	Passeriformes
Game bird	Galliformes
Woodpecker	Piciformes

Appendix D. Photographs of 3 target species (Douglas squirrel, western gray squirrel, and fisher respectively) captured on remote cameras in the northern Sierra Nevada Mountains of California in 2017.

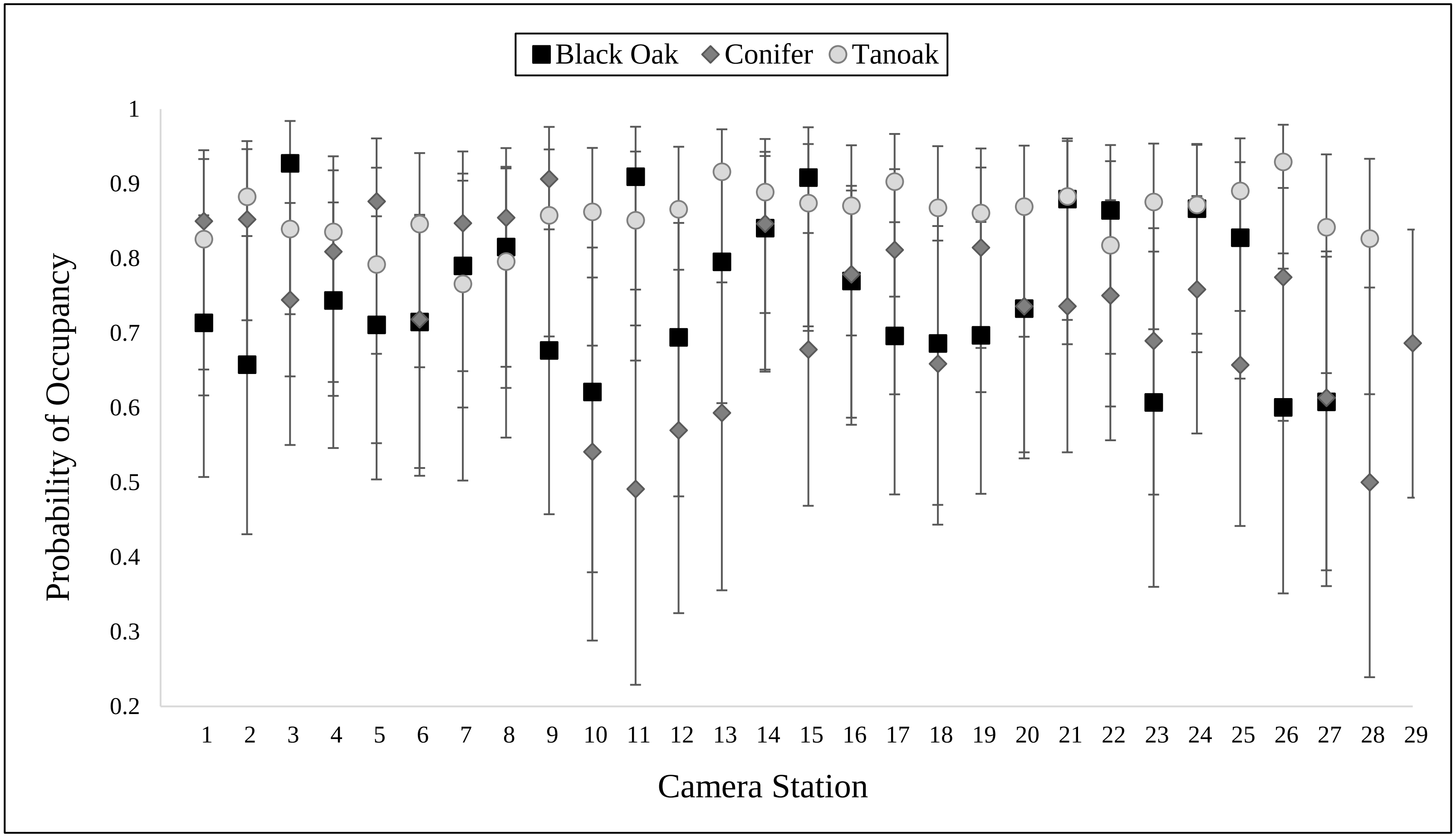
Appendix E. Results from a chi-squared parametric bootstrap (n = 1000 simulations) goodness of fit test on a global single-season occupancy model for tree squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017.



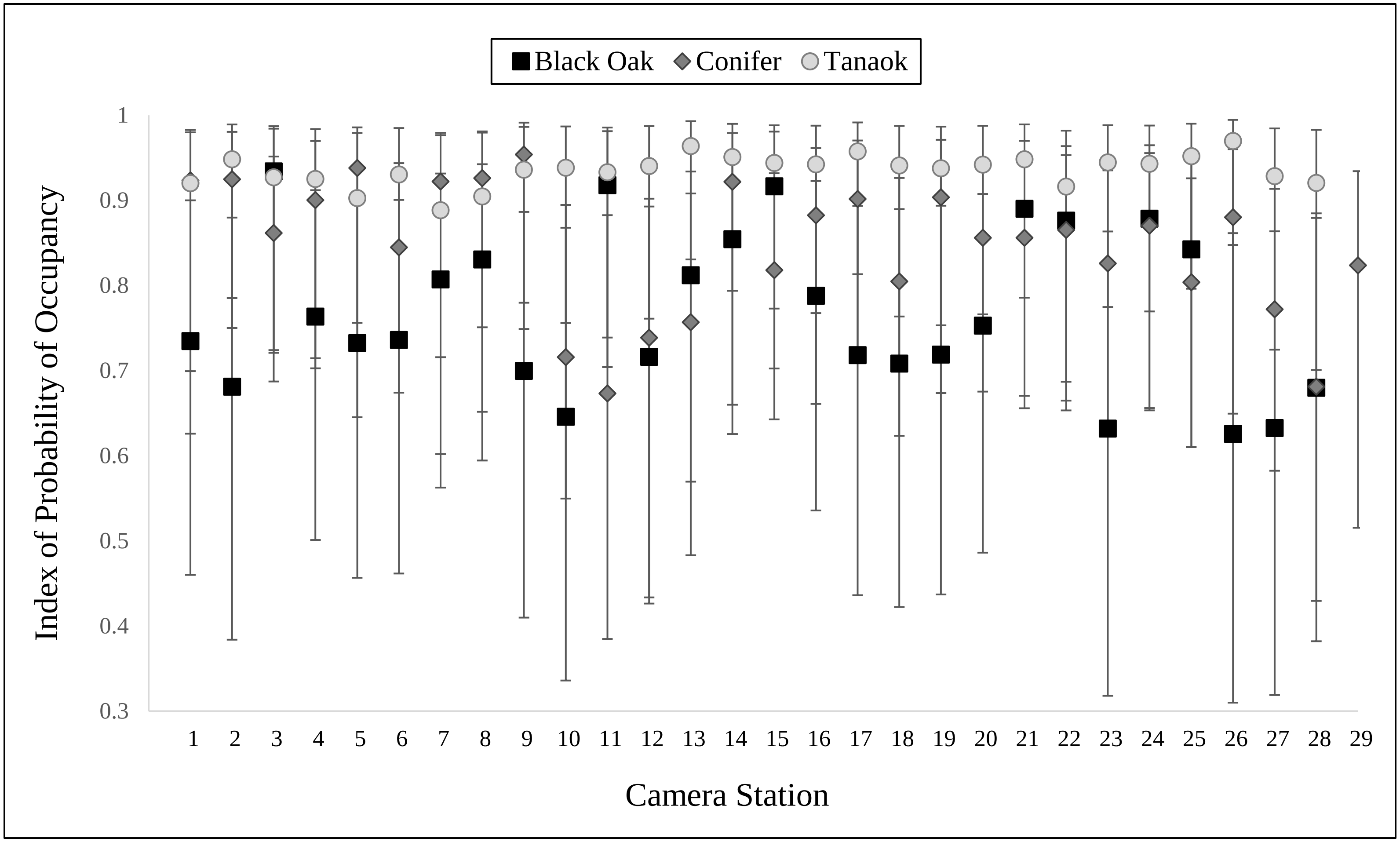
Appendix F. Results from a chi-squared parametric bootstrap (n = 100 simulations) goodness of fit test on the top single-species occupancy model based on AIC ranks for tree squirrels and fishers in the northern Sierra Nevada Mountains of California in 2017.



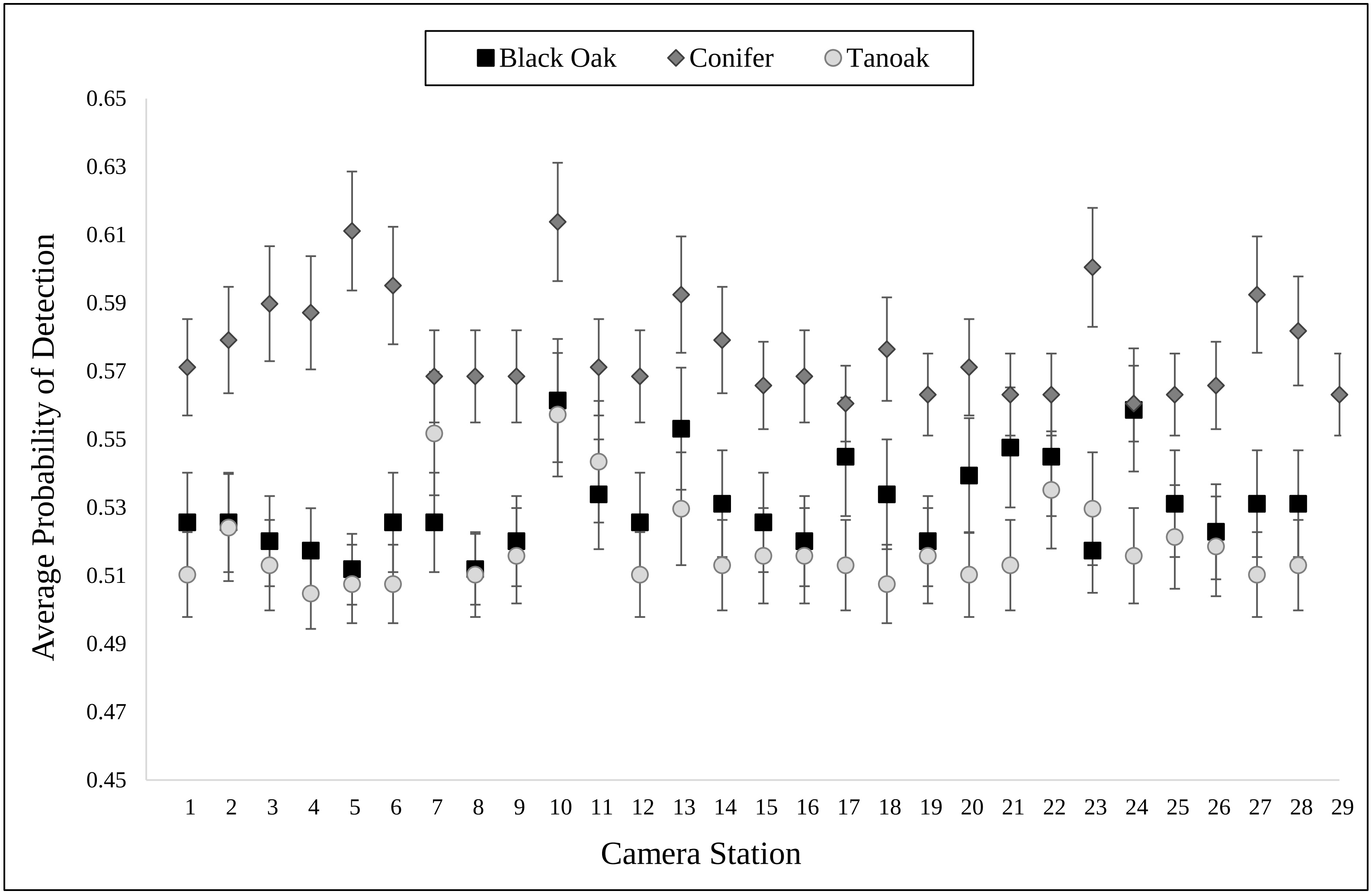
Appendix G. Site specific occupancy probabilities ±95% confidence intervals for western gray squirrels at 85 sites across 3 forest stand types, estimated from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017.



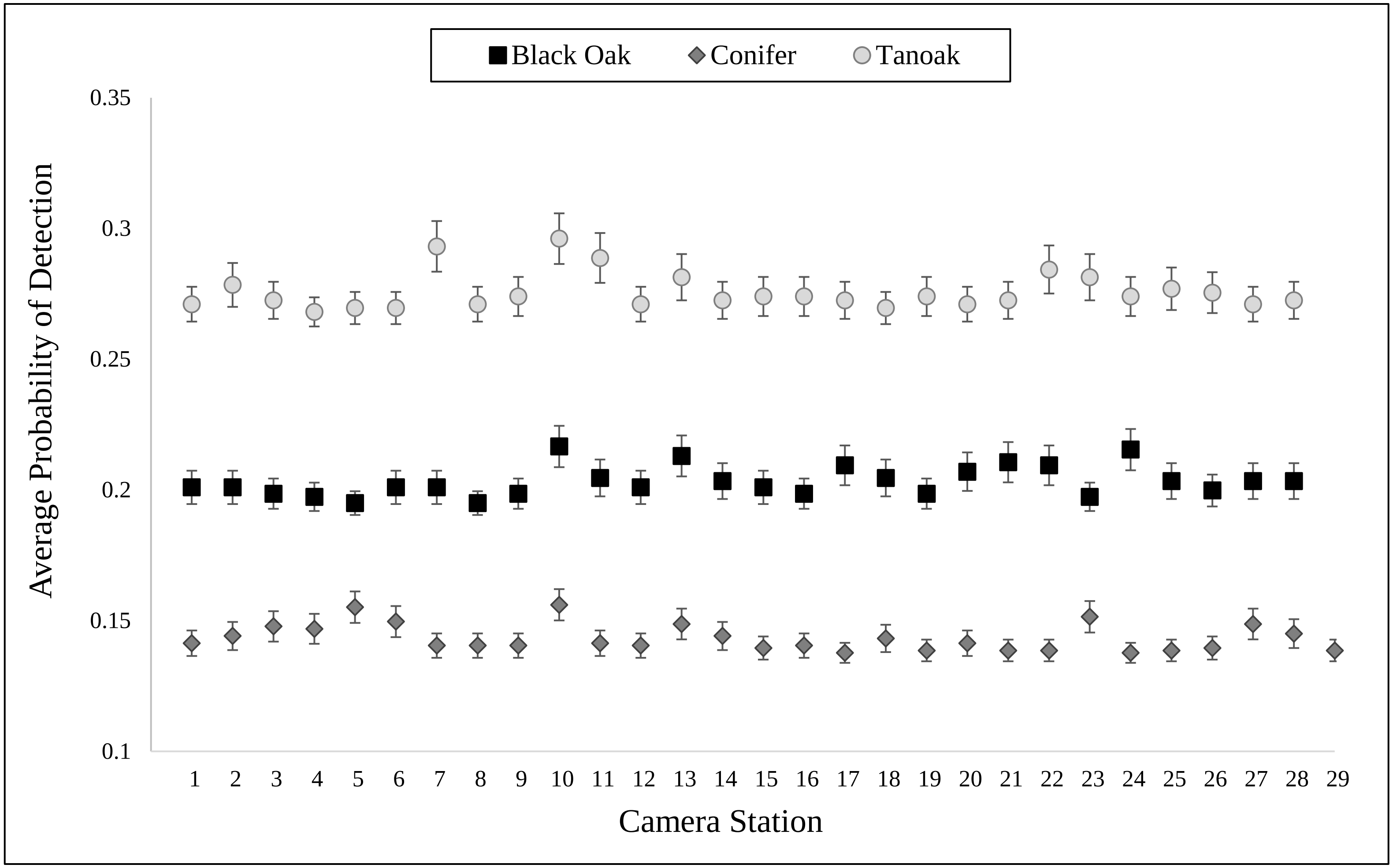
Appendix H. Site specific index of occupancy probabilities ±95% confidence intervals for fishers at 85 sites across 3 forest stand types, estimated from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017.



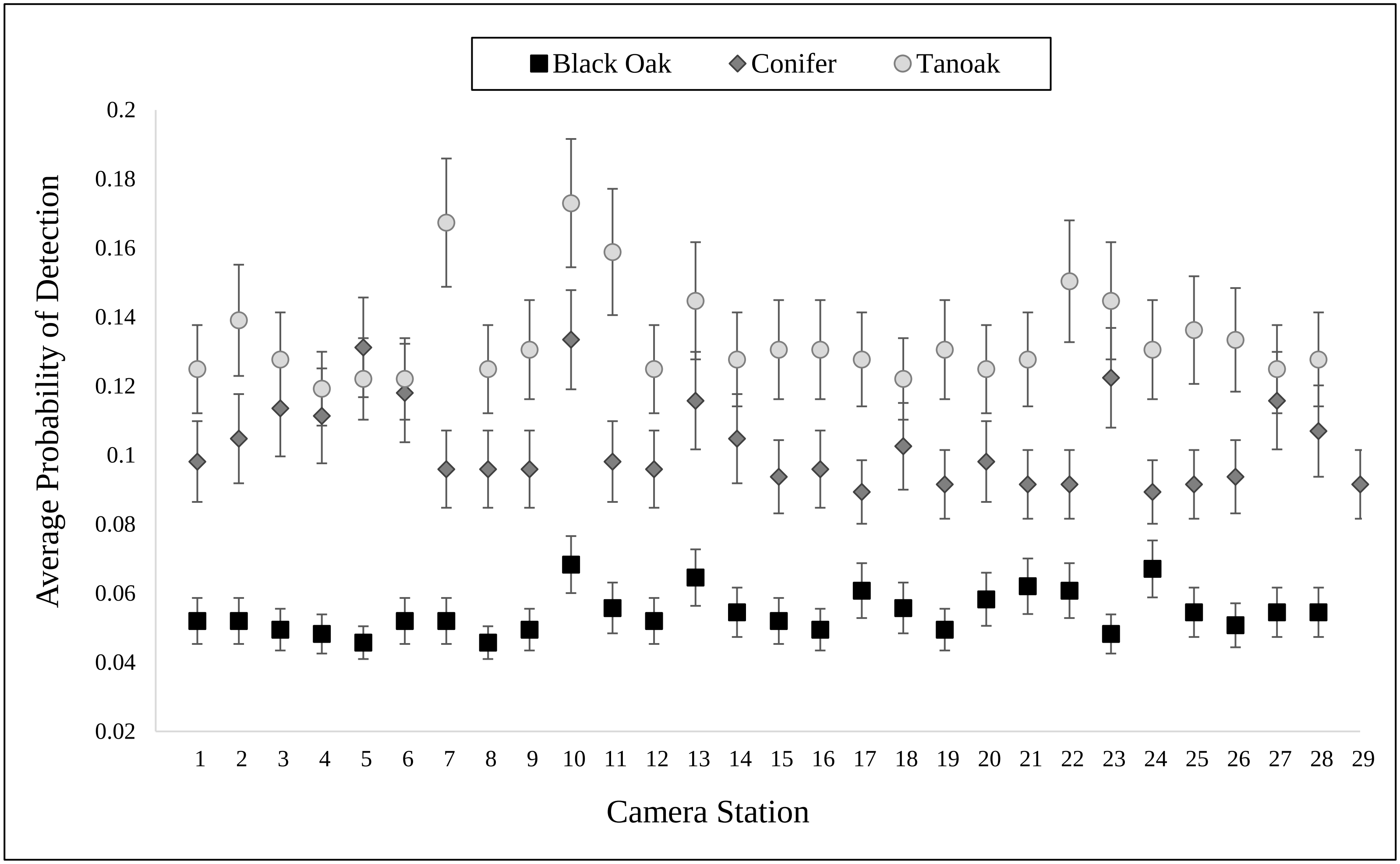
Appendix I. Average site-specific probability of detection ±95% confidence intervals of Douglas squirrels at 85 sites across 3 forest stand types, estimated from remote camera data collected in the northern Sierra Nevada Mountains of



Appendix J. Average site-specific probability of detection ±95% confidence intervals of western gray squirrels at 85 sites across 3 forest stand types, estimated from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017.



Appendix K. Average site-specific probability of detection ±95% confidence intervals of fishers at 85 sites across 3 forest stand types, estimated from remote camera data collected in the northern Sierra Nevada Mountains of California in 2017



Appendix L. Detection data for western gray squirrels (Species A) and fishers (Species B) collected at 85 sites across 3 forest stand types, calculated from remote camera data collected in the northern Sierra Nevada Mountains of California over a 44-week period in 2017.

Site	Stand Type	Species A Absent	Neither Present	Only B Present	Species A Present	Only A Present	Both Present
1	Black Oak	37	37	0	2	2	0
2	Black Oak	32	32	0	8	8	0
3	Black Oak	20	18	2	1	0	1
4	Black Oak	26	25	1	0	0	0
5	Black Oak	10	10	0	11	9	2
6	Black Oak	37	34	3	0	0	0
7	Black Oak	29	29	0	8	8	0
8	Black Oak	16	16	0	4	4	0
9	Black Oak	32	32	0	0	0	0
10	Black Oak	31	26	5	4	4	0
11	Black Oak	37	36	1	5	5	0
12	Black Oak	16	16	0	20	19	1
13	Black Oak	41	37	4	1	0	1
14	Black Oak	38	33	5	4	3	1
15	Black Oak	29	27	2	6	6	0
16	Black Oak	37	34	3	0	0	0
17	Black Oak	25	22	3	9	9	0
18	Black Oak	39	39	0	0	0	0
19	Black Oak	39	38	1	0	0	0
20	Black Oak	21	20	1	2	2	0
21	Black Oak	18	18	0	15	14	1

Site	Stand Type	Species A Absent	Neither Present	Only B Present	Species A Present	Only A Present	Both Present
22	Black Oak	32	31	1	10	8	2
23	Black Oak	25	25	0	6	6	0
24	Black Oak	39	38	1	2	2	0
25	Black Oak	15	15	0	26	25	1
26	Black Oak	36	36	0	0	0	0
27	Black Oak	29	29	0	2	2	0
28	Black Oak	34	33	1	5	5	0
1	Conifer	32	31	1	10	10	0
2	Conifer	35	29	6	2	1	1
3	Conifer	34	25	9	2	1	1
4	Conifer	38	33	5	4	3	1
5	Conifer	29	25	4	13	11	2
6	Conifer	32	30	2	7	7	0
7	Conifer	38	38	0	3	3	0
8	Conifer	43	28	15	1	1	0
9	Conifer	27	21	6	16	9	7
10	Conifer	33	31	2	7	6	1
11	Conifer	27	26	1	10	10	0
12	Conifer	34	33	1	1	1	0
13	Conifer	29	28	1	11	10	1
14	Conifer	30	30	0	0	0	0
15	Conifer	37	33	4	0	0	0
16	Conifer	18	17	1	2	2	0
17	Conifer	12	10	2	1	1	0

Site	Stand Type	Species A Absent	Neither Present	Only B Present	Species A Present	Only A Present	Both Present
18	Conifer	24	19	5	0	0	0
19	Conifer	33	32	1	0	0	0
20	Conifer	25	24	1	5	5	0
21	Conifer	37	36	1	0	0	0
22	Conifer	22	20	2	1	1	0
23	Conifer	27	27	0	10	9	1
24	Conifer	35	30	5	1	1	0
25	Conifer	39	38	1	3	2	1
26	Conifer	37	37	0	0	0	0
27	Conifer	36	36	0	0	0	0
28	Conifer	38	38	0	0	0	0
29	Conifer	36	35	1	1	1	0
1	Tanoak	44	33	11	0	0	0
2	Tanoak	26	22	4	13	13	0
3	Tanoak	41	38	3	3	3	0
4	Tanoak	13	10	3	7	5	2
5	Tanoak	19	18	1	10	9	1
6	Tanoak	32	30	2	5	5	0
7	Tanoak	34	25	9	8	5	3
8	Tanoak	15	13	2	3	3	0
9	Tanoak	11	10	1	8	8	0
10	Tanoak	39	39	0	3	3	0
11	Tanoak	22	20	2	18	16	2
12	Tanoak	19	15	4	7	5	2

Site	Stand Type	Species A Absent	Neither Present	Only B Present	Species A Present	Only A Present	Both Present
13	Tanoak	36	27	9	6	2	4
14	Tanoak	42	34	8	2	1	1
15	Tanoak	29	22	7	15	7	8
16	Tanoak	23	20	3	9	8	1
17	Tanoak	33	27	6	5	4	1
18	Tanoak	22	19	3	0	0	0
19	Tanoak	32	31	1	11	9	2
20	Tanoak	12	12	0	17	17	0
21	Tanoak	31	29	2	1	1	0
22	Tanoak	16	15	1	25	24	1
23	Tanoak	13	9	4	16	13	3
24	Tanoak	43	38	5	0	0	0
25	Tanoak	37	36	1	5	4	1
26	Tanoak	14	13	1	28	26	2
27	Tanoak	35	34	1	0	0	0
28	Tanoak	26	26	0	13	12	1