

## ABSTRACT

PACKA, AARON NEIL. Conservation Translocations as Opportunities for Scientific Advancement: A Case Study with Fishers (*Pekania pennanti*) (Under the direction of Dr. Roger A. Powell).

Humans intentionally translocate organisms to facilitate any number of management, conservation and scientific goals. Intentional translocations are subdivided into three types: the restoration of organisms into locations where they previously, but no longer, exist (reintroductions), movement of organisms into places where they never exist (introductions), or movements of organisms into places where other members of the species already exist (augmentations). For at least 30 years, researchers have recognized the importance of incorporating scientific design and evaluation into translocations. This focus on science was advocated to increase the relatively low rates of founding self-sustaining populations. Throughout the history of intentional translocations, success was defined by establishing viable populations of organisms. This concept remains important for guiding future translocations and their goals. Nevertheless, the success of a translocation should not depend exclusively on establishing viable populations. The scientific value of a translocation – the value associated with acquiring general scientific information and not strictly associated with establishing a new population – is largely ignored when determining translocation success and designing translocations.

Translocations offer unique and important opportunities to test hypotheses about organisms and natural systems. Ideally, all translocations would occur in places with optimal habitat and in places that can support high rates of population growth, high population densities, and long-term population persistence.

From 2009 to 2015, I studied a population of reintroduced fishers (*Pekania pennanti*) and their progeny on an intensively logged landscape in California. Using several different approaches, I demonstrate how well-designed and well-executed translocations provide important information that tests basic ecological and management hypotheses. I tested the hypothesis that logged timberlands can provide sufficient habitat to support the establishment of a population of fishers. Reintroduced fishers remained at the study site (>90% of all fisher locations were within 2 km of the study site) in high enough numbers to support an incipient population. Long-term patterns of survival (monthly survival > 0.95) and reproduction indicate a stable to increasing population. My results indicate that the area and habitat were sufficient to establish a population of fishers thought to be negatively affected by the effects of moderate to heavy logging

Using data from our reintroduced and another reintroduced population of fishers in Washington, I demonstrate that releasing female fishers close to the time of implantation reduces the probability that they will produce kits by 66%. Matrix population models indicate that populations with a reduction in birth rate in the year of reintroduced may have subsequent long-term population consequences, including reduced population sizes and increased probabilities of extinction.

By purposively releasing male and female fishers inside and outside of the known home ranges of other, already-released fishers, I deduce that the perceived costs of competition with conspecific are high among female fishers. Females released within the home ranges of other females traveled longer distances and established home ranges further than those released outside of conspecific competition. Males appeared indifferent to the presence of conspecifics and were likely driven by the absence of females.

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Conservation Translocations as Opportunities for Scientific Advancement: A Case Study  
with Fishers (*Pekania pennanti*)

by  
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## **DEDICATION**

I dedicate this dissertation to the working man. For every man (or woman), who puts in eight or ten hours a day of work and toil and sweat and always has someone looking down his neck trying to get more out of him than he really ought to have to put in. Johnny Cash wrote those words (or something like them) and they seem appropriate. I specifically dedicate this to men and women who worked hard so that I might have opportunities in life. I specifically wish to dedicate this to Pete Jaquez for his hard work, perseverance, and great humility.

## **BIOGRAPHY**

Aaron Facka was born in Farmington New Mexico. With any luck he will die somewhere on a mountain side taking his last breath of crisp autumn air. In between those two moments he wastes a lot of time coming up with ideas that will likely never come to fruition, following animals in the places where they live, eating good food, drinking good beer, conversing with family and friends, and trying to understand himself and the world.

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## CHAPTER 1: Introduction

In late 2008, I was invited to become a member of a collaborative project that intended to reintroduce fishers (*Pekania* [formerly *Martes*) *pennanti*) into a portion of their historic range in northern California. I had done research for my Masters of Science degree on reintroduced populations of black-tailed prairie dogs (*Cynomys ludovicianus*) in southern New Mexico and I had always been extremely curious about mustelids (mammals in the family *Mustelidae*). Thus, working on a PhD that involved both a weasel (the fisher) and a reintroduction seemed like a perfect fit for me and I accepted the invitation. I thought I knew a lot about moving and reintroducing organisms. I had spent much time thinking and reading about methods and approaches that increased the likelihood of establishing persistent populations (e.g., Griffith et al. 1989, Lomolino and Channell 1998, Wolf et al. 1998). Further, new perspectives and directions on science and reintroductions were emerging that I was eager to explore and to implement into my own research (Seddon et al. 2007, Armstrong and Seddon 2008). At the time, I knew little about fishers other than that they lived in forested parts of North America and that they were one of the few predators that routinely preyed on porcupines (*Erethizon dorsatum*). I knew virtually nothing else about their life-history, mating strategies, space-use, or their ecology. I was completely ignorant that in western North America they were a source of concern and controversy driven, in part, by conflicts between fishers and land management practices (logging) in the forests where fishers dwelled (USDI 2004, USDI 2006). In many ways, I was as ignorant about reintroductions as I was about fishers. The project I was joining was unique and innovative in diverse and important ways compared

to other reintroductions. That uniqueness would alter my own way of thinking about translocations, and specifically reintroductions, and would guide much of my dissertation research.

Our project was a collaborative venture between Sierra Pacific Industries (a private timber company), the California Department of Fish and Wildlife, the Yreka office of the United States Fish and Wildlife Service, and North Carolina State University. All four of these stakeholders were contributing different resources and ideas to the project and all had a diverse perspectives and expectation for the project. Nonetheless, all the parties were eager to learn if fishers could live on a landscape devoted primarily to logging and all were interested in expanding the range of fishers in California and the western United States. Establishing a new population would diminish the risks of more local extinctions of fishers in the Pacific states and would increase the population of fishers in northern California, thereby influencing fisher conservation both directly and positively. All parties were also convinced that careful study of the fishers at the release site would provide important insights into how fishers survive and reproduce, or did not, on landscapes that are intensively managed. All the collaborators sensed that understanding how fishers behaved in the presence of logging and on logged landscapes would be useful in predicting the likelihood that fishers could survive in other places where logging occurred and would be valuable in assessing the risks of future management activities. Thus, the information gleaned from the project about fisher management could affect regulations about the type and intensity of logging and, consequently, could affect the management, the ecology and the economics of fishers in the western United States. Of course, all the answers to all those questions are not found within this dissertation, but I

am hopeful that it is useful nonetheless.

Evaluation of the feasibility of reintroducing fishers and development of the reintroduction plan occurred before I became part of the team (Callas and Figura 2008). Ergo, much of the groundwork that supported my research was conceived, designed and initiated by the many bright and innovative people involved with the project before I came aboard (see my Acknowledgments). Consequently, I have always thought of the research presented in this dissertation as a collaboration with other folks, even though I have designed and largely carried out the research myself. For these reasons, I have chosen to write the chapters that follow in a form that reflects the collaborative aspects of the research and assumes co-authorship by several different people of published versions of the chapters.

Somewhere along my long academic journey at North Carolina State University, I began to realize that that the greatest value of this fisher reintroduction was the science that would come from it. Moreover, I was convinced that the fisher reintroduction provided an important template for other projects to consider prior to and through the development of translocations. Thus, in this dissertation, I have attempted to provide general considerations and approaches that I hope will be useful and important to other people working on translocation of all types. I've tried to build on what the people that started his project have initiated and to create a single cohesive message about how researchers, managers and others can conceive, design and execute translocations of organisms to maximize their effectiveness and value.

In chapter 2, I outline how translocations provide unique opportunities to address scientific hypotheses that resolve issues related to general questions and that are not

restricted to reintroduction science. I contend that considering translocations as opportunities for testing general hypotheses increases their value and is important for their design and implementation. In chapter 3, I discuss definitions of success in translocations relative to diverse goals that are not strictly relegated to establishing new populations. Further, I provide as an example of how we defined success and failure for our fisher reintroduction in northern California and that explains the importance of our project to fisher ecology and conservation more thoroughly. In chapters 4, 5, and 6, I test hypotheses related to the suitability of habitat for fishers on managed landscapes, to the timing of releasing fishers during reintroduction, and to the influence of conspecifics on movement and use of space by fishers. Throughout these last 3 chapters, I use both simulation models and empirical data to evaluate specific hypotheses and the effects of my research results on conservation and management of fishers and other species, especially other mammalian carnivores. Thus, the last 3 chapters provide further examples of the points I raise in Chapters 2 and 3.

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## **CHAPTER 2: Maximizing the value of conservation translocations through science**

**Abstract.** Translocations for the purposes of conservation are widely used, but often controversial, actions aimed at preserving or restoring organisms or ecosystems. Traditionally, the decision to move organisms is based on the potential conservation benefit they provide weighed against the risks to the species of concern, source and release ecosystems, or human communities and society. Yet, all translocations have scientific value and provide unique opportunities to test hypotheses relevant to diverse fields of biology. The information translocations can generate, add benefit and purpose to conservation translocations. Translocations provide control over research design including the locations organisms are moved and the number or types of co-occurring organisms. Conservation translocations are squandered when scientific questions are not a major aspect of the project or when relegated to only questions that indicate successful establishment of populations. Considering the scientific value inherent in translocations, improves translocations and conservation and, thus, should be an important aspect of their design. In particular, testing scientific hypotheses elucidates habitat requirements of organisms by allowing researchers to link fitness or population viability with specific environments. We advocate that researchers and managers consider the value of the science that translocations can produce, and design translocations to derive the maximum scientific value. Each translocation is an opportunity to design and conduct meaningful science. Translocations are diminished when we do not maximize this opportunity.

**Keywords:** augmentation, collaborations, experiment, habitat, reintroduction, resources, movement, species interactions, viable populations

## INTRODUCTION

Translocations of organisms for conservation or management are often controversial because the outcomes are difficult to predict and to assess, resulting in long planning and implementation processes (Pérez et al. 2012, IUCN 2013). Investments in time and resources become especially costly if translocations fail to meet their objectives, which is often the case. A relatively high percentage of all animal (33%), and an even higher percent of translocations of threatened or endangered species (47%), fail to produce viable populations (Griffith et al. 1989, Wolf et al. 1996, Seddon et al. 2012). Similar estimates (as high as 48%) are also reported for plant reintroductions (Godefroid et al. 2011). Translocations are often implemented haphazardly without consideration for the evolutionary, ecological or population level processes, or risks for the target and non-target species and systems (Sarrazin and Barbault 1996, Bullock and Hodder 1997, Pérez et al. 2012). Hence, many translocations are controversial after implementation as well (Kloor 1999, Balčiauskas and Kazlauskas 2014).

A small number of researchers and managers have advocated strongly for rigorous science to increase the probability of successfully establishing viable populations (Falk et al. 1996, Pavlik 1996, Sarrazin and Barbault 1996, Guerrant Jr and Kaye 2007, Armstrong and Seddon 2008). Yet, with respect to translocations aimed specifically at conserving threatened or endangered species or populations (hereafter conservation translocations), little consideration has been given to their potential to elucidate important, but untested scientific hypotheses (see Pavlik 1996). All translocations have

innate scientific value as natural experiments that can increase knowledge and that can address scientific questions. The potential knowledge gained from conservation translocations can resolve habitat issues, can clarify the distribution of organisms, and elucidate interactions among conspecifics, and among members of ecological communities, and between human and wild organisms (Fischer and Lindenmayer 2000, Pople et al. 2001, Hargreaves et al. 2014, Betts et al. 2015). The mechanisms that influence the abundances and distributions of organisms are central process of ecology, evolution and conservation but can be difficult to understand fully when multiple environmental, biological and human drivers affect organisms and systems simultaneously (Brown 1984, Sutherland et al. 2006, Crooks et al. 2011, Runge et al. 2014). Translocations provide valuable scientific knowledge irrespective of whether populations are established or become self-sufficient. Thus, well designed, scientifically-based translocations offer a return on investment even when some aspects fail (Pavlik 1996, Redford and Taber 2000, Knight 2006; Chapter *Broadening the definition of success*).

Endler (1980) noted that questions concerning adaptation to environments or to biotic forces are often impossible to address without well designed experiments. Nevertheless, many studies aimed at understanding translocations or natural systems are descriptive and devoid of experimental treatments or sufficient replication (Romesburg 1981, Morrison 2012, Hayward et al. 2015). Translocation provides an opportunity for well-structured research designs and experimental methodologies (e.g., Pelini et al. 2009 and Hargreaves et al. 2014). Experiments that have used translocated or transplanted organisms have provided important insight into life-history theory and adaptation to new environments

(Endler 1980, Reznick et al. 1990, Reznick and Travis 1996, Gordon et al. 2009).

Translocations have informed the movements of animals. Specifically, movement experiments have demonstrated how animals move through fragmented landscapes, select habitat, and locate themselves (Bovet 1984, Bowman and Fahrig 2002, Bakker and Van Vuren 2004, McDonald and St Clair 2004, Lawes et al. 2012, Volpe et al. 2014). Other translocation experiments have used ecological equivalents or surrogates (different taxa that perform similar ecological roles in different geographical areas) to test ideas including: release strategies relative to predation risk and foraging experiences of endangered or rare species (Powell et al. 1985, Biggins et al. 2011a, Biggins et al. 2011c). Researchers that are working on conservation translocations are in unique positions to address important and unresolved hypotheses while furthering conservation and restoration objectives. We contend that conservation translocations are squandered when scientific questions are not a major aspect of the project or when relegated to be only questions that indicate successful establishment of populations (e.g., post-release movements of animals; Fritts et al. 1984, Stüwe et al. 1998, Mosillo et al. 1999, Berger-Tal and Saltz 2014).

Many, and probably nearly all, conservation translocations are not constructed with specific hypotheses in mind beyond those that relate specifically to improving success of re-establishing populations of organisms or improvements of translocation methods (Seddon et al. 2007, Armstrong and Seddon 2008, Seddon et al. 2012). Yet, in some instances, conservation translocations have led to important insights when researchers did not propose and test specific hypotheses but did observe emergent phenomenon following the release of organisms. Stüwe and Nievergelt (1991) noted that offspring of

the Alpine ibex (*Capra ibex ibex*) that were hybridized with Nubian ibex (*C.i. nubiana*) or domestic goats (*Capra aegagrus*) were unable to establish viable wild populations. Alpine ibexes were adapted to give birth in the early spring with highest food availability whereas hybrids were born months too early and starved when food was unavailable. The translocation of large blue butterflies (*Phengaris arion*) revealed that their breeding habitat was based on coevolution with a specific ant (*Myrmica sabuleti*) (Thomas 1991, Hodder and Bullock 1997). In some instances, post-hoc analyses from the results of many translocations reveal mechanism that limit populations (e.g., Short et al. 1992, Jachowski et al. 2011). Yet, these results come only after great expense, many failures to establish populations, and long periods of time where important drivers of population limitation or viability were unknown (Griffith et al. 1989, Packer et al. 2013). We reiterate the view proffered by others, that scientists and managers should put explicit thought and energy to testing hypotheses related to translocations (Kleiman 1989, Guerrant Jr and Kaye 2007, Armstrong and Seddon 2008).

Hypothesis testing and experimental approaches in translocations lead to definitive findings that further both science and conservation. Conservation translocations are often well designed to test specific hypotheses related to translocation efficacy. For example, Pople et al. (2001) experimentally released captive-bred versus acclimatized wallabies (*Onychogalea fraenata*) and showed high rates of mortality in the captive-raised individuals. Armstrong and Perrott (2000) experimentally tested the hypothesis that Hihi (*Notiomystis cincta*) were limited by food. In rejecting this hypothesis, they eliminated a specific mechanism from further consideration and likely saved resources and time.

Facka et al. (2016) demonstrated how the timing of stressful events (release) into novel

environments reduced the birth rates of fishers (*Pekania pennanti*) and how these small reductions could have long-term population impacts. Without specific *a priori* hypotheses, observing differences in reproductive success based on timing of release could have been considered an aberrant event that occurred at one study site. Bottin et al. (2007) experimentally reintroduced 6 different populations of sandworts (*Arenaria grandiflora*) and revealed that some sites were not suitable, as previously thought, and that predation was an important limiting factor for *Arenaria*. Without experimental designs deducing mechanisms of population failure may not have been possible. Using translocations to test hypotheses aside from those related to developing translocation methods (or reintroduction science) remains a largely unaddressed aspect of moving organisms for conservation.

Hypotheses should be prominent parts of translocation plans and feasibility assessments. The discoveries that come from testing hypotheses that are broader than a single translocation will provide additional incentive and benefit for doing translocations. Pérez et al. (2012) outlined criteria for considering and undertaking translocations (also see the IUCN 2013). These guidelines incorporate numerous and diverse criteria, including biological, economic, and societal considerations. Yet, their framework did not consider the benefits of gaining general scientific knowledge as the result of undertaking a translocation. Future management and conservation requires clear mechanisms that apply to both known and unknown conditions (or likely conditions) including those of novel systems and locations where species may never have existed (Hobbs et al. 2009, Ricciardi and Simberloff 2009, Seddon et al. 2014a, Seddon et al. 2014b, Svenning et al. 2015). Understanding those likely conditions and the responses of organisms requires

knowing what organisms need and their interactions with other organisms (Harris et al. 2006, Hobbs et al. 2009, Pelini et al. 2009). Researchers that emphasize projects that consider and test hypotheses contribute more and, thus, increase the value of their work. Here, we discuss approaches to gaining information from translocations designed for conservation.

## TRANSLOCATIONS INFORM HABITAT REQUIREMENTS

Habitat quality at release sites is a key consideration when assessing the feasibility of translocations (e.g., Pearce and Lindenmayer 1998, IUCN 2013). Yet, the habitat needs of organisms are often inferred from correlated sampling where populations natively occur, providing little mechanistic understanding of habitat quality that can be used to predict resource selection or habitat quality (Mitchell and Powell 2003, Mitchell and Hebblewhite 2012, Morrison 2012). Rarely do researchers use translocation data to assess their own *a priori* ideas of habitat quality for released organisms, but when they do, the results provide important insights (Bottin et al. 2007, Welch et al. 2016). For example, Noël et al. (2011) used experimental reintroduction of wetland plants to demonstrate that plant populations grew faster when they were moved between ecologically similar locations. Translocations offer important opportunities to identify the mechanisms that drive distributions, range limits and abundances of animals as a product of the habitats where they occur (Hargreaves and Eckert 2014, Hargreaves et al. 2014, Chapter *Habitat conflicts and reintroduction decisions*). Translocations allow researchers to test critically the understanding of what organisms need because release sites are independent of locations where previous data and habitat models were generated. Translocation sites may differ radically from previous study locations, demonstrating the ability of

organisms to survive in different ecoregions or ecosystems. Alternatively, release sites may differ from source locations in small but quantifiable ways.

The responses of organisms released in new locations have the potential to reveal important relationships to habitat. Movements are important indicators of how animals may evaluate landscapes and habitat (Young and Shivik 2006, Kemink and Kesler 2013, Berger-Tal and Saltz 2014). Subsequent to release, organisms will survive and reproduce in relation to habitat quality and thus relate demographic rates and growth directly to habitat (Hargreaves and Eckert 2014, Hargreaves et al. 2014). Evaluating survival and reproduction may demonstrate which habitat types are ecological traps or sinks versus those that function as sources and are inherently self-sustaining (Van Horne 1983, Pulliam 1988, Battin 2004). Designing a translocation carefully to release organisms in the presence, absence or along gradients of a specific habitat or community element can identify specific habitat elements and their commensurate effect on population growth or the fitness of individuals. For example, an experiment on reintroduced European wild rabbits (*Oryctolagus cuniculus*) created treatments with varied abundances of food and shelter and determined that food positively influenced rabbit abundance (Cabezas and Moreno 2007). Attempting to understand effects of habitat on native rabbit populations without experimentation may have failed to identify the important components of habitat.

Contemporary ranges of many organisms are contracting rapidly and areas they do inhabit often exhibit small population sizes or decreases in population growth rate (Dirzo et al. 2014). Moreover, human habitation and development often cause conflict between existing populations and organisms. For examples, thousands of gopher tortoises (*Gopherus agassizii* and *G. polyphemus*) in California and Florida have been translocated

to accommodate solar energy projects or housing developments (reviewed in Germano et al. 2015). Such mitigation translocations appear to be increasing as human expansion requires new areas for development (Germano et al. 2015). Many animals are translocated without consideration for the areas they will be moved to and little or no post-release monitoring. Carefully designing experiments where animals are moved to habitats with specific elements would be illustrative of specific habitat requirements as well as movements and conspecific interactions.

Small or isolated populations limited by carrying capacity may produce surplus individuals (e.g., juveniles) that will not be recruited under the current conditions and causing those individuals to die or disperse into poor habitat (Emslie and Brooks 1999, Foley et al. 2014, Foley and Foley 2016). Because surplus individuals will not contribute in their natal location, removing and translocating individuals into areas that are considered marginal or even sink habitats provides additional opportunities to evaluate habitat requirements. Locations that are unoccupied could hypothetically be limited by dispersal and, thus, moving new animals into these areas is a critical test of whether habitat is poor or simply unconnected (Hargreaves et al. 2014). Habitat restoration projects that improve habitat or develop potential corridors between populations may also be a viable use of individuals from populations where they were moved to mitigate human needs or because they would have died in their natal range. In the event that such translocations fail they may provide information on the expected time a habitat may support a population in the event that radical measures, such as assisted migration, become necessary (Hoegh-Guldberg et al. 2008).

## INTERACTIONS AMONG ORGANISMS

### *Intraspecific Interactions*

Releasing organisms into places where they have not occurred for long periods, or ever, provides unique insights into the interactions and relationships within populations, communities, and ecosystems. During the early stages of reintroductions and introductions, the newly released individuals are largely uninfluenced by conspecifics. As a population grows, through newly released individuals and reproduction, conspecific density increases, providing opportunities to evaluate changes in home range or territory development, size, overlap and competition (Jetz et al. 2004, Berger-Tal and Saltz 2014). For example, Nolet and Rosell (1994) sequentially translocated beavers (*Castor fiber*) into initially unoccupied areas to reveal that beaver densities were limited because of territorial behavior. For plants, changes in densities may elucidate limited, critical resource thresholds, or reveal novel components of competition (Kuang and Chesson 2009, Epperlein et al. 2014). Populations with low numbers of individuals, may lend themselves to testing models or hypotheses regarding negative density dependence, which is often difficult to observe in naturally occurring populations (Allee and Bowen 1932, Allee et al. 1949, Courchamp et al. 2008). For animals, translocations provide a template for assessing societal and familial bonds and how those interactions, or lack of them, affect survival and space-use such as dispersal distances (Linklater et al. 2006, Fryxell et al. 2008). The reintroduction of prairie dogs (*Cynomys ludovicianus*) provided an experimental platform where individuals were moved with and without family groups and demonstrated that societal or familial bonds affected mortality of individuals directly (Shier 2006a, b). Similarly, solitary animals also benefit from being released with

neighbors, suggesting that interactions with conspecifics may be important for survival (Shier and Swaisgood 2012). Augmentations of individuals to already existing population provide opportunities to test ideas concerning competition, territorial boundaries and development of territories (Lewis et al. 1997, Potts and Lewis 2014). Researchers may waste such opportunities. For example, augmentations of American martens (*Martes americana*) could have been used to test hypotheses of territory structure and development between already existing and newly arriving individuals, but would have required understanding pre-release home ranges and considerations for how and where to release new martens (Woodford et al. 2013). In contrast, Ruth et al. (1998) evaluated movements and home ranges of cougars (*Puma concolor*) before and after translocation to test hypotheses that native individuals dispersed and had home ranges of similar size to those translocated.

### *Interspecific Interactions*

Interspecific interactions within communities can be difficult to address in many naturally occurring systems and studies. Removing or adding destructive or ubiquitous organisms (e.g., diseases) to or from ecosystems may not be practical or ethical. Translocations allow researchers to test the effects of translocated individuals in the absence of other confounding variables. Pople et al. (2001) translocated wallabies to islands that had few predators to assess survival of captive-reared animals. Such approaches may elucidate top-down or bottom-up effects on communities in the absence of predators (Berger et al. 2008, Beschta and Ripple 2009, Ripple and Beschta 2012). Reintroduced ungulates like caribou (*Rangifer tarandus*) have been documented as having dramatic negative impacts on vascular plant communities that eventually reduced

ungulate populations (Hansen et al. 2007). Generally, the effects of removing and reintroducing predators that lead to trophic cascades or to mesopredator release are investigated after the release of organisms (Litvaitis and Villafuerte 1996, Linnell et al. 1997, LaPoint et al. 2015). Yet, these observations do provide examples that future translocations can use to guide tests of hypotheses about the structure of communities. Presently, few restoration or reintroduction researchers appear to have investigated interactions between plants and animals (McAlpine et al. 2016). Conservation translocations could provide important empirical data about interactions between plants and first and second order consumers in novel situations and environments.

Translocations allow researchers to investigate the importance of parasites or diseases by removing them from the translocated individuals prior to movement (Kock et al. 2010). Diseases interact with an animal's condition and the environment and potentially obfuscate the influences of other attributes (Cunningham 1996, Sainsbury and Vaughn-Higgins 2012). Cabezas et al. (2011) evaluated European rabbits for the diseases myxomatosis and rabbit haemorrhagic disease before releasing them on food-predator treatment plots. Consequently, the authors determined that short-term survival was most affected by predation whereas long-term survival was most affected by incidence of myxomatosis and food availability. Animals or plants can be inoculated prior to translocation to ensure that they do not influence the outcome of a project. Genetically selected or modified individuals could be released in areas with specific disease prevalence to evaluate their efficacy for disease resistance (Thomas et al. 2013). Research designs for translocated animals are only just maturing but offer multiple opportunities to address general questions and those that apply directly to current management decisions

(Betts et al. 2015). Many examples of successful experiments within translocations exist and future researchers should think deeply and critically about addressing hypotheses through manipulative experiments (e.g., Pople et al. 2001, Cabezas et al. 2011, Welch et al. 2016).

## CAPTIVITY

Recovery of animal populations often requires periods during which individuals are held in captivity for short periods, prior to translocation, or because of intense captive-breeding programs (Kleiman 1989, Miller et al. 1994, Phillips et al. 2003). Periods in captivity offer opportunities to evaluate traits (e.g., shy vs bold) of animals that may relate to survival and reproduction in different circumstances. Sinn et al. (2014) evaluated behavioral traits of Tasmanian devils (*Sarcophilus harrissii*) held in captivity and rejected the hypothesis that predilections towards boldness or shyness influenced post-release movements. Such behavioral differences can be important in other species (Watters and Meehan 2007). More tests are needed to infer effects on fitness based on individual behavior and these are uniquely possible in translocation projects. Such comparisons are useful for understanding the importance of learned behaviors during development including the timing and amount maternal care (Biggins et al. 2011b). Many possibilities exist for experiments between captive animals or wild animals temporarily in captivity.

Much about stress responses is unknown. Acute stress responses are inevitable in wild animals captured, held in captivity and moved to new locations (Romero et al. 2009, Dickens et al. 2010). Though stress is clearly important to understand from the perspective of influencing translocations, translocations can serve to inform the processes of stress by monitoring behaviors related to stress (e.g., fecal glucocorticoids; Busch and

Hayward 2009). Scarlata et al. (2012) measured fecal glucocorticoids in the feces of captive pygmy rabbits (*Brachylagus idahoensis*) to evaluate their relationship to reproduction. Fecal samples are relatively easy to acquire from captive animals and evaluating them through time (e.g., from 1<sup>st</sup> to last day in captivity) provides baseline and elevated measures of stress that can be associated with reproduction or survival.

Understanding the evolutionary history of stress responses of individuals to different types of stress may elucidate population processes as well as mechanisms that may negatively influence animals (Boonstra 2013). Much research has been done on glucocorticoids, particularly their metabolites in feces, but few baseline measurements are available for most animals to interpret these changes in the wild. Though studies can be undertaken in other venues, translocations provide opportunities to understand how specific stress will affect wild populations. Captive animals can also be used in studies on dietary requirements, food preferences and energetic expenditure (Davison et al. 1978, Powell 1979, Parker 2003).

#### ADAPTATION AND EVOLUTION

Organisms may be locally adapted to specific environmental or habitat conditions (Knaus et al. 2011, Weeks et al. 2011) causing organisms from different source locations to have differential habitat preferences, for example, and to perform poorly at release sites to which they are not adapted (Kephart 2004, Stamps and Swaisgood 2007, Mabry and Stamps 2008). If local adaptations exist among individuals from different populations, hybrids may do poorly compared to non-hybridized variations (Stüwe and Nievergelt 1991, Allendorf et al. 2001). Generally, whether hybrids have advantages, disadvantages or are similar to non-hybrid parents will be unknown prior to releasing

organisms. Thus, identifying local adaptations may be difficult due to lack of environmental variation or without controlled comparisons to other individuals (Garland and Adolph 1994). Translocations provide a way of quantifying the fitness of organisms from different locations as well as hybridized offspring to evaluate if differences exist and indicate local adaptations. For example, experimental translocations with populations of butterflies have demonstrated that local adaptations could be limiting under specific conditions brought about from climate change (Pelini et al. 2009). Such observations would have been difficult or unethical outside of a translocation framework. Thus, conservation-based translocation may be in position to test similar models or mechanisms.

#### IMPLEMENTATION AND DESIGN

Translocations provide control over the individuals that will be part of the study. Such control is often not available in other studies of natural systems. Thus, translocations lend themselves to studies of dominance hierarchies or the effects of age or sex on interactions among individuals. Individuals at different life stages (e.g., reproduction vs non-reproductive) or sexes can be assigned randomly across treatments of habitats, absence or presence of predators, or types of food supplementation (e.g., Pople et al. 2001, Chauvenet et al. 2012). During planning of translocations, researchers should strongly consider the types of hypotheses that they can address and select appropriate treatments and study subjects to include in their translocations.

Translocation programs provide ideal templates for studying the effects of local climate-habitat interactions and meta-populations dynamics (Facka et al. 2010, Davidson et al. 2014). Further, translocated populations can be compared to natural populations

occurring in both similar and different conditions. Wide-scale experimentation offers important opportunities for research. Nevertheless, broad experimentation requires coordination and collaboration among agencies interested in conservation and those considering translocation in the future. Indeed, the feasibility and design of translocations should consider the scientific questions that are most important. For example, selection of translocation sites could be predicated on replication in new habitat types or in the absence of important predators, and provide critical tests of ideas about the range limits of species or where populations will be most robust. Within a paradigm of using translocations as broad-scale experiments, the design of individual translocations would be, in part, guided by the scientific value attainable across multiple well designed sites. General scientific knowledge should be an integrated part of an integrated concept of how translocations are conceived and considered.

Scientific value of translocation will generally be a secondary consideration relative to conservation goals, though they need not be. Yet, scientific inquiry and conservation goals may be synonymous in many circumstances. If a translocation is warranted without consideration of scientific merit, then adding scientific value strengthens the reasons to progress with the translocation. Therefore, researchers and managers should consider the potential scientific information they can gain, especially when the risks to populations and ecosystems are negligible. Alternatively, if a proposed translocation has expected risks that could harm founder (source), release populations or ecosystems, then the benefits of scientific results could make a translocation feasible or even desirable if those risks are identified and lead to appropriate strategies in the future (Pérez et al. 2012, IUCN 2013). Researchers should think deeply about potential ideas and hypotheses that

resolve questions that cannot be addressed in other typical ways or at other study sites. Translocations are valuable because they may be difficult to undertake or get to get approved; thus, they are relatively rare and exploring all reasonable scientific avenues is important less opportunities be missed. Translocation projects have limited funds for basic monitoring. Collaborations with researchers with unique expertise and ideas may provide additional funds or resources that allows different entities to support both traditional translocation goals and scientific goals beyond the translocation.

Conservation of imperiled species have often resulted in numerous spatially varied, independent translocations (Short et al. 1992, Hayward et al. 2007, Lewis et al. 2012, Powell et al. 2012, Simon et al. 2012, Anderson et al. 2014, Hedrick 2014). Single translocations projects could consider each individual released as an independent replicate which helps resolve hypotheses about a site or a specific mechanism when *a priori* hypotheses are in place before moving individuals. Yet, general information about ecological or evolutionary mechanisms, habitat quality or individual species will come from replications across many translocation projects. Ideally, individual translocations can be treated as replicates to increase statistical power and to identify similar patterns across diverse circumstances (Hayward et al. 2007, Facka et al. 2008, Powell et al. 2012, Facka et al. 2016). Many individual translocation projects create multiple populations with little, or no, connectivity. We advocate that high scientific value of translocations, or of series of translocations, can mitigate risks and help to resolve decisions to move organisms. Such opportunities may be missed without serious thought and planning before organisms are moved.

Traditionally, the evaluation of success of a translocation is based on whether a population persists at the release site or not (see Chapter *Broadening the definition of success in animal and plant translocations*). Ultimately, however, the success of a project is contingent on the contributions to its many goals. In many cases, the conservation benefit to populations or meta-populations will be given the most weight, but testing scientific hypotheses provides an additional route for translocations to reach goals related to managing and conserving important organisms and ecosystems. Our perspective is that an appropriately designed translocation has the potential to create a viable population that positively influences the conservation, restoration, or management goals, but also has the potential to acquire new information related to diverse biological disciplines that may be more beneficial to the target species than a single new population. In this way, translocations that do not establish persistent populations can make important contributions. Moreover, within the scope of science, well designed and executed experiments have the ability to reject or support specific hypotheses. Establishing a viable population is not a sure thing (Griffith et al. 1989, Wolf et al. 1996, Wolf et al. 1998, Godefroid et al. 2011, Guerrant Jr 2012) but testing hypotheses using sound scientific design should always give meaningful results. Elucidating causal mechanisms that inform habitat quality and population viability, among other possible outcomes, are valid goals to conservation and to our understanding of our natural world and should be considered seriously. Each translocation is an opportunity to design and conduct meaningful science. Translocations are diminished when we do not maximize this opportunity.

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### **CHAPTER 3: Broadening the concept of success in animal and plant translocations**

**Abstract.** Translocations are a common tool used in the conservation and management of organisms. Generally, the success of such translocations is based exclusively on the establishment of viable populations of organisms. Yet, translocations are conducted for diverse reasons including conservation, economics, scientific advancement, and to restore ecosystem function or ecosystem services. Further, all translocations have inherit effects on source and release communities and populations. A definition of success that only considers population viability may be restrictive of the diverse reasons for conducting translocations or of the novel ways that conservations can be achieved through translocations (e.g., ecosystem functions). We argue that the definition of success of translocations can be broadened to accommodate diverse goals that include establishing viable populations. Success should be predicted on *a priori* goals that are designed to achieve specific outcomes or to reduce risks including those to release locations. Developing a broader definition of success allows projects to judge success and failure on many project goals and to conceptualize success as a continuum rather than a simple binary outcome. Further, defining and thinking about success from different perspectives, and for different types of goals, encourages those designing translocations to think seriously about both positive and negative outcomes beyond the population they hope to establish. We discuss an example for considering success and failure through the reintroduction of fishers (*Pekania pennanti*) released in northern California.

**Keywords:** augmentation, ecological restoration, ecosystem services, establishment, introduction, Population Success, Project Success, reintroduction, source population

## INTRODUCTION

The last 30 years has brought immense change to the conception, design and implementation of translocating organisms (Griffith et al. 1989, Seddon et al. 2007a, Armstrong and Seddon 2008, IUCN 2013). Translocations can include either intentional or unintentional movements of organism from one location to another. We view success as related to goals and so focus exclusively on intentional movements of organisms.

Intentional translocations are subdivided into three types: *Reintroductions* are the movements of organisms into places they historically occurred but are presently extinct, *Introductions* are movements of organisms to places where they are not known to ever have existed, and *Augmentations* are movements of organisms into place with known populations of conspecifics (Seddon et al. 2012, IUCN 2013).

Research has greatly improved the understanding of how to move organisms and to establish viable populations (Griffith et al. 1989, Fischer and Lindenmayer 2000, Armstrong and Seddon 2008). Improved research and methods have provided important insight into common biological mechanisms, including the number of founders and habitat quality, and their influence on the outcomes of projects (Armstrong and Seddon 2008, Powell et al. 2012, Seddon et al. 2014). Various mechanisms can affect the biological outcomes of translocations including diseases, random catastrophes, and demographic stochasticity (Sarrazin and Barbault 1996, Hodder and Bullock 1997, Miller et al. 1999). Simultaneous to recognizing that science can improve translocations, awareness about ecological function and ecosystem services provide new motivations to

move organisms in scientifically interesting and important ways (Donlan 2005, Harris et al. 2006, Armstrong and Seddon 2008, van Andel and Aronson 2012, Svenning et al. 2015, McAlpine et al. 2016). Translocations may be planned for varied reasons that include ecosystem rehabilitation, ecosystem services, conservation and even human aesthetics (e.g., Irvine et al. 1964, Hodder and Bullock 1997, Seddon et al. 2012). Removing organisms for release elsewhere has the potential to alter ecosystems and, therefore, is included design and evaluation of translocations (McLoughlin et al. 2003, van Wieren 2006, Berger et al. 2008, Pérez et al. 2012).

Despite advancement in approach and the broadening of purpose, translocations are often judged successful, or not, based only on the viability of the resultant population. Griffith et al. (1998) stated that “*A translocation is a success if it results in a self-sustaining population*”. Nearly all translocation projects and analyses since have adopted this defining principle for planning and evaluation (Sarrazin and Barbault 1996, Guerrant Jr and Kaye 2007, Seddon et al. 2007b, Powell et al. 2012, Anderson et al. 2014). Individual translocation programs often do not define success explicitly because of this convention (Pavlik 1996). Indeed, the international guide to translocations and nearly all published reports that discuss success refer to this definition either explicitly or implicitly (IUCN 2013).

A definition that emphasizes the viability of populations is pertinent when the main goal of a translocation is to ensure long-term persistence of a population, metapopulation, or a species. Several authors have recognized that success depends on the stated goals of a project (Kleiman 1989, Pavlik 1996, Guerrant Jr and Kaye 2007, Hayward et al. 2007). Perhaps because the goals of most projects ostensibly are related only to viability of

populations, the stated or unstated goals, seem consistently to pertain to viable, self-sustaining populations. Continued scrutiny of biological processes that affect establishment and persistence of populations remains a critical aspect of planning and implementing future translocations (Seddon et al. 2007b, Armstrong and Seddon 2008, Seddon et al. 2014). Nevertheless, the definition of Griffith et al. may be restrictive when translocations are undertaken for reasons that may not rely on creating self-sustaining populations, such as moving animals to test a specific method or hypothesis (Phillips et al. 2003; see Ch 1 *Maximizing the value of conservation translocations through science*). A definition that focuses solely on the population-related outcomes of a translocation ignores effects to the founder or source ecosystems, which are scientifically interesting and pertinent to population and ecosystem management, and possibly to human economies (Phillips et al. 2003, van Wieren 2006, Armstrong and Seddon 2008, Packer et al. 2013). Researchers, managers and agencies should not be encumbered by a definition of success that is predicated only on viable populations and be able to consider translocations successful under a variety of criteria (Fig. 1). Ultimately, human societal values and desires, are, effectively the main determination for all successful translocations (Pavlik 1996, Pérez et al. 2012).

Here we discuss the success of translocation projects in terms of both goals that are specific to establishing self-sufficient populations and goals that do not require a self-sufficient population. We highlight these principles through an example from a reintroduction of fishers (*Pekania pennanti*) in northern California. Others researchers have noted that success can be defined in different ways based on different specific goals and taxa (e.g., plants; Pavlik 1996, Guerrant Jr and Kaye 2007, Hayward et al. 2007) but

often alternative goals are simply means to achieving a viable population. We argue a more general treatment is needed.

We propose that translocation goals can be divided logically into a minimum of two categories: (1) *Population Success* pertains to establishing and sustaining a viable population and (2) *Non-Population Success* pertains to a goal or goals that do not require the creation of a viable population. Collectively, achieving *Population* and *Non-Population* goals determines the cumulative success of a project (hereafter *Project Success*; e.g., Pavlik 1996; Fig. 1). Thus, if the only goal of a project is to have a self-sustaining population, the *Project* success reduces to *Population* success. *Population* or *Non-Population* goals (or both) may be complex and be divided into multiple sub-goals. Identifying multiple goals expressly acknowledges that a project meets some success if some goals are met even when a new population is not established (Fig. 1).

#### ARE DEFINITIONS IMPORTANT?

The definition espoused by Griffith et al., and by others, appears to have been motivated primarily by a need to quantify successful and unsuccessful translocation for analyses (Griffith et al. 1989, Sarrazin and Barbault 1996, Wolf et al. 1996, Fischer and Lindenmayer 2000). So long as *Population* success strictly equates to *Project* success, this definition poses no issues. The reintroductions of prominent North American animals such as bison (reviewed in Kleiman 1989), black-footed ferret (*Mustela nigripes*), red wolves (*Canis rufus*), and California condors (*Gymnogyps californianus*) had few goals beyond creating viable populations; thus, a definition focused on population objectives was appropriate and valuable (Miller et al. 1994, Toone and Wallace 1994, Phillips et al. 2003). If, however, translocations are designed to accomplish goals other than, or in

addition to, establishing a new population, they could be falsely identified as completely successful if a new population is created but other goals are not, or a failure if no population was established but other goals were met. For example, global analyses of fisher and marten translocations (*Martes* spp.) identified success based on the determination of the agencies or researchers that conducted the translocations (Powell et al. 2012). Generally, those definitions of success were roughly equivalent to Griffith et al., but for some augmentations in the Union of Soviet Socialist Republics success was based on improvement of fur quality of native sable (*Martes zibellina*) populations (Powell et al. 2012). Powell et al. accounted for these differences within their analyses but this example illustrates that goals set out for different projects can be equally successful, but “success” represents different biological processes. Translocations are often closely scrutinized for their ability to meet goals associated with establishing a population and their cost effectiveness (Kleiman 1989, Pérez et al. 2012, Packer et al. 2013). Yet, well designed and well executed translocations can may be useful and important investments of money and time even if they fail to establish persistent populations (Pavlik 1996, Guerrant Jr 2012, Chapter 1 *Maximizing the value of conservation translocation through Science*). Translocation failures may promote conservation by identifying important threats and causes of population failure. For example, Short et al. (1992) demonstrated that the presence of exotic predators caused the population failures of 6 reintroductions of wallabies (macropods). These data in combination with the results from other reintroductions demonstrated that islands without predators had a high proportion of population successes. Identification of the causal

mechanisms that limited reintroductions provided information useful to future translocations as well as other restorations.

Translocations that are concerned primarily with restoring a population of a single species have effectively become a sub-branch of biology (e.g., Seddon et al. 2007a, Armstrong and Seddon 2008). Many subfields of ecology and conservation including ecological restoration, invasive species biology, and pest control have relevant literature that should be incorporated in these varied, but related, branches of science (Lipsey and Child 2007, Polak and Saltz 2011, McAlpine et al. 2016). Even among researchers that do reintroductions, divisions exist within the literature because some are focused exclusively on plants (Guerrant Jr 2012) or animals (Seddon et al. 2007a) but few that study the interactions between translocated or restored plants and animals (McAlpine et al. 2016). Plant and animal translocations have fundamental principles tied to population biology, as do other fields of study mentioned. Important differences in the life histories of plants and animals do exist that require specialization of knowledge and approaches and, therefore, are less useful to researchers from other specialties. Nonetheless, these differences can be overcome by common concepts and definitions of translocation success or failure. Thus, a definition that is shared and understood among diverse research fields is important, but a definition exclusive to viable populations is now insufficient to be useful completely across different fields of study.

Defining success in a broad and comprehensive framework may increase the rigor and thoroughness of translocation design. The definition of success used on a particular project affect the ideas of appropriate or important goals held by project personnel. Labeling success only from a population perspective may give some researchers or

managers a reasonable excuse to think that population processes are the only aspects of a translocation that are important. A broad concept of success necessitates the incorporation, or at least the consideration, of diverse goals into all translocations. A broadening of success, and the goals that determine success, can facilitate researchers and managers to think deeply about their translocation's core functions, benefits and potential costs. Thus, a broad and inclusive set of goals and success is important. Translocation design and implementations improve by thinking more clearly about one commonly advocated idea of success that transcends different types of goals for doing translocations.

#### BEYOND A POPULATION-SPECIFIC VIEW OF SUCCESS

When translocations are conceived with the goal of producing ecological or economic services, these goals need to be emphasized (van Wieren 2006, Stoskopf 2012).

Reintroduction projects should identify all requirements of a population or system and emphasize meeting those diverse needs as specific goals. Restoring ecological processes and ecological services is important and should be integrated into as many translocation projects as possible (van Andel and Aronson 2012). If definitions of success do not accommodate, or promote, ecological restoration, planners that are focused on establishing a viable population may not consider ecosystem benefits. Ecosystems and communities are highly dynamic and often modified from their historic conditions and translocations can restore environmental services. For example introducing native predators can lead to control of native herbivores (Powell 1981, Earle and Kramm 1982, Powell 1993). Translocations of ecological surrogates may restore communities and increase their overall function (Donlan 2005, Svenning et al. 2015). Such translocations

also increase biodiversity (Hodder and Bullock 1997) and ecosystem services should be considered a central goal contributing to project success. Some biologists have even advocated using translocations as actions that create communities proactively in the face of new or accelerated threats (e.g., climate change; Seddon 2010, Aitken and Whitlock 2013, Seddon et al. 2014). For such translocations, population success is more complex than for standard translocations and understanding and accounting for this complexity belongs in the goals of projects (Polak and Saltz 2011). The reintroduction of a predator may alter the local community in ways that humans perceive as beneficial such as the trophic cascade in Yellowstone National Park (Berger et al. 2008, Beschta and Ripple 2009, Ripple and Beschta 2012); however, the complex interactions of new predators with new communities often is negative (Jones et al. 1997, Chipman et al. 2008, Letnic et al. 2009, Roemer et al. 2009).

Many translocations are motivated in part by economics. (Hayward et al. 2007, Spear and Chown 2009). Thousands of translocations occur for human recreation, including stocking fish and game for sport-fishing and hunting (Thorne and Williams 1988, Hodder and Bullock 1997, Chipman et al. 2008). Animals are often translocated to mediate the impacts of urbanization or development (Germano et al. 2015) or to alleviate human-animal conflicts caused by predation or destruction of human property (Miller and Ballard 1982, Fritts et al. 1984, Walsh and Whitehead 1993, Stüwe et al. 1998). In these instances the central goal of moving animals is to alleviate problems without killing animals directly. Such economically motivated translocations may be more common than conservation-based projects and their goals may be emphasized in spite of the usual emphasis of the Griffith et al. definition (Germano et al. 2015). Less information on

biological processes or ecological services, or damage, may be associated with these types of translocations without consideration for their specific goals.

In some circumstances, translocated populations may exist only when humans intervene for an extended time. Such interventions may include supplemental feeding, predator removals or continuous augmentation with new individuals (Oro et al. 2008, Chauvenet et al. 2012). Ultimately, these populations will become self-sufficient or go extinct without human intervention. Translocations that result in non-viable populations and that go extinct may offer important temporary conservation benefit that was an expected outcome of the translocation. For example, colonies of black-tailed and Gunnison's prairie dogs (*Cynomys ludovicianus* and *gunnisoni*) that were reintroduced to the southwestern United States were predominantly not self-sustaining (Fig. 2; Facka et al. 2010, Davidson et al. 2014). Prairie dog populations could be maintained with augmentations that could benefit the ecosystem even if they ultimately went extinct. The presence of prairie dogs, through their burrowing and herbivory, had positive effects on burrowing owls (*Athene cunicularia*) and soil invertebrates (Duval and Whitford 2009, Duval and Whitford 2012). Additionally, the burrows provided an important resource if future reintroductions were attempted after the mechanisms that limited prairie dogs were overcome. In such instances, non-viable populations may be important to consider partially successful in terms of their non-population goals.

Some methods of genetic pest control (e.g., Sterile Male Technique) use translocated, genetically modified organisms that express characteristics that reduce or eliminate populations of pest species (Knipling 1955, Klassen and Curtis 2005). Recently, these methods have, at times, been developed as conservation measures for the

purpose of eliminating or reducing invasive organisms from localized areas (Gould 2008). Clearly, such translocations have important conservation benefits but their success emerges via the elimination or reduction of populations. Currently, these types of translocations are not considered within our concept of successful translocations because their goal is not conservation of the organisms being translocated. Reconsidering success of these translocation based on diverse goals allows assessment of these projects within the context of the specific population biology associated with translocation as well their contribution to conservation or restoration.

Conservation translocations that simply move individuals may re-establish populations but still be insufficient to improve the status of imperiled organisms and such translocations should not be considered completely successful. Slotow and Hunter (2009) concluded that dozens of successful reintroductions in South Africa made little impact on the conservation status of African lions (*Panthera leo*) because they had not re-established a viable metapopulation. In this specific case, the success of translocations should be, at least partly, evaluated with respect to formation of viable meta-populations rather than on individual populations. Meeting multiple goals may demand more integrated and collaborative planning of conservation actions beyond single independent translocation efforts.

#### INCORPORATING THE NEGATIVE IMPACTS OF TRANSLOCATIONS

Even if re-establishing a population is the only goal for a translocation, planning must still address effects of the new organisms on the release environment and the effects of removing organisms from source populations and communities. Reintroduced flora or fauna may be ill-adapted to, or cause severe perturbations at, their release locations (Caro

2007, Caro et al. 2012). Consequently, “reintroduction” of a species to a portion of its range where it has long been absent may be functionally equivalent to an introduction (Thorpe and Stanley 2011, Osborne and Seddon 2012). In these instances, a translocation that yields a viable population may have many unintended consequences that are not the designed or desired outcomes. Comprehensive success is only achieved if the population persists and adds value to the ecosystem to which it is introduced. If a translocation hinders species or populations that were extant before the reintroduction or services then the project should not be fully considered a success.

An overlooked aspect of assessing success in translocating organisms is the impact that a translocation has on source populations or source communities (Armstrong and Seddon 2008, Swiers 2013). Source populations are often chosen to provide genetic diversity within the new population (Jamieson 2011, Weeks et al. 2011). Yet, few researchers or managers consider negative effects of removing many individuals, or the timing of those removals, on the source population as an important aspect of the total project success (Armstrong and Seddon 2008). We know of only one study that has monitored actively a source population, of fishers, and documented little impact to population numbers during or after removing animals (Swiers 2013, Green et al. In Prep). Creating a new population at the cost of damaging an established, naturally-occurring population is counterproductive. While most managers would acknowledge this principle, they have not acted upon it or have not reported their findings. Monitoring and reducing impacts on source populations should be a stated consideration, and goal, for translocations.

Translocating diseased, parasitized, or immuno-compromised organisms may lead to reduced vigor of a new population (Cabezas et al. 2011, Sainsbury and Vaughn-Higgins 2012, Sepúlveda et al. 2014). Additionally, unintentional translocations of diseases and parasites to areas where they are novel can decimate local populations and ecosystems (Gaughan 2001, Kock et al. 2010, Ewen et al. 2012). Translocation efforts that damage the local community should be considered unsuccessful, or only partially successful, even when translocated populations are established. Few translocation efforts appear to monitor diseases actively after organisms are released (Kock et al. 2010).

Released organisms can be either novel food for extant consumers or are themselves novel consumers with which novel foods have no experience (Frair et al. 2007, Biggins et al. 2011). Often translocated organisms are both the consumers to some local organisms and the food of another. Released animals may be prey for native predators (Shier and Owings 2006, Cabezas and Moreno 2007, Moseby et al. 2011, Anson and Dickman 2013). Conversely, prey at a release site may be naïve and highly susceptible to novel, though native, predators. Predators and prey may alter their behaviors in response to the translocated animals, leading to cascades through the community (Gittleman and Gompper 2001). Even over short timeframes, these interactions can reduce the resiliency of that ecosystem to recover in the long-term (Lundberg et al. 2000).

Disease and predation are only two examples of community effects that influence *Project Success* for translocations. Mladenoff et al. (1997) argued that species-specific management must be placed in the context of ecosystem health and function. Long-term

ecosystem effects are part of the total success of a translocation. Minimally, the benefits of a translocation on the recipient community should offset any damage they do.

## RECOMMENDATIONS

A broad view of success for an intentional movement of organisms promotes diverse goals, motivations and approaches to restoration and conservation (Guerrant Jr and Kaye 2007, Thorpe and Stanley 2011). We recommend that intentional translocations be designed and evaluated based on diverse goals that include population viability, ecosystem function, and scientific advancement that is identified *a priori* (also see Pavlik 1996). We also recommend that translocation projects formally incorporate monitoring and report negative outcomes that relate to overall *Project Success*. Monitoring known possible effects should be incorporated into translocation plans and, if possible, be noted as an unanticipated outcome in reports and publications. Ideally, conservation translocations should not commence until the factors that led to their necessity are ameliorated (Morrison 2012, Stoskopf 2012, IUCN 2013). Thus, all projects are responsible for some minimally evaluating the conditions before translocating any organisms, making identification of changes in communities post release not an onerous task.

Armstrong and Seddon (2008) suggested that translocated populations exist in two distinct phases: establishment and persistence (also see; David et al. 2013). This distinction increases the precision of defining population success. The establishment phase comes during and soon after the release of individuals. In this phase the incipient population is small and reliant on the founding individuals. Hence, we suggest that the establishment phase concludes when normal population processes (e.g., breeding and

recruitment) are ongoing and independent of augmentation from further releases. In the persistence phase, populations of sufficient size experience smaller effects from environmental or demographic stochasticity (Armstrong and Seddon 2008). Nevertheless, if populations are relatively small or live in poor habitat they may still be prone to extinction. We recommend that projects identify important milestones for the persistence phase rather than generally arbitrary end dates that may have little biological relevance. Identification of these milestones, *a priori*, is crucial for projects and populations, and may be revisited throughout the life of the project (Morrison 2009).

#### AN EXAMPLE OF SUCCESS AND SCIENCE: FISHER REINTRODUCTION

In the mid-2000s, Sierra Pacific Industries, a company that owned and managed >2 million acres in California for timber production, proposed a reintroduction of fishers onto one of five of their properties in the southern Cascade mountains and the northern Sierra Nevada (Callas and Figura 2008). Most forests where fishers live in the western portion of their range are also valuable private and public timberlands with intensive logging (Haynes 2003, Shaw et al. 2011, Morgan et al. 2012). Yet, the functional relationships between fisher populations and logging were unknown but important, for both future management and regulatory decisions (USDI 2004, USDI 2014). We reasoned that using robust scientific theory and methodology, a reintroduction project could provide answers about fishers and their habitat requirements in the presence of logging. We estimated that the benefit of understanding these complex relationships better was greater than the cost of the population failing to establish. Thus, after a feasibility assessment was made to choose an appropriate reintroduction site, fishers were moved to the Stirling Management Area, where the southern Cascades and the northern

Sierra Nevada meet and located between the 2 extant fisher populations that occurred in California at the time (Fig 3; Callas and Figura 2008).

The population, if it became established, would expand the range of fishers (Fig. 3). If, however, the population did not become established, we would be in a position to understand the reasons for that failure and make recommendations for fisher habitat management and reintroduction efforts in other parts of California and in western North America (Lofroth et al. 2010). We outlined 3 primary goals for our project on which to evaluate success: 1) Understanding fisher habitat use and persistence on an industrial timberland, 2) understanding the effects of removing fishers from source locations and monitoring one source population to assess the effect of removal, and 3) establishing a viable population of fishers (Table 1). Were the new population not viable, and we learned why it failed, we would consider that a success because the knowledge learned could profoundly influence management of fishers elsewhere (Table 1). Alternatively, if fishers persisted and expanded their new population beyond the Stirling Management Area, but our research failed to elucidate the reasons for their persistence, then the project could not be considered a full success (Callas and Figura 2008). Ultimately, like all translocations, we hoped to meet all our primary goals but we considered many potential outcomes for achieving or failing to achieve our specified goals.

## CONCLUSIONS

Thinking about success of translocations only through the lens of establishing viable populations fails to include and to consider translocations that are undertaken for other diverse purposes. Broadening the concept of success in translocations does not diminish the importance of establishing viable populations or for understanding the mechanisms

that lead to viable populations. Rather, a broad definition for translocation success incorporates diverse goals that consider both positive and negative outcomes of moving organisms. Some translocations may be easily defined as successful or unsuccessful based on 1 or few goals but others may be more aptly viewed as a continuum where each goal is weighted equally and contribute to comprehensive success and, thus, modest levels of success are possible. A broad definition of success is a strong motivator for researchers and managers that undertake translocation projects to develop their goals fully and to reflect on the true purpose of their proposed actions. If those planning a project determine that it's only goal is to have a viable population, perhaps they should reconsider other important aspects of their design that include scientific inquiry, effects to source and release ecosystems or to their own human communities.

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Table 1. Goals and sub-goals and their importance to a reintroduced population of fishers in northern California. Meeting all goals would signify success to the project whereas only reintroducing a viable population or monitoring a source location would represent failure or partial success.

Major Goals	Sub-Goals	Importance to Project Success†
<b>Understand fisher habitat use on industrial timberland</b>	a. Estimate Survival & Reproduction	High
	b. Predict use of habitat by fishers	High
	c. Predict placement, sizes, and shapes of home ranges using models of optimal home range choice	Moderate
	d. Predict patterns of breeding by males from home range placement and familiarity with landscapes	High
	e. Collect information on the use of structures for natal dens, maternal dens, and for resting.	Moderate
	f. Determine causes of fisher mortality and monitor health	High
	g. Use the results of items 1-6 above to provide the foundation for understanding the results of the reintroduction.	High - Ultimate Goal

Table 1. Continued

<b>Reduce and understand impacts to one source location prior to, during, and after removal of fishers</b>	h. Monitor from 2006 to 2017	Moderate
	i. Non-invasive techniques (DNA marking w/ spatial mark-recapture)	Moderate
	j. 10 adult fishers removed in 2009 and 2010	High
	k. Moved fishers from diverse locations (reduced individuals from any one)	High
<b>Reintroduce a viable population of fishers in northern California</b>	l. Release 40 fishers (24F: 16M) over three years (2009 – 2012)	High
	m. Adults favored to increase likelihood of reproduction in first years	High
	n. Captured from multiple locations in northern California (genetic diversity)	High

<sup>†</sup> Different cooperators to the project could potentially ranked the importance of these goals modestly differently.

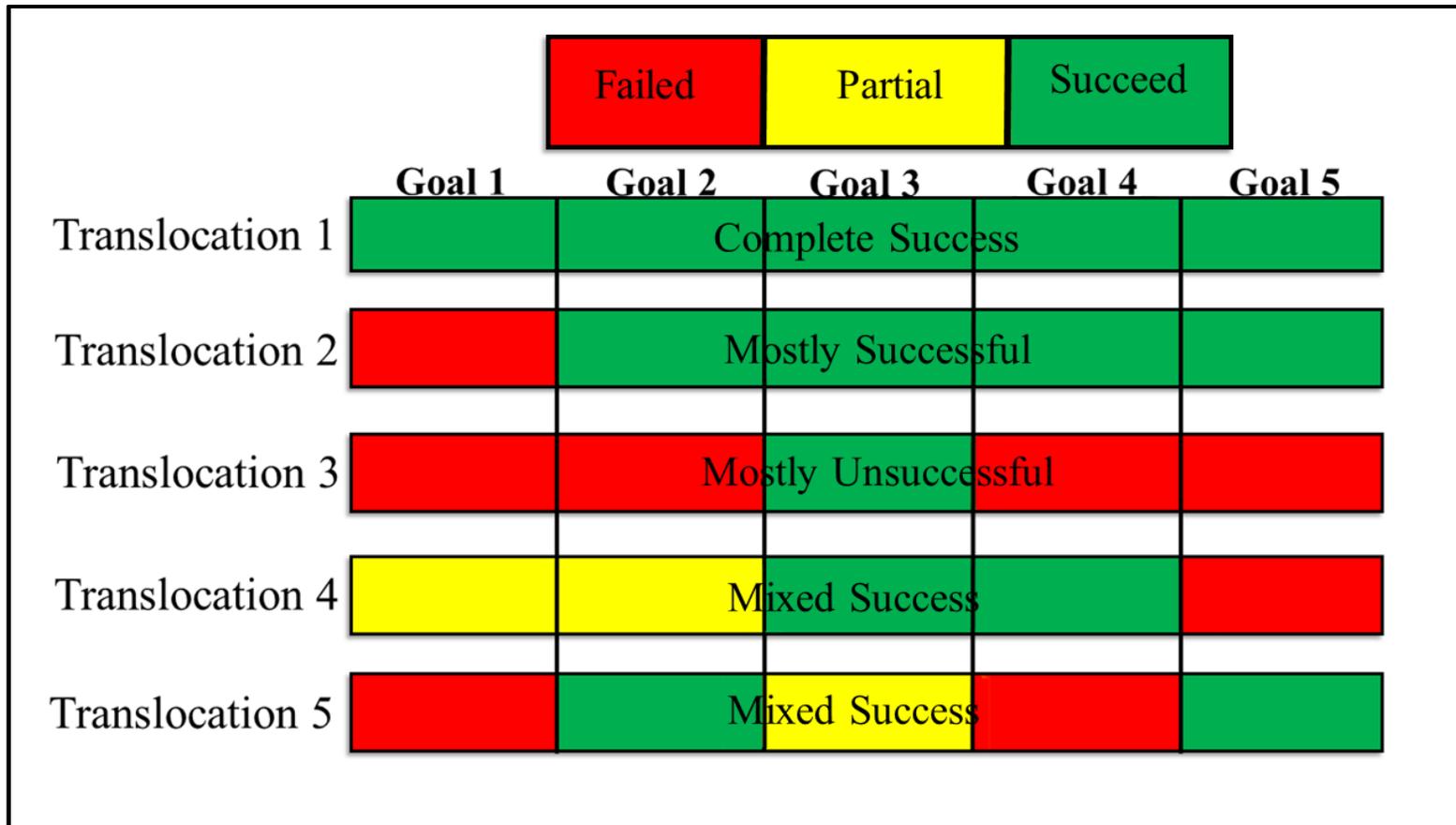


Figure 1. Five scenarios where Project success is met by achieving different types of goals that could pertain to both establishing self-sustaining populations and achieving goals not related to self-sustaining populations

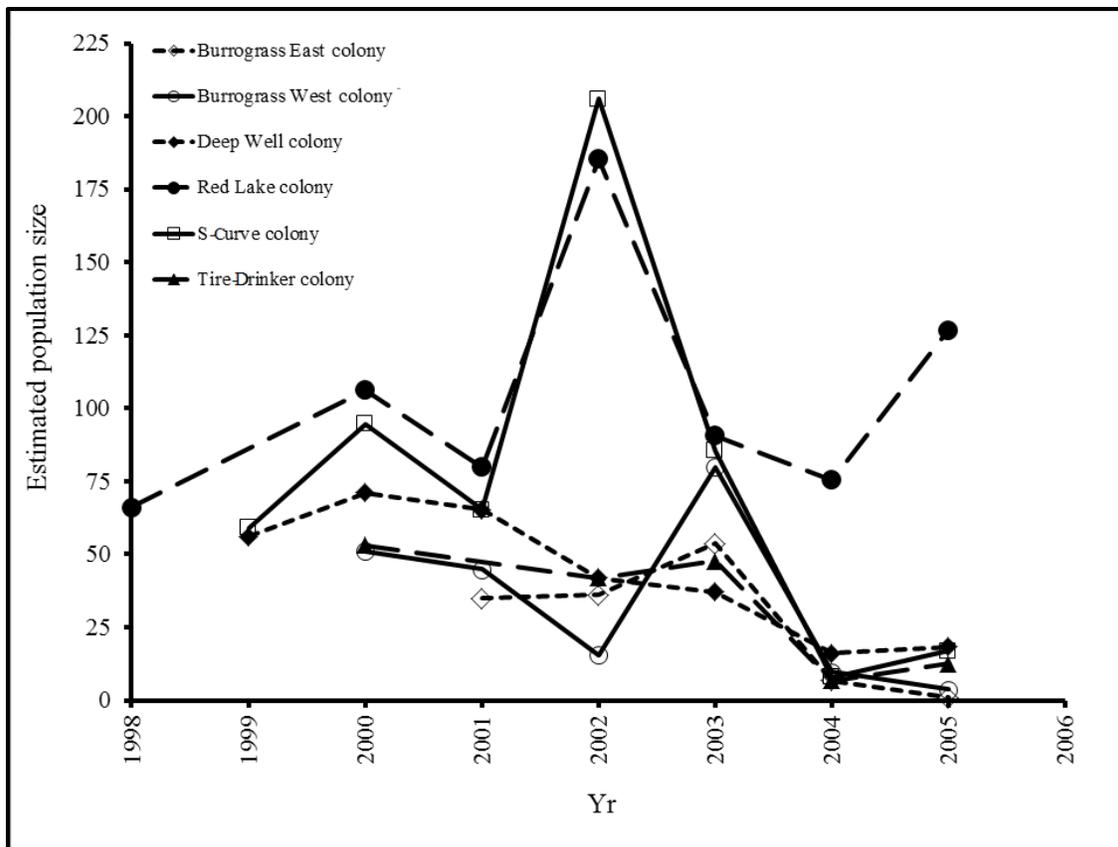


Figure 2. Annual estimates of population size for 6 reintroduced populations of black-tailed prairie dogs (*Cynomys ludovicianus*) colonies in southern New Mexico from 1998 (earliest release) through 2005 (Facka et al. 2010).

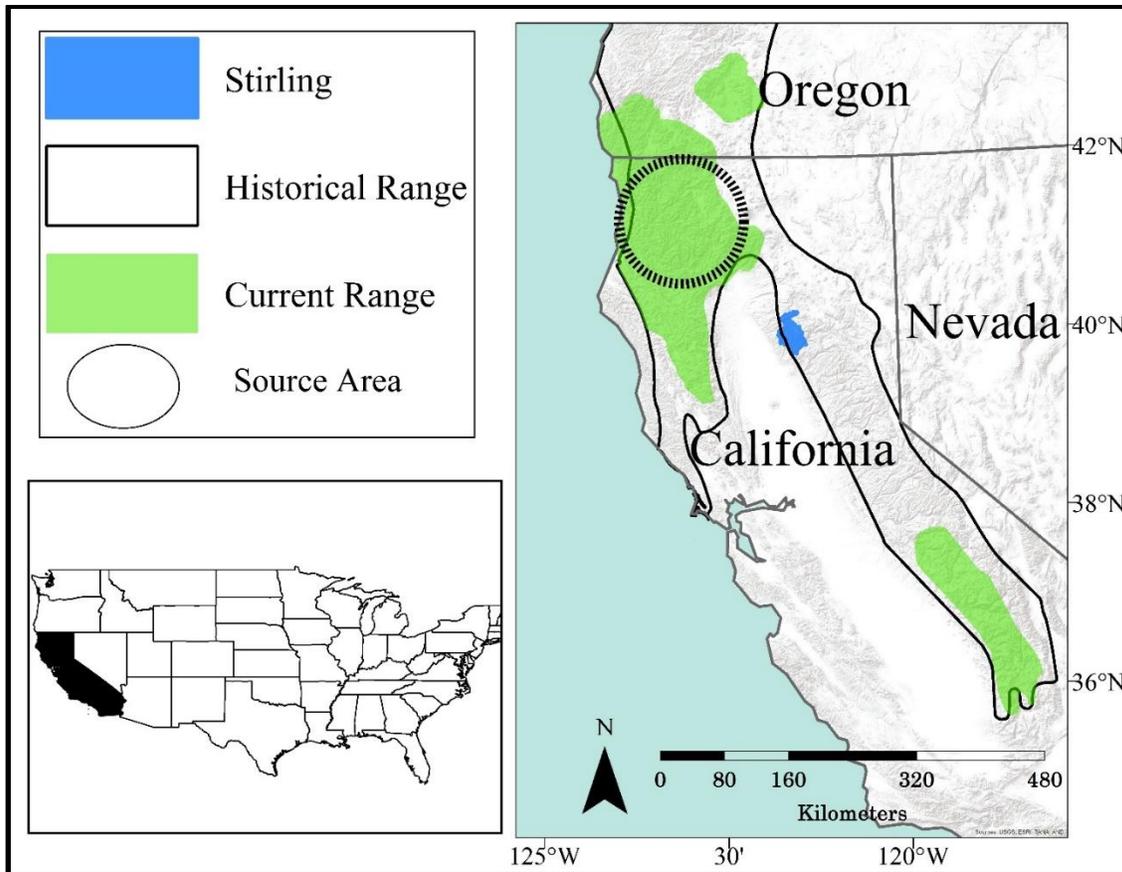


Figure 3. Historical and current range of fishers, release location (Stirling) and source area (dashed circle) for reintroduction of 40 fishers in northern California from 2009 to 2012.

#### **CHAPTER 4: Habitat conflicts and reintroduction decisions: establishing a forest-specialist on an industrial timberland**

**Abstract.** Translocations should ideally occur in places with optimal habitat that leads to high rates of population growth and long-term persistence of populations. Because humans have affected natural systems dramatically, few places may exist that have optimal or unaltered habitat. Additionally, researchers and managers may not know the true habitat quality of a location. Experimentally reintroducing organisms to test the understanding of habitat is one approach that may provide important information that is applicable for research and conservation. The fisher is a species of concern in much of western North America due in part to the perceived inability of fishers to live on landscapes logged commercially. From 2009 to 2011, we reintroduced 40 fishers (24F:16M) onto an industrial timber landscape, and studied these initial founders and their progeny through 2015 to understand if the land management methods and landscape could support establishment of a new fisher population. Through 6 years after release, and concurrent with active logging operations, >90% of all locations of fishers were on or within 2 km of the study site. Female and male fishers had high monthly survival (>0.95). We documented that on average 79% of adult females gave birth with an average litter size of  $1.7 \pm 0.41$ . Mean rates of survival and reproduction were constant across years and all vital rates were similar to populations of fishers elsewhere in California. By 2013, population processes, in particular reproduction, was independent of the founding fishers. After 6 years the population consisted mostly of young fishers born on the study site. Estimates of populations size indicated a relatively small (< 70 fishers) but increasing population of fishers. Stochastic population simulations suggest that the population is unlikely to go extinct within the first 10 years after moving fishers. We conclude that

logged landscapes offer opportunities to establish and manage populations of fishers at similar levels of logging intensity observed on our study site.

**Keywords:** defaunation, fishers, forest management, habitat alteration, logging, *Pekania pennanti*, persistence, success, translocation

## INTRODUCTION

The extent and effect of human activities are affecting populations of animals greatly at a global scale (Dirzo et al. 2014, Marco and Santini 2014). To combat extinctions or decreases in population sizes (defaunation) people attempt to restore or rehabilitate populations or metapopulations through diverse actions that include translocations of animals (Seddon 2010, Seddon et al. 2012, Seddon et al. 2014). Translocations can be controversial because they fail relatively often owing to complex and diverse effects including small founder sizes and poor quality of release habitats (Griffith et al. 1989, Lomolino and Channell 1998, Wolf et al. 1998, Seddon et al. 2014)

Humans have altered more than an estimated 50% of the terrestrial land covers of earth (Vitousek et al. 1997, Thomas 2011, Hooke et al. 2012). Human induced alteration of habitat is a primary mechanism causing declines and extinctions of animal populations and loss of biodiversity (Foley et al. 2005, Caro et al. 2012, Marco and Santini 2014). Altered environments may influence animals in diverse negative ways including reducing important vegetation for food or cover, fragmentation that isolates individuals and populations, and loss of connectivity that reduces genetic flow or makes movements risky (Fischer and Lindenmayer 2007, Crooks et al. 2011, Haddad et al. 2015). Conservation of animals, and therefore translocation efforts, are usually forced to move animals into places affected by habitat alteration.

Ideally, all translocations whose goal is to re-establish populations for conservation would occur in places with optimal habitat that meets all the biological needs of an organism and, thus, lead to high rates of population growth, high population densities, and long-term persistent populations (Seddon 2010, IUCN 2013). Realistically this idealized notion should be tempered because humans have affected natural systems so dramatically that few places exist that may have optimal habitat. Moreover, a complete understanding of what makes optimal, or even suitable, habitat may be lacking for specific animals and locations, and conventional approaches may give wrong or incomplete information (Romesburg 1981, Morrison 2009, Cromsigt et al. 2012). Further, competing ideas or models of habitat may give conflicting views of the suitability of locations; even opinions among experts may be at odds (e.g., Cromsigt et al. 2012, Kueemmerle et al. 2012; see below). Common approaches to quantifying habitat are not based on direct links between viability of populations, or fitness of individuals, to habitat, and are often based on data from a single study that are assumed to be applicable for other locations (Morrison 2001, 2012). If the best scientific information available leads to conflicted views of habitat, and its potential to foster a viable population, how should decision making progress? One option is to refine our understanding of habitat through experimental reintroductions by evaluating how animals perform in places with unknown or disputed habitat quality (Young and Shivik 2006, Cromsigt et al. 2012, Hargreaves et al. 2014, Chapter Maximizing the value of conservation translocations through science).

Logging is one specific type of habitat alteration that can affect forest-specialized animals negatively (Carey and Johnson 1995, Fisher and Wilkinson 2005, Burivalova et

al. 2014). Among many potential effects, logging affects animals by removing mature trees or downed woody debris with structural elements, like cavities, that provide denning or roosting sites (Gumtow-Farrior 1991, Paclík and Weidinger 2007, Weir et al. 2012, Manning et al. 2013). Removal of trees that provide food (e.g., acorns or pine nuts) may eliminate species that rely on those resources as well as their predators and thereby have multi-trophic effects (McShea 2000, Wilson et al. 2008, Fauteux et al. 2012). Openings in forests left after cutting increase fragmentation that alter how animals move or increase their susceptibility to predation (Bakker and Van Vuren 2004, Mortelliti and Boitani 2008). Moreover, the regenerated forests that come after initial felling may contain fewer important elements or configurations that are important for recovery or sustainability (Bunnell et al. 1999, Bunnell et al. 2002, Linden and Roloff 2013)

Fishers (*Pekania pennanti*) are medium sized carnivores in the Mustelidae weighing between 2 and 6 kg. Throughout their range, which is restricted to northern North America, they thrive in large, dense stands of late successional forests (Allen 1983, Powell 1993, Powell and Zielinski 1994). Throughout the fisher range, these forests are highly valued for timber production and logged intensively (Haynes 2003, Shaw et al. 2011, Morgan et al. 2012). Throughout their historical range, fishers decreased in abundance through the 19<sup>th</sup> and early 20<sup>th</sup> centuries, due primarily to over-trapping for fur, to habitat alterations, most often attributed to timber harvest, and to climate changes at the end of the little ice age (Aubry and Houston 1992, Powell 1993, Krohn 2012). These declines and petitions to list them under the U.S. Endangered Species Act have instigated several reintroduction efforts throughout North America (USDI 2004, Lewis et al. 2012, USDI 2014).

In the mid-2000s, Sierra Pacific Industries (SPI), a company that owned and managed >2 million acres in California for timber production, proposed a reintroduction of fishers onto one of five of their properties in the Sierra Nevada (Callas and Figura 2008). The proposal, and subsequent consideration by the California Department of Fish and Wildlife, was controversial because at least 2 fisher habitat models indicated that the proposed site had poor to marginal habitat quality (Carroll et al. 1999, Carroll 2005, Davis et al. 2007, Appendix A) whereas another model indicated reasonable habitat (Airola 1988, Callas and Figura 2008). Ultimately, based on expert opinions that enough high quality habitat existed to support fishers, and to understand better how fishers survive on altered landscapes the reintroduction, was approved (Chapter *Broadening the definition of success in animal and plant translocations*).

Generally, mature, unlogged, forests are thought to be optimal habitat for fishers, but the extent to which logged forests are sufficient to maintain fisher population is unknown (Powell et al. 2016). Fishers generally avoid places with no overhead canopy such as occurs after clear-cut logging (Powell 1993, Sauder and Rachlow 2014, Lewis et al. 2016). Fishers, and similar animals like American martens (*Martes americana*) are demonstrably affected by logging when forests are completely cleared (Bissonette et al. 1997, Hargis et al. 1999, Moriarty et al. 2015). Mature trees, or those with cavities, are essential for females of these species to effectively den and reproduce and, hence, logging could reduce the numbers of these structures. Additionally, marten and fisher foraging is negatively affected by a reduction in forest floor complexity indicative of regenerated or thinned stands of timber (Andruskiw et al. 2008, McCann et al. 2014,

Moriarty 2014). Despite these potential negative effects from logging, fishers do exist on logged landscapes.

In western North America, many fishers exist on privately and publicly owned lands with relatively high amounts of timber harvest under various intensities of forest management practices (Lofroth et al. 2010, Zielinski et al. 2010, Swiers 2013). Fishers living on logged landscapes may have dispersed from neighboring un-logged landscapes that function as source populations (Van Horne 1983, Pulliam 1988, Carroll et al. 1999, Carr et al. 2007, Mitchell and Hebblewhite 2012). Alternatively, logged landscapes may attract fishers but function as ecological traps where populations cannot persist (Battin 2004, Weldon and Haddad 2005). Fishers may find some logged landscapes suboptimal but be able to persist on such landscapes (Powell 1979a). Presently, researchers cannot fully disentangle these complex relationships where fishers naturally occur.

Estimates of fisher densities vary widely in the western portion of their range (Weir and Courbould 2006, Jordan et al. 2011, Matthews et al. 2011). Logging is concurrent with fisher populations in many places but no data elucidate how, or if, logging influences population viability or size directly. Fishers do occur in the presence of logging at high densities but in productive climates and in proximity to large tracts of mature forests (Thompson 2008, Matthews et al. 2011). Native and reintroduced fisher populations in the western US appear less productive compared to fisher populations studied in the eastern and central US (Powell 1993, Powell et al. 2012, LaPoint et al. 2015). Yet, such observations are confounded by environmental differences among study sites, the types and degree of logging practices, and other processes such as predation and poisons (Gabriel et al. 2012, Wengert et al. 2014, LaPoint et al. 2015). Currently, much

of the historical range of fishers in California, Oregon, and Washington do not have fisher populations on large tracts of land that appear potentially suitable for fishers (Aubry and Lewis 2003, Lofroth et al. 2010). Whether fishers are not present on those landscapes because of poor habitat quality, owing in part to logging, or because of restrictions on dispersal is unknown (Lofroth et al. 2010).

We tested the hypothesis that intensively logged landscapes can support fishers in the absence of source populations from adjacent lands. We reintroduced 40 fishers onto an industrial managed landscape and evaluated movements, reproduction, survival, population growth and population viability during the establishment phase of the reintroduction (Fig. 1) (Kemink and Kesler 2013, Berger-Tal and Saltz 2014). We predicted that, if our methods were suitable and habitat adequate for establishing a population, we would observe stable to increasing survival and reproduction through time with commensurate rates of population growth. If habitat decreased in quality through time, as logging activities continued, and affected survival or reproduction, then we would observe decreases in those rates subsequent to releasing fishers.

#### FIELD METHODS

*Study Site*—We reintroduced fishers to the Stirling Management Area (hereafter Stirling) owned and managed for industrial timber production by Sierra Pacific Industries (SPI). Stirling lies in portions of Plumas, Butte and Tehama counties in northern California (Lat 39.9° Lon -121.5°; Fig. 2) that straddle where the southern Cascade Mountains meet the northern Sierra Nevada. Stirling encompassed 648 km<sup>2</sup> with elevations ranging from 424 to 2080 m and with peaks of up to 2400 m located to the east. The climate on Stirling was temperate with the majority (>85%) of precipitation

coming in late fall and winter as snow fall and rain (Pandey et al. 1999). Vegetation on Stirling was typified by Sierra Nevada mixed conifer forest with 6 dominant tree species: Ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertinia*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), and California black oak (*Quercus kelloggii*). Tanoak (*Lithocarpus densiflorus*) and canyon live oak (*Quercus chrysolepis*) also formed some dense stands in some locations (Griffin and Critchfield 1972, Beesley 2007).

Stirling has a diverse history of management regimes. From the early 1900s through 1992, Stirling was managed primarily with single tree selection every 10-15 years while the remainder of a stand was left as growing stock (termed uneven-age management). In 1992, even-aged management, where nearly all merchantable trees were removed at each harvest by clearcutting, became the major forestry strategy. In each clear-cut 2% of a harvested area was retained, with the goal of retaining structures and diversity in a stand while it regenerated with planted tree seedlings. California timber practice rules required, with few exceptions, that no more than 8 hectares (20 acres) were harvested in any one clear-cut and that adjacent stands must be retained for 5 years (Brandow and Cafferata 2014). Additionally, SPI's policies required retention of select structures, such as snags and live hardwoods, in harvested units. Units were commercially thinned after 20 and 40 years, with harvest rotations planned every 80 years. Approximately 5-15% of a watershed, or area, is harvested during a cycle.

*Reintroductions*— In late 2009, the state of California approved a plan that would reintroduce 40 fishers (24 F; 16 M) over three years from their range in northwestern California (Callas and Figura 2008). Live-capture to evaluate and to move fishers began

in late autumn 2009. We captured fishers from diverse locations in northern California to minimize the impact to any one source area and to infuse genetic diversity into the founding population (Fig. 2; Callas and Figura 2008). We transported all captured fishers to a central processing area near Anderson, California, and evaluated them for potential release at Stirling. For females, we sought individuals approaching their 2<sup>nd</sup> or 3<sup>rd</sup> birthdays to increase the likelihood they would reproduce in their first year. For males, we selected individuals we estimated were at least 3-years old because we surmised that old, big males would be better breeders than young males (Lewis et al. 2012). We removed one pre-molar from each fisher to estimate age by counting cementum annuli (Arthur et al. 1992, Poole et al. 1994), but the actual ages were unknown at the time we selected and moved fishers. At least one field biologist and one wildlife veterinarian evaluated each fisher we considered for reintroduction.

We immobilized fishers chemically with Tiletamine HCL and Zolazepam HCL (Telazol, Fort Dodge Animal Health, Fort Dodge, IA) at dosage of 7 mg/kg to fit transmitters properly and to collect data on sex, reproductive status, general condition, disease exposure, weight, and morphology. At initial capture, we collected a blood sample for genetic identification and gave each fisher a Passive Integrated Transponder (PIT) tag for future identification. We vaccinated all released fishers against canine distemper virus with Purevax (Merial Limited, Duluth, GA) and against rabies virus with Imrab 3 (Merial), and treated them for endo- and ecto-parasites with Ivermectin and Frontline (Merial Limited, Duluth, GA). We held fishers in captivity for 3-14 days while we tested them for previous exposure to distemper virus and canine parvovirus (Gabriel et al. 2012). We transported individual fishers that passed this disease quarantine period

to Stirling within 2 days. We returned one fisher that tested positive for CDV to his original capture location and held one female in captivity until she was no longer shedding canine parvovirus. The Institutional Animal Care and Use Committees from North Carolina State University (09-007-O) approved handling and sedation procedures. Our handling methods were consistent with the guidelines of the American Society of Mammalogists recommendations (Sikes and Gannon 2011)

We could not capture all the fishers we planned to release at once and we wanted to minimize the time any fisher spent in captivity and, thus, released fishers in groups of 1-5 individuals. From December of 2009 through January of 2010, we released the first 15 fishers (9 F, 6 M) onto Stirling (Fig. 3). In November 2010 and through early February 2011, we released an additional 13 fishers (7 F, 6 M) and in late 2011 we released the final 12 (8F, 4 M) fishers (Facka et al. 2016, *Conspecific competition Chapter*). We released fishers throughout Stirling but emphasized central locations (Fig. 3), which encouraged a widely distributed population that reduced potential intra-sex conflict (Powell 1979b). We released fishers without acclimation because extensive data fail to show that this improves survival of fishers or influences population establishment (Lewis et al. 2012, Powell et al. 2012). To monitor fisher movements, reproduction and survival, we outfitted female fishers with either Telonics (IMP-325 or MOD-125; Mesa, AZ) or Holohil (MI-2i, Carp, Ontario) Very High Frequency (VHF) transmitters. We outfitted adult males with Platform Terminal Transmitter (PTT [Argos]; Kiwisat 202 or 303, Sirtrack, Havelock North, NZ) collars. We programmed the PTT transmitters to turn on and ideally, to provide a minimum of one location estimate per day. Different PTT collars

were active during different time blocks to allow inference about male locations and movements throughout a 24 hour cycle.

*Field Methods at Release Site*—We attempted to locate all fishers carrying transmitters (both reintroduced and those born at the reintroduction site) once per day using either VHF or PTT telemetry. We estimated locations with VHF data by triangulation (e.g., White and Garrott 2012) using program Location of a Signal (LOAS, Ecological Software Solutions LLC), using fixed-wing or helicopter based aerial surveys, or homing on a transmitter signal until we saw the fisher or could identify the tree or other structure it used. We used location estimates from PTT data processed through the Argos system with Kalman estimation and filtering (Collecte Localisation Satellites [CLS]; Ramonville-Saint-Agne, France). Both VHF and PTT transmitters had mortality sensors that alerted us to dead fishers. When we detected a mortality signal, we attempted to find fishers immediately to confirm that they had died and to collect information on the possible causes of mortality (Wengert et al. 2013). We outfitted 8 fishers with Minitrack Global Positioning Systems (GPS) collars (Lotek Wireless, Newmarket, Ontario, CAN) during the autumns of 2012 through 2015 and set those collars to collect a location at <15 minute intervals over 10 days.

We used telemetry location estimates to document reproduction by females. Female fishers produce 1 litter per year of 1-4 kits, always in a tree cavity, beginning on or near their second birthdays, in late-March and April. Within several days to 2 weeks after giving birth, female fishers breed and, approximately 2 weeks later, their blastocysts delay implantation until winter of the following year, followed by a normal pregnancy of ~32 days (Enders and Pearson 1943, Enders and Enders 1963, Frost et al. 1997).

Generally, we followed females through the year but with increased intensity from mid-March through May to find their denning trees (detailed by Facka et al. 2016). We confirmed reproduction by placing 1-6 remotely-triggered cameras (PC800 Hyperfire Professional, Reconyx, Inc., Holmen WI) within 6 m and facing the base of a suspected den tree to photograph a female and her kits (Facka et al. 2016). Photographs showing repeated use of a tree indicated that a female was attending kits, and photographs of females with kits confirmed reproduction and documented minimum litter sizes.

In each autumn beginning in 2011, we conducted extensive live-capture efforts to document and capture fishers living on Stirling. Live-trapping occurred over the full extent of Stirling and on adjacent lands within 2 km. In each year, we used between 90 and 110 live-traps that we spaced roughly 1.6 km apart (range 0.5 to 4 km). Spacing and the numbers of traps were similar among years. Trapping lasted 14 days in 2011 and 28 days, in other years and began in mid-October. We baited traps with a chicken drumstick and placed a scent lure (Gusto, Minnesota Trapline Products, Pennock MN) at trap locations. We checked all traps daily and replaced bait and scent as needed but a minimum of 2 times per trapping session.

We brought all captured fishers to a central processing location for evaluation and handling following the same protocol used for all initial captures for reintroduced fishers. We took a genetic sample and injected subcutaneously a PIT tag into all newly captured fishers. We weighed all captured fishers, examined them for parasites and disease, and fitted them with new transmitters, if appropriate. During physical examinations, we graded a fishers' general condition based on its teeth, skin and fur, musculature, obvious wounds or injuries, ecto-parasite load, weight, and our assessment of fat over their hips

and ribs. We defined poor condition as having obvious, serious injuries or disease; worn, broken, diseased or dead teeth; low levels of body fat; and high ecto-parasite load. We defined excellent condition as having no signs of serious injury, having all carnassial and canine teeth and little wear on teeth generally, and having high levels of fat over hips and ribs. We defined average condition as being not obviously in poor or excellent condition. Fishers in average condition might have minor injuries and missing or worn teeth but no ailments that obviously affected the fisher. We did not give transmitters to fishers we deemed too small (e.g., juvenile males) or for whom the burden of a transmitter was inappropriate. Fishers we had reintroduced to Stirling were re-vaccinated annually for rabies with (Imrab 3, Merial Limited, Duluth GA) and distemper (Purevax, Merial Limited). Fishers born on Stirling were vaccinated only through 2011.

#### ANALYSIS

We considered the reintroduction in two phases: establishment and persistence (Fig. 1; Pavlik 1996, Armstrong and Seddon 2008). Evaluation of reintroductions in these phases provides temporal precision in evaluating population-level success and in elucidating reasons for failure when failure occurs. Our analyses relate specifically to the establishment phase and thus do not necessarily reflect processes or changes that could occur after this phase.

Our central premise was that both the methods of our reintroduction and the habitat quality at the release site were sufficient to establish a population of fishers. Hence, we evaluated broad patterns of movement, reproduction and survival to assess our main premise. We hypothesized that if our methods were suitable for establishing a population, we would not see differences in movement or in survival and reproduction between animals translocated (once they had settled into home ranges) and those born on the study

site (we would not see a *reintroduction* effect). If habitat decreased in quality through time, as logging activities continued, and if this habitat change affected survival or reproduction, then we would observe commensurate decreases in survival and reproduction in successive years (*year* effects). We hypothesized that variables related to the individual fisher would describe rates of survival and reproduction including *weight*, *sex*, *age*, or metrics of seasonal changes such as animals that reproduced successfully or not (survival only; *Reproduction*) or simple monthly patterns (*Month*).

*Site Fidelity*—We assumed that site fidelity of fishers on Stirling indicated whether fishers perceived their new environment as suitable or not (Young and Shivik 2006, Kemink and Kesler 2013, Berger-Tal and Saltz 2014). For analyses of site fidelity, we used only VHF telemetry location estimates with error radii < 1000 m. For Argos location estimates, we used only those with error < 1500 m. We analyzed locations of males and females separately because fishers are sexually dimorphic and use space differently (Powell 1979b). Additionally, we evaluated reintroduced fishers separately from fishers born on Stirling. We examined the proportions of locations of reintroduced male and female fishers and Stirling-born fishers that occurred either within, or near, the Stirling boundary. Because the radii of large home ranges of females in California are roughly 2 km, we considered this a reasonable distance that fishers might settle outside the Stirling border. We created a 2-km buffer around the boundary of Stirling and calculated the proportion of all locations within this buffer including those occurring on Stirling.

*Habitat availability and selection*— To categorize habitat use and selection by fishers we used forest inventory data provided by Sierra Pacific Industries. These data are

based on 39,871 variable radius plots that were spaced roughly every 80.5 m (North-South) by 201.2 m (East-West) or approximately every 1.7 acres (see Niblett et al. 2015). Professional foresters sampled each plot every 5-10 years and SPI used models of tree growth to estimate changes to forest stands on an annual basis. Thus, for each year, the forests on Stirling are quantified for a number of forest-metrics including tree size, stand volume, canopy cover, and numbers of trees by species (Appendix A).

We categorized habitat quality for fishers by classifying forest types based on 2 variables: Overhead canopy closure and quadratic mean diameter at breast height (QMD). These metrics were classified in 4 categories: Habitat Form 1 (HF1), Habitat Form 2 (HF2), Habitat Form 2 heavy (HF2hv), and Habitat Form 4 (HF4). Habitat Form 2 (HF2), was defined by forests with canopy cover greater than 40% and  $QMD \geq 15.2$  cm. A subset of HF2 is Habitat Form 2 heavy (HF2hv) which were forest stands with canopy closure greater than 50% and  $QMD \geq 27.9$  cm. The final classification level, and the one considered most appropriate for fishers, is Habitat Form 4, which was defined by forests with canopy closure greater than 60% and QMD greater than 33 cm. The forest classification we considered as least important, or most avoided, by fishers is HF1. It is defined as all other forest types not defined by the other 3 classifications. For the purposes of analysis we arbitrarily assigned the habitat form categories the values of  $HF1 = 0$ ,  $HF2 = 0.50$ ,  $HF2hv = 0.75$ , and  $HF4 = 1.0$ .

We used all locations from female and male fishers from 2009 through 2015 that occurred within the Stirling boundary. This data set included all locations for females from estimated triangulations, walkins, flights, and captures and for males from locations from Argos locations of classes 1, 2, and 3, Global Positions Systems (GPS) collars,

capture, and walkins (Table 2). We quantified the proportion of locations used by fishers and available habitat to fishers for each of the 4 land cover categories for each year from 2010 to 2015. Thus, allowing comparison of the habitat fishers used and avoided in each specific year. We used the proportion of used and available habitat to calculate a resource selection function (RSF) based on the modified Ivlev electivity index (Manly et al. 2007) as:

$$\textit{modified Ivlev} = \frac{2 \times (\textit{proportion used} - \textit{proportion available})}{1 + (\textit{proportion used} + \textit{proportion available})}$$

We calculated the mean values for the modified Ivlev across years to generate a mean values for the resource selection function. We used ordinary least squares linear regression in the statsmodels package for Python to evaluate the relationship between predicted habitat quality and the resource selection function to identify land cover categories that fishers used or avoided based on their availability.

*Population estimation*– We calculated the minimum number of fishers known alive (MNA) for each of our autumn live-capture sessions beginning in 2011. We calculated this index by summing the total number of fishers captured plus the total number of fishers with active telemetry units that were not captured. Further, we adjusted retrospectively this value to include fishers that were not detected in a given year, or whose statuses were unknown because their transmitters failed, but were detected later. We calculated separate MNA values for males and females as a conservative index of changes in population size. In a prior analysis with data from 2011 to 2014, we estimated population size using our autumn trapping data in a mark-recapture approach. Nevertheless, these estimates were relatively uninformative because they only

recapitulated the pattern of MNA, and had very large confidence intervals because of low probability of capture ( $<0.10$ ).

*Survival*—We analyzed survival with telemetry records in the “known fates” analyses within program MARK (White and Burnham 1999). Known fates analyses account for each month when we documented each fisher as alive or dead. We censored fishers that we could not document as alive or dead in any month. We evaluated fisher survival based on the effects of time (*month* and *year*), and a null model effect with survival constant through time. We evaluated if fishers differed in survival based on *age*. We could only estimate juvenile survival directly from the time of initial capture (~6 months old) until their first birthday in April.

We could not estimate directly juvenile survival from birth until capture in the first autumn after birth. When females with kits died, we assumed that their entire litters were lost. Yet, some juvenile fishers also die when their mothers live. Thus, we created an index of kit survival in their first six months by calculating the total number of kits we documented during spring and summer. We remove from this count all kits of mothers that died prior to 1 – September. We used this minimum total count of kits in the denominator and the total captured kits from each autumn in the numerator to estimate a minimum kits survival index.

*Reproduction*—We examined reproduction as a composite variable (reproductive output) that included whether a female gave birth and the number of kits we observed. We classified adult females for each denning season as: 1) did not give birth, 2) gave birth and had one kit, and 3) gave birth and had at least 2 kits. Females that were 1 year old and, consequently, not old enough to give birth in April were not included in these

analyses. We hypothesized that covariates unrelated to time or reintroduction status might explain reproductive rates. Thus, we included the *weight* of a female in the fall or winter before the denning season as well as her age on 1-April. We analyzed denning rate as a multinomial response using polytomous (multinomial) logistic regression (PROC LOGISTIC, Statistical Application Software [SAS], Cary, NC). We considered females that were tracked in multiple years as independent events because our main goal was to investigate broad-scale changes in reproduction through time. We modeled the dependent variable (reproductive output) to covariates that may affect its including effects from *age*, *translocation*, *weight*, and *year*. To evaluate how the models we tested compared to simple random variation we included a normally distributed, randomly-generated covariate to include within our analyses (random). We converted the beta estimates for the direction and magnitude of effects to odds-ratios using an exponential transformation ( $e^{\beta}$ ).

We estimated rates of survival, the probability of a female reproducing (denning), and minimum litter size with similar approaches. We tested the several competing hypotheses that potentially explained those vital rates. We ranked those hypotheses using Akaike's Information Criteria corrected for small sample size (AICc; Burnham and Anderson 2002). When a model had clear support ( $\Delta AICc \geq 4$  for other models ) we used the top model to provide parameter estimates for vital rates or population sizes. Otherwise we used model averaging across all competing models to provide estimates of specific effects.

*Population Viability Analysis*—We evaluated population size, population growth rate, and likelihood of extinction for our reintroduced fisher population using stochastic

simulations. In MATLAB (The Mathworks Inc, Natick MA), we constructed 4-stage Leslie matrices that described the life history pattern of female fishers (Fig. 4; Buskirk et al. 2012, Facka et al. 2016). We simulated the release of female fishers for 3 years, with 9 released in year-1, 7 in year-2, and 8 in year-3 (equal to our actual releases). The population structure of released females was biased towards adult females (19 of 24) with fewer yearlings (4 of 24) and only 1 juvenile female released among all years.

For each discrete age class (juvenile, yearling, 2-yr old, and adult) and vital rate we used the mean estimates from our data as the mean parameter in our simulation (Table 1). For each of the 4 age classes, we generated survival and denning rates randomly using the beta distribution (betarnd function). For the beta distribution, the parameters alpha and beta define the shape of the distribution and were calculated from the values for these parameters from the mean and standard deviation from our data (Morris and Doak 2002). We generated litter size randomly using the normal distribution (normrnd function) parameterized, again, by the mean and standard deviation from our data. For each run, each vital rate was generated randomly and independently in each year of the simulation without correlation among years or vital rates. A female fisher's litter includes both sexes but our simulations were for females only; thus, we simulated the number of females born by setting the sex ratio at birth to 0.50 with a standard deviation of 0.05. We had the least information on juvenile survival from birth through their 1st year. Therefore, we simulated 2 low estimates of mean juvenile survival (0.20 and 0.30) based on values in the literature (York 1996, Buskirk et al. 2012), a medium value of 0.50, and a high value of 0.60. Mean juvenile survival was the only parameter we varied in this manner. We arbitrarily set the maximum number of females to be 200. If a simulation reached this

number of females, reproduction in the next year of all cohorts fell to 0, but survival of all non-juvenile class was unaffected. This model assumes that habitat remains constant, such that mean and variance of the vital rates remain constant. Finally, we assumed that numbers or quality of males did not limit reproduction.

We replicated a 50-year reintroduction 1000 times, for each mean value of juvenile survival, to evaluate the likelihood of extinction and population trajectory. For all 4 simulated values of mean juvenile survival we calculated the percent of 1000 replicates that went extinct (population size  $\leq 2$  females), the year of extinction, and the geometric mean of the population size.

## RESULTS

*Population Structure*— Average age at time of release was 2.6 years old (range 0 – 5) for females and 3.0 years old (range (0 – 6) for males (Fig. 5). A single juvenile male and female (<1 year old) were reintroduced. All other fishers (n = 38) were adults (>1 years old), capable of breeding and reproduction when released. Subsequent to the initial releases, the population remained biased towards females with a trend toward an increased ratio of females to males. From 2009 to 2015, the ratio of females to males increased as we detected fewer males in the population. The average age of known males from 2010 to 2015 declined below 3. Relatively old fishers (>6 years) have remained within the population since the release.

The number of fishers reintroduced compared to fishers born on Stirling decreased through time (Fig. 5). We documented one juvenile male in the autumn of 2010 using a remote camera. We captured 2 other fishers (1F:1M) in subsequent years whose ages indicated they were born in spring of 2010. In the fall of 2011 we captured the first fishers that we had not released; subsequently, the proportion of fishers born on Stirling

increased in each year (Fig. 5). From 2011 on, we captured 72 (44F: 28M) individual fishers born on or near Stirling and, thus, have collected data from 112 total fishers at Stirling. At the end of 2015, 3 (1F;2M) reintroduced fishers still lived on or near Stirling (Fig. 5). Stirling-born fishers comprised 90% of the total known population (both female and male fishers). Thus, after 6 years, female fishers < 3 years old and born on Stirling were the most common fishers encountered.

*Locations & Site Fidelity* –At the conclusion of 2015, we had estimated 29,491 locations for female and male fishers using diverse tracking approaches (Table 2). A majority of total locations came from PTT Argos data (43%). Generally, Argos locations were from the low precision classes (63%; Table 2). Thus, only 17% of locations with an estimated error were from Argos. The majority of all VHF-based locations came from triangulations (85%) and relatively few locations came from estimates where we homed in on a signal (10%) or from aerial surveys (5%). We collected 8,618 locations (27% of total locations) from GPS collars.

The majority of locations for fishers occurred on or within 2km of the boundaries of Stirling. For females, 98% and 99% of translocated and Stirling-born fishers were within the Stirling boundary. The locations of translocated male fishers occurred on Stirling 96% of the time whereas those born on Stirling occurred 99% of the time. All 152 den locations occurred on or within 2km of the study site. This rate is similar between fishers we translocated and those born on Stirling. Through time the proportion of locations found near Stirling has increased because we tracked few fishers off the study site. In all years >65% of locations of females and males were within 2km of Stirling. Fishers may have established home ranges on adjacent lands but the location

data indicated that many fishers from the inception of the project to the present have found habitat sufficient to stay on the study area. Incidental detections from adjacent lands have provided documentation that fishers exist beyond Stirling (Figura unpublished data).

*Habitat availability and selection*— The mean available habitat quality on Stirling across all years was  $0.59 \pm 0.37$  SD. Across all years, forest stands classified as HF4 were the most abundant on Stirling (Fig. 6). Stands classified as HF2hv were the second most abundant followed by stands classified as HF1 and HF2 (Fig. 6). The amount of each forest stand type relative to other remained the same throughout the study with slight increases in both HF4 and HR1. Both HF2 and HF2hv declined modestly from 2010 to 2015. There was almost no change in mean available habitat from 2010 (0.60) to 2015 (0.59), but stands with younger trees and less overhead canopy (HF1) increased through time as logging occurred. Some stands that were classified as HF2hv in earlier years matured into HF4 stands whereas many stands logged 20-30 years ago had not mature sufficiently to be classified as HF2 or HF2hv.

Fishers preferentially used stands of higher quality (mean  $0.72 \pm 0.30$ ) than were available. The relationships between predicted habitat quality and the modified Ivlev resource selection function demonstrated a positive relationship that is statistically different from zero across all years ( $\beta = 0.16$ ,  $R^2 = 0.49$ ,  $p = 0.03$ ,  $n = 20$ ). Suggesting that fishers selected stands with high overhead canopy and large mean diameter trees (RSF value for HF4 = 0.1) and avoided stands with low canopy cover and small mean diameter trees (RSF value HF1 = -0.19). We detected similar patterns of selection and

avoidance using different models published in the literature and indicates that fishers on Stirling generally selected old, mature, stands of forest (see Appendix A).

*Population Trends* –At the end of our trapping effort in autumn, 2015, the MNA population size on Stirling was 49 total fishers (Fig. 7). The MNA shows an overall positive trajectory since 2011 with an apparent increase in population size since 2013. The decreases in MNA size during 2013 were likely attributable to changes in the number of adult males. We observed a relatively high numbers of male mortalities during 2013 and early 2014 (n= 5). The minimum numbers of females known alive was relatively stable throughout the study period and with the highest MNA for females in 2015 (33 females; Fig. 6). Dividing the total MNA by the area of Stirling provides a conservative estimate of density that ranged from 5.4 to 7.6 fishers/100 km<sup>2</sup> from 2011 to 2015.

*Survival*–Through December of 2015, we confirmed the deaths of 26 fishers (16 F, 9 M, 1 unknown). Fishers whose sex was unknown represent kits we found with 2 adult female fishers, presumably their mothers, but that were too badly decomposed to determine sex. We documented an average of  $3.7 \pm 1.3$  ( $\pm$ SD) fisher mortalities per year since the start of the project. The total number of mortalities was highest in 2014 with 6. As a proportion of the total numbers of fishers we tracked in each year, mortality in 2014 (20%) was higher than the mean proportion across all years ( $13\% \pm 3\%$ ). Total mortalities (4) in 2015 were lower than in 2014 and were closer to the overall mean (14%). Thus, we detected little evidence for changes in mortality rates during the 6 years. The causes of most of mortalities (61%) could not be determined specifically because we did not find the carcass before extensive decomposition occurred. At least 1 female fisher died from drowning in an abandoned water tank and 4 other dead fishers were found in

water tanks. One male fisher died after being hit by a vehicle. Three other fishers appeared to have died from predation (Wengert et al. 2014).

We documented the mortalities of 17 (43% of 40 total) reintroduced fishers, and the average time after release until their deaths was  $21 \pm 20$  months. Reintroduced fishers comprised the majority of deaths we have documented and only 9 deaths (8% of 112 fishers captured or tracked) were from individuals born on Stirling. Captured fishers that were born on Stirling have lived an average of  $21 \pm 9$  months (omitting the 2 kits discovered with their mothers).

Our known fates analysis reflected differences in the number and proportion of deaths associated with the reproductive seasons for males and females (Table 3). The highest ranked hypotheses indicated that survival was lowest for males from March to July and lowest for females from May through August (Table 3). Females and males had similar rates of survival during their reproductive and non-reproductive seasons. The second and third most well supported hypotheses incorporated the reproductive season effect but incorporated juvenile survival that was modeled as equal to adults in the non-reproductive seasons and differences between the sexes in all seasons (Fig. 8A). Other hypotheses of survival for fishers including effects from sex, weight, age, and condition were not well supported. Our analysis revealed no apparent change in survival across years (Fig. 8B)

When we assumed that kit mortality occurred only when mothers died, we estimated kit survival at 78% (44 of 56; Table 4). We assume some kits die in dens even when their mothers live. When we combined our estimate of kit survival through denning (93%) with estimates from autumn survival following capture (80%), we produced an index of

juvenile survival (from time of litter size counts to age 1 yr) of 74%.

*Reproduction*—We tracked 42 females in the denning seasons of 2010-2015 for 63 denning opportunities. We documented 50 dens for an overall average denning rate of 79% (Table 4). Of the 42 total females, 19 (45%) were tracked for multiple years and 13 were tracked for  $\geq 3$  years. We tracked equal numbers of reintroduced and Stirling born (21 of 42) adult females during denning seasons. In 2014, we tracked fewer females because of logistics, including fewer experienced field technicians. Nevertheless, in the 2014 and 2015 seasons the number of potentially reproducing females was biased towards those born on Stirling. We acquired minimum litter counts from 30 of the 42 actively denning females. We documented 77 kits and the mean minimum litter size across all years was  $1.7 \pm 0.4$  kits/litter (Table 4). Yearling females had lower mean litters sizes ( $1.6 \pm 0.50$ ) than did adults females ( $1.72 \pm 0.72$ ). The lowest mean litter size occurred in 2010 as all 4 females documented with kits produced at least only 1 kit. The highest mean litter size occurred in 2011 when females produced at least 2.2 kits/litter (Table 4).

Hypotheses related to individual females described reproductive output better than did those related to time (Table 5). The best supported models included an effect from a females' age during the previous fall (Table 5). Age had the lowest AIC<sub>c</sub> score but nearly all other variables we tested had  $\Delta\text{AIC}_c < 4$ , including the random variable. The odds-ratio point estimate for age for reproductive class 2 compared to 1 (not producing kits) was  $1.67 \pm 0.97$ , 2.865 and for reproductive class 3 compared to 1 was  $1.60 \pm 0.946$ , 2.671. The model estimates from this top model suggest that young females  $< 3$  were less likely to reproduce compared to older females, but the 95% confidence limits bounded 1 and

indicated a non-informative metric for understanding reproductive output. We found weak functional relationships among other covariates and reproductive output. Thus, a null model describing reproductive output as constant through time and among females was relatively well supported among other covariates.

*Population Viability Analysis*—Our stochastic simulations suggest that juvenile survival potentially has large effects on fisher population growth. When we set mean juvenile survival to 0.60, the mean female population size grew, approaching 180 females at 50 years, and no simulated populations went extinct (Fig. 9). Conversely, when we set mean juvenile survival to 0.20, the mean female population size was 0 at 20 years and all simulated population extinct with the mean year of extinction  $11.5 \pm 2.66$ . Mean juvenile survival rates of 0.30 and 0.50 showed concordant increases in mean population size but the average population growth was negative at low rates of juvenile survival (Fig. 9). In the 1000 simulations where juvenile survival was 0.30 (99%) of the populations went extinct by year-50 and the mean year of extinction was year-22  $\pm 8.20$ . When juvenile survival was 0.50, 14% of the simulation reintroductions went extinct and the mean year of extinction was year-32  $\pm 10.0$ . We inferred that populations with a mean juvenile survival of 0.45 would be stable assuming other vital rates were similar to those in our model.

Regardless of the true juvenile survival rate, the simulated populations grew rapidly during the first 3 years, while releases were ongoing. No simulated population went extinct before year-5 even at the lowest rate of juvenile survival. Simulated reintroductions that strongly decreased or increased could not be differentiated clearly before year-10, because of the influence of the releases during the first 3 years (Fig. 9)

and large variation in population growth.

## DISCUSSION

The reintroduction of 40 fishers into the southern Cascade and northern Sierra Nevada mountain ranges of California led to an established a population by year 5 (2014) (Fig. 1). The reintroduced fishers remained on the study site, and sufficient numbers of their progeny occupied the area to continue population growth. The population presently functions without need of augmentation. Processes such as mating, reproduction and recruitment into the population are ongoing and not restricted to the founding fishers. The population has grown to an estimated population size that is larger than the number of originally released fishers and at the low end of the range of densities observed for other fishers population in California and in north America (5 – 52 fishers/100 km<sup>2</sup>; Fig. 6; Powell 1993, Matthews et al. 2011). Our estimates of the vital rates from 2009 to 2015 suggest no negative trends in population parameters, which agree with our estimates of population size for this same period. Overall, these results indicate the methods and the habitat present on the landscape from reintroduction through 2015 did not preclude establishment. Our analyses focused on broad population processes that should represent the average habitat condition, but we recognize that there were likely important differences in survival and reproduction for fishers living in different habitat conditions. Future work will more closely evaluate these individual metrics with respect to specific habitat metrics where fishers lived. Specifically, we hypothesize that fishers with the highest amount of high quality habitat, including denning structures and forage, will have commensurate rates of survival or reproduction.

Our reintroduction is an important example demonstrating that experimental, perhaps controversial, reintroductions can effectively test the potential viability of populations reliant on marginal or suboptimal habitats (Young and Shivik 2006; Chapter *Maximizing the value of conservation translocations through science*, Crooms et al. 2012). Had most fishers dispersed from Stirling we could infer that conditions, either from habitat or other exogenous forces, were insufficient to support a population (Kemink and Kesler 2013, Berger-Tal and Saltz 2014). Moreover, if the fishers that did stay, died or failed to reproduce we could have inferred that habitat quality was poor and insufficient to support viable populations (Fig. 1; Davis et al. 2007, Hargreaves et al. 2014). A failure from any of these mechanisms would have provided compelling evidence that Stirling, and other logged landscapes, represented poor habitat quality and thus informed further management actions. We do not know if the population will decline through time as more of the landscape is logged and regenerates, but the apparently growing population at the end of 2015 suggests fishers can endure relatively high levels of timber harvest. This observation supports the hypothesis that fishers can live on logged or otherwise fragmented landscapes (Thompson 2008, Matthews et al. 2011, LaPoint et al. 2013, Swiers 2013). Thus, our approach may be valuable for other projects to consider when designing reintroductions where habitat quality is controversial.

The vital rates we have estimated from the first six years of the project are similar to those at other sites in the west (Weir and Corbould 2008, Jordan et al. 2011, Matthews et al. 2011, Matthews et al. 2013, Thompson et al. 2014, Sweitzer et al. 2015a). Estimates of adult survival from the southern Sierra Nevada populations indicate annual survival rates from 0.62 to 0.94; and, that short term rates from northern California populations

were 0.64 (Jordan 2007, Jordan et al. 2011, Swiers 2013, Thompson et al. 2014, Sweitzer et al. 2015b). Our estimates of adult annual survival were 0.80 across all years and similar to average estimates of survival for California (Fig. 7). We found little evidence of strong differences between sexes in survival but males may endure a higher survival in some years during the reproductive seasons (Fig 7A). One study from coastal California shows rates of denning (0.87; range = 0.73 – 1.0) and average litter size (1.8; range 1.5 – 2.0) that are higher, though similar, to ours (Matthews et al. 2013). Denning rates in the first 2 years of the reintroduction were depressed modestly by the timing of when we released some females (Facka et al. 2016) and potentially litter size was similarly affected. Obtaining long-term population parameters that are reliable takes as long as 5-7 years for black-bears (*Ursus americanus*) (Brongo et al. 2005). Thus, we considered data from 2-3 more years post-establishment critical to estimate accurately the mean values for reproduction.

The roles of habitat quality and forest management on fishers are key questions facing regulators, managers and conservationists in the western United States. Fishers in the western portion of their range appear to fare poorly compared to fishers in the east (Lewis et al. 2012, Powell et al. 2012, LaPoint et al. 2015). Fishers in their eastern range live in places with high rainfall, low temperatures and high primary productivity, and those conditions also describe locations with high fisher densities in the west (Weir and Courbould 2006, Thompson 2008, Matthews et al. 2011). We hypothesize that regional climate regimes (e.g., maximum temperature and rainfall) are an important correlates of fisher population densities and population viability. Few studies on fishers consider the innate differences that occur between study areas and population of fishers that result

from climate or other abiotic factors. Thus, inferences to forest management are confounded by these innate differences and should be addressed. Forest management practices are easier to modify than are climates, and may influence fishers directly by altering populations of prey and competing predators (Powell 1993, Wengert et al. 2014). The specific types of logging and the configuration of habitat modifications are likely important mechanisms that can affect placements of fisher's home range, fitness of individuals, and ultimately populations (Sauder and Rachlow 2014).

Forests that regenerate after heavy logging may lack important components that fishers, martens, and other forest carnivores require such as coarse woody debris on the forest floor (Powell and Zielinski 1994, Powell et al. 2003, Andruskiw et al. 2008). Alternatively, forests that are comprised primarily of regenerated timber may need only have sufficient canopy cover, denning trees and large prey species (e.g., gray squirrels [*Sciurus griseus*]). Understanding the subtle differences, if they exist, between old-growth or mature forests and old regenerated stands will require specific understanding of what fishers, or similar species, need from those forests to meet each aspect of their lives.

The population on Stirling is isolated and relatively small. Future work must illuminate if this population has reached an asymptote that indicates a carrying capacity because newly born fishers – particularly females - cannot maintain home ranges. Moreover, if such an asymptote exists and changes through time it may reflect affects from changes in habitat that we can correlate to specific metrics including logging intensity. Currently, several studies address native fisher populations throughout California, Washington, and British Columbia and these provide important comparisons to Stirling. In particular, they provide the opportunity to evaluate the influence of

climates and forest management practices on fishers. If the population of fishers on Stirling expands and exists on neighboring USDA Forest Service and private lands, new monitoring and research programs should be developed to track and compare these sub-populations. Presently, only incidental monitoring occurs on lands adjacent to Stirling. We documented unknown male fishers living in these areas

Our research suggests managed landscapes have value for reintroduced fishers. Fishers are finding habitat within a matrix of clear-cut logging that supports survival and reproduction. Fishers appear to be able to use fragmented or patching landscapes even in urban environments (LaPoint et al. 2013). Our project suggests that fishers in much of their range are adaptable and capable of finding pockets of suitable, if not optimal, habitat. Additionally, our project provides a baseline of both protocols and conditions where fishers were released and subsequently performed well enough to establish a new functioning population.

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Table 1. Mean values used in matrix population models. The mean values S01 through S04 are four different parameterization used for juvenile survival. All other mean values remained constant.

Stage	Metric	Mean	Standard Deviation
F0	Juvenile Fecundity	0.000	--
	Juvenile Den Rate	0.000	0.000
	Juvenile Litter Size	0.000	0.000
S01	Juvenile Survival	0.200	0.300
S02	Juvenile Survival	0.300	0.300
S03	Juvenile Survival	0.500	0.300
S04	Juvenile Survival	0.600	0.300
F1	Yearling Fecundity	0.500	--
	Yearling Den Rate	0.550	0.100
	Yearling Litter Size	1.600	0.500
S1	Yearling Survival	0.500	0.090
F2	2-yr Fecundity	0.586	--
	2-yr Den Rate	0.733	0.100
	2-yr Litter Size	1.600	0.550
S2	2-yr Survival	0.600	0.100
F3	Adult Fecundity	0.797	--
	Adult Den Rate	0.840	0.100
	Adult Litter Size	1.833	0.790
	Adult Survival	0.600	0.140
	Sex Ratio	0.500	0.050

Table 2. The total number (Number) of locations used in analyses based on estimation method with the proportion of each location type, and the proportion of each location type relative to all methods for used estimates of female and male fishers in northern California from 2009 to 2015.

Method	Type	Number	Proportion Method	Proportion Total
VHF	Total	8195	1.00	0.28
	Triangulation	6927	0.85	0.23
	Homing	836	0.10	0.03
	Aerial	392	0.05	0.01
PTT(Argos)	Total	12678	1.00	0.43
	3 (<250 m)	1215	0.10	0.04
	2 (>250<500 m)	1599	0.13	0.05
	1 (>500<1500 m)	1837	0.14	0.06
	others	8027	0.63	0.27
GPS		8618	1.00	0.29
<b>Total Locations</b>		<b>29491</b>		<b>1.00</b>

Table 3. Model selection comparison for 20 models of survival from a known fates analysis in program MARK based on monthly fates of reintroduced fishers and their offspring in northern California, December 2009 – December 2015. Model selection criteria are the AIC<sub>c</sub> scores,  $\Delta$ AIC<sub>c</sub> compares top model to other competing models, the model weight for each competing model ( $w$ ), the likelihood, and the number of estimated parameters (K).

Model	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w$	Likelihood	K
Repro Season <sup>†</sup>	223.85	0.00	0.66	1.00	2
Age + Repro Season <sup>‡†</sup>	226.48	2.62	0.18	0.27	2
Sex × Repro Season <sup>†</sup>	226.97	3.12	0.14	0.21	4
Repro Season (Mar-Aug) <sup>§</sup>	232.84	8.98	0.01	0.01	2
Repro Season (Mar-Aug) <sup>¶</sup>	235.07	11.22	0.00	0.00	4
Constant (null)	235.38	11.53	0.00	0.00	1
Head length	236.06	12.21	0.00	0.00	2
Sex	236.42	12.57	0.00	0.00	2
Weight	236.55	12.70	0.00	0.00	2
Age (juv, 1-yr, ad)	238.88	15.03	0.00	0.00	3
Condition	239.38	15.53	0.00	0.00	3
Reintroduction	240.18	16.33	0.00	0.00	4
Sex × Age (juv, 1-yr, ad)	242.26	18.41	0.00	0.00	6
Sex × Age at first capture	242.56	18.71	0.00	0.00	16
Month	244.20	20.34	0.00	0.00	12
Sex × Year	246.10	22.24	0.00	0.00	13
Year	246.32	22.47	0.00	0.00	7
Sex × Month	249.52	25.67	0.00	0.00	24
Year × Month	328.30	104.44	0.00	0.00	73

<sup>†</sup> Reproductive seasons for females were May thru August and for males were March thru June

<sup>‡</sup> Juveniles and 1-year old fishers estimated as having same survival as non-reproductive adults

<sup>§</sup>Sexes modeled as unequal

<sup>¶</sup>Sexes modeled as equal

Table 4. The number of females that were radio-tracked, the number that denned, the percent of females that denned, the minimum number of kits known to have been produced (Min # kits), the mean minimum litter size (Litter Size  $\pm$  95% CI), the ratio of kits known to have been produced to females (Kits/Female), the number of natal dens found, and the number of maternal dens found for females tracked in 2010-2015 on the Stirling Management Area of Sierra Pacific Industries in the northern Sierra Nevada and southern Cascade Mountains of northern California.

Metric	2010	2011	2012	2013	2014	2015	Total
Females	8	9	10	11	7	18	63
Females denned	5	7	9	9	6	14	50
% Dened	63%	78%	90%	82%	86%	78%	79%
Min # kits	4	13	14	17	8	21	77
Kits in fall	1	8	17	13	12	21	72
Females Died in Den	2	1	2	1	2	1	9
Kits Died Den	2	3	3	2	2	1	13
Litter Size	1	2.2	1.8	1.9	1.6	1.9	1.7
Juvenile Spring:Fall	0.25	0.62	1.21	0.76	1.50	1.00	0.9
Kits/Female	0.5	1.4	1.4	1.5	1.1	1.2	1.2

Table 5. Comparison of 7 competing models hypothesized to explain denning rate and litter size of female fishers in California from 2009 to 2015. Metrics used to compare models follow the form of Burnham and Anderson (2002) where the log likelihood multiplied by -2 natural log ( $-2\ln[L]$ ), the number of estimable parameters ( $K$ ), number of observation ( $n = 63$  for all) are used to construct Akaike's Information Criterion corrected for sample size ( $AIC_c$ ), the difference between top model and other models ( $\Delta AIC_c$ ), the model likelihood, and model weight ( $w$ ).

Model	$AIC_c$	$\Delta AIC_c$	Likelihood	$w$	$k$
Age	133.615	0.000	1.000	0.358	4
Weight	135.511	1.896	0.388	0.139	4
Body Condition Index <sup>†</sup>	136.073	2.458	0.293	0.105	4
Year <sup>‡</sup>	136.167	2.552	0.279	0.100	12
Reintroduction	136.645	3.030	0.220	0.079	4
Random	137.115	3.500	0.174	0.062	4
Head Length	137.213	3.598	0.165	0.059	4
Year <sup>§</sup>	137.473	3.858	0.145	0.052	4
Body Length	137.688	4.073	0.130	0.047	4

<sup>†</sup> The weight of the fisher divided by body length

<sup>‡</sup> Year was modeled as a discrete variable and different in each year.

<sup>§</sup> Year was modeled as continuous.

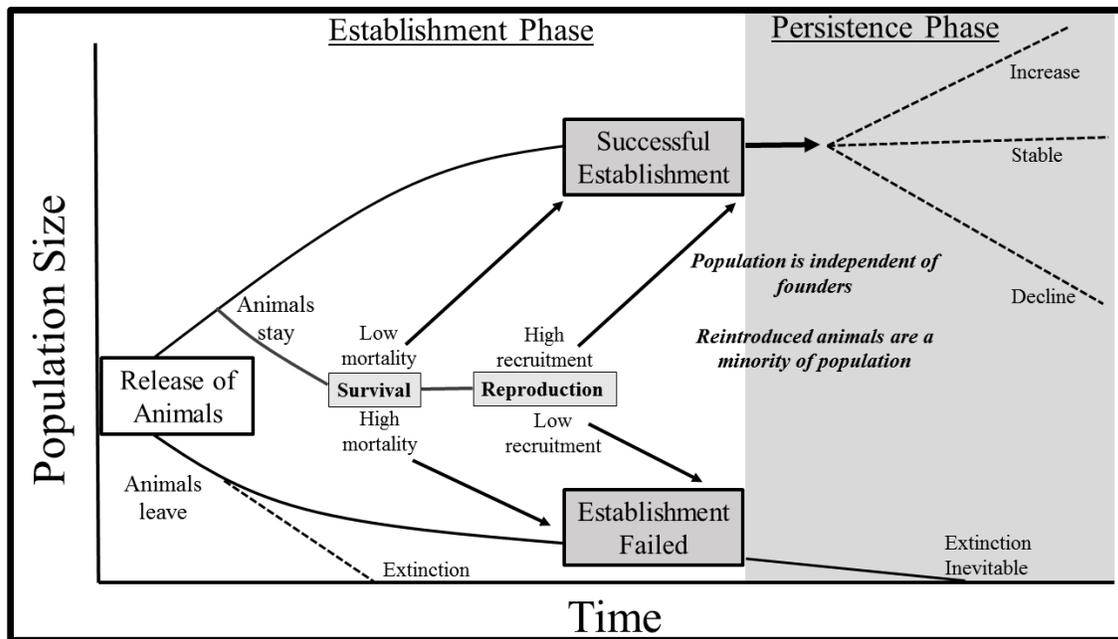


Figure 1. Phases of reintroduction

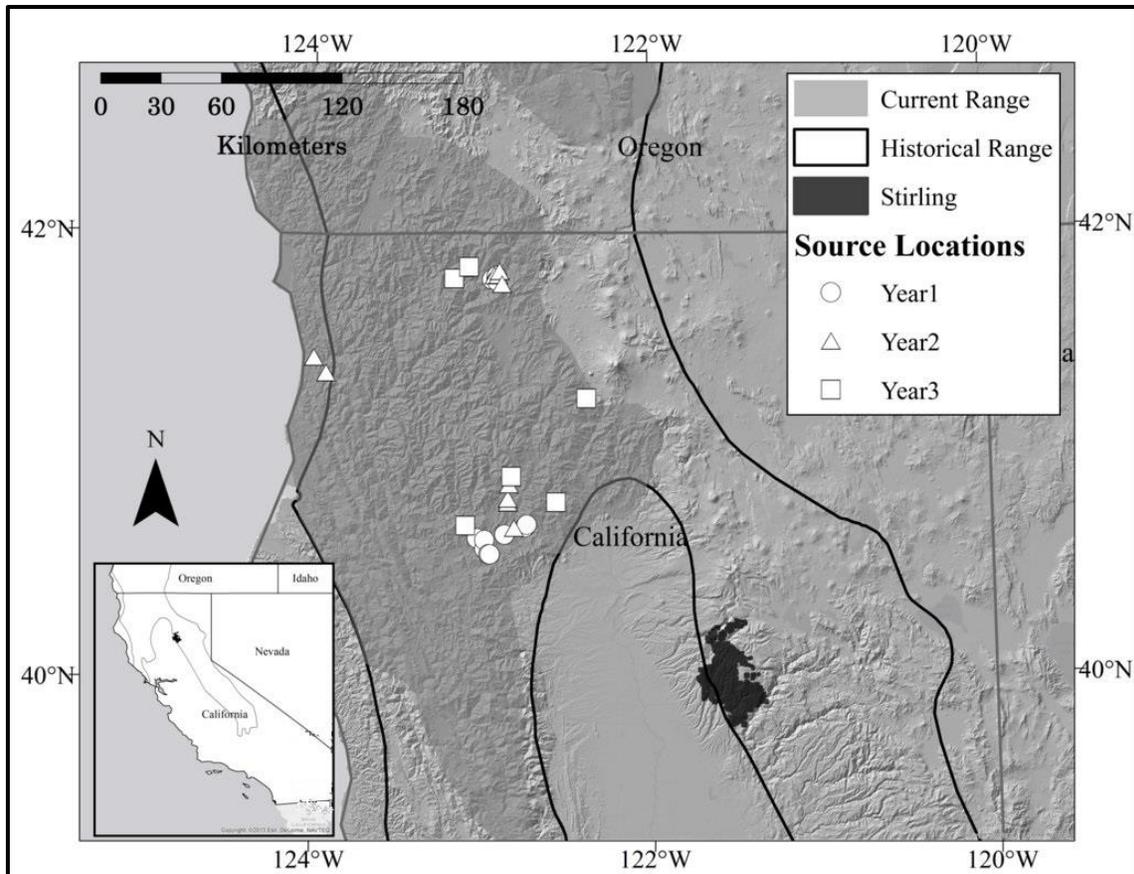


Figure 2. Locations, by years, where we captured fishers for release on the Stirling reintroduction site in northern California overlain with the estimated historical (Grinnell 1937) and current distributions (Lewis et al. 2012) of fishers.

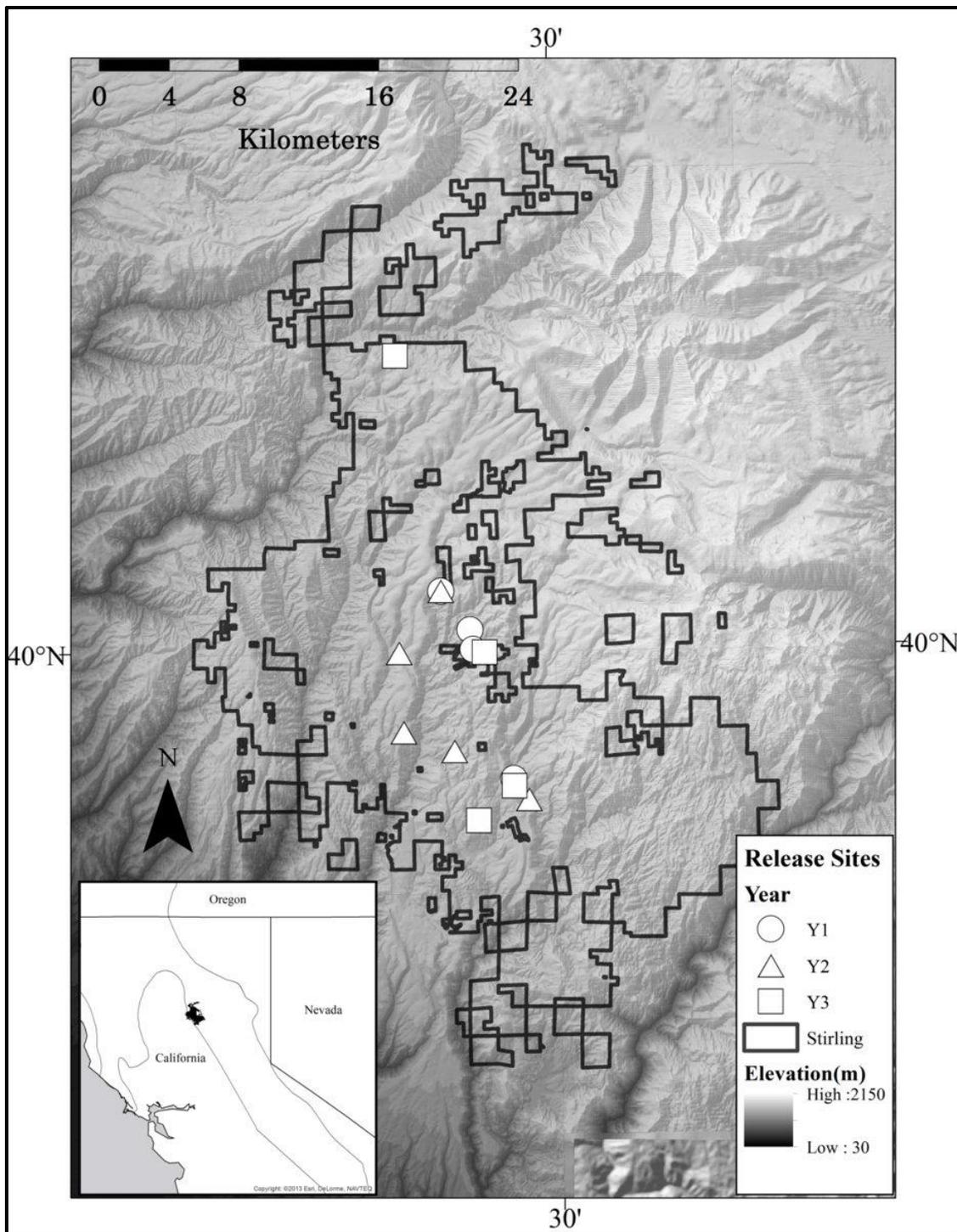


Figure 3. Release locations, by year, of fishers on the Stirling reintroduction site at the boundary of the Southern Cascade and northern Sierra mountain ranges in northern California.

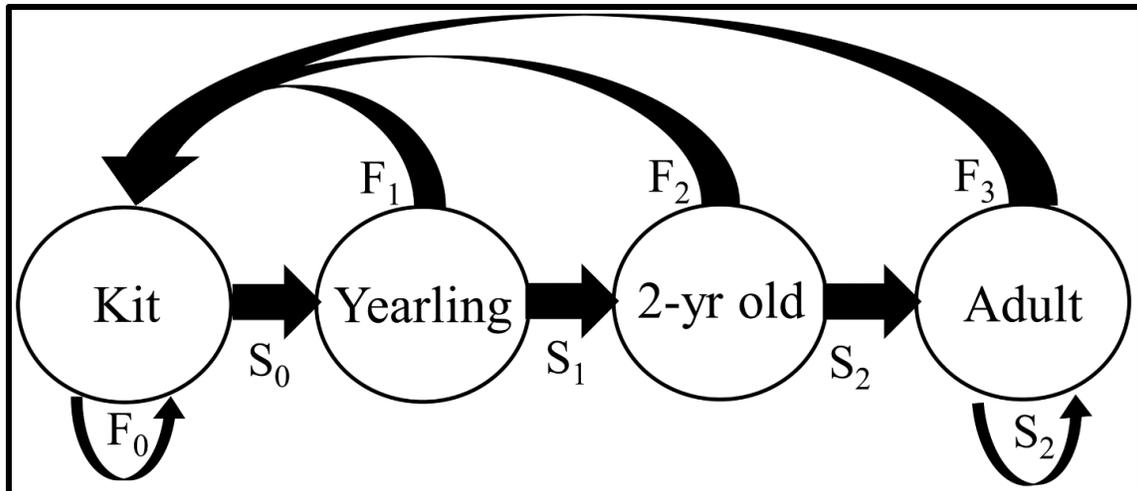


Figure 4. Life-stage model of the fisher life cycle used to construct projection matrices to simulate reintroductions. Each circle represents the discrete life-stage of a female fisher with the kit life-stage consisting of all females ages 0 to <1 year old, the yearling life-stage is females 1 to <2, and the adult life-stage is all females ages 2 and older. The arrows connecting the circles represents the transition values between the life-stages:  $S_0$  = probability of surviving from birth until 1<sup>st</sup> birthday,  $S_1$  = probability of surviving between 1<sup>st</sup> and 2<sup>nd</sup> birthday,  $S_2$  = probability of surviving in to successive birthdays after the 2<sup>nd</sup>,  $F_0$  = probability of a newborn giving birth (always 0),  $F_1$  = the probability of a yearling female denning on her 2<sup>nd</sup> birthday, and  $F_2$  = the probability of a 2-yr old female denning

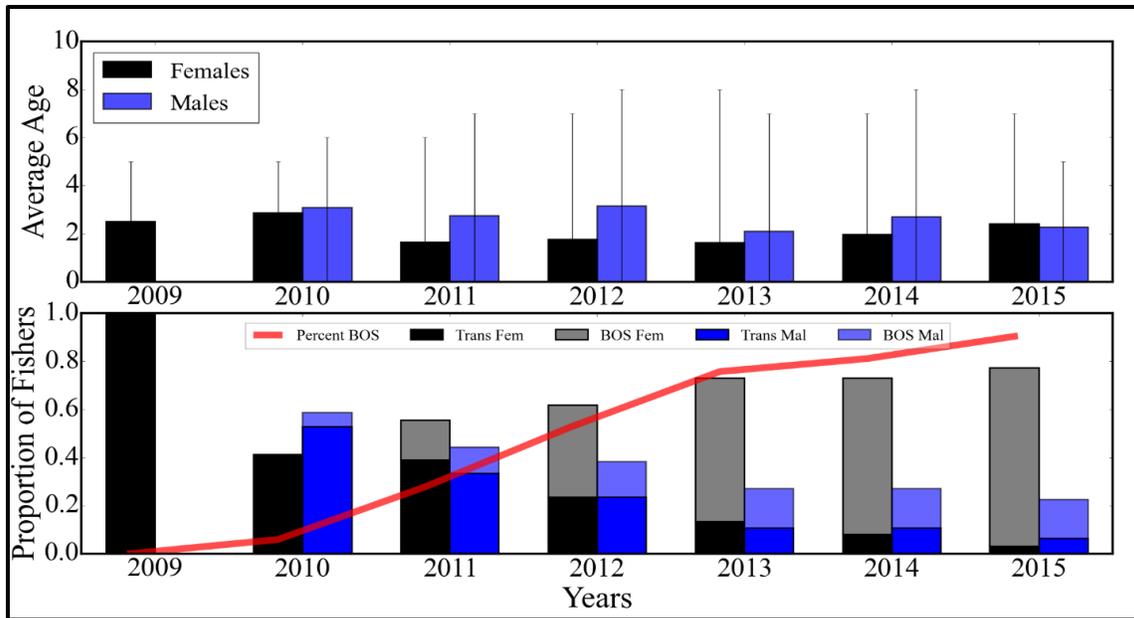


Figure 5. Age structure of the reintroduced fisher population in northern California at the each of each year from 2009-2015. Top) The average age  $\pm$  range of female (dark columns) and male (blue columns) fishers by year, Bottom) The proportion of known individuals in the population by year for reintroduced female (black bars) and male (blue bars) fishers and for females (gray bars) and males (light blue) fishers born on the study site. The total proportion of fishers born on the study site by year is represented by a red line.

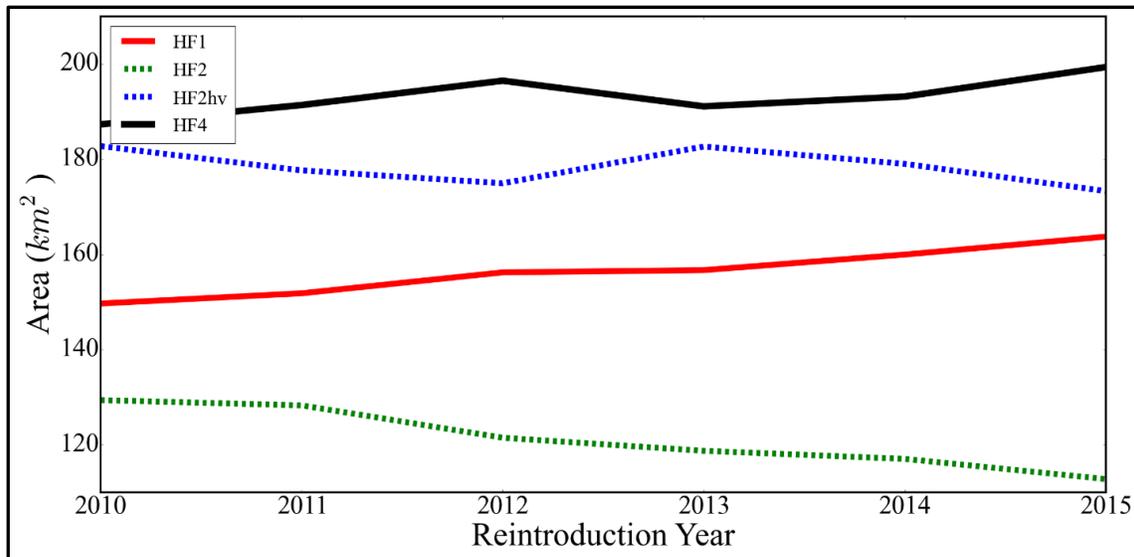


Figure 6. Total acreage, by year, for 4 forest classes occurring on Stirling in northern California. Habitat Form 1 (HF1) represents forests stands with mean values for quadratic mean diameter at breast height less than 15.2 cm and canopy closure less than 40%, Habitat Form 2 (HF2) was defined by forests stands with mean canopy cover greater than 40% and mean quadratic mean diameter at breast height  $\geq 15.2$  cm, Habitat Form 2 heavy (HF2hv) were forest stands with canopy closure greater than 50% and mean quadratic mean diameter at breast height  $\geq 27.8$  cm, and Habitat Form 4 defined by forests with canopy closure greater than 60% and mean quadratic mean diameter at breast height greater than 33 cm.

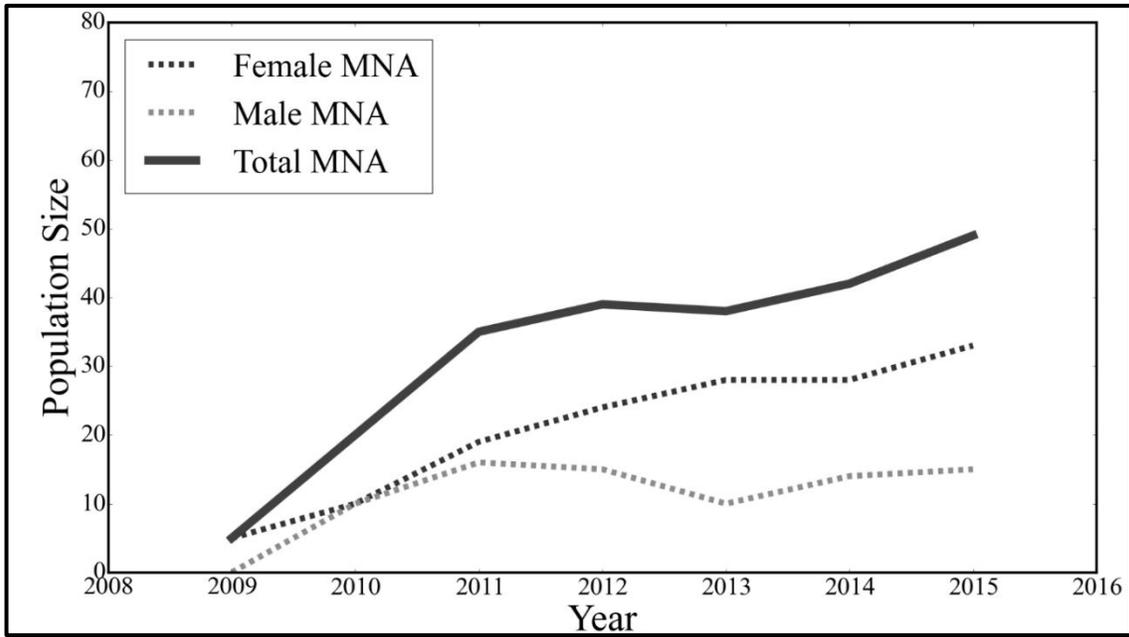


Figure 7. The minimum number of fishers known alive for females (Female MNA) and males plus females (Total MNA) for each year from 2009 to 2015 for fishers in the northern Sierra Nevada.

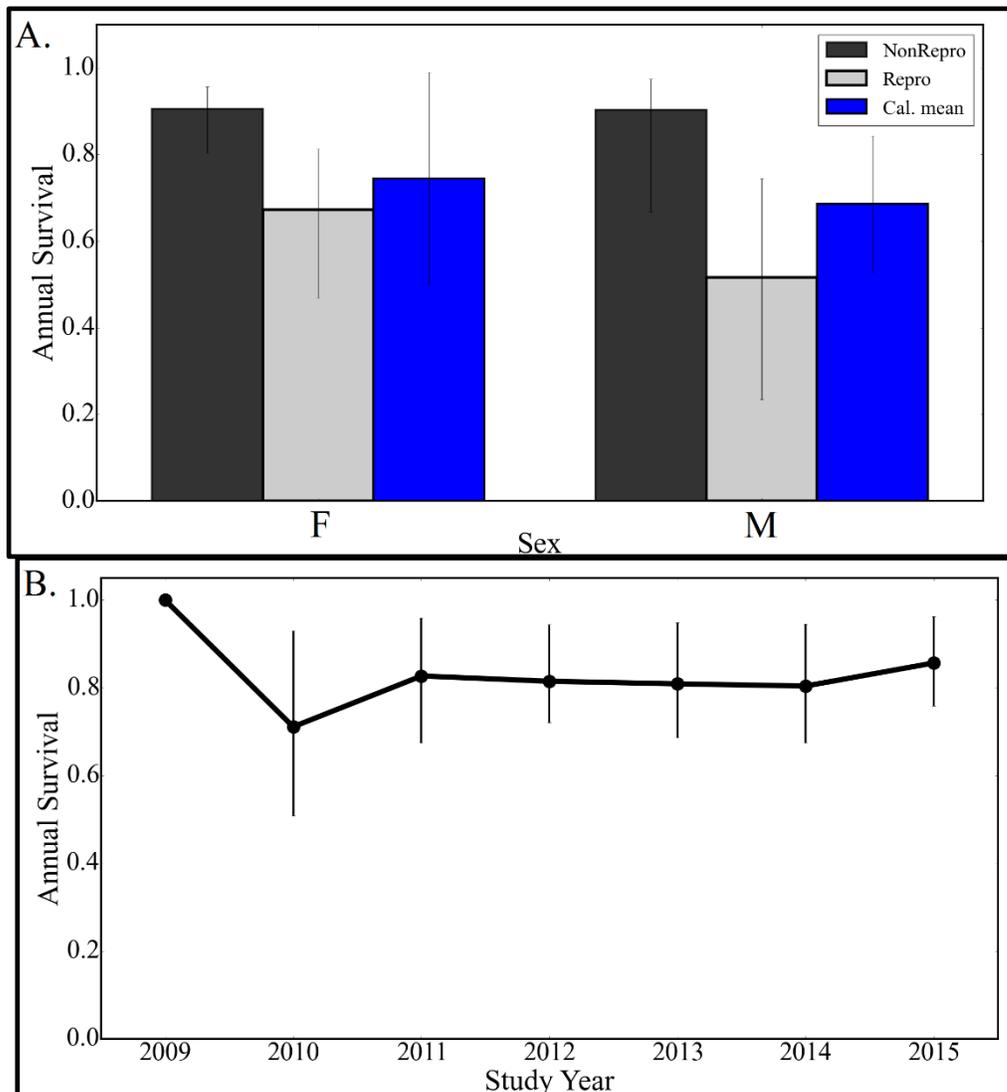


Figure 8. Annual estimates of adult survival for female and male fishers in northern California from 2009 to 2015 from model known-fates analysis (telemetry data) Top) Survival estimates for females and males during the non-reproductive season (Fem NonRepro and Male NonRepro) and during the reproductive season for females from May to August (Female Repro) and for males from March to July (Male Repro) compared to mean estimates of annual survival from other studies in California (Cal. Mean) and Bottom) Annual survival by year for all fishers. The estimate from 2009 represent 1 month of data on 4 female fishers in December.

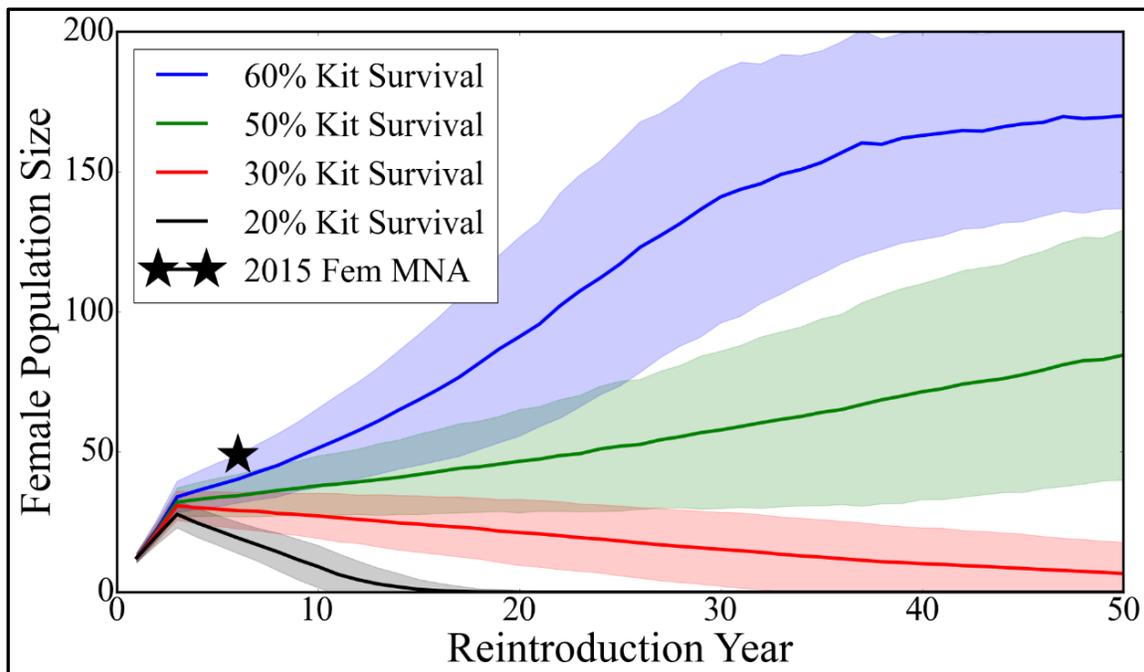


Figure 9. Projections of mean female population size (from 1000 simulated reintroductions) with the mean values  $\pm 1$  standard deviation (shaded portions) for simulated populations where mean juvenile (kit) survival was 20% (black), 30% (red), 50% (green) and 60% (blue).

## CHAPTER 5: Timing of translocation influences birth rate and population dynamics in a forest carnivore

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ECOSPHERE

### Timing of translocation influences birth rate and population dynamics in a forest carnivore

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**Abstract.** Timing can be critical for many life history events of organisms. Consequently, the timing of management activities may affect individuals and populations in numerous and unforeseen ways. Translocations of organisms are used to restore or expand populations but the timing of translocations is largely unexplored as a factor influencing population success. We hypothesized that the process of translocation negatively influences reproductive rates of individuals that are moved just before their birthing season and, therefore, the timing of releases could influence translocation success. Prior to reintroducing fishers (*Pekania pennanti*) into northern California and onto the Olympic Peninsula of Washington, we predicted that female fishers released in November and December (early) would have a higher probability of giving birth to kits the following March or April than females released in January, February, and March (late), just prior to or during the period of blastocyst implantation and gestation. Over four winters (2008–2011), we translocated 56 adult female fishers that could have given birth in the spring immediately after release. Denning rates, an index of birth rate, for females released early were 92% in California and 38% in Washington. In contrast, denning rates for females released late were 40% and 11%, in California and Washington, a net reduction in denning rate of 66% across both sites. To understand how releasing females nearer to parturition could influence population establishment and persistence, we used stochastic population simulations using three-stage Lefkovich matrices. These simulations showed that translocating female fishers early had long-term positive influences on the mean population size and on quasi-extinction thresholds compared to populations where females were released late. The results from both empirical data and simulations show that the timing of translocation, with respect to life history events, should be considered during planning of translocations and implemented before the capture, movement, and release of organisms for translocation.

**Key words:** California; carnivore; delayed implantation; fisher; life history; Olympic Peninsula; *Pekania pennanti*; population extinction; reintroduction; reproduction; timing; translocation; Washington.

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#### INTRODUCTION

Timing is important in nature. The life histories of organisms are often timed to cues from

their environment that increase survival and reproduction through specific mechanisms such as exploitation of important or seasonally abundant resources (Siekmann et al. 2001, Ryan et al. 2007,

Love et al. 2010, Fletcher et al. 2013, Lodge et al. 2013). The timing of specific life history traits (e.g., migration or reproduction) spans a continuum temporally from invariant to highly plastic to account for environmental change (Smith et al. 2010, Monteith et al. 2011), and the alteration in one trait, such as reproduction, may have cascading effects on other traits or interactions with other species (Mitchell et al. 2012, Touchon et al. 2013). Mistiming of key life history events may reduce individual fitness and lead to population decreases or even collapse (Seeley and Visscher 1985, Boonstra 2004). Failure to consider how timing influences management actions may reduce effectiveness, or result in total failure, of efforts to restore species or populations (Stüwe and Nievergelt 1991).

Translocation has become an often used management tool aimed at the establishment, augmentation, or reestablishment of functional populations of imperiled animal and plant populations (IUCN 2013, Seddon et al. 2014). Throughout history, humans have translocated wild animals (reviewed by Bolen and Robinson 2003, Powell et al. 2012) and plants, but researchers have begun only relatively recently to examine factors that influence the success of such conservation actions (Griffith et al. 1989, Reading and Clark 1996, Sarrazin and Barbault 1996, Wolf et al. 1996, Armstrong and Seddon 2008). Several factors consistently predict population establishment and persistence following translocations, including the size of the founding population, habitat quality at the release sites, and the release location relative to the historical and contemporary range of the species (Griffith et al. 1989, Lomolino and Channell 1998, Wolf et al. 1998, Lewis et al. 2012, Powell et al. 2012). The reproductive potential of the translocated individuals or the presence or abundance of potential consumers (predators or herbivores) and diseases are also important for some species (Cunningham 1996, Griffin et al. 2000, Letty et al. 2000, Sarrazin and Legendre 2000, Cabezas and Moreno 2007). Despite advances in recognizing the primary attributes that influence translocation success, many modern translocations still fail, which has led to a demand for rigorous scientific methods in their planning and implementation to deduce the mechanisms affecting success (Miller et al. 1999, Seddon et al. 2007).

The initial numbers of founder individuals in a translocated population are nearly always small relative to naturally occurring, self-sustaining populations (Hayward et al. 2007). Small populations are vulnerable to extinction due to demographic and environmental stochasticity and negative density-dependence (Allee effects; Allee and Bowen 1932, Shaffer 1981, 1987, Courchamp et al. 2008). Thus, minimizing mortality and maximizing the reproduction of translocated organisms is particularly important because they have a disproportionate effect on persistence of small populations.

The process of translocating animals likely depresses reproduction of individuals through a variety of physiological, ecological, and behavioral mechanisms. Physiologically, translocation elevates the stress responses of animals through multiple, often additive, mechanisms including capture, time in captivity, handling, and releasing individuals into unfamiliar environments (Teixeira et al. 2007, Dickens et al. 2009, 2010, Scarlata et al. 2013). Elevated stress in animals affects gonadotropins directly and, ultimately, impairs or curtails reproduction (Teixeira et al. 2007, Busch and Hayward 2009, Breuner 2011, Scarlata et al. 2012). Additionally, animals released into new environments are unfamiliar with the locations and types of important resources, thus affecting their energetic balances and, potentially, reproduction (Armstrong and Perrott 2000, Kemink and Kesler 2013, Lodge et al. 2013). Stress in combination with the challenges experienced within new environments may reduce or curtail short-term reproductive success individually or interactively (Busch and Hayward 2009). The effects of stress may last for many weeks but are likely to be highly variable based on individual species as well as the circumstances of translocations (Dickens et al. 2010).

Translocations, and specifically reintroductions (release of animals into areas once occupied by members of the species; IUCN 2013), have been used extensively to restore populations of martens (*Martes* spp.) and fishers (*Pekania pennanti*) throughout North America and Eurasia (reviewed by Powell et al. 2012). Fishers (Fig. 1) were reintroduced often to restore populations that were extirpated due to overharvesting and habitat alteration (Lewis et al. 2012, Powell et al. 2012). Many of these reintroductions succeeded



Fig. 1. Female fisher moving her approximately 3-month-old kit to a new den in the northern Sierra Nevada of California.

in the eastern portion of the fisher's range but in California, Oregon, Washington, and western Canada more than 50% of reintroductions have failed (Lewis et al. 2012). To increase the success of translocations of fishers and martens, researchers have experimented with release-based effects, such as hard vs. soft releases (allowing for a period of adjustment before release). Proulx et al. (1994) found that translocating fishers during summer increased site fidelity, but did not link this observation to the long-term success of the reintroduction. The reasons most reintroductions fail are unknown and, moreover, few novel mechanisms that may affect population establishment and persistence are hypothesized or tested (Powell 1993a, Lewis et al. 2012, Powell et al. 2012). Here, we use a rigorous approach to consider how translocating fishers during critical periods of their reproductive cycle affects reproduction and population establishment.

Fishers have relatively low rates of reproduction and population growth. Females can give birth for the first time on or near their second birthdays, in late March or April, and they produce at most one litter per year of 1–4 kits. Natal dens are always cavities in trees or standing snags. Kits depend on their mothers until autumn of their first year (Powell 1993a, Frost 1994, Frost et al. 1997). Within several days to 2 weeks after giving birth, female fishers breed and their blastocysts suspend development (delayed implantation) until winter of the following year, at which time blastocysts implant concurrent with increasing day length, followed by a normal pregnancy of ~32 d (Enders and Pearson 1943, Enders and Enders 1963, Wright and Coulter 1967, Mead

1971, Frost et al. 1997). Generally, fisher translocations occur in autumn and through late winter, with late releases coinciding with the time when blastocysts implant and active gestation occurs (Proulx et al. 1994, Frost et al. 1997). Trapping fishers for translocation cannot easily begin before autumn for many reasons, but the chief concern is that adult females have dependent young that are difficult to locate and to trap, introducing an unacceptable risk of mortality to kits if mothers are captured and translocated (Proulx et al. 1994). By and large, managers translocating fishers have not considered that moving female fishers during late winter could prevent implantation of blastocysts, leading to complete reproductive failure, or could affect maternal stress *in utero*, reducing the total number of kits born.

In planning the reintroduction of fishers in northern California, we hypothesized that fishers translocated just prior to or during the period of implantation would have lower reproductive success immediately following translocation than females that were captured and released earlier (autumn or early winter). We were concerned enough with these potential effects that we proposed to move all fishers prior to January 1 in each of the 3 yr of reintroduction (Callas and Figura 2008). In our concurrent, but independent, reintroduction of fishers in Washington, we also attempted to release fishers early (Lewis and Hayes 2004, Lewis 2006). In both cases, however, the logistics of planning and capturing enough fishers necessitated the capture and movement of individuals across a range of dates from November through March. Here, we test our *a priori* hypothesis that the timing of the release of female fishers affected their abilities to give birth in the first spring after their release. Furthermore, through simulation we evaluated the consequences of a depressed reproductive rate, as the result of releases in late winter, on reintroduction success.

## METHODS

### *Fisher reintroductions*

We reintroduced fishers to both California and Washington as independent efforts to restore fishers to unoccupied portions of the species' historical range (Lewis and Hayes 2004, Lewis 2006, Callas and Figura 2008). Many of

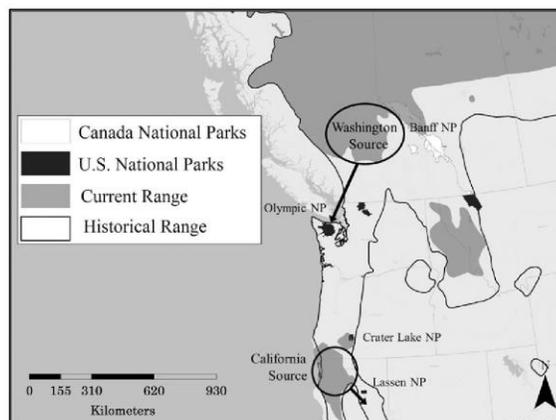


Fig. 2. General locations of source (labeled circles) and release areas (arrows) of fishers for both the California and Washington reintroduction projects, 2008–2011 compared to the current range of fishers in western North America (gray shading) and their historical range (thin black outline; Lewis et al. 2012).

the approaches and methods used during these reintroductions, though similar, varied in meaningful ways. For example, source populations and the duration that we held fishers in captivity differed. Additionally, the final release locations are found in different ecoregions with presumably different biotic and abiotic influences (Olson et al. 2001). For both projects, we immobilized fishers chemically to fit transmitters and to obtain information on sex, reproductive status in previous years, general condition, body mass, and morphological measurements. We immobilized fishers with tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Animal Health, Fort Dodge, Iowa) in California, and in Washington with a combination of ketamine hydrochloride (Ketaset, Zoetis, Florham Park, New Jersey) and detomidine hydrochloride (Dormosedan, Zoetis, Florham Park, New Jersey). We outfitted female fishers with either Telonics (IMP-310 or MOD-125; Mesa, Arizona, USA) or Holohil (MI-2i, Carp, Ontario, Canada) Very High Frequency transmitters. We removed one of the first premolars from each fisher to estimate age by counting cementum anuli (Arthur et al. 1992). We released fishers into the wild with no acclimation period (i.e., hard releases). The

Institutional Animal Care and Use Committee from North Carolina State University (09-007-O) approved the handling protocol for the California reintroduction, whereas the translocation and monitoring conducted during the Washington project were approved by the Animal Care and Use Committee of the Wildlife Science Division of the Washington Department of Fish and Wildlife. For both projects, handling of fishers was consistent with the guidelines of the American Society of Mammalogists for the use of wild mammals for research (Sikes and Gannon 2011).

In California, we reintroduced 40 fishers (24 F; 16 M) from early November 2009 to December 2011 to the region where the southern Cascades and northern Sierra Nevada mountain ranges meet (Fig. 2). We live-trapped fishers from across a large source area in northern California (Fig. 2). At least one field biologist and one wildlife veterinarian evaluated each fisher to determine its suitability for reintroduction. In California, we sought to reintroduce only individuals that were old enough to reproduce (females anticipated to give birth the next spring, males able to breed), and those that had body mass at or above average and appeared in good general health. To decrease the likelihood that we would inadvertently

move diseases or parasites to the reintroduction site, we vaccinated all candidate fishers for canine distemper virus and rabies and treated them for both ecto- and endo-parasites. We held all fishers selected for reintroduction in captivity for 3–14 d, while we tested them for previous exposure to distemper and canine parvovirus (Larkin et al. 2011, Keller et al. 2012). We transported individual fishers that passed this disease quarantine period to their release sites within 2 d, whereas fishers that tested positive for previous exposure to distemper were returned to their original capture locations. We released all fishers onto the Stirling Management Area (Lat 39.9 Lon -121.5°) owned by Sierra Pacific Industries. We released fishers across Stirling to encourage a widely distributed population and to reduce potential intra-sex conflict (Powell 1979). Our goal was to release all fishers from October through December so that females could overcome stress responses incurred during translocation and become familiar with the release site well before blastocyst implantation and active gestation began. Nevertheless, we released some fishers in January and February because we were unable to trap sufficient numbers of fishers before January 1 (Fig. 3).

We reintroduced 90 fishers (50 F; 40 M) onto the Olympic Peninsula in northwestern Washing-

ton (Lewis et al. 2010). We captured and housed fishers in central British Columbia, where we assessed their general health and vaccinated them for canine distemper and rabies (Lewis et al. 2010, Fig. 2). In Washington, our goal was to introduce ~100 fishers, and our relatively low rates of capture necessitated accepting all apparently healthy fishers regardless of age. Because of the high costs of transportation associated with the long distance from the capture site to the release site, we held fishers in captivity until ~10 were available to move to Washington. Mean duration of captivity was  $21 \pm 12$  d (range 2–55), but we held five fishers for 32–55 d for special medical treatment (e.g., treatment of wounds, impacted canine teeth). We released fishers across sites in Olympic National Park (lat 47.9° lon -123.4°; Lewis et al. 2010), usually in groups of 3–7 that included both males and females of variable ages. Originally, our intent was to release all fishers as early as possible (late fall or early winter) but limited capture success during this period necessitated a greater duration of trapping effort (into January and February) and resulted in late releases (as late as early March; Fig. 3).

#### Documenting reproduction

We tracked all female fishers 1–5 times per week in California using a combination of ground and aerial telemetry, whereas in Washington we located females ~1 time per week using aerial telemetry. In Washington, we located females 1–3 times weekly during the breeding season (March–June) to identify denning sites. At both sites, a female was suspected of having given birth in a den when she was repeatedly located in a restricted area, especially in the same tree, in late March and early April. We confirmed reproduction by placing three remotely triggered cameras (PC800 Hyperfire Professional, Reconyx, Inc., Holmen, Wisconsin, USA) within 6 m, and facing the base, of a suspected den tree to photograph kits (Fig. 1; e.g., Matthews et al. 2013). Photographs showing repeated use of a tree indicated that a female was attending kits, and photographs of females with kits confirmed reproduction as well as provided documentation of minimum litter size (Fig. 1). If kits were not photographed, we deduced that a female had given birth if we observed her, through

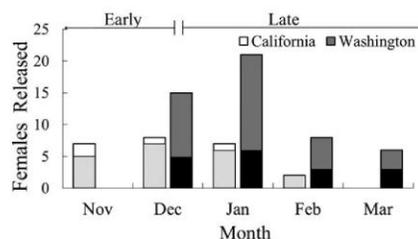


Fig. 3. Full column lengths show the total numbers of female fishers released at each site in each month (total is 24 for California and 50 for Washington), whereas the darker portions represent the numbers of adult females for whom we could confidently assess denning status and that were used in our analysis. Females released prior to January were considered early releases, whereas fishers released in January or later were considered late releases.

pictures or telemetry, returning to the same locality for several weeks. As we tracked females regularly, we could confidently identify patterns of location indicating that a female was using a confined area more often than was normal for prereproductive location patterns. A female that we never photographed with kits and who was never found in a confined portion of her home range for a 2–4 week period we designated as non-parous. Our analyses did not include females <2 yr old ( $n = 18$ ) that could not have given birth or those whose denning status could not be determined. We only evaluated birth rate, as indicated by the denning rates of females, and thus we did not remove females from the analysis that died after we confirmed that they had denned.

#### Analysis

We analyzed whether a female denned (yes or no) as a binary response using logistic regression (PROC LOGISTIC, Statistical Applications Software, Cary, North Carolina, USA). We modeled the response of denning rate to covariates that we hypothesized *a priori* might affect the probability that a female would establish a den (i.e. give birth). We categorized females into two groups based on the time we released them: “early” (November or December release) or “late” (January, February, or March release). We compared the proportions of early- vs. late-released females that denned in each study area. Additionally, we compared these proportions to the mean denning rate for reintroduced females (California only) that denned in the years subsequent to translocation and to the mean denning rate for resident (not reintroduced) female fishers studied elsewhere in western North America (Aubry and Raley 2006, Weir and Corbould 2008, Matthews et al. 2013). Proulx et al. (1994) found that the distance that female fishers traveled after release had stabilized after 2–4 weeks, suggesting they had established home ranges. Moreover, the lengths of time that stress responses last and influence fishers are unknown but are likely to be on the order of several weeks (Dickens et al. 2010). We reasoned that fishers released before January 1 had at least 1 month to establish home ranges and overcome stress responses before blastocysts implanted. Therefore, we used January 1 as

the dividing line between early and late releases. This dividing date also bisected our releases into two relatively equivalent periods (Fig. 3). We considered these two periods as reasonable proxies for evaluating the effect of release time on birth rate; nonetheless, we also recognized that if our hypothesis was correct we might observe a continuous decline in denning rate with later dates of release. Consequently, we included in our analysis a continuous variable quantifying the number of days beyond November 1 on which we released a female. We predicted that denning rate would decrease as date progressed. Our discrete and continuous variables evaluated the same effect and, therefore, we did not include both in the same models.

We tested several other covariates that we hypothesized might influence denning rate. The two reintroduction projects differed in many ways such as the source locations of fishers, biotic and abiotic differences at the source and release locations, and our protocols for handling fishers while in captivity. Therefore, we hypothesized that project differences could influence denning rate. We included the project variable in both additive and interactive models for both discrete and continuous time analyses. We also hypothesized that a female's body condition influenced denning rate. Because fishers from British Columbia were heavier than those from California, we standardized female body mass relative to the mean body mass of each study area (i.e., [(body mass – mean body mass)/standard deviation]). We hypothesized that a female's age and the variation in conditions associated with the year of release affected denning rate.

We evaluated and ranked our candidate models using Akaike's information criterion adjusted for small sample size ( $AIC_c$ , Burnham and Anderson 2002). We followed the general approach and suggestions of Burnham and Anderson (2002) and considered the model with the lowest  $AIC_c$  value to be the hypothesis best able to describe our data. Our main objective was to evaluate the hypothesis that the timing of release influenced denning rate; hence, we summed the  $AIC_c$  weights ( $w$ ) for individual variables across models to quantify their relative importance (Burnham and Anderson 2002).

We examined the direction and magnitude of covariate effects on denning rate with both parameter estimates from the top-ranked model (containing a specific covariate), and with estimates from model averaging across all models in the candidate set (Burnham and Anderson 2002). We used an exponential transformation ( $e^{\beta}$ ) to convert both the model-estimated, and model-averaged, beta parameters to an odds ratio, with the associated 95% confidence interval (Hosmer and Lemeshow 2004).

We hypothesized that the time a female spent in captivity would be highly correlated with the stress she endured and, therefore, would explain some amount of the variation associated with the project variable (Teixeira et al. 2007). Consequently, we tested this covariate (days in captivity) within our analysis but did not consider it *a priori*; nevertheless, we compared it with other variables and models to evaluate this hypothesis and how it explained observed project differences.

#### Simulating effects of release date on population growth and probability of extinction

We evaluated the potential effects of release timing on population size, population growth rate, and the likelihood of extinction of reintroduced fisher populations using stochastic simulation in MATLAB (The Mathworks Inc., Natick MA). We constructed a three-stage Lefkovich matrix (Lefkovich 1965) that described the life history pattern of fishers (Fig. 4). Because the number of animals released affects the probability of success for a reintroduction (Lewis et al. 2012, Powell et al. 2012), we simulated reintroductions of 9, 30, and 60 female fishers over 3 yr with 1/3 of those totals released each year (Powell et al. 2012). We chose 20 yr for the length of each simulation because it is a common period of time for evaluating success of reintroductions for fishers and martens (Lewis et al. 2012, Powell et al. 2012). For each number of females released, we simulated two release strategies, one in which all females were released early with no effect on their denning rate in the first year and a second strategy in which all females were released late and denning rate was diminished in the first year. For the late strategy we simulated a small (34% reduction), medium (66% reduction, matching our field

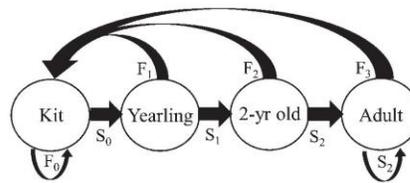


Fig. 4. Life-stage model of the fisher life cycle used to construct projection matrices to simulate reintroductions. Each circle represents the discrete life-stage of a female fisher with the kit life-stage consisting of all females aged 0 to <1 yr old, the yearling life-stage is females 1 to <2, 2-yr olds aged 2 to <3, and the adult life-stage is all females aged 3 and older. The arrows connecting the circles represents the transition values between the life-stages:  $S_0$  = probability of surviving from birth until 1st birthday,  $S_1$  = probability of surviving between 1st and 2nd birthday,  $S_2$  = probability of surviving from 2nd to 3rd birthday and annually after 3rd birthday,  $F_0$  = probability of a newborn giving birth (always 0),  $F_1$  = the probability of a yearling female denning (also always 0),  $F_2$  = the probability of a 2-yr-old female denning (giving birth)  $\times$  the number of her female offspring, and  $F_3$  = the probability of an adult female denning (giving birth)  $\times$  the number of her female offspring.

data), and large (90% reduction) effect of late releases on denning rate (Table 1). All other population parameters were unaffected by the timing of release and the effect on denning rate applied only to females the first year immediately following their releases.

We generated model parameter values as random deviates from distributions based on estimated vital rates reported from other populations of fishers (Powell 1993a, Higley and Matthews 2006, Buskirk et al. 2012, Matthews et al. 2013, Table 1). We evaluated many different combinations of mean vital rates but ultimately used three sets of mean values for vital rates that simulated habitat quality as poor, fair, or good. For each life stage, we randomly generated survival and denning rates using the beta distribution (betarnd function of MATLAB) where the alpha and beta parameters define the shape of the distribution and are transformations from the means and standard deviations taken from the empirically derived distributions (Morris and

Table 1. Mean values  $\pm$  SD for life history parameters used to simulate fisher populations resulting from releases where the habitat quality was poor, fair, or good.

Parameter	Life stage	Poor	Fair	Good
Apparent survival	Kit	0.25 $\pm$ 0.20	0.35 $\pm$ 0.30	0.35 $\pm$ 0.20
Apparent survival	Yearling	0.60 $\pm$ 0.10	0.70 $\pm$ 0.10	0.70 $\pm$ 0.10
Apparent survival	2-yr old and adult	0.84 $\pm$ 0.10	0.84 $\pm$ 0.10	0.84 $\pm$ 0.10
Den rate	2-yr old	0.50 $\pm$ 0.12	0.50 $\pm$ 0.12	0.70 $\pm$ 0.12
Den rate	Adult	0.90 $\pm$ 0.08	0.90 $\pm$ 0.08	0.90 $\pm$ 0.08
Litter size	2-yr old and adult	1.80 $\pm$ 0.41	2.1 $\pm$ 0.41	2.4 $\pm$ 0.41
Sex ratio	2-yr old and adult	0.50 $\pm$ 0.05	0.50 $\pm$ 0.05	0.50 $\pm$ 0.05
Low den rate <sup>†</sup>	2-yr old and adult (Low)	0.34 $\pm$ 0.00	0.34 $\pm$ 0.00	0.34 $\pm$ 0.00
Moderate den rate <sup>†</sup>	2-yr old and adult (Med)	0.66 $\pm$ 0.00	0.66 $\pm$ 0.00	0.66 $\pm$ 0.00
High den rate <sup>†</sup>	2-yr old and adult (High)	0.90 $\pm$ 0.00	0.90 $\pm$ 0.00	0.90 $\pm$ 0.00

<sup>†</sup>The percent reduction on reproduction of releasing female fishers in the late period.

Doak 2002). Litter size was similarly generated randomly using the normal distribution (normrnd function) and parameterized by the mean ( $\mu$ ) and standard deviation ( $\sigma$ ) from the empirically derived distribution. Each vital rate was randomly generated (random number seeded by the computer clock) independently for each year of the simulation without correlation among years or vital rates. We set the maximum number of home ranges available after establishment at 200 and after these home ranges were occupied reproduction and juvenile survival fell to 0, but survival of animals  $\geq 1$ -yr old was unaffected.

We replicated each 20-yr reintroduction 1000 times for each combination of release size, time of release strategy (including the three effect sizes for late releases), and three levels of habitat quality. For all simulations, we calculated the percent of 1000 replicates in which the population fell below each of three quasi-extinction thresholds of 5, 10, and 20 female fishers during years 4 through 20 (Morris and Doak 2002). We calculated the geometric mean of population size and population growth rate at each time step of the reintroduction to evaluate the average response to the simulated release scenarios and effect sizes.

## RESULTS

### Denning rate

We released 24 females in California and 50 females in Washington from 2008 to 2011 (Fig. 3). Because some female fishers were too young and because we could not document

denning for all females, we included only 37 of these 74 females in our analyses. Twenty-three of 24 (95%) and 33 of 50 (66%) fishers released in California and Washington were old enough to give birth in the April following their releases. We determined the denning status of 87% (20 of 23) and 52% (17 of 33) of the potentially parous females in California and Washington. We could not determine the denning status of one adult female in California because her VHF transmitters failed prematurely and two others died prior to the denning season. In Washington, we could not determine the denning status of 18 adult females. Six died prior to the denning season and the others we could not confidently designate due to our inability to track them thoroughly in the National Park. In California we released 12 adult females, whose denning status we could determine, early and 8 late, whereas in Washington we released 5 early and 12 late. Photographs of kits from cameras set at den sites confirmed reproduction for 80% and 86% of females we suspected of denning in California and Washington, respectively. For the remaining females, we documented that denning by observing them repeatedly at the same tree via remote cameras.

The date when we released female fishers was the most important variable influencing denning rate in both California and Washington (Table 2, Fig. 5). Our seven highest ranking models included either the discrete or the continuous *date of release* variable. The best supported model included the discrete *date of release* variable with

Table 2. Metrics used to compare 17 models hypothesized to explain the initial denning success of female fishers in their first year following reintroduction to California and Washington in 2008–2011, where the  $-2\log$  likelihood (not shown), the number of estimable parameters ( $k$ ), number of observation ( $n = 37$  for all) are used to construct Akaike's information criterion corrected for sample size ( $AIC_c$ ) and calculate the difference between top model and other models ( $\Delta AIC_c$ ), the model likelihood, and model weight ( $w$ ).

Model description	$k$	$AIC_c$	$\Delta AIC_c$	Likelihood	$w$	$\tilde{R}^2$
Date <sub>D</sub> † + Project	3	42.73	0.00	1.00	0.42	0.45
Date <sub>D</sub>	2	45.40	2.67	0.26	0.11	0.32
Date <sub>D</sub> + Body mass	3	46.04	3.31	0.19	0.08	0.37
Date <sub>C</sub> ‡ + Project	3	46.08	3.35	0.19	0.08	0.37
Date <sub>C</sub>	2	46.40	3.67	0.16	0.07	0.29
Date <sub>D</sub> + Days held captive§	3	47.06	4.33	0.11	0.05	0.34
Date <sub>D</sub> + Year	6	47.10	4.37	0.11	0.05	0.47
Project	2	47.34	4.61	0.10	0.04	0.27
Date <sub>D</sub> + Age	3	47.77	5.04	0.08	0.03	0.32
Date <sub>C</sub> × Project	4	48.57	5.84	0.05	0.02	0.37
Date <sub>C</sub> + Days held captive	3	48.71	5.98	0.05	0.02	0.30
Date <sub>D</sub> × Day held captive	4	48.95	6.22	0.04	0.02	0.36
Date <sub>C</sub> × Days held captive	4	51.20	8.47	0.01	0.01	0.30
Days held captive	2	52.36	9.63	0.01	0.00	0.11
Body mass	2	53.35	10.62	0.00	0.00	0.05
Age	2	55.58	12.85	0.00	0.00	0.00
Year	4	56.44	13.71	0.00	0.00	0.14

†Date<sub>D</sub> is a discrete variable that places females into two release groups, those that were released prior to January (early) and during or after January (late).

‡Date<sub>C</sub> is a continuous variable that was defined as the number of days after November 1 when a female was released.

§The number of days a female was held in captivity (Days Captive) was a post hoc variable used to test the idea that variance between projects was associated with this factor. All models with the variable are not considered *a priori* tests of our central hypotheses.

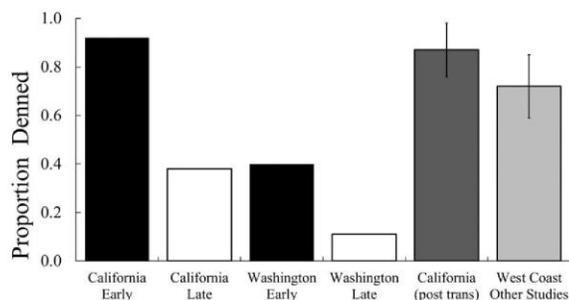


Fig. 5. The percent of female fishers released early or late and confirmed to have denned in their first year following reintroduction to California and Washington, 2008–2011. The dark gray bar shows the average percent  $\pm$  SD of females that denned in all years, excluding their first, following their reintroduction at the California site while the light gray bar shows a mean value  $\pm$  SD for denning rate in non-reintroduced fisher populations in the western United States (Aubry and Raley 2006, Weir and Corbould 2008, Matthews et al. 2013).

an additive effect of *project* differences (Table 2 and Fig. 5). Models that did not include an effect of release date received nearly no support ( $\Delta AIC > 4$ ). The discrete *date of release* variable had the highest summed Akaike's weight (Table 3) indicating that, relative to other variables tested, it was able best to describe denning rate across models. Additionally, differences between the

Table 3. Summary statistics for variables included in logistic regression models including the summed Akaike weight ( $\Sigma w$ ) for each variable, the odds-ratio estimates from the top-ranked model that included the variable ( $OR_{Top}$ ) and the model-averaged value ( $OR_{avg}$ ) and their associated 95% confidence intervals.

Variable	$\Sigma w$	$OR_{Top}$	95%CI $_{Top}$	$OR_{avg}$	95% CI $_{avg}$
Date <sub>D</sub> (Late vs. Early)	0.76	0.124	0.024, 0.637	0.429	0.003, 52.060
Project (Wash vs. Cal)	0.56	0.164	0.032, 0.849	0.610	0.008, 43.320
Date <sub>C</sub>	0.20	0.966	0.941, 0.991	0.994	0.893, 1.106
Days held captive	0.10	0.970	0.900, 1.045	0.997	0.828, 1.199
Body mass	0.08	1.799	0.705, 4.588	1.049	0.206, 5.320
Year 2008 vs. 2011	0.05	0.069	0.004, 1.180	0.923	0.093, 9.107
Year 2009 vs. 2011	0.05	0.250	0.015, 4.198	0.982	0.102, 9.377
Year 2010 vs. 2011	0.05	1.058	0.114, 9.781	0.951	0.118, 7.658
Age	0.03	0.989	0.540, 1.811	1.000	0.506, 1.974

projects and the continuous *date of release* variables had relatively high weight compared to other factors we tested (Table 3). We found good support that the date of release influenced denning rate but little support that *body mass*, *year* effects, and female *age* beyond reaching maturity influenced denning rate (Tables 2 and 3).

Denning rate across both sites for adult females released early was 76% (13 of 17) whereas that for females released late was only 25% (five of 20). Compared to females released early, the denning rate for late-released females was reduced by 58% in California and 73% in Washington, respectively, demonstrating similar patterns at both sites (Fig. 5). Females released early had similar rates of denning to those of females that survived and denned beyond their first year after reintroduction in California (similar data were not available for Washington), and were similar to the rates of naturally occurring populations of fishers in western North America (Fig. 5). All candidate models that included either a discrete or a continuous *date of release* variable indicated a negative influence of late release on denning rate (Table 3). Females released late were only 12% as likely to den compared to females released early indicating a negative relationship between denning rate and the number of days from November 1 a female was released (Table 3 and Fig. 6). Evaluation of the odds ratio for females released 100 d from November 1 indicate they had only a 3% (0.04% to 41%) probability of denning compared to females released on November 1.

The *project* variable was included in our top model, indicating a difference in denning rates between the projects. Additionally, an effect due

to the *project* had the second highest summed Akaike's weight, indicating a relatively high importance (Table 3). Nonetheless, the *project* variable as a single-variable model was less well supported than either of the single-variable *date of release* models. Females released in California denned at a higher rate than in Washington, and this pattern was apparent in both early and late-released females, consistent with models with additive effects and ranking higher than those with interactive effect (Table 2, Fig. 5).

As a single-variable model, the number of *days in captivity* had a lower AIC<sub>c</sub> value, as well as a higher adjusted  $R^2$  value, and thus described our data better, than did either *body mass* or *age* (Table 2). When combined with a *date of release* variable, *days in captivity* described only 75% of the variation compared to our top model. The longer a female was held in captivity the lower the denning rate, but the estimated 95% confidence intervals for both the beta and odds-ratio estimates bounded 1, indicating a weak relationship (Table 3).

#### Population simulations

Our reintroduction simulations demonstrated an effect of release date on average population size (Fig. 7). For all simulations, reintroductions based on an early release strategy showed higher average population sizes compared to reintroductions where females were released late (Fig. 7). Average population sizes tended to converge through time between early and late strategies when the simulated population occurred in poor habitat yielding negative population growth. The differences in mean

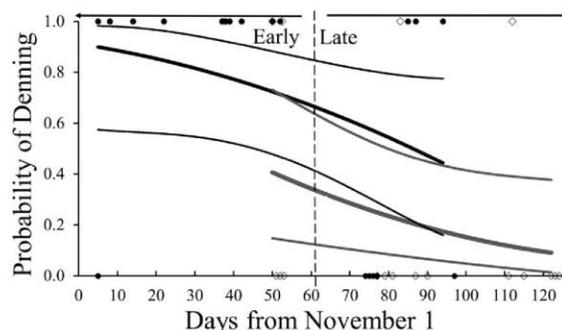


Fig. 6. Estimated logistic relationship between the time of a female fishers' release (days after November 1) and the probability that she denned (gave birth) after reintroduction for two studies, 2008–2011 where heavy solid lines represent the California (black lines) and Washington (gray lines) study sites with thinner solid lines as the 95% confidence intervals, and the vertical dotted line is January 1 which divided the transition between early and late releases. Black-filled circles represent females reintroduced in California, whereas open diamonds represent females reintroduced to Washington that were included in the analysis and whether they denned (value = 1) or did not (value = 0).

population sizes were greater for large founder populations living in fair or good habitats. Population growth was most strongly affected by reintroduction time during the first 4 yr of simulated reintroductions (Fig. 7). In fact, for simulations with large reductions in denning rates, the average population size decreased in the first 2 years after release. Subsequent to the final releases of all animals, simulated populations stemming from both early and late reintroduction strategies had nearly identical average rates of growth (Fig. 7), which only makes sense because they had the same mean values for life history rates.

Within our simulations, the reduction of the denning rate associated with releasing females late resulted in small increases in the probability that a population edged toward extinction (Fig. 8). Late releases and small founder group sizes caused populations to fall closer to extinction on more occasions than did reintroductions with early releases. The number of animals released and the population growth rate had the largest effects on whether a reintroduction fell below any quasi-extinction threshold (Fig. 8). Yet, the effect of releasing females late did increase the number of times we observed a reintroduction to fall below these thresholds (Fig. 8).

Scenarios with high effect sizes, as the result of late release, had a concordant influence on the probability of extinction (Fig. 8). In general, the effect of timing of release on the probability of extinction was small relative to the population release size and the quality of the release habitat but did increase the risk of extinction for reintroduced populations (Fig. 8).

## DISCUSSION

The female fishers that we released late denned at a lower rate in the spring following their release than did females we released early. For the California and Washington projects, we observed decreases in denning rates of 58% and 73% for females that we released after January 1 compared to females released prior to this date (Fig. 5). A discrete model (early vs. late release) described our data better than did a continuous model. We interpret the strong support for the models including a discrete date to suggest that individual female fishers either have a discrete threshold for when denning would be affected (such as implantation of blastocysts) or that other unrecognized factors influenced denning rate during these distinct periods. Releasing females late affected females

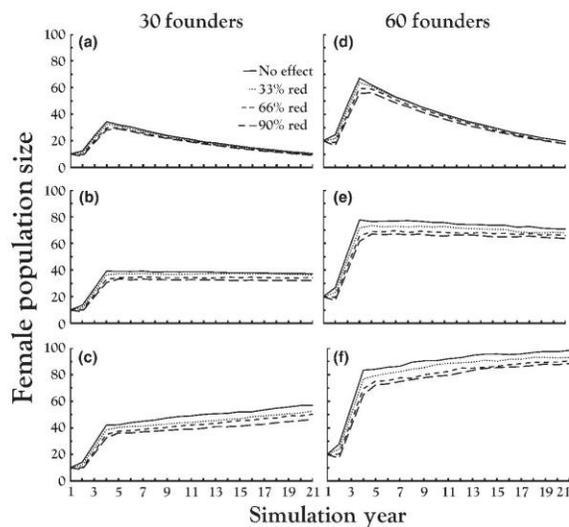


Fig. 7. Mean population sizes for female fishers over time from 1000 replicates of stochastic simulations of reintroduced populations for founding sizes of 30 and 60 females with 1/3 released in each of 3 yr. We simulated growth rates for reintroduced populations in poor (panels a and d), fair (panels b and e), and good (panels c and f) habitat after the final release (year 3). We simulated early releases of females (solid line), which did not reduce denning rates, and we simulated late releases with a 34% reduction in denning rate (dashed lines), a 66% reduction in denning rate (dotted lines), and a 90% reduction in initial denning rate (long-dashed line) in the year following translocation.

in all years, irrespective of a female's age, body mass, or other potentially confounding factors we tested. These results support our hypothesis that late releases, just prior to or during the time when dormant blastocysts were implanting and active gestation was beginning, had a substantial effect on the reproduction of adult female fishers.

Many factors may affect whether translocations succeed but the timing for releasing animals is heretofore unconsidered in analyses or planning (Griffith et al. 1989, Wolf et al. 1998, Armstrong and Seddon 2008). In the few instances when timing, in any capacity has been discussed or studied it has related to the time animals spend either in captivity or the mistiming of vital rates as a consequence of the reintroduction, rather than a product of when animals were released (Stüwe and Nievergelt 1991, Teixeira et al. 2007).

In contrast, we demonstrate that the timing of the release of fishers produced changes in their reproductive rates and that those short-term changes have the potential for long-term consequences. Our results are explicit for this effect on reproduction by fishers but the timing of specific life history traits affects vital rates of individuals in non-translocated populations of other animals (Seeley and Visscher 1985, Siekmann et al. 2001). Thus, it makes sense that other species may be influenced by translocations that coincides with important times in their natural history. If the untimely release of animals occurs during a period when they are acquiring important resources, reproducing, migrating, or entering torpor, they may experience subsequent effects on their general health or rates of survival or reproduction (Monteith et al. 2011, Mitchell et al. 2012). Our observations implicated the timing of release on

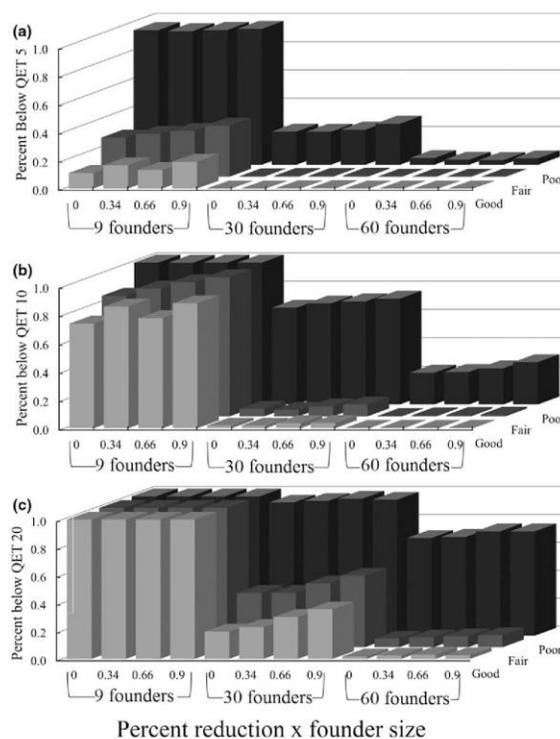


Fig. 8. Percent of simulated, reintroduced fisher populations monitored for 20 yr and that fell below a quasi-extinction threshold of 5, 10, and 20 fishers (panels a, b, and c). These scenarios depict different founding populations (9, 30, and 60 fishers), different habitats (good, fair, and poor), and an early release strategy (no effect on reproduction the first year following release) and a late release strategy (reduced reproduction of 0.34, 0.66, and 0.90).

reproduction directly but we hypothesize that such direct effects may not always be obvious. Rather, the effects of release may be cryptic or influence aspects of life history occurring at later times for some organisms. For example, animals released late (or early, depending on the species) may be at competitive disadvantages to animals released early or may miss critical resources prior to events like migration or hibernation (Monteith et al. 2011). Intra-species comparisons of translocations that occurred within and outside of hypothetically important periods may pro-

vide insight into if, and how, timing has affected the outcomes of translocations. Researchers and managers considering translocation should carefully consider a species' life history to determine an optimum season to release animals.

The effect of translocation timing on reproduction is important and warrants further consideration; nonetheless, we view the actual moving of fishers as a proximate mechanism for our observations. Many mechanisms can alter reproductive rates of animals and may correlate with translocation, and of these we

hypothesize that stress incurred from trapping, handling and transport as well as the novelty of new environments as the most important and ultimate mechanisms. Stress is a ubiquitous by-product of translocating animals, and though we did not measure stress directly, we assume that our fishers had stress responses that are similar to those of other species (Teixeira et al. 2007, Dickens et al. 2009, 2010). Because stress can affect reproduction directly (Breuner 2011, Scarlata et al. 2013), we expect that female fishers experiencing the highest levels of stress at the time when reproductive was re-activated had a concordant depression in reproduction during that year. Stress responses are advantageous because they modulate different aspects of the life history of animals (Busch and Hayward 2009). Newly released individuals are unfamiliar with the landscape, its potential resources, and the threats that occur there (Dickens et al. 2010, Powell and Mitchell 2012). With respect to reproduction by fishers, females released in autumn should have an advantage compared to females released in late winter and spring because they will be better acquainted with, and able to exploit, resources in the new landscape when reproduction re-activates. For example, fishers have unique denning habitat requirements and give birth only in tree cavities (Powell 1993a, Weir et al. 2012). Female fishers that are released just before the denning season will have less time to find suitable den sites and their kits may be more vulnerable to severe weather conditions or predation if females select poor-quality den sites due to time constraints. Trade-offs, as the result of translocations, between survival and reproduction could also have important consequences for both individuals and populations and warrant investigation in future theoretical and empirical work.

Our analyses documented clear differences in denning rates between our two projects. The two projects used different drugs to immobilize fishers. All three of the main drugs used for sedation are contraindicated for use during pregnancy (Plumb 2011). Yet, adverse effects on reproduction from these drugs appear most likely during late embryonic development rather than during implantation of blastocysts and no evidence suggests that these drugs are teratogens (Plumb 2011). Regardless, the role that sedatives play in

reproduction of mammals is largely unknown and should be investigated more.

Additionally, the logistics of tracking fishers in California differed from those in Washington. The California study site had extensive road networks that provided relatively close access to females. In Washington, road access was limited because Olympic National Park made up a large portion of the study area and it is largely without roads. These differences may have contributed to identifying the denning status of fewer females that could have given birth and, thus, affected the estimated rates of denning in Washington. We emphasize that these potential differences occur between projects but not among females based on when they were released. Moreover, errors that occurred in designating a female parous or not would have been distributed randomly among females and unlikely to influence the pattern related to timing, though such errors could influence the precision of our estimates.

The length of time that females spent in captivity described some variation between projects. In Washington, we held fishers in captivity longer (mean =  $21 \pm 23$  d) than in California (mean =  $6 \pm 13$  d) because they had to be transported farther and, therefore, more individuals were transported at any one time to reduce expenses. We assumed that females captured in British Columbia and northern California had similar numbers of fertilized but un-implanted blastocysts, but if this assumption was incorrect it could describe some of the differences we observed between projects (Wright and Coulter 1967, Frost et al. 1997). Another factor that may have contributed to differences between release sites is the variation in the respective environments between source and release locations. The source sites for both California and Washington existed within ecoregions that differed from the release locations (Olson et al. 2001), and differed in climate, vegetation and, potentially, prey type, and availability. Though we have not quantified these differences for either project, the California source sites were closer to the release site and we hypothesize more similar, and therefore familiar, to newly reintroduced fishers. We hypothesize that fishers released in Washington were less familiar with their new environments compared to fishers in California,

which may have resulted in energetic, or other unknown, deficits. How animals select and respond to their release environments remain key questions in studies on translocations that may relate to how and when management activities, like translocation, should take place (Seddon et al. 2007, Stamps and Swaisgood 2007, Mabry and Stamps 2008).

We recognize that releasing animals early vs. late has only a secondary effect on potential reintroduction success relative to factors like founder population size and habitat quality. Nevertheless, it represents a non-trivial influence on how a population may establish or thrive. The simulations we used here demonstrate that releasing animals late may increase the likelihood of extinction. We note that these simulations likely underestimated the extinction rate because the variation in vital rates, and population change, was potentially low because we did not include scenarios in which vital rates were correlated temporally. Nor did we include unexpected, random catastrophes (e.g., wildfires). Incorporation of such dynamics in reintroduced populations may increase the likelihood of extinction for populations where fishers are released late.

Timing of translocation of animals should be considered in conjunction with other risks and the time of life history traits of the animals during the planning of any translocation effort. In particular, reproductive phenology should be considered when species are proposed for translocation. Releases should be scheduled at times most advantageous for maximizing rapid reproduction of the founding members of the population. Maximizing reproduction in early years of a translocation is important because founding populations are typically small, additional source animals may be limited, and relatively rapid initial population growth should increase the probability of establishment. We contend that this research has important implications for timing and management that extend beyond translocations. Management activities like logging or trapping for research may also induce stress responses or change foraging behaviors in animals, and specifically fishers (Powell 1993b). If these activities occur during the birthing season then effects on reproduction may occur similar to those we observed. Additionally, we contend that timing of

translocations may have impacts on factors other than reproduction and, therefore, should be evaluated for life stages that are crucial for the species of interest. We suggest that, for species with life histories similar to fishers, consideration for the time at which they are captured, moved, or released may decrease negative effects on their reproduction and, thereby, increase the viability of populations, especially small populations typical of translocations.

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**CHAPTER 6: Conspecific competition and resource depression affect movement and home range establishment of translocated fishers (*Pekania pennanti*)**

**Abstract.** Experience and information should be advantageous to residents of a home range but put invaders to the home range at a disadvantage and, thus, should cause them to move and establish their home ranges elsewhere. Conspecifics, especially, should avoid the home ranges of one another to ensure they are not altering resource availability through resource depression or depletion. Yet, encountering one competitor (e.g., dominant or of a different sex) may cause an individual to discount resource patches differently compared to encountering another. We tested these ideas by developing simulations of movements for animals that developed a home range in the absence of conspecific competition (Colonist) and animals that began home range development within the home range of a conspecific (Intruder). We found that Intruders moved further, and settled further from their starting locations than did Colonists. We compared our simulation results to the post-release movements of fishers (*Pekania pennanti*) that we reintroduced into northern California over 3 years from late 2009 to 2011. Using satellite transmitters (Argos) and land-based (VHF) telemetry we made daily observation of fisher locations, movements and area of their minimum convex polygons during their first 200 hundred time steps after release. Females that encountered the home range of any conspecifics moved further, had larger minimum convex polygons and settled further from their release locations than did females that did not encounter a conspecific home range. Males did not avoid, or appeared indifferent, to the home ranges of all conspecifics but males released in the absence of females moved more. Our results suggest that female fishers avoid conspecific competition from both males and females in accordance with

results from our simulations. Males appear indifferent to competition and likely invoked overlapping home ranges on females.

**Keywords:** carnivore, conspecific competition, discount rate, home range, movement, resource depression

## INTRODUCTION

Conspecific competition affects how animals perceive habitat quality and, consequently, how they behave and use space. Competitors may remove resources and apply them to their own fitness (Nunes et al. 1997, Goubault et al. 2005). Alternatively, conspecific competitors may also depress foraging opportunities by changing prey behavior or availability, making resources more difficult to acquire (interference competition; Charnov et al. 1976, Jetz et al. 2004, Mitchell and Powell 2007). Changes in resource availability induced by conspecifics causes individuals to forage further or more often to acquire resource (Brown and Orians 1970, Waser and Wiley 1979, Lewis and Murray 1993, Nunes et al. 1997, Mitchell and Powell 2004, Moorcroft et al. 2006a, Mitchell and Powell 2007).

Territories and home ranges represent an important link between habitat quality and fitness (Burt 1943, Mitchell and Powell 2003, Powell 2004, Mosser et al. 2009, Mitchell and Hebblewhite 2012, Powell and Mitchell 2012). Home ranges are collections of places where animals have information that aids them in obtaining the resources they need, and territories are specialized home ranges, or parts of home ranges, for which individuals have exclusive access to resources (Burt 1943, McNab 1963, Brown and Orians 1970, Carpenter and MacMillen 1976, Powell and Mitchell 2012). Territories should arise when resources are scarce enough such that the benefits of guarding a territory exceed the

benefits and lead to exclusive use areas (Krebs 1980, Davies and Houston 1981, Powell 1993 pg. 292, Davies and Hartley 1996, Powell et al. 1997, Powell 2012a). When resources are limiting, but costs to maintain a territory are too high, animals leave. Intruders are at a disadvantage in the home ranges of conspecifics and, hence, should avoid those locations in favor of finding and developing their own home ranges.

The mechanisms by which conspecific competitors affect home range development and maintenance is little studied. Both conceptual models and empirical data for mammals demonstrate that cues, such as scent-marking, can result in distinct territory boundaries (Peters and Mech 1975, Krebs 1980, Lewis and Murray 1993, Moorcroft et al. 2006b, Potts and Lewis 2014). Animals may actively defend territories through direct contact including intimidation (e.g., threat displays) or combat (Brown and Orians 1970, Kitchen and Bromley 1974, Jaeger 1981). Direct confrontation and non-direct cues, like scents, are likely important for communication and maintenance of home ranges, but the degree to which either is used likely varies, depending on how limiting resources are and on the benefits of defending them (Gosling 1982, Lewis and Murray 1993, Buesching and Macdonald 2004, Moorcroft et al. 2006a). When direct confrontation is limited between individuals, non-direct cues, specifically scents for many mammals, provide information that affects the structure of home ranges or territories (Gosling 1982, Richardson 1991). Scent also communicates reproductive receptivity, sex, age, and individual identifications to conspecifics (Mech and Peters 1977, Gosling 1982, Hagey and MacDonald 2003, Buesching and Macdonald 2004, Zhang et al. 2005, Kent and Tang-Martínez 2014). Moreover, the freshness or concentrations of scents convey information concerning the last use of the locations, and hence, the time of depletion or

depression (Spencer 2012, Stockley et al. 2013, Potts and Lewis 2014).

Studies that have incorporated the effects of conspecific competition have demonstrated that resource depression does have important effects on space-use (Jetz et al. 2004, Moorcroft et al. 2006a, Mitchell and Powell 2007). Nevertheless, much remains unknown about conspecifics, resource depression and the commensurate effects on home range structure and animal movements. The cost of resource depression on perceived habitat quality from one individual to another is largely unknown. Discount rates likely change from one animal to another depending on the relative time since potential depression (e.g., the last scent mark) and for different types of conspecific competitors (Polis 1984, Field et al. 2005, Spencer 2012). Mitchell and Powell (2003 and 2007) arbitrarily assigned a discount rate of -0.20 for black bears (*Ursus americanus*), which matched modeled expectations of home range structure. Individuals encountering the home ranges of a dominant individual of the same sex may discount the habitat more than compared to that of subordinate (Holmes and Powell 1994, Powell 1994, Yamaguchi and Macdonald 2003, King and Powell 2007).

Translocation experiments provide important insights into animal movements, habitat connectivity, and habitat quality (Young and Shivik 2006, Hargreaves et al. 2014, Betts et al. 2015). Early during reintroductions, animals exist in the absence of conspecific competitors. As more animals are released, competitors encounter and react to the existing home ranges of conspecifics of different sexes and ages (Linklater et al. 2006, Berger-Tal and Saltz 2014, Chapter *Science in Reintroductions*). These interactions across a range of conditions provide the opportunity to test hypotheses related to perceptions of conspecifics and existing home ranges and resource depression.

During a reintroduction of fishers (*Pekania pennanti*) in northern California, we investigated the effects of conspecific competition on movements and home range establishment by fishers after release in each of 3 years. Fishers (Fig. 1) are medium sized carnivores in the Mustelidae weighing 2-6 kg. Throughout their range, which is restricted to northern North America, they thrive in large, dense stands of late successional northern forests (Allen 1983, Powell 1993, Raley et al. 2012). Through the 19<sup>th</sup> and early 20<sup>th</sup> centuries, fishers decreased in abundance throughout their range and subsequent efforts to restore their populations resulted in numerous reintroductions and augmentations (Aubry and Houston 1992, Powell 1993, Krohn 2012, Lewis et al. 2012).

Like many carnivores, fishers develop home ranges with little intrasexual overlap, but the home ranges of males overlap those of several females (Powell 1979b, Powell 1993, Weir 1995, Badry et al. 1997, Rennie 2015). Fishers have large home ranges because of their high metabolic rates and large travel distances in search of prey (McNab 1963, Harestad and Bunnell 1979, Powell 1979a, 1994). Females and males can travel relatively large distances when dispersing or after reintroductions but males, on average, travel further (Powell 1993, Proulx et al. 1994, Badry et al. 1997, Lewis 2014). Because of their large home ranges and solitary nature, fishers are unlikely to have direct interactions outside of breeding and kit-rearing. Little is known about fisher communication, but captive fishers do not vocalize loudly or often (Powell personal communication); thus, communication through olfaction is likely important (Powell 1993). Adult fishers seldom use the same locations simultaneously, indicating, high resource depression resulting from competition (Rennie 2015). Exactly how habitat is discounted by different types of competitors is unknown. Powell (1994) hypothesized that females have little overlap

among home ranges but that males impose home range overlap and competition on females because of their large size. Adult male fishers are larger than females but anatomical structures related to capturing and killing prey (e.g., teeth and jaws) of the 2 sexes are less dimorphic than are the rest of their bodies, indicating similar resource use (Holmes and Powell 1994). Males may tolerate direct competition with females for food to ensure mating opportunities (Erlinge and Sandell 1986, Sandell 1986). Yet, males should avoid the home ranges of other males, especially males dominant to them (e.g., an older, larger male). Females should avoid existing home ranges of males and females.

We hypothesized that conspecific competition would affect fisher movements and establishment of home ranges after release. Specifically, we hypothesized that female and male fishers would move further and faster when released into home ranges of conspecifics. We hypothesized that newly released female fishers would avoid male and female home ranges but that males would be indifferent to or attracted by females' home ranges while avoiding those of established males. We hypothesized that established home ranges (2 months or older) from previously released fishers affect newly released fisher's movements and use of space more strongly than insipient home ranges because sufficient scent had accumulated within established home ranges to signal avoidance to new animals. Nevertheless, we reasoned that if one animal came across scents from fishers released only days earlier, he or she could be affected and move further and faster.

To understand better what specific movement characteristics we should expect from newly released fishers, we simulated animals that took random walks plus animals that developed home ranges inside and outside of the established home ranges of conspecifics.

## METHODS

### *Study Site*

We reintroduced fishers to the Stirling Management Area (hereafter Stirling) owned by Sierra Pacific Industries in portions of Plumas, Butte and Tehama counties in northern California (Stirling; Lat 39.9° Lon -121.5°; Fig. 2) where the southern Cascade Mountains meet the northern Sierra Nevada. Stirling is 648 km<sup>2</sup> with elevations ranging from 424 to 2080 m. The climate on Stirling is temperate with the majority (>85%) of precipitation coming in late fall and winter as snow and rain (Pandey et al. 1999). Vegetation on Stirling is typical of Sierra Nevada mixed conifer forest and Ponderosa pine (*Pinus ponderosa*), Sugar pine (*Pinus lambertinia*), Incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), and California black oak (*Quercus kelloggii*) were dominant tree species. In some locations tanoak (*Notholithocarpus densiflorus*) and Canyon live oak (*Quercus chrysolepis*) also formed some dense stands (Griffin and Critchfield 1972, Beesley 2007).

Stirling was owned by Diamond Match Company from 1903 to 1988 and by Roseburg Forest from 1988 to 1992. Both companies harvested select trees within stands every 10-15 years while the remainder of a stand was left as growing stock (termed uneven-age management). In 1992 Sierra Pacific Industries bought Stirling and began using even-aged management, where nearly all merchantable trees were removed at each harvest. Roughly two percent of a harvested area was retained, with the goal of retaining structures and diversity in a stand during regeneration with planted tree seedlings. California timber harvest laws required, with few exceptions, that no more than 8 hectares (20 acres) were harvested in any one clear-cut and that adjacent stands must be

retained for 5 years (Brandow and Cafferata 2014). Select structures, such as snags and live hardwoods, are retained within harvested units. Units were commercially thinned after 20 to 40 years after harvest, with major harvests planned to cycle every 80 years. Approximately 5-15% of a watershed, or area, is harvested during a cycle. Since 2008, Sierra Pacific Industries has harvested 9145 ha on Stirling (mean = 1829 ha/yr), with 6344 ha associated with salvage logging of large burns from previous years. Excluding salvage logging from large wildfires, an average of 772 ha was logged annually with the majority (621 ha; 80%) as clear-cuts.

### *Field Methods*

*Reintroduction*— In late 2009, the state of California approved a reintroduction plan to move 40 fishers (24 F; 16 M) from across the fisher range in northwestern California over three years (Callas and Figura 2008). Trapping to evaluate and to move fishers began in late fall of 2009. We captured fishers from diverse locations in northern California to minimize the impact to any one area and to infuse genetic diversity into the founding population (Callas and Figura 2008, Facka Chapter *Establishment of a reintroduced carnivore population on an industrial timberland*). We transported all captured fishers to a central processing area near Anderson, California and evaluated them for potential release at Stirling. For females we sought individuals that were approaching their 2<sup>nd</sup> or 3<sup>rd</sup> birthdays, and therefore reproductive lives. For males, we sought individuals that we estimated to be at least 3-years old and weighing >4 kg, because we surmised that big males would be the best breeders (Table 1; Kovach and Powell 2003). Actual ages were unknown at the time we selected and moved fishers but for future analysis we removed one upper pre-molar from each fisher to estimate age by

counting *cementum annuli* (Arthur et al. 1992, Poole et al. 1994). At least one field biologist and one wildlife veterinarian evaluated each fisher we considered for reintroduction. We immobilized fishers chemically with Tiletamine HCL and Zolazepam HCL (Telazol, Fort Dodge Animal Health, Fort Dodge, IA) at a dosage of 7 mg/kg to evaluate their sex, reproductive status, general condition, disease exposure, weight, and to fit transmitters properly. At initial captures we collected a blood sample for genetic identification and gave fishers a Passive Integrated Transponder (PIT) tag identification. The Institutional Animal Care and Use Committees from North Carolina State University (09-007-O) approved handling procedures.

During late autumn autumns and early winters of 2009-2010 to 2011-2012 we released fishers in three release cohorts by year (Table 1). We released fishers in groups of 1-5 across much of Stirling, but emphasized the center (Fig. 2). After the first releases, we released female and male fishers in each year in locations where fishers had established home ranges and in areas where we had not documented fishers (Table 1). We released fishers in or out of known home ranges in alternating groups. We released fishers without acclimation (hard release) because acclimation appears not to affect population establishment (Lewis et al. 2012, Powell et al. 2012). To estimate fisher movements and survival post-release, we outfitted female fishers with either Telonics (IMP-325 or MOD-125; Mesa, AZ) or Holohil (MI-2i, Carp, Ontario) Very High Frequency (VHF) transmitters. We fitted adult males with Platform Terminal Transmitter collars (PTT [Argos]; Kiwisat 202 or 303, Sirtrack, Havelock North, NZ). In 2011, we began capturing fishers that were not reintroduced and presumably born on Stirling. These fishers were given the same transmitters as those given to reintroduced fishers based on sex and age.

*Field Methods at Release Site*—We attempted to locate all fishers carrying transmitters on Stirling (reintroduced and those born at the site) once per day using either VHF or PTT telemetry. We estimated fisher locations with VHF data using three methods, based on conditions, activity and the relative distances that individual fishers were from the field researcher. Most commonly we collected azimuths in the field to triangulate fisher locations (e.g., White and Garrott 2012) using program Location of a Signal (LOAS, Ecological Software Solutions LLC). Less often we located fishers from fixed-wing or helicopter based aerial surveys. Finally, we sometimes homed in on the signal of a fisher until we saw the fisher or could identify the tree or other structure where it was currently hidden. Location estimates from PTT data were processed through the Argos system with Kalman estimation and filtering (Collecte Localisation Satellites [CLS]; Ramonville-Saint-Agne, France) and delivered via email daily. Ideally, the PTT transmitters provided a minimum of one location estimate per day. Different PTT collars were active during different time blocks to allow inference to males' movements throughout a 24 hour cycle. We estimated VHF and PTT error by comparing locations estimated for collars and fishers to known locations. Median VHF error was 112 m and generally within the error radius produced from the LOAS software. The Argos (PTT) system classifies locations into distinct classes based on predicted error rates (Sauder et al. 2012). The expected precision of estimates descend from those designated class-3 ( $\leq 250$  m) to class-2 ( $\leq 500$  m), class-1 ( $\leq 1500$  m), and class-0 ( $>1500$  m). Our estimates of error for Argos locations did not depart from these categories and was similar to results from other studies on fishers carrying Argos collars (Sauder et al. 2012). Both VHF and PTT transmitters were equipped with a mortality sensor to document fisher deaths.

### *Simulations*

We simulated stochastic movements of animals in Python (version 2.7 available at <http://www.python.org>) to model the effects of conspecifics on the movements of fishers. We simulated landscapes with different habitat quality distributions based on values that ranged from 0 (low quality) to 1 (highest quality). We constructed these landscapes using the beta distribution where the alpha and beta parameters define the shape of the distribution and are transformations representing mean and standard deviation. We simulated 5 landscapes with varied distributions of habitat quality from low to high (Fig. 3).

We simulated 3 types of movement-models: 1) *Random*: Animals moved with a standard random walk and did not develop home ranges (e.g., Turchin 1998), 2) *Colonist*: Animals developed home ranges based on returning to the highest quality habitat patches encountered in the absence of conspecifics and 3) *Intruder*: Animals developed home ranges after being released into already developed home ranges from a previously released animal. Intruders ultimately become colonists in new locations. To understand how many times steps were needed to see differences between random walking animals and those that established home ranges we simulated scenarios with increasing time steps from 10 to 1000 to see where the standard deviation of the means ceased to overlap (Fig. 4).

At each time step for *Random* movements we generated a direction based on a uniform random distribution 0-360° and random distance (Gaussian distribution parametrized by mean distance and standard deviation). Animals moved further in low quality habitat compared to high quality habitat as a negative exponential function related

to habitat quality as

$$\text{Distance} = 1500e^{-2.4 \times q}$$

where  $q$  equals the habitat quality at a location. The standard deviation movement parameter followed a similar relationship.

$$\text{SD} = 400e^{-2.4 \times q}$$

We calculated the linear distance between the current location and the start site at each time step as well as a minimum convex polygon that bounded all points after the walk began.

*Colonist* and *Intruder* simulations on constrained random walks remembered locations that had high quality habitat, and thus, developed home ranges (Van Moorter et al. 2009, Spencer 2012). At each time step, the animal compared habitat qualities of its last 5 locations to locations prior. If the average or maximum habitat quality of past locations was higher than the last 5 locations, and had value greater than 0.5, then the animal changed course to an angle within  $45^\circ$  of the past location with greatest habitat quality. The azimuth between current locations and the highest habitat patch encountered were calculated using the arctangent ( $\text{atan2}$ ) function parameterized with the distance traveled in the X and Y directions. If present and past conditions were similar the animal showed no bias in direction of travel. To simulate how animals respond if released into an already existing home range, we generated an already present animal with 10,000 locations and that depressed habitat quality to the intruder by 10%, 50% and 90%.

Because of simulation to determine step numbers, we used 200 time steps for all other analyses and replicated these 1000 times. At the conclusion of each simulation we calculated the mean and maximum distance the animal traveled from the start location,

the area of the minimum convex polygon (MCP) that bounded all points, and the distance from start location to the center of MCP.

### *Analyses of Field Data*

*Release Habitat*- We estimated habitat quality on Stirling using Thomasma's version of the Allen fisher habitat suitability index (HSI; Allen 1983, Thomasma et al. 1994). The Allen model, and subsequently the Thomasma model, have been tested at other study sites and describe fisher habitat selection reasonably well (Thomasma et al. 1991, Powell 1993, Powell 2004). The Thomasma model quantifies fisher habitat quality based on 4 vegetative metrics: 1) percent tree canopy closure, 2) mean diameter at breast height (DBH) of overstory trees, 3) tree canopy diversity (*i.e.*, number of canopy and ground layers), and 4) percent of overstory trees that are not coniferous (hereafter hardwoods; Fig. 5; Allen 1983). Proximity among habitat patches and spatial configuration (e.g., fragmentation) do not contribute to habitat quality in the Thomasma model. We used the gradient nearest neighbor (GNN) dataset downloaded from <http://lemma.forestry.oregonstate.edu/data> (Ohmann et al. 2011) to create habitat suitability indices for each of the 4 vegetative metrics and then combined these into the final habitat suitability index (HSI) as:

$$HSI = (Canopy\ Closure + Mean\ DBH + Canopy\ Layer)^{\frac{1}{3}} \times \\ Percent\ Hardwood,$$

where canopy closure, Mean DBH (Diameter at Breast Height), canopy layering and percent hardwoods are HSI values that range from 0 to 1 (Fig. 5). We calculated the mean habitat value at each release point and within a 1 km circular buffer around each release points for all reintroduced fishers (Fig. 5). To evaluate the habitat quality of home ranges of reintroduced fishers, we used all their locations (if  $\geq 20$ ) during a calendar year (1-Jan to 31-Dec) to estimate an annual utilization distribution with a fixed kernel density

estimator and smoothing parameter set to 750 m (Seaman and Powell 1996). For each utilization distribution, we bounded the 0.50 isopleth, representing an area where we could find a fisher on 50% of occasions, and calculated the mean habitat quality in this isopleth.

*Reintroduced fishers-* We tested the hypothesis that conspecific competition influenced fisher movement and space-use. To account for the differences in time that some fishers were tracked we calculated movement and space-use metrics at 10, 20, 50, 100, and 200 relocations. We could not obtain a location for fishers each day after release; hence, the number of relocations generally represented longer periods (e.g., 100 relocations equated roughly to 1 year). Because we wanted to account for differences in fisher movements through time we included data from all time steps into one data set.

For each fisher, we calculated its mean and maximum distance from its release location. After each relocation we also calculated the area of the minimum convex polygon that bounded all locations. Finally, we calculated the distance between the fishers release location and the center of the 50% isopleth, which we interpreted as the fisher's home range center. For comparison, we calculated similar measures of distance and area for fishers that were not reintroduced but that were captured for the first time on Stirling. We used the initial capture locations of these fishers to represent release locations.

Prior to releasing fishers, we knew that male and female fishers move and behave differently (Powell 1979b, Powell 2012b). Thus, we considered sex differences in movement and space-use as the null model (*Sex*). Because we included data from multiple time steps we accounted for changes through time by including an effect for

time in all statistical models (*Step*). We hypothesized that both *Sex* and *Step* would interact with our other hypothesized effects from conspecifics (e.g., the presence of males could affect female movements differently at step 10 vs 100) and included both them in additive or interactive terms in our statistical models. To capture effects occurring over short time periods we included in our models the *Order* of release and order by sex (*Sex order*). We tested for an effect on movement patterns from encountering a female's home range within a week after release (*EncFem*), a male's home range (*EncMale*) or either a female's or male's home range (*EncFisher*). We tested for differences among the 3 release cohorts (*Cohort*), which may have reflected large-scale signals about habitat quality from one release cohort to the next. We postulated that large fishers could keep or claim areas from conspecifics that were small, young or simply less dominant. Therefore, we tested if either *age* or *weight* of fishers better described their movement and space-use than metrics related to habitat or the mere presence of other fishers. Poor habitat at the release sites or better habitat quality elsewhere could also affect fisher movements and settlement locations. Hence, we tested models of habitat at the source locations using the average habitat quality within a 1-km buffer around the release (*Average Habitat*) and mean habitat in the 50% isopleth of a fisher (*HabitatSettle*).

We tested four metrics of distance and space-use with general linear models (PROC GENMOD) in SAS assuming an underlying gamma distribution using a log link: area of the minimum convex polygon, distance from release location to center of home range (utilization distribution), maximum observed distance from release location, mean distance from release location. Because we had relatively few individuals we kept the structure of our statistical models relatively simple. For all models and metrics we ranked

competing hypotheses using Akaike's Information Criteria corrected for small sample size (AICc; Burnham and Anderson 2002). We took beta parameter estimates from the top models when they had high support (weight > 0.95). Otherwise beta parameters were estimated with model averaging across all competing models.

## RESULTS

### *Simulations*

Our simulations demonstrated clear differences in patterns of movement and space-use based on differences in animal behavior and habitat. Simulated animals that walked randomly (*Random*) moved further, on average, from their start locations at each respective time step they moved (Fig. 6). Simulated animals on constrained random walks stayed closer to their starting site irrespective of how long after release they were sampled (Fig. 4). Mean habitat quality of a landscape influenced the movements of simulated animals as expected based on the simulation structure. Animals in landscapes with low habitat quality moved further on average from their release locations than did animals in high quality habitat (Table 2, Fig. 7).

Simulated animals released within the home range of another animal moved further than those released without conspecifics and had larger average minimum convex polygon sizes compared to animals released without conspecifics (Table 2). These patterns were constant regardless of the habitat quality of the releases site, though the magnitudes of difference did change with habitat (Fig. 7). Animals that developed home ranges without conspecifics (*Colonists*) moved less far and had smaller areas of space used than those developing home ranges in competition (Table 3, Fig. 8). Animals behaving *Randomly*, as *Colonists*, or as *Intruders* moved relatively large distances in the first 10 time steps, but animals that formed home ranges decreased their mean

movements away from their starting points quicker than did those behaving randomly (Fig. 8). *Intruders* often moved further distances in shorter times, in the first 20 steps after starting than animals that were walking randomly, and remained further from their starting locations than did *Colonists* (Fig. 8). *Intruders* that discounted the habitat of an occupied home range greatly (90% reduction) moved slightly further, on average, than those that discounted habitat less (10% reduction; Fig. 8). Nevertheless, any discounting of habitat, as the result of encountering a conspecific, was more influential than the specific rate of discount. Releasing animals in the presence of conspecifics had a greater effect on speed from the release site than did habitat.

#### *Reintroduced fishers*

Roughly equal numbers of fishers were reintroduced over a 3 year span and with similar average ages in all years of release (Table 1). The males we released were on average older than females and all but 2 fishers were adults at release (Table 1). In the first year, 4 females were released in early December and the other females were released in late January or February and all males were released on January 14th of 2010 (~ 1 month after the first females). In both the 2<sup>nd</sup> and 3<sup>rd</sup> year of the reintroduction males and females were released in the late fall or early winter with males and females released in groups. For reintroduced fishers across all years we estimated an average of 55 locations for females and 97 locations for males within the first 12 months after release (Table 1). We captured and radio-collared the first fishers born on the study site in the fall of 2011 and subsequently estimated 330 locations for females and 1144 for males through September of 2012. We followed 8 of 9 females released in year-1 through June of their first year. From June to August 2010, three females died and we lost contact with 2 others

from apparent transmitter failure. Similarly, for males we were able to track most fishers through the summer of 2010 (5 of 6). We tracked all year-2 females for their entire first year except for one females that died in August. One male from the year-2 cohort died within 2 months after release. We had fewer estimated location for the year-3 cohort because 1 female died 2 days after release and another died within 2 months.

Differences in movements and space-use were apparent between the sexes (Table 3). Male fishers moved further from their release locations (both mean and maximum values), had larger areas of use (minimum convex polygon area), and settled into home ranges further from their releases locations. Differences in movement and space-use were evident among the release cohorts particularly among females. Females released in year-2 and year-3 moved further away from their release locations than females in year-1. Moreover, females in year-1 had smaller areas of total use (Table 3) than females in either years-2 or year-3. Male fishes showed far less differentiation in patterns of movement among release cohorts than did females. In contrast to the patterns we observed in females, males in year-1 tended to move further than males released in subsequent years (Table 3).

Female and male fishers demonstrated patterns of space-use indicating that they developed home ranges relatively quickly. Similar to our simulations, the mean area of a fishers' minimum convex polygon plateaued, or increased slowly, after roughly 100 relocations and indicating they found areas to form home ranges (Fig. 9). Notably, males that did not encounter the home range of pre-existing fishers increased their mean MCP during much of their first 200 time steps (Fig. 9), because they appear to have explored further from their release sites before returning to the study area (Fig. 9). Males,

generally, were far more variable in their patterns of movement and space-use than females (Fig. 9).

The mean habitat at the point of release was  $0.75 \pm 0.4$  with a mean value within a 1-km buffer of  $0.79 \pm 0.02$  ( $n = 12$ ; Fig. 2). Generally, fishers established home ranges in higher quality habitat quality than their releases, but there was high variance around mean habitat in settled areas  $0.80 \pm 0.67$ . On average, females settled in areas of higher quality habitat ( $0.80 \pm 0.075$ ) than males ( $0.70 \pm 0.08$ ). Additionally, fishers released in year-1 and year-2 tended to establish home ranges in areas of higher quality habitat ( $0.77 \pm 0.09$  and  $0.77 \pm 0.08$ ) than fishers released in year-3 ( $0.73 \pm 0.11$ ). Nevertheless, fisher movement and space-use did not appear to be based exclusively on finding quality habitat.

The movements of reintroduced fishers were best described by the presence of previously released conspecifics compared to other variables including habitat (Table 4). The top ranked hypothesis included effects from encountering male home ranges (*EncMale*) for area of minimum convex polygons of fishers during their first 200 relocations. This top model had high  $AIC_c$  weight (0.98). The second highest ranked hypothesis for minimum convex polygon area included effects from habitat quality of settled home range. Similarly, a hypothesis with effects from encountering a female home range (*EncFem*) was best supported for describing the distance from release to the home range center (Table 4). For both mean and maximum distance, the best hypotheses included effects from encountering male home ranges (mean distance) or encountering any home ranges from previously released animals (maximum distance). As with the other metrics there was high support for the top models ( $AIC_c$  weight  $> 0.95$ , Table 4).

For the top hypotheses in all 4 metrics, the main effects of sex, time, and conspecific completion were better explained with inclusions of interactions terms between *Sex* and *Step* the main effects (Table 4, Fig. 9).

Female fishers that encountered the home ranges of conspecifics soon after release moved further and had large areas of space use compared to females that did not (Fig. 10). The effect of conspecific fishers toward females was apparent regardless of the metric of movement used or which type of conspecific home range they encountered (females or males). Additionally, the pattern of females moving further in apparent response to conspecifics was consistent through the time period of analysis. The relationship between male fishers that encountered or did not encounter conspecifics was less distinct than was that of females (Fig. 9 and 10). Generally, the mean values between males encountering or not encountering conspecific home ranges, for all metrics of movement and space use, overlapped and had high variation. Soon after release (<50 relocations) males that did not encounter other fishers did travel further than males that did encounter conspecifics. Several males in the first year of release, when few females were present, travelled long distances only to return to the study site later (Fig. 9). Generally, our results indicate the females avoided the home ranges of all types of conspecifics whereas males were indifferent or more likely to move when conspecifics, especially females, were not present. Reintroduced fishers, both females and males, moved further away from their release locations compared to individuals born on the study site and that had established home ranges. Reintroduced female fishers that did not encounter the home range of a conspecific were similar, though they moved marginally further from their release site, to female fishers born on the study site (Fig. 10). Few

differences existed between movement patterns between males that were reintroduced or that were born on Stirling.

## DISCUSSION

Conspecific competition affects movements and home range development of simulated and real animals. Our simulations showed that animals moved further and used more space when encountering the home ranges of conspecifics. Fishers moved less in the absence of competition regardless of habitat quality. The amount that animals discount habitat quality based on the presence of a conspecific may be less important to structuring their movements than experiencing conspecific competition at any discount rate. Our empirical results for females matches the patterns we observed from our simulations for animals released in existing home ranges. All metrics of movement and space-use showed that female fishers avoided the home ranges of previously released males and females. Males, in contrast, appeared indifferent to existing home ranges of other males, but appeared to move further for longer when they did not encounter the home range of a female. These results support the hypothesis that female fishers avoid the home ranges of any conspecific and that there is a high discount rate on areas inside the home ranges of competitors as a product of resource depression. Additionally, our findings support the hypothesis that female avoidance of male home range means they are generally intolerant of competition and that males invoke overlapping home ranges on females probably to ensure opportunities for mating (Powell 1994).

Large male movements in the absence of encountering females may indicate that maintaining information on mating opportunities even outside of the breeding season is important to males (Sandell 1986, Holmes and Powell 1994). Males only seem to have

moved long distances, relative to other males, in response to the absence of females and for short periods after release. This may occur because males are indifferent to competitors, but we hypothesize that the movements of males that encounter home ranges of other males will be explained by specific attributes of the males. On at least two occasions we released young, relatively small males whose movement patterns appeared relatively stable a short time after release. After the introduction of larger males, the small males moved further and into locations we characterized as poor habitat. When males are in the absence of females or in the presence of large, dominant males, their travel (dispersal) distances are similar to those observed for male fishers elsewhere (Proulx et al. 1994, Lewis 2014). These types of interactions may occur relatively infrequently but likely influence structure of home ranges considerably and are important considerations for future translocation efforts when they decide how to release specific types of individuals.

The process of moving animals to a new landscape has important impacts on their movements after release. Animals experience stress during reintroductions and their behaviors may be aberrant compared to behaviors in their natal ranges; thus, their behavior may be an unreliable metric of what naturally occurring animals do (Young and Shivik 2006, Betts et al. 2015). We hypothesize that these biases are likely to be similar among reintroduced animals and comparisons of treatment types are additive to the reintroduction process. Thus, they may represent a biased, but meaningful comparison.

Fishers appeared to be responding to the scents left by conspecifics. We could not directly observe the interactions of fishers, and thus, cannot rule out direct interactions including guarding or defense behaviors. Nevertheless, because fishers have large home

ranges we think it unlikely that fishers were encountering one another within days after release. Indeed, direct interactions that lead to our observations seem very unlikely. Thus, scents left throughout the home ranges of previously released fishers provided important information to newly released individuals (Gosling 1982, Linklater et al. 2006, Kent and Tang-Martínez 2014). Fishers may visit specific latrines but we hypothesize that the majority of information between fishers occurs as they deposit scents as they forage, rest and den. Thus, female home ranges may be effectively territories with respect to other females. Generally, researchers know very little about how most species within the *Martes* complex communicate and how it influences their home range development and fitness.

Future studies should investigate the time that scents from mammalian carnivores, and mammals generally, last and influence the behavior of individuals that invade an existing home range (Gosling 1982, Potts and Lewis 2014). Understanding how animals respond to scent through time may provide important insights into shifts in home ranges and the birth of new home ranges within the spaces of existing home ranges. Sound theory for interactions exists for territorial animals, but basic theory and empirical data still lag behind in situations when animals develop home ranges (Lewis and Murray 1993, Potts and Lewis 2014). We observed females that had relatively stable home ranges that they shifted after the death of neighboring animals. Yet, we do not know if these shifts resulted because new areas of better habitat opened up or if the death of one individual facilitated expansion by another. Shifts often happened in the fall and often about 1 month after the death of a neighbor. We hypothesize that home range shifts or home range invasions after the death of conspecifics will provide important insight the time one

animal detects and respects the cues (e.g., scents) of other individuals of different types.

Familial or past-mating relationships between animals are particularly interesting to understand in the context of home range development and shifts in home range structure. One hypothesis suggests that closely related females will be more willing to incur overlap between their home ranges (Rennie 2015). We further hypothesize that familiarity with another animal during home range development may have important implications for how animals discount habitat quality. If females are intolerant of competition because of the risks of resource depression then they may simply incur the costs of foraging with related individuals which could cause them to be less effective foragers and travel further to find food.

Conspecific competition is an important aspect of assessing habitat quality for animals. Because habitat quality is inherently related to the fitness of individuals, the presence of competitors should have consequences for fitness of the resident of a home range (Mitchell and Powell 2003, 2004, 2007, Mosser et al. 2009). Our simulations suggest that the resource discount rate may cause only subtle changes in the mean movement and space-use of animals. Yet, even small discount rates may cause animals to forego home ranges of otherwise high quality. We hypothesize that assessing the difference between the habitat quality of foregone areas, or patches, and the habitat quality of used, or settled, home ranges provides a quantifiable metric that will relate to the true discount rate. Further, we hypothesize the using habitat models and observations about good habitat in apparently unused locations provides a way of identifying home ranges for animals that are undocumented by live-capture or non-invasive detection.

Some researchers demonstrate that home range size decreases with increased

competition and poor habitat quality or highly clumped resources may cause animals to change their behavior (Jetz et al. 2004, Mitchell and Powell 2007). Yet, little is known about the cognitive maps of animals are structured around the presence of conspecifics. How animals decide where and how to move from one portion of their home range to another, or into the home ranges of others, remains effectively unknown for most animals (Nunes et al. 1997, Powell 2012b, Powell and Mitchell 2012). We surmise that animals consider strongly the cues from conspecifics when deciding both which resource patch to use and how to get between them.

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Table 1. The total number of female (F) and male (M) fishers released by cohort, average weight  $\pm$  range, mean numbers of locations  $\pm$  range per individual in the first 12 months, and whether fishers were released within the home ranges of female released at least 2 months previously (Rel In HR) and whether they encountered any home ranges of other fishers (Enc HR) released at least 2 months previously.

Sex	Cohort	Years	Num	Age	Rel IN HR	Enc HR
F	Year1	2009-2010	9	2.6 $\pm$ 1,5	3	6
	Year2	2010-2011	7	2.4 $\pm$ 1,5	4	7
	Year3	2011-2012 <sup>†</sup>	8	2.0 $\pm$ 0,3	5	5
	All F	--	24	2.3	12 (50%)	18 (75%)
M	Year1	2009-2010	6	3.0 $\pm$ 1,5	0	0
	Year2	2010-2011	6	3.8 $\pm$ 2,6	6	6
	Year3	2011-2012 <sup>†</sup>	4	1.8 $\pm$ 0,4	1	3
	All M	--	16	3.0	7 (43%)	9 (57%)

<sup>†</sup> Final releases occurred in December of 2011

Table 2. The mean values  $\pm$  SD for 4 metrics calculated from simulations where animals randomly walked after release (*Random*), had constrained random walks in the absence of conspecifics (*Colonist*), and had constrained random walks started in the home ranges of conspecifics (*Intruder*): Mean distance moved from the start site (MeanDist), the mean maximum distances from the start site (MaxDist), and the mean minimum convex polygon area (MCParea), and distance between the start site and final home range center (Relast\_to\_HR) for simulated animals released on landscapes with 5 habitat quality distributions (Habitat) from 1000 simulated releases and 200 relocations post-release.

Behavior	Habitat	MeanDist (km)	MeanMaxDist (km)	MCParea (km <sup>2</sup> )	Rel_to_HR (km)
Random	Low	16.1 $\pm$ 6.8	23.0 $\pm$ 4.4	486 $\pm$ 117	12.4 $\pm$ 4.4
	Mod	8.5 $\pm$ 3.5	13.7 $\pm$ 5.7	131 $\pm$ 41	10.7 $\pm$ 6.0
	Mixed	11.4 $\pm$ 4.7	19.3 $\pm$ 8.3	240 $\pm$ 181	13.1 $\pm$ 7.0
	High	8.3 $\pm$ 3.6	10.2 $\pm$ 4.4	126 $\pm$ 52	9.7 $\pm$ 5.1
	Very high	7.8 $\pm$ 3.2	9.3 $\pm$ 3.9	105 $\pm$ 41	7.0 $\pm$ 4.8
Colonist	Low	4.2 $\pm$ 2.1	4.9 $\pm$ 2.5	43 $\pm$ 16	5.1 $\pm$ 2.6
	Mod	2.1 $\pm$ 1.1	3.7 $\pm$ 1.8	31 $\pm$ 8	6.3 $\pm$ 4.4
	Mixed	3.0 $\pm$ 1.5	5.0 $\pm$ 2.5	50 $\pm$ 13	4.1 $\pm$ 2.1
	High	2.45 $\pm$ 1.2	2.6 $\pm$ 1.4	16 $\pm$ 4	4.0 $\pm$ 2.4
	Very high	2.1 $\pm$ 1.1	2.4 $\pm$ 1.3	16 $\pm$ 5	3.3 $\pm$ 3.7
Intruder	Low	5.4 $\pm$ 2.0	7.8 $\pm$ 2.7	50 $\pm$ 22	6.8 $\pm$ 3.7
	Mod	2.9 $\pm$ 1.5	5.3 $\pm$ 1.9	37 $\pm$ 10	5.4 $\pm$ 2.1
	Mixed	4.4 $\pm$ 1.6	6.5 $\pm$ 2.3	56 $\pm$ 16	6.7 $\pm$ 3.7
	High	3.2 $\pm$ 1.4	3.5 $\pm$ 1.8	18 $\pm$ 6	5.6 $\pm$ 3.4
	Very high	3.2 $\pm$ 1.5	3.8 $\pm$ 1.8	20 $\pm$ 6	4.3 $\pm$ 1.9

Table 3. Mean values  $\pm$  SD for 4 metrics, mean minimum convex polygon area (MCP km<sup>2</sup>), the mean distance from release site to 50% isopleth centroid (HR Dist), the mean observed maximum distance from release site (Max Dist), the mean distance from release point (Mean Dist), for female and male fishers reintroduced in 2009-2010 (year-1), 2010-2011 (year-2) and 2011-2012 (year-3) with a minimum of 50 relocations after release in northern California.

Sex	Cohort	MeanDist (km)	MaxDist (km)	MCParea (km <sup>2</sup> )	Release_to_HR (km)
F	year-1	2.8 $\pm$ 0.9	7 $\pm$ 2.2	34 $\pm$ 25.3	2.9 $\pm$ 1.3
F	year-2	7.1 $\pm$ 3.6	13 $\pm$ 2.6	119 $\pm$ 45	6.7 $\pm$ 2.8
F	year-3	6.2 $\pm$ 2.1	11.1 $\pm$ 2.4	86 $\pm$ 33	3.5 $\pm$ 2.2
M	year-1	16.5 $\pm$ 15.5	23.7 $\pm$ 18.2	415 $\pm$ 39	13.4 $\pm$ 10.5
M	year-2	8.8 $\pm$ 4.2	17.1 $\pm$ 5.5	596 $\pm$ 662	12.4 $\pm$ 6.1
M	year-3	6.9 $\pm$ 0.5	14.9 $\pm$ 4.3	816 $\pm$ 1043	11.8 $\pm$ 8

Table 4. Model selection criteria including the AIC<sub>c</sub> scores,  $\Delta$ AIC<sub>c</sub> comparing top model to other competing models, the likelihood of each model, and the model weight for each competing model ( $w$ ) for the top five models from analyses of 4 dependent variables of fisher movements after reintroduction in the northern California from 2009-2012. Dependent variables are: the area of the minimum convex polygon (MCParea), the distance from release location to 50% isopleth centroid, the mean distance traveled from a fishers release location (MeanDist), and the maximum observed distance traveled from release location (MaxDist). Total sample size was 130 (fisher  $\times$  steps)

Dependent	Model Description	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Likelihood	$w$
MCParea	Sex+ Step + EncMale + Sex $\times$ EncMale+Step $\times$ EncMale	4430.2	0.00	1.00	0.98
	Sex + Step + HabitatSettle	4437.7	7.50	0.02	0.02
	Sex $\times$ ReleaseOrder	4444.0	13.78	0.00	0.00
	Sex + Step + EncFisher + Sex $\times$ EncFisher + Step $\times$ EncFisher	4445.0	14.77	0.00	0.00
	Sex $\times$ Release Order ( Sex-Specific)	4448.5	18.35	0.00	0.00
Release to HR	Sex+ Step + EncFem + Sex $\times$ EncFem + Step $\times$ EncFem	2188.8	0.00	1.00	1.00
	Sex + Step + EncFisher + Sex $\times$ EncFisher + Step $\times$ EncFisher	2199.8	11.04	0.00	0.00
	Sex + Step + EncFem	2205.7	16.97	0.00	0.00
	Sex + Step + EncFem + Step $\times$ EncFem	2205.8	16.99	0.00	0.00
	Sex + Step + EncFisher	2206.1	17.28	0.00	0.00
MeanDist	Sex + Step + EncMale + Sex $\times$ EncMale + Step $\times$ EncMale	2208.2	0.00	1.00	0.99
	Sex $\times$ Order	2218.4	10.21	0.01	0.01
	Sex + Step+ EncFisher + Sex $\times$ EncFisher + Step $\times$ EncFisher	2220.4	12.17	0.00	0.00

Table 4. Continued

MeanDist	Sex × SexOrder	2222.0	13.75	0.00	0.00
	Sex +Step + EncFem	2222.2	14.01	0.00	0.00
MaxDist	Sex+ Step +EncFisher + Sex×EncFisher + Step×EncFisher	2282.9	0.00	1.00	0.96
	Sex +Step + EncFem	2291.8	8.96	0.01	0.01
	Sex + Step + EncFem + Sex×EncFem + Step×EncFem	2291.9	9.03	0.01	0.01
	Sex + Step+ EncFem + Sex×EncMale + Step×EncMale	2292.1	9.24	0.01	0.01
	Sex + Step+ EncFem + Step×EncFem	2292.2	9.29	0.01	0.01



Figure 1. A fisher (*Pekania pennanti*) running after being reintroduction onto an industrial timberland in the fall of 2011 in northern California.

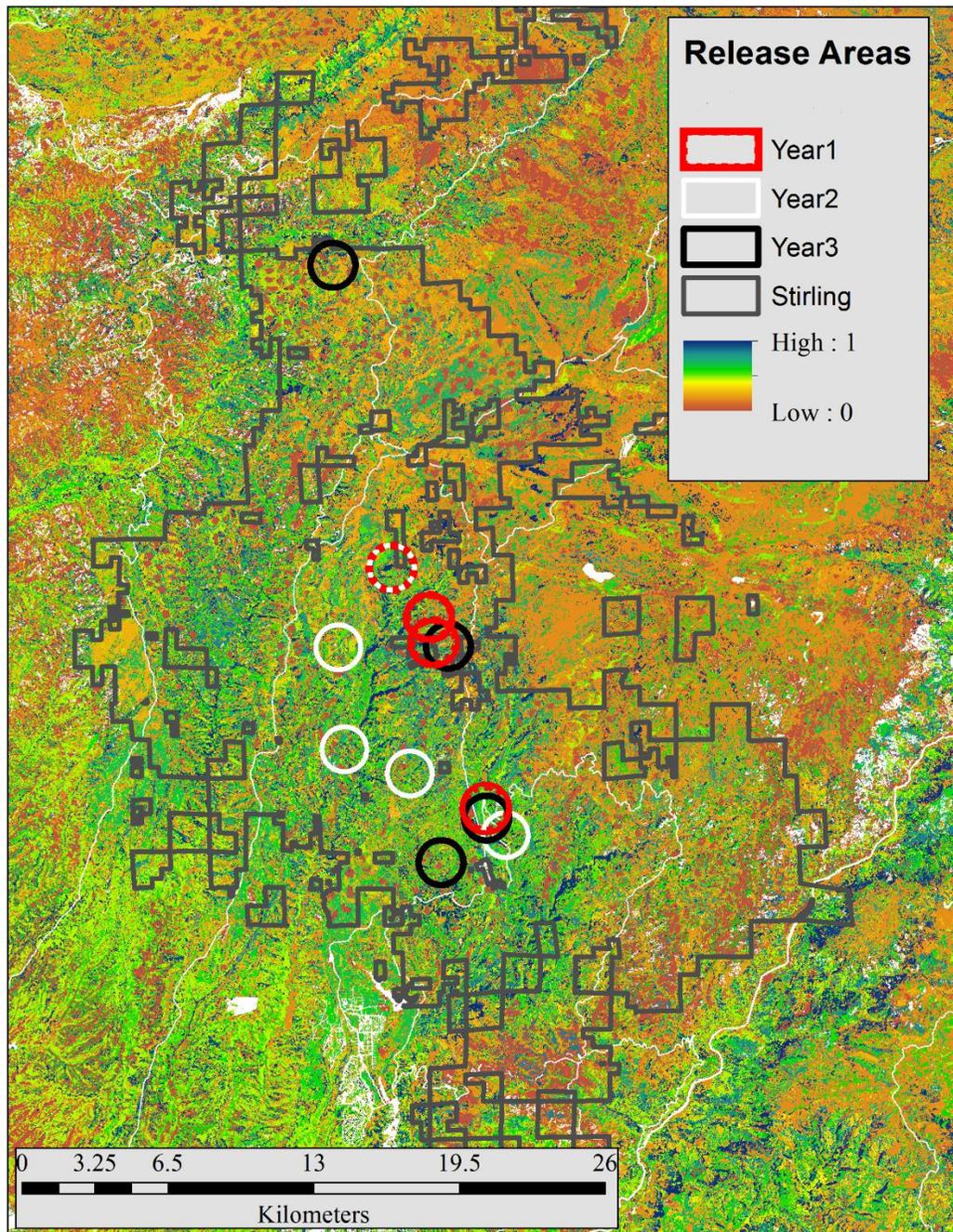


Figure 2. Release areas by year (black circles = 2009-2010, white circles = 2010-2011, and red circles = 2011-2012) for fishers on Stirling study site in northern California with estimated habitat quality (blue is highest) based on the Thomasma et al. (1996).

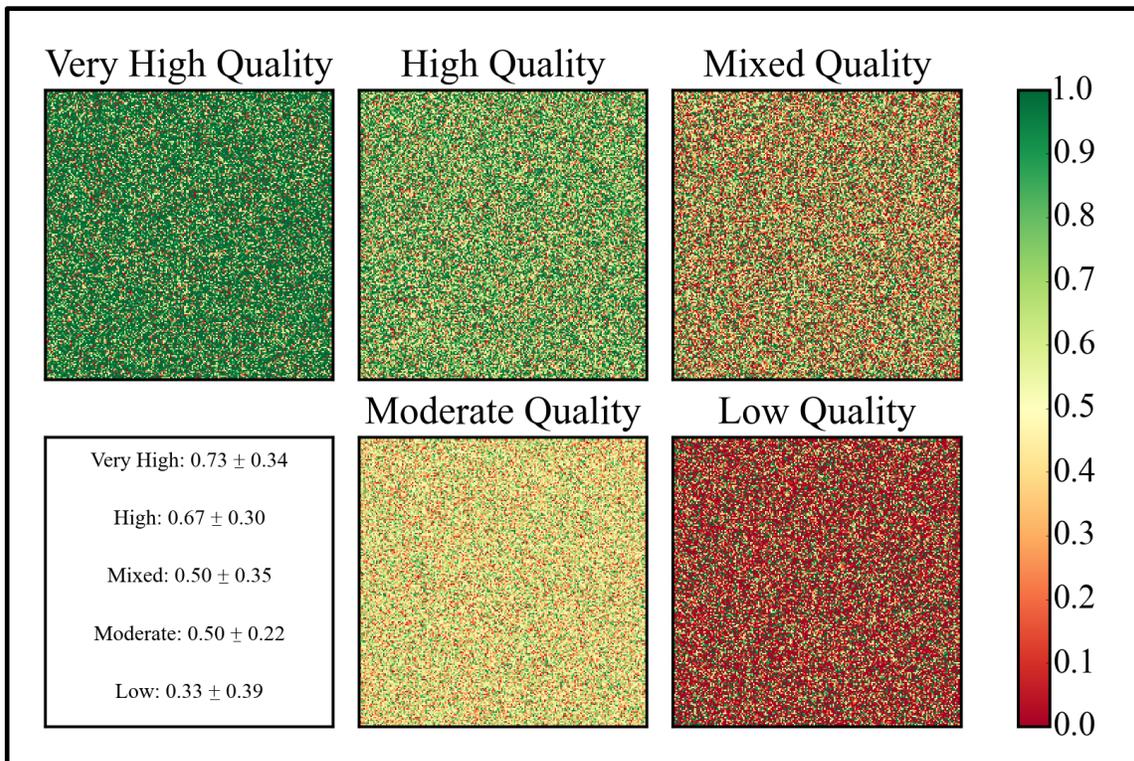


Figure 3. Visual representations of five simulated landscapes with patch sizes (grid cells) of  $100 \times 100$  m and randomly distributed mean habitat qualities ranging from low to very high. Mean  $\pm$  standard deviation for each simulated landscape in lower left panel.

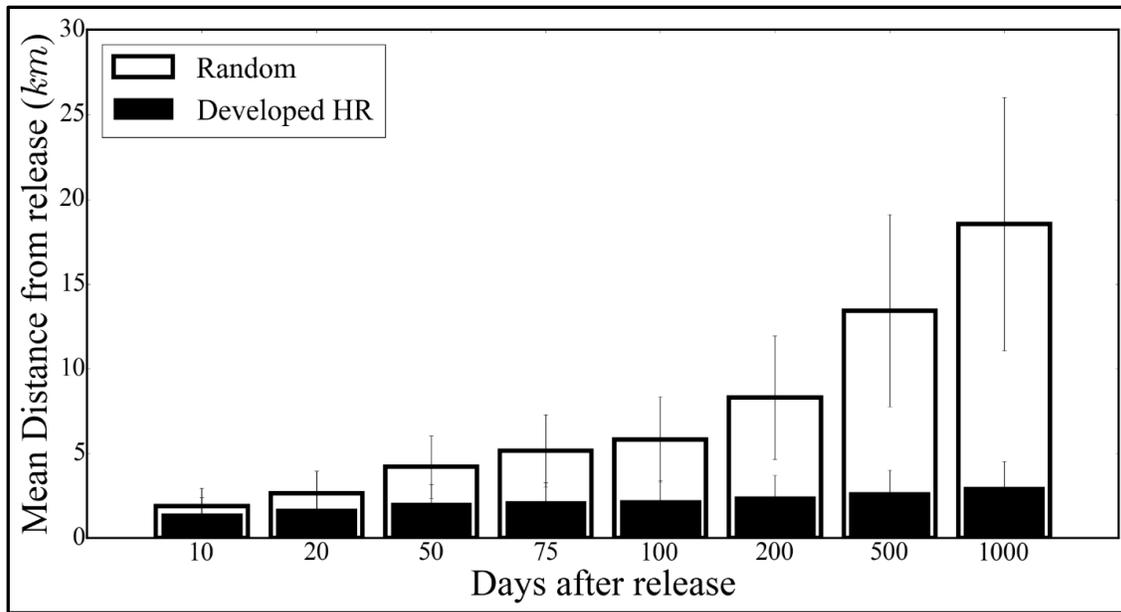


Figure 4. Mean distance (meters)  $\pm$  standard deviation from the release location at time steps 10 to 1000 for simulated animals that took random walks (*Random*; open bars) and animals that develop home ranges in the absence of competition (*Colonist*; black bars).

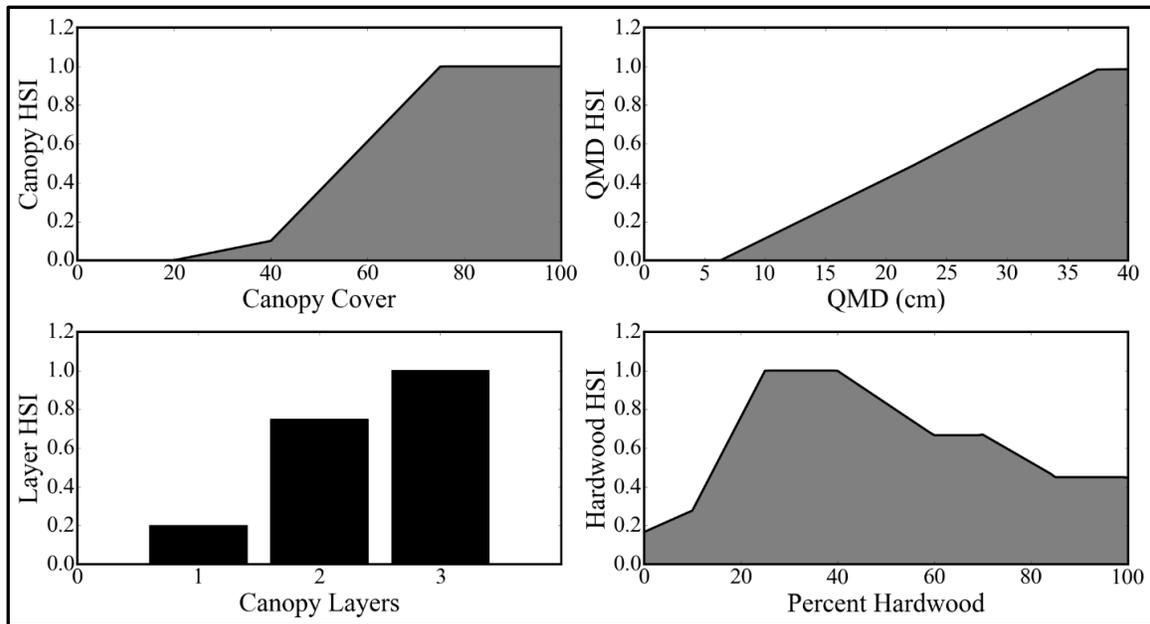


Figure 5. The relationships between habitat suitability for fishers and percent canopy closure, quadratic mean diameter at breast height (QMD) of overstory trees, tree canopy diversity, and percent of hardwoods.

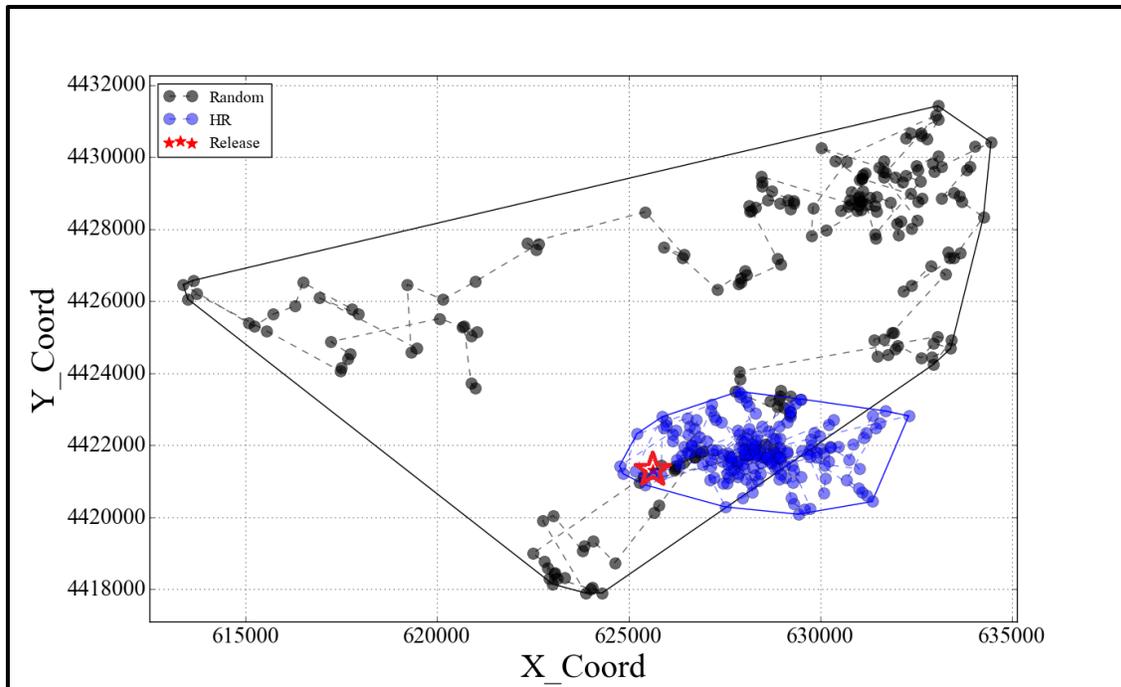


Figure 6. Single run for a simulated animal on a random walk (black dots, dashed lines) and an animal that develops a home range based on returning to high value habitat patches (blue dots, dashed lines) released from the same location (red star). Black and blue solid lines represent the minimum convex polygon bounding all points for each animal.

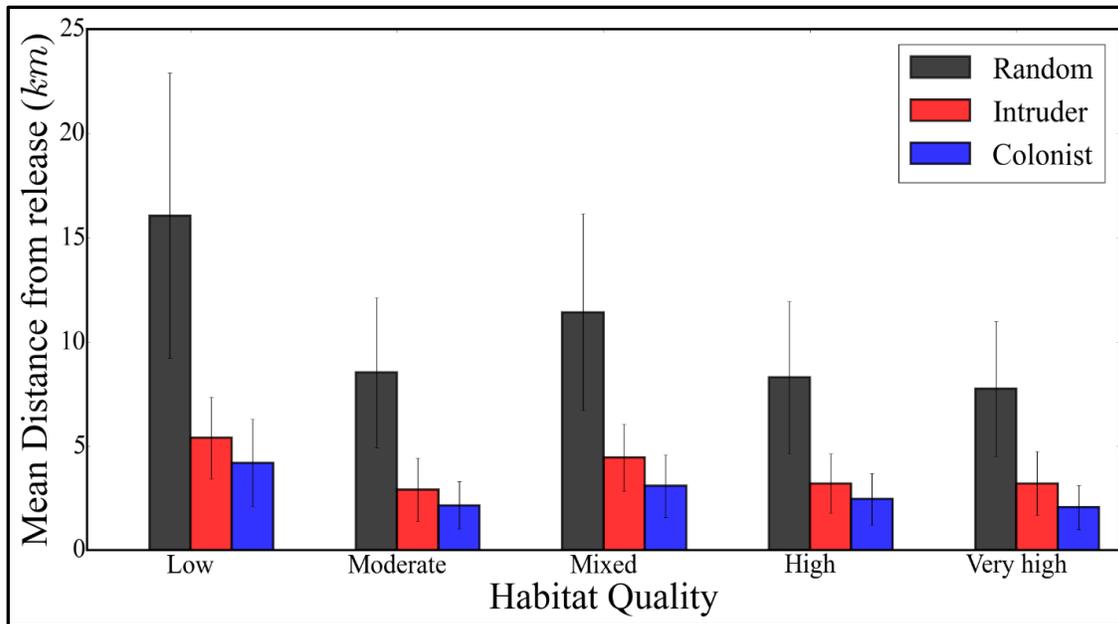


Figure 7. Mean distance from start location  $\pm$  standard deviation after 200 steps for simulated animals in landscapes with 5 different habitat quality distributions and that walked randomly (*Random*; black bars), were released into the home range of an existing animal before developing a home range (*Intruder*; red bars) and developed home ranges in the absence of conspecific competition (*Colonist*; blue bars).

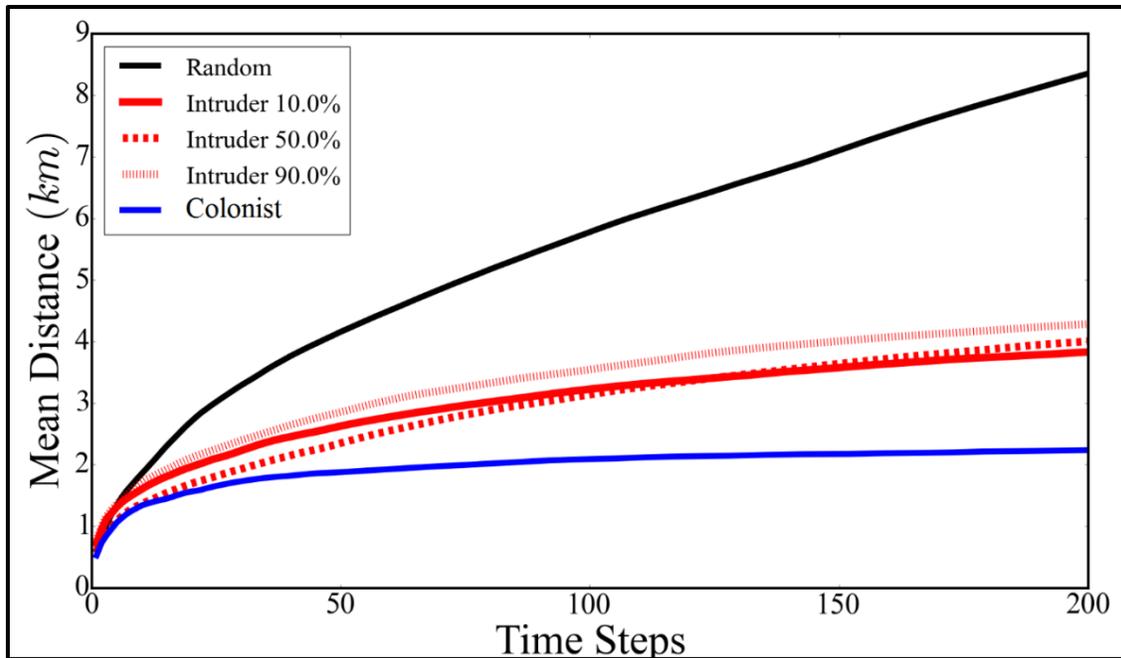


Figure 8. The average distance from the start point for simulated animals that walked randomly (*Random*; black line), animals that were released and established a home range without competition (*Colonist*; blue line) and an animal released into the established home range of a conspecific (*Intruder*; red lines) where there intruder discounted habitat quality at 90%, 50% and 10% of the value to the resident after 200 time steps. All releases occurred in landscapes where the average resource patch had high habitat value.

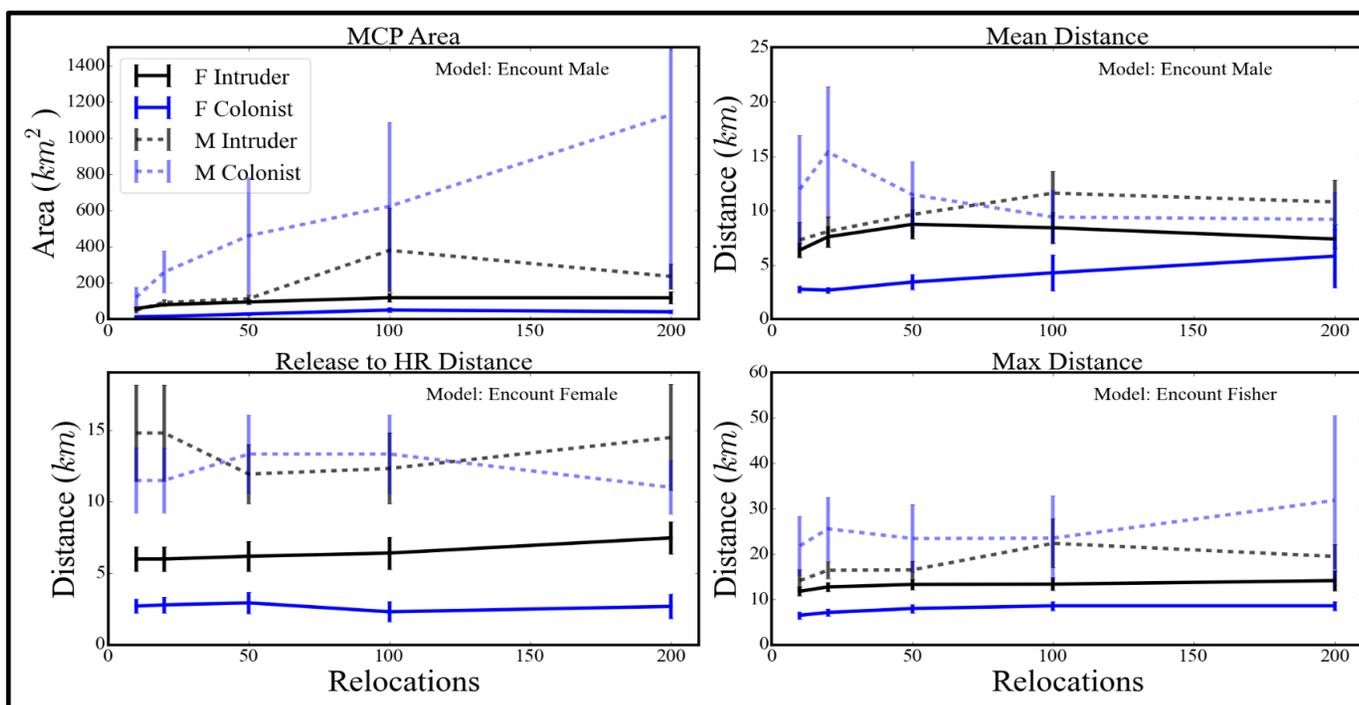


Figure 9. Mean values  $\pm$  95 confidence limits of the minimum convex polygon area (MCP Area), mean distance travelled from the release location (Mean Distance), the distance from the release site to the home range center (Release to HR Distance) and mean maximum distance observed from the release point (Max Distance) for females that encountered (F\_Enc) or did not encounter (F\_NoEnc) and males that encountered (M\_Enc) and did not encounter (M\_NoEnc) home ranges of conspecifics previously released fishers (*Pekania pennanti*) reintroduced into northern California from 2009 to 2012, based on the top selected general linear model.

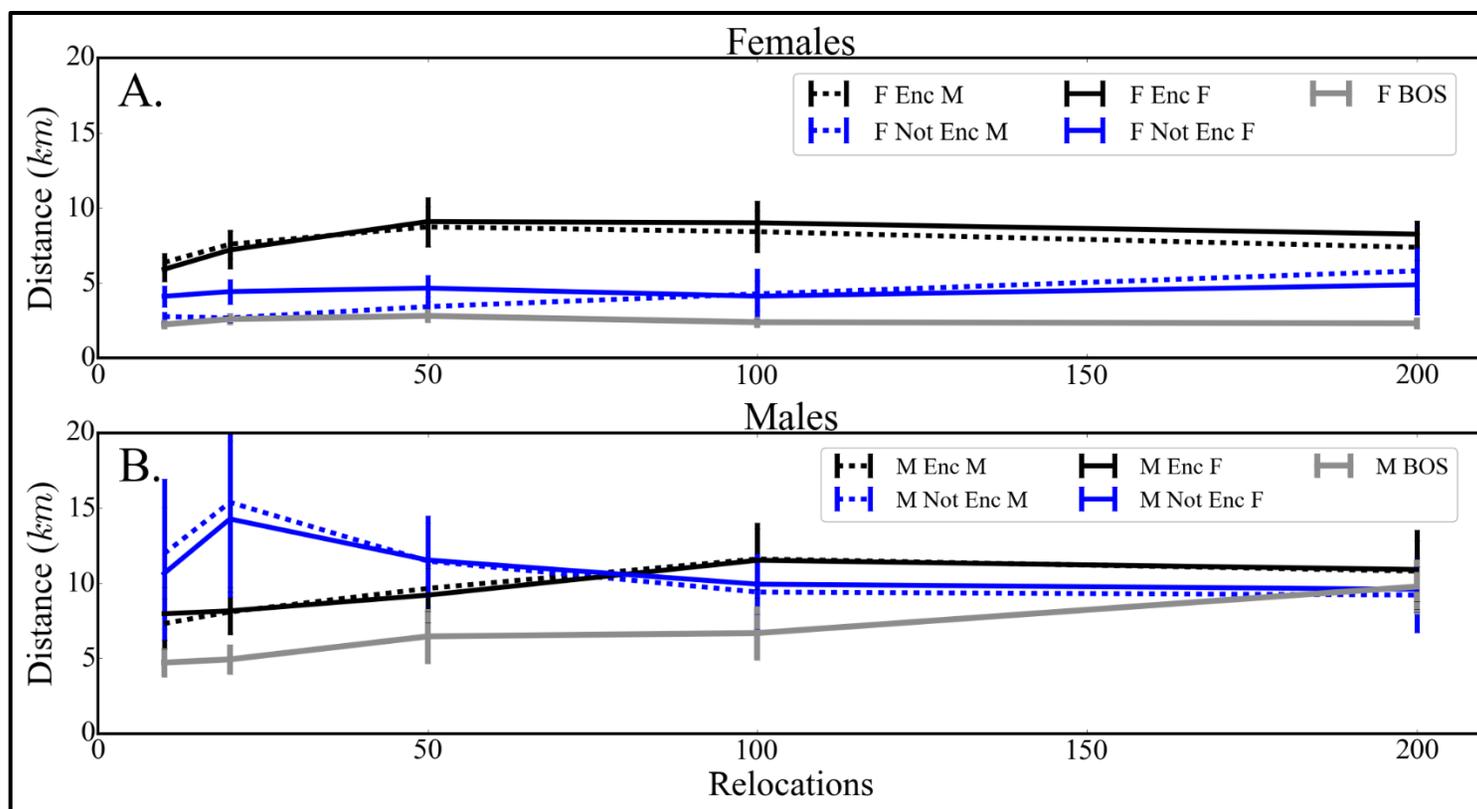


Figure 10. The mean distance traveled from the release point of reintroduced fishers in northern California from 2009 to 2012 showing differences among A). Females that encountered (Enc) or did not encounter (Not Enc) the home ranges of females (F) and males (M) compared to females born on the study site (F BOS) and B). Males that encountered (Enc) or did not encounter (Not Enc) the home ranges of females and males compared to males born on the study site (M BOS).

**APPENDIX**

## APPENDIX A – Habitat Selection by fishers

**Fisher Habitat Selection on Stirling management district from 2010-2014: A critical test of our understanding of fisher habitat needs**Aaron N. Facka<sup>a</sup>, Sean Matthews<sup>b</sup>, and Roger A. Powell<sup>a</sup><sup>a</sup>Department of Applied Ecology, North Carolina State University, Raleigh, NC 27612<sup>b</sup>Institute for Natural Resources, Oregon State University, Portland OR 97207**Executive Summary**

Understanding the habitat requirements and habitat selection of fishers (*Pekania pennanti*) on lands managed primarily for timber production is a key concern for their management and conservation throughout the western portion of their range. Several models of fisher habitat need have been developed, but most have never been tested with data independent of those used to construct those models. Independently testing habitat models provides an important way of assessing our basic understanding of the needs of fishers, both generally and specifically on managed landscapes. Fishers are generally associated with forests of high canopy closure and large mean diameter trees. Most fisher models incorporate measures of these two components, but there is wide variation in other attributes of models including environmental variables, such as precipitation and terrain, other vegetation-based attributes like canopy layers, stand types (e.g., hardwoods vs conifers), and relationships to human-caused disturbance (e.g., road density, edge density). We tested 12 models of fisher habitat quality to evaluate how well they predicted use of space by a population of fishers reintroduced to the Stirling district owned by Sierra Pacific Industries. We tested the models of Allen, Carroll (1999 & 2005), California Wildlife Habitat Relationships (CWHR), Davis (2007), SPI and a composite mean model. With the exception of the Davis models we used vegetation data from SPI's forest inventory to create annual habitat models. We evaluated these models across multiple scales of selection including across the landscape (Stirling and surrounding areas), within female home ranges, and within the short-term areas of

movement for 4 fishers with GPS collars. We found that the Allen model predicted the highest overall habitat quality, followed by the SPI habitat form model, the CWHR model, Carroll (1999), Carroll 2005, and the David models. Across all models, fishers avoided areas predicted to have low habitat quality. These areas are characterized by low (<20%) canopy closure, and trees with mean quadratic mean diameter at breast height (QMD) of 30 cm (11’’). Thus, there is strong support that fishers avoid areas with little over story tree component. Additionally, there was high agreement among models that fishers used areas of canopy closure >60% and QMD > 60cm (24’’). At moderate levels of habitat quality there was little agreement among models. An index of the Carroll 2005 (simple model) which included Terrain Ruggedness and canopy closure predicted fisher selection of habitat best with the highest correlation coefficients as well as the strongest indices of habitat avoidance at low values and selection at habitat values >0.50.

Nevertheless, we find that terrain ruggedness was correlated to other vegetative metrics including percent of a stand in hardwoods, tree diversity and logs per acre. Further, areas of high terrain ruggedness are areas likely most unaffected by management, and hence the terrain ruggedness index captured multiple aspects of habitat quality in one metric. That is, areas with high terrain ruggedness were also likely to have more tree diversity, hardwood trees, and less active management. We also find that the Allen model displays relatively high indices of avoidance and selection at the highest and lowest values; however, fishers consistently avoid areas within the predicted habitat quality range of 0.8-0.9. Further, we found that these areas, on average, have a low component of hardwoods within these stands though they have relatively large trees and overstory canopy closure. Thus, the Allen model seems to have been diagnostic to detecting areas that fishers avoided despite conforming to what might be considered high habitat quality without inclusion of hardwoods. Additionally, we found that fisher avoided values within the CWHR model that were similar to the Allen model. Further analysis revealed high overlap between the CWHR and Allen model at these ‘moderate’ habitat values that fishers avoided. Thus, suggesting fishers avoided similar places that were low in hardwoods. The SPI habitat form model, which relies on canopy, QMD and counts of trees over >22’’, accurately predicted fisher avoidance at low and high values and with indices of selection similar to other models. Fishes avoided all other areas classified by

the SPI model other than the top category (Habitat Form 4). Evaluation of the SPI territory opportunity model indicated that female fishers established home ranges in all 3 hexagon types proposed by SPI. Logistic regression analysis suggests that hexagon classified as support cores or territory cores are more to contain a female home range compared to hexagons classified as currently below threshold. Nevertheless, there is not statistical difference in the probability of a hexagon containing a home range, or more than one home range, based on the hexagon classification. Across all models we tested, the highest habitat quality are areas that have undergone little clear-cut logging within the last 50 years. Thus, areas of highest quality have commensurately high canopy and QMD, but also are correlated with components such as hardwoods and tree diversity not seen at lower classification levels. Thus, we urge additional work to evaluate the importance of hardwoods as well as other vegetative components such as tree diversity and understory diversity. Additionally, we find no statistical difference in habitat use and avoidance based on the sex of fishes or among the years we evaluated habitat use. Thus, we find no strong evidence that fishers we originally reintroduced used habitat differently than did fishers born on the study site in later years.

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## INTRODUCTION:

To understand how fishers (*Pekania pennanti*) respond to intensive forest management the California Department of Fish & Wildlife (DFW), the US Fish & Wildlife Service (FWS), Sierra Pacific Industries (SPI) and North Carolina State University (NCSSU) started collaborating in 2007 to re-establish a fisher population in the northern Sierra Nevada and southern Cascade Mountains of California. How fishers use and respond to habitat alteration, particularly alterations occurring because of industrial logging, is a central concern for fisher management ((USDI 2014). Thus, a major objective of our project is to evaluate models of habitat for fishers, those already existing and ones we develop. No less than 12 models of habitat have been developed, including those of Allen (1983), the California Wildlife Habitat Relationship model (Airola 1988), Carroll (1999, 2005), Davis et al. (2007), Zielinski et al. (2010), and a model developed by Sierra Pacific Industries for its Candidate Conservation Agreement with Assurance with the FWS. We view the applicability, or generality, of models to predict use of space by fishers in multiple and novel areas as most important. Unfortunately, none but the Allen model have been tested with independent data or at locations aside from those where the models were developed and, thus, their abilities to predict fisher use of habitat generally is unknown. Since the Allen model has been validated at 2 independent locations (Thomasma et al. 1991, Powell & Zielinski 1994a, Thomasma et al. 1994b, Powell 2004), it represents an important model to test and refine first, as a baseline. Therefore, we present here an examination of the use of habitat by fishers and in particular we evaluate several habitat models using data from the Stirling reintroduction and location data for fishers for 2009-2014.

Allen (1983) developed the first quantitative model of fisher habitat from the literature and from expert knowledge and indexed how use of space by fishers varied with 4 variables tied to fishers' resources: number of canopy layers, canopy closure, overstory tree diameter at breast height, and the ratio of deciduous to conifer trees in the canopy (Figure Allen). Despite its simplicity, this model has been tested 3 times in 2 vastly different forest ecosystems (the Laurentian forests of the northern Great Lakes region and the mixed conifer-hardwood forests of the northern Sierra Nevada of California) and shown to predict use of space by fishers (Powell 2004, Thomasma 1991, 1994). Over the decades, models of fisher habitat have employed ever more sophisticated multivariate statistical algorithms to produce maps of fisher probability of occurrence or use of space. Recent models have used diverse, GIS-based environmental variables, including traditional land cover data, climate variables, and remotely sensed variables, along with fisher location data to map use of space by fishers (Scheller et al. 2011, Zielinski et al. 2012) across spatial scales. Nevertheless, most models of fisher habitat include identical or very similar metrics to the Allen model. In particular, canopy cover, tree size and hardwood/conifer components are common among many models (see Table 1).

In general, field observations and habitat models agree that fishers are associated with forests with high overhead canopy and large trees (Powell 1993, Powell & Zielinski 1994b, Carroll et al. 1999, Sauder & Rachlow 2015). Hardwood and deciduous tree components, though commonly considered in the literature, have variable and inconsistent effects on predicted fisher habitat quality. Snow-tracking of fishers suggested that, though fishers travel through deciduous stands, they concentrate their

foraging within isolated pockets of conifers with complex structure within forest stands that are otherwise largely deciduous (Powell 1978, McCann et al. 2014). Thus, Allen viewed an abundance, or prevalence, of deciduous trees as a negative effect on overall habitat quality, but viewed few or even no deciduous trees as having only marginal negative influence on habitat quality. In contrast, Thomasma (1994) suggested that stands with no deciduous component have low overall habitat value. Often studies using telemetry and available raster GIS databases have mistakenly concluded that fishers used deciduous stands extensively (Gilbert et al. 1997) but may be stands that they actually avoid (McCann et al. 2014, Powell 1994a).

Habitat models can be too specific, reducing their generality. Some habitat models for fishers developed for northern California emphasize terrain ruggedness (Carroll 2005, Davis et al. 2007) because fisher locations were correlated with steep terrain. Yet, such correlations may be spurious or may reflect other processes. For example, steep terrain may simply hinder logging or road building and thus provide for forests with few disturbances. Fishers exist elsewhere in California and east of the Rocky Mountains where steep terrain does not exist. Hence, terrain is unlikely a limiting factor of itself.

Testing models with independent data has provided feedback and new insight into why habitat characteristics are important to fishers (Powell 2004, Thomasma et al. 1991, 1994). Research on fishers has also shown where caution is needed with habitat modelling (Gilbert et al. submitted, McCann et al. 2014, Zielinski et al. 2010). Habitat models are being developed from the bottom up (e.g., Mitchell & Powell 2003), starting with fishers' requirements, establishing how the conditions for requirements can be represented by environmental variables in such a way as to be applicable throughout the fisher's range. Testing such a model will show how well we understand how and why habitats meet fishers' requirements.

Information on the locations, home ranges, and habitat selection of fishers on a managed landscape are particularly relevant to development of a Candidate Conservation Agreement with Assurances (CCAA) between the USFWS and SPI. Recent discussion between the USFWS Yreka Field Office staff and the research team at NCSU have identified several key information gaps relative to habitat selection and habitat avoidance of fishers on managed forests. Thus, the research team at NCSU is in a singular position to evaluate fisher habitat associations and their needs on managed landscapes.

Here we perform analyses aimed at evaluating and predicting habitat quality for fishers using several existing habitat models. We will test the appropriateness of each of these models by evaluating what fishers have selected since their initial release in 2009 through 2014. Further, we will quantify which, if any, habitat model is appropriate for describing fisher habitat and rank them in terms of their abilities compared to one another.

#### Tested Models

A wide variety of fisher habitat models have been proposed and constructed with various statistical methods and techniques. Some habitat models address specific requirements or life-history needs for fishers such as denning or resting habitat (Zielinski et al. 2012, Niblett et al. 2014). Other models aim to describe and predict the likelihood of occurrence of fishers over specific landscapes (Airola 1988, Carroll et al. 1999, Carroll 2005, Davis et al. 2007, Zielinski et al. 2010, Sauder & Rachlow 2014, 2015). Fewer fisher habitat models have been developed, and tested, that are general to all aspects of

fishers habitat associations throughout their range (e.g., Allen 1983, Thomasma et al. 1991, Thomasma et al. 1994a). For our analyses and tests we did not include, or test, models that were specific to habitat, denning or other specific fisher needs or to other life-history traits or events. We chose to focus on models that had explicit or implicit goal of creating an integrated (or complete) representation of fisher habitat quality.

Additionally, we chose models that were both specific to Stirling and California as well as any that were spatially and temporally general (Table 1). We built models put forth by Allen (1983), Carroll et al (1999) and amended in 2005, the most recent California Wildlife Habitat Relationships model (CWHR; Airola 1988), and habitat relationship models proposed by Sierra Pacific Industries (Ed Murphy personal communication). For these aforementioned models we used SPI forest inventory data in all years from 2010 to 2015 to construct annual habitat models for the Stirling tract. Additionally, we used the Gradient Nearest Neighbor (GNN) data sets downloadable at (<http://lemma.forestry.oregonstate.edu/data>)(Ohmann et al. 2011), to construct some, but not all, models from a different data set for testing and evaluation. The GNN data set is fundamentally different than stand-level inventory data provided by SPI. The GNN data is pixel-based (30 × 30m) and compiled from various sources. Additionally, these data are not temporally consistent since the field data that are used to construct it are available from different sources and potentially collected at disparate times.

#### MODEL CONSTRUCTION AND DATA

##### Allen HSI

The Allen model is relatively simple and is based on 4 vegetative metrics: 1) percent tree canopy closure, 2) quadratic mean diameter at breast height (QDBH) of overstory trees, 3) tree canopy diversity (*i.e.*, number of canopy layers), and 4) percent of overstory trees that are hardwoods. Allen's original conception was to use the percentage of deciduous trees (Figure Allen; Allen 1983). Nevertheless, we included all hardwood trees in our models because Allen's original models considered deciduous trees as important components for denning habitat. Therefore, we assumed that all hardwood trees provide increased opportunities for denning habitat (among other possible ways they can contribute to habitat quality). The canopy layer component of this model is somewhat nebulous based on what is considered important to fishers as well as the needed data to quantify this metric. Layering could potentially include only vertical layers that are off the ground and in this conception stands with shrub (or sapling), mid-aged, and dominant canopies could be considered to have high values for fishers. Additionally, layering could be important for foraging and could include structure (layers) that occur on the ground including logs, rocks and low hanging tree limbs. In our development of the Allen model with SPI-based data we chose to parameterize the layer component with data based on the overall area covered by dominant, codominant, intermediate and suppressed trees. For all 4 components of Allen's model we used mean stand-level forest inventory data from SPI, we were able to approximate the 4 components of Allen's model and created an overall habitat suitability index (HSI) for Stirling for 2010 to 2015 (equation 1). The Allen model constructed with SPI-based data is explicit to land within the Stirling boundary (Figure AllenSPI).

Eq. 1:

$$\text{Allen HSI} = (\text{Canopy Closure} + \text{QMD} + \text{Canopy Layer})^{\frac{1}{3}} \times \text{Percent Hardwood}$$

In addition to developing the Allen model with SPI-based inventory data we also constructed a model with GNN/Lemma data. We used 4 variables found with the GNN dataset to parameterize the Allen model: quadratic mean diameter of all dominant and codominant trees (QMD\_DOM), canopy cover (CANCOV), number of canopy layers (CANCOV\_LAYERS), and proportion of hardwood basal area (BAH\_PROP). These layers were classified and implemented in the Allen HSI exactly as was the model using SPI-inventory data. Because the GNN data set covers Stirling and the surrounding area it was implemented for the entire region around Stirling as well as Stirling proper (Figure AllenRegion).

Carroll 1999 – adjusted

The Carroll (1999) habitat model is a logistic regression model based on the probability of detecting fishers at a location. Similar to Allen, the Carroll model uses measures of canopy closure and quadratic mean diameter of trees (Table 1). Additionally, the Carroll model uses the percent of conifers (Per\_Conifer) within a stand, mean annual precipitation (AnnPrecip), the north-south position of locations (UTM\_N) and north-south position raised to the second power (UTM\_N<sup>2</sup>). The equation also includes two interaction terms between canopy and percent conifer as well as QMD and annual precipitation. Data concerning tree size, canopy closure and percent conifer was taken from SPI-inventory data and UTM position was extracted from ArcGIS 10.3. Mean annual precipitation data from 1999 to 2010 were taken from the ClimateWNA website at <http://climatemodels.forestry.ubc.ca/climatebc/downloads/libraryfiles.zip> (Wang et al. 2012). These data are on 1-km<sup>2</sup> resolution that covers the entire study area and surrounding areas. These variables were used with the beta-parameter estimates found in Carroll (1999; equation 2).

Eq.2

$$\text{Carroll} = (1/(1+\exp(-(-2401+(0.6023 \times \text{canopy}) + (-12.07 \times \text{QMD}) + (0.4911 \times \text{Per\_Conifer}) + (-0.01307 \times \text{AnnPrecip}) + (0.001059 \times \text{UTM\_N}) + (-0.0000000001176 \times \text{UTM\_N}^2) + (-0.006251 \times (\text{canopy} \times \text{Per\_Conifer})) + (0.005004 \times (\text{QMD} \times \text{AnnPrecip}))))$$

In Carroll's original model the vegetative parameters were averaged across a 10-km<sup>2</sup> moving window (Carroll 1999). We did not average vegetative parameters because we were interested in fisher use at the scale of individual locations and home ranges; whereas, the scale of the original paper was across the state of California. Our first implementation of the Carroll model provided results that were contrary to our understanding of the original model's overall pattern. Areas that should have low habitat values (e.g., recently logged areas with 0 canopy closure and QMD) were estimated with values approaching 1 (Fig. CarrollA). The misrepresentation of habitat quality at these low canopy and QMD values was likely an aberration that never occurred in the original model because those values would likely never have appeared in the averaged landscapes. Thus, we corrected this model by replacing all cells with habitat quality > 0.90 and that had canopy values < 0.10 to have habitat quality = 0. This adjustment produced results that were visually consistent with our interpretation of the original model (Figure Carroll B). We constructed the Carroll model with this adjustment for all year from 2010 to 2015 on Stirling. Nevertheless, we recognize that the model we produced is fundamentally different from that of Carroll 1999, but incorporates the same

variables and patterns of habitat quality. We did not construct the Carroll model based on GNN data.

#### Carroll index

Carroll (2005) revisited the analysis from the 1999 paper and amended it with new data that generated new beta-parameters estimates. Additionally, Carroll constructed additional logistic regression models. We attempted to implement these models, but could not because the Carroll 2005 report lacked all parameters (the y-intercepts) from all models. Preliminarily, we constructed these models with specific assumptions about the y-intercepts but could never find a solution that was satisfying. Nevertheless, Carroll created and reported a model (model 3; Carroll 2005) that included only 2 parameters: Terrain Ruggedness Index (TRI; Riley 1999) and canopy cover. Though we could not find a satisfactory solution based on the beta-parameters for this model we created an index that incorporated both parameters. We calculated TRI within ArcGIS 10.2 using a  $30 \times 30$  m digital elevation model (DEM) following the methods of Riley (1999; the same method as Carroll 2005). This resultant raster produced values between 0 and 160 with the highest values being the most rugged locations. We then scaled the TRI raster to values between 0 and 1 by dividing each cell by 160. We then calculated a mean value between the canopy raster and the TRI raster. Because the beta parameters for both TRI ( $\beta = 0.0226603$ ) and canopy ( $\beta = 0.0456$ ) were positive (Carroll 2005), the resultant value simply quantifies areas that have high, or low, values for both canopy and TRI and thus indexing the model results. We calculated this index using SPI-inventory data from 2010 to 2014 for Stirling. Additionally, we constructed this index for the entire area on and around Stirling using GNN data for canopy in addition to the TRI values for the same area.

#### SPI habitat classification

These analyses were performed based on the classification (hereafter “habitat model” or “model”) of forest types provided by Sierra Pacific Industries through a series of white papers and in conversations with Ed Murphy. The model, as constructed for use in this analysis, is comprised of three variables: Overhead canopy closure, quadratic mean diameter at breast height (QMD [reported in inches]), and the number of trees per acre over 22 inches (TPA).

Sierra Pacific Industries uses canopy closure, QMD, and TPA to classify their forests in 4 categories: Habitat Form 1 (HF1), Habitat Form 2 (HF2), Habitat Form 3 (HF3), and Habitat Form 4 (HF4). Additionally, SPI creates a sub classification of forests in the HF2 class known as Habitat Form 2 heavy (HF2hv). These classifications are briefly described below with the exception of HF3 which has very limited distribution on Stirling and is therefore not considered further (Ed Murphy personal communication). For the purposes of this report we use those classifications as a discrete variable with a predicted hierarchy of importance to fishers. The forest classification we assume is least important, or most avoided, by fishers is HF1. It is defined as all other forest types not defined by the 3 remaining classifications. The next classification, Habitat Form 2 (HF2), is defined by forests with canopy cover greater than 40% and  $QMD \geq 6''$ . A subset of HF2 is Habitat Form 2 heavy (HF2hv) which are forest stands with canopy closure greater than 50% and  $QMD \geq 11''$ . The final classification level, and the one considered most appropriate for fishers, is Habitat Form 4, which is defined by forests with canopy closure greater than 60% and QMD greater than 13''. For the purposes of analysis we arbitrarily assigned the

habitat form categories the values of HF1 = 0, HF2 = 0.50, HF2hv = 0.75, and HF4 = 1.0. The classification described above where implemented in ArcGIS with the following raster algebra implementation:

Eq. 2.

$$\text{SPI HabitatForm} = \text{Con}(\text{canopy} \geq 60) \ \& \ (\text{QMD} \geq 13) \ \& \ ((\text{TPA}_{22}) \geq 9), 1, \\ \text{Con}(\text{canopy} \geq 50) \ \& \ (\text{QMD} \geq 11), 0.75, \text{Con}(\text{canopy} \geq 40) \ \& \ (\text{QMD} \geq 6), 0.50, \\ \text{Con}(\text{canopy} < 40) \ | \ (\text{QMD} < 6), 0))))$$

Where “Con” is a conditional function requiring the stated arguments (conditions) to be met to include in the classification. The “canopy” and “QMD” arguments are generic arguments that are substituted with canopy cover and mean QMD rasters for each specific year. We used forest inventory data provided by Sierra Pacific Industries for each year to construct spatial representations of their forest classification system on Stirling. We used these data to create a separate model for forest classification in each calendar year from 2010 to 2014. We did not create the SPI habitat form classification model using GNN data or other sources beyond SPI inventory data.

CWHR

The California Wildlife Habitat Relationships (CWHR) models exist for most animal species occurring in California. The CWHR model for fishers are based on the dominant woody vegetative types (e.g., Ponderosa pine, Sierran Mixed Conifer) as well as classification of canopy closure and average tree size (Airola 1988; Figure CWHR). Canopy closure is classified into 5 bins: none (0-10% canopy), sparse (10-24% canopy), open (25-39% canopy), moderate (40-59% canopy) and dense (>60%). We arbitrarily gave these bins the index values 0,1,2,3, and 4. Tree size (QMD) is classified into 6 bins: 1) seedling (<1” QMD), 2) Sapling (1”-6” QMD), 3) Pole (6”-11” QMD), 4) Small (11”-24” QMD), 5) Medium/large tree (>24”), and 6) Multi-layered trees which are stands with class 5 trees over a layer of 4 or 3 trees. We gave these classification bins the value 10,20,30,40, and 50, and 60. The classified values for canopy and tree size were added together to produce a raster (code10) with discrete values ranging from 0 to 65. We did not to include stands classified as 60 (or multi-layered trees), because preliminary analysis demonstrated fewer than 2 km<sup>2</sup> across Stirling that could be potentially be classified (mean tree QMD > 24”) in this category. The values from the ‘code10’ raster were assigned a habitat classification value with equation 4 (Figure CWHR).

Eq. 4:

CWHR Habitat Quality =

$$\text{Con}(\text{code10} \leq 31, 0, \text{Con}(\text{code10} == 32) \ | \ (\text{code10} == 33) \ | \ (\text{code10} == 41) \ | \\ (\text{code10} == 51), 0.11, \text{Con}(\text{code10} == 34) \ | \ (\text{code10} == 51), 0.22, \text{Con}(\text{code10} \\ == 42) \ | \ (\text{code10} == 52), 0.33, \text{Con}(\text{code10} == 43), 0.66, \text{Con}(\text{code10} == \\ 44), 0.89, \text{Con}(\text{code10} == 53), 0.77, \text{Con}(\text{code10} \geq 54), 1.0))))))$$

We used SPI-inventory data to classify canopy and tree size according to those rules. Habitat quality within the majority of tree stand types is identical with the highest habitat values occurring at the highest classification of both canopy and tree size (Figure CWHR). We constructed our final habitat model to follow these rules exactly as in the CWHR model with the exception of stands classified as Ponderosa pine dominated. The only differences between other stand types and Ponderosa pine stands occur in low

quality stands (low canopy and tree class). Thus, we assigned habitat quality values to Ponderosa pine stands the same as implemented for all other stand types (equation 4, Figure CWHR).

#### Mean values

We recognized that most of the models in our tests have some variables in common (e.g., canopy and tree size). Generally, there is agreement among those models about how canopy and tree size affect fisher habitat quality (positively). Nonetheless, the final predictions about habitat quality among habitat models are variable. We hypothesized that fisher use of habitat might be well predicted by identifying areas of agreement among models. Thus, we calculated the arithmetic mean habitat quality produced from the Allen, Carroll (1999), Carroll 2005 (index), CWHR, and SPI values. We considered this a 6<sup>th</sup> model that we chose to include in our analysis. We used only models constructed using SPI-inventory data to calculate this mean value. Additionally, because we constructed annual versions of each of the models used we likewise constructed a mean model for each year across Stirling. We also calculated the standard deviation among the models to evaluate areas, or components of habitat quality, that were consistent among models and those that were different.

#### Davis

We included the original 6 habitat models from Davis et al. (2007). The Davis models were directly downloaded from <ftp://ftp.biogeog.ucsb.edu/pub/org/biogeog/users/fd/fisher/> and were used as originally constructed by Davis et al. The Davis models were not constructed using either SPI or GNN datasets. Rather, they are the exact models produced by Davis et al. and based on the vegetation, terrain, and environmental data available during their original analysis. Clearly, these models are flawed with respect to predicting current habitat quality because of changes that occurred since their analysis. Changes within stands of trees and forests, including logging and wildfires, that occurred since 2006 are most obvious and important for the scope of our analysis. Additionally, the vegetation data used to construct these models are unlikely as accurate as those produced by SPI's forest inventory data. Nevertheless, the Davis models do incorporate data that would have been consistent across the region of our study area and thus provides insight into how well those models predict habitat quality at a landscape scale. We did not attempt to reconstruct these models, as well as other models that used Generalized Additive Modelling (GAM) (e.g., Zielinski et al. 2010) because those models were not published with parameters that could be used to construct models with new data and new places (J. Dunk and B. Zielinski, personal communication).

#### Methods and Analysis

##### Analysis: Fisher Use and Resource Selection Functions

##### Individual Locations Analysis

We used locations of both female and male fishers from 2009 through 2014. Because we constructed habitat models for both area bounded by the Stirling boundary (hereafter Stirling) as well as the area on and around Stirling (hereafter 'area') we also used data from fisher locations at two different scales. For habitat models on Stirling we used fisher locations that occurred only on Stirling as well (10,011 total). This data set included a total of 4025 locations for females from estimated triangulations, walkins, flights, and captures. For males we used 5986 locations deriving from Argos locations of classes 1, 2,

and 3, Global Positions Systems (GPS) collars, capture, and walkins. We generated 10,011 random points distributed throughout Stirling to estimate the proportion of habitat occurring on Stirling. We calculated the habitat quality of all locations for each habitat model and for the calendar year that the location occurred (Figure LocYear). Similarly, the habitat value for each model was calculated for all random points by year. Thus, allowing direct comparison of the habitat fishers used and that was available in each specific year. We quantified the proportion of both used and available habitat occurring within 0.10 bins for all models. We used the proportion of used and available habitat to calculate a resource selection function (RSF) based on the Ivlev electivity index (equation 5) and modified Ivlev electivity index (equation 6; Manly et al. 2007).

Equation 5:

$$Ivlev\ electivity\ index = \frac{proportion\ used - proportion\ available}{proportion\ used + proportion\ available}$$

Equation 6:

$$modified\ Ivlev = \frac{2 \times (proportion\ used - proportion\ available)}{1 + (proportion\ used + proportion\ available)}$$

We calculated the mean values for both the Ivlev and modified Ivlev across years, for each model, to generate a mean resource selection function. Habitat models that capture important aspects of what fishers are selecting should have a positive relationship between the predicted habitat quality values and the selection index of used vs available habitat. Thus, we used ordinary least squares linear regression in the statsmodels package for Python to evaluate the relationship between predicted habitat quality and the resource selection functions. We performed separate analyses for males and female as well as for all locations combined.

In our analysis we also constructed models for the region including Stirling and the surrounding area. Because SPI-inventory data is only available for Stirling but fisher selection occurred both on and off Stirling we needed data sets that were comparable. For these analyses we used all locations collected from males and females on both Stirling and off. In total, we used 12,591 points from fishers for this analysis to calculate locations and habitats that fishers used. To represent available habitat in the study area we calculated a Minimum Convex Polygon (MCP) in the minimum bounding geometry tool within ArcGIS 10.2 around all locations (see Figure AllenGNN). Within this MCP we generated 12,591 random points and the calculated the habitat value for each of those points based on the Allen (GNN data type), Davis (all six models), and Carroll Index models. We then calculated both the Ivlev and modified-Ivlev resource selection functions (eq 5 & 6) and used regression to evaluate the relationship of predicted habitat quality to fisher use and avoidance for each model tested.

#### Female Utilization Distribution Analysis

Analysis of individual locations provides one measure of fisher use and avoidance of habitat. More specifically, analyses that focus on all points as equal, compared to the entire landscape, provide insight into where fishers settled after reintroduction and which habitat model describes these general patterns best. Nevertheless, fishers, and all animals, select home ranges because they provide important resources for their lives. In particular, female fisher habitat use is important to understand because they may have the most

restrictive habitat requirements (e.g., appropriate dens and foraging requirements during reproduction). Thus, analysis of where female fishers establish home ranges, and their associated habitat quality, as well as the specific locations used within those home ranges provides a level of precision that goes beyond our more broad analyses. To evaluate home range habitat selection we created utilization distributions for female fishers using Kernel Density Estimation (KDE) approaches. We used a fixed kernel approach with a bandwidth of 750 m to smooth female locations during each calendar year from 2010 to 2014. We did not estimate a utilization distribution for a female if she had fewer than 20 locations for a single year. We categorized each utilization distribution by isopleths that bounded 25%, 50%, 75%, 90%, and 95% of the cumulative probability of occurrence. The smaller isopleths hypothetically represent areas of highest use, and ostensibly importance, for females. Larger isopleths are likely to envelope points on the periphery of a home range and should have the weakest level of habitat selection. To estimate the proportion of available habitat we extracted the habitat value at each cell within the estimated utilization distribution of a female (by year). We then calculated the resource selection functions (eq 5 & 6) for each female by year and isopleth. We calculated a mean yearly mean RSF (both Ivlev and modified Ivlev) across females and regressed this value on predicted habitat quality. We next calculated a mean RSF values across years but by isopleth. Finally, we calculated a mean RSF score across isopleth. Analyses for the utilization distributions of females focused on the habitat models exclusively on Stirling and built with SPI-inventory data.

#### GPS Data Analysis

Most fisher locations used in previous analyses come from either Argos (male) or VHF telemetry (Powell et al. 2014, Facka et al, in preparation). Both these types of location data give accurate though relatively imprecise locations for fishers (>200 m error). Additionally, both these types of locations usually provide a maximum of 1 or 2 locations per day. As such, examining fine-scale spatial use or habitat use over fine scales is difficult. In 2012, 2013, and in the fall of 2015 we have opportunistically placed GPS collars on 2males and 2 females. These collars have been programed to record data at short intervals (<10 minute), but over a short total duration (<10 days) and on average provide relatively high precision for location estimates. Thus, we performed habitat selection analyses using GPS by itself for these four individuals. The GPS location data for both male (2012 & 2013) are included in our other location data; however, these data for females became available only in the fall of 2015.

We visually examined the GPS data from all four fishers and eliminated all data points that were obvious errors. For example, locations that was aberrantly distant from all other locations but within a similar time window was eliminated. As with our other analyses we then calculated the habitat value across for the Allen, Carroll (1999), Carrol index, SPI model, and the mean habitat models. We then quantified the proportion of points that fell within specified 0.1 habitat quality bins. To quantify the proportion of random points we created a minimum convex polygon around all points for each individual fishers GPS locations. We then generated a number of random points within the MCP equal to the total points collected by the GPS collar for those fishers. We then used these proportions to calculate the Ivlev and modified Ivlev RSF and used regression to evaluate the general relationship between predicated habitat quality and habitat selection.

### SPI Territory Opportunity

A proposed component of SPI's habitat designation and planning is the identification of "Territory Opportunities" for fishers. Territory Opportunities rely on the classification of forests into habitat forms, as described above, and then to classify hexagons on the landscape. Hexagons are classified into one of three categories: 1) A territory core (TC; hexagons with the highest habitat value for fishers), 2) A support core (SC: moderate habitat value), and 3) hexagons currently below threshold (CBT; hexagons with little or no value to fishers). The three categories are delineated by quantifying the amount and proportion of each hexagon and then identifying whether the hexagon meets the following three conditions:

1. Hexagon  $\geq 30\%$  HF4
2. Hexagon  $\geq 50\%$  HF4 and/or HF2H
3. At least one contiguous 30 ac. stand of HF4, which is also contiguous to at least an additional 20 ac. of HF2Hv (HF4 + HF2Hv  $\geq 50$  ac)

Hexagons that meet all three criteria are considered Territory cores whereas hexagons that only meet conditions 1 and 2, 2 and 3, or 3 are classified as support cores. Hexagons that do not meet the criteria for a territory core or support core are classified as currently below threshold (CBT).

To evaluate this approach we constructed a series of hexagons on and around Stirling that were 1.95 km<sup>2</sup> (481.5 acres). We then quantified the proportion and amount of HF1, HF2, HF2Hv, and HF 4 within each of those hexagons and used Zonal Statistics tools in the Spatial Analyst toolbox in ArcGIS 10.3. Each hexagon was then classified as a territory core (index value 2), support core (index value 1) or CBT (index value 0) for each year from 2010 to 2014.

Initially, we simply described the basic composition of female home ranges by hexagon value (type). We overlaid the utilization distributions of female fishers with the territory opportunity values for each hexagon. For each utilization distribution we calculated the proportion and value for each hexagon. We calculated the mean values across years and female utilization distribution. We calculated the types of hexagons that comprised female home ranges by examining the variety (range) of hexagons used and which type were most common.

The purpose of the territory opportunity method is to identify areas (hexagons) that can support fisher home ranges. Thus, we used two different, but similar analytic techniques to evaluate if a hexagon's classification was related to the likelihood that a hexagon contained a female's home range and number of female home ranges. We used logistic regression to determine if a hexagon's territory opportunity classification increased the likelihood that the hexagon intersected at least one female home range. Additionally, we used polytomous logistic regression to evaluate if a hexagon's territory opportunity classification increased the likelihood of a hexagon intersecting 1, 2, 3, or  $\geq 4$  female home ranges. For both analyses we used the portion of a utilization distribution that bounded 50% of the total probability distribution. The 50% isopleth is conservative in eliminating areas that are less often utilized and thus stresses areas that are ostensibly more important to females. Additionally, the 50% isopleth minimized intersections among multiple females within a specific hexagon that were attributable to short-term forays or that occurred after major events (e.g., the death of a female). For both the logistic and polytomous logistic regression we also evaluated how differences among

years, and geographic position may have influenced the probability of encountering a home range within a hexagon. Both forms of logistic regression rely on comparison between positive events (a home range within a hexagon) and negative events. Thus, in all years we randomly selected an equal number of hexagons that did not have a female home range to those that did. We performed logistic and polytomous logistic regression in Statistical Applications Software (SAS; Cary, NC) using Proc Logistic.

## RESULTS AND DISCUSSION

### Allen

#### Stirling locations

For locations occurring only on Stirling, the Allen model consistently predicted the highest amount of high quality habitat across Stirling. Mean available habitat quality on Stirling across all years was  $0.71 \pm 0.38$  SD. Mean habitat quality decreased from  $0.71 \pm 0.38$  in 2010 to  $0.70 \pm 0.39$  in 2014. The distribution of habitat quality was similar among years with the approximately 50% of Stirling occurring at the highest habitat quality values (Figure AllenRandom). Habitat quality values below 0.2 comprised  $>0.15$  percent of Stirling in all years with a slight increase from 2010 to 2014. Habitat quality values from 0.2 to 0.8 were a relatively small proportion of the landscape.

The average habitat quality of fisher locations was  $0.83 \pm 0.31$ . Mean habitat quality used by fishers was constant and showed no strong patterns in change from 2010 to 2014 (range = 0.82 – 0.83; Figure AllenSPI). The relationships between predicted habitat quality and both the Ivlev and modified Ivlev resource selection function were not statistically different from 0 with an  $R^2$  value of 0.06 (Table 3; Figure AllenRSFalla). Nevertheless, the beta-estimate for this relationship was positive ( $\beta = 0.14$ ) and both the Ivlev and modified-Ivlev RSFs indicate fishers avoided habitat quantified at low ( $<0.20$ ), but selected habitat values greater than 0.90 (Figure AllenRSFalla). Habitat values from 0.80 – 0.90 were most obviously deviant from the predicted relationship. Fishers used areas quantified in the 0.80 – 0.90 far less than would be predicted by the amount of those habitats available indicating avoidance of those areas despite having relatively high predicted values according to the Allen model.

Female and male fishers appear to have used habitat similarly based on the Allen model. Mean used habitat for females ( $0.82 \pm 0.31$ ) and males ( $0.83 \pm 0.30$ ) was nearly identical across all years. Mean female habitat use was similar from across years with the minimum value occurring in 2012 (0.74), but in all other years this value ranged from 0.82-0.88 with no obvious trend through time indicating that fishers used habitat markedly different among years. Mean male habitat use was also relatively consistent from 2010 to 2014 (range = 0.75 – 0.88). Generally, male mean habitat use was slightly lower than females, but within the 95% confidence intervals. The mean Ivlev and modified Ivlev resource selection functions showed similar patterns among females and males (Table 3). Both demonstrated positive relationships between predicted habitat quality and patterns of usage, but neither were significantly different from zero. As with the more general analysis, female and males both avoid habitat that is quantified below 0.1 and select habitat over 0.90. Additionally, both females and males show a pattern of avoidance for habitat values from 0.80 – 0.90 (Figure Allensex).

#### Area locations

The Allen model, constructed using GNN data for the area on and around Stirling, had a mean available habitat value of  $0.54 \pm 0.39$  (Figure AllenGNN). The highest

predicted habitats with GNN data were within the 0.8 – 0.90 value bins (36%). Habitat values less than 0.1 represented 27% of the total area whereas habitat with the highest values (0.9 – 1.0) comprised 21% of the area sampled. Moderate values of available habitat quality (0.1 to 0.79) totaled 17% of the total area (Figure AllenGNN). High quality habitat was distributed throughout much of Stirling as well as areas with similar elevation to Stirling. Low habitat quality was associated with elevations below Stirling. Fishers selected higher quality habitat ( $0.78 \pm 0.29$ ) on average than was available. Fishers also appeared to avoid areas with low predicted habitat quality and selected for the highest quality habitat (Figure AllenGNNb). At moderate values of habitat quality fishers seems indifferent and used habitat in approximately the same proportion as was available on the landscape. Similar to the Allen model with SPI-inventory data, fishers used areas in the 0.8 – 0.9 habitat quality bin less than would be expected (Figure AllenGNNb). The relationship between predicted habitat quality and both the Ivlev and modified-Ivlev RSF were significantly different from zero ( $\beta = 0.35$ ; Table 3). The results between the GNN and SPI-based models were similar in pattern but different with respect to how well predicted habitat quality related to either resource selection functions. Obviously, the models were produced using different vegetation information and different scales (stand vs cell based). Thus, differences between using  $30 \times 30$  m pixels compared to entire stands may be important to the observed differences. Additionally, the GNN-based model sampled a wider area than just Stirling and resulted in different proportion of available habitat. The estimated differences in available habitat likely reflected a strong signal of habitat avoidance at very low habitat quality (e.g., more negative RSF scores). Differences between the estimation of vegetative components of the habitat model (e.g., percent hardwoods) may also explain differences between the model results. Importantly, the pattern of avoidance of the 0.8 – 0.9 habitat quality is apparent across all analyses (model types, years, sex) and suggested an actual avoidance by fishers rather than a statistical anomaly or error in the way the models were constructed.

#### Female Home Ranges

The available habitat within female home ranges as quantified by the Allen model was similar to that observed for the entire study area (Fig. Allenrandom). Across all years the highest amounts of habitat (range = 0.56 – 0.67) were found in the highest habitat quality bins (0.9-1.0). Female home ranges incorporated the lowest habitat quality within their home ranges in low proportions compared to the highest (range across years = 0.10 to 0.13). The proportions of other habitat quality were also low compared to the highest habitat quality with values from 0.80 – 0.90 relatively common within female home ranges (range = 0.08 – 0.12).

The mean habitat value selected by females within their home ranges was  $0.82 \pm 0.31$ . The mean habitat quality selected by females across years was nearly identical to the values from all female locations (range = 0.73 – 0.89) with no obvious trend through time. The relationship between female selection (resource selection functions) and predicted habitat quality was similar, though variable, across years (Figure AllenHRbyyear A). For the Allen model a consistent pattern emerged at every level of analysis – female, year, isopleth, and mean values (Table HRresults; Figure AllenHRbyYear). The pattern mirrors the pattern seen for other analyses with the Allen model – avoidance at low levels of habitat quality with relatively strong selection at the

highest levels of habitat quality (Figure AllenHRbyYear). As with our previous analyses there was a strong avoidance in the range of habitat values from 0.8 to 0.9. This deviation appears to be the main reason that the Allen model predicted habitat quality does a poor job in explaining patterns of selection (Table HRresults). In fact, the RSF scores for this relatively high habitat quality are often more strongly avoided than locations with the lowest habitat quality. At moderate habitat quality values (0.2 – 0.79) fishers show neither strong avoidance nor selection. Rather, fishers appear indifferent to these areas or perhaps use them only within the context of other high quality habitats. Because none of the models we tested is spatially explicit by taking into account distance between patches of different habitat quality we cannot dismiss that some areas are used simply because they are close to patches of high quality habitat.

### GPS

The proportion of available habitat within the convex polygons of fishers with GPS collars was high variable (Figure GPSallen). Few fishers (n=4) were included in the GPS analysis and they occurred over different areas of the district. Thus some fishers had high proportions of high quality habitat (Figure GPSallen A) whereas other fishers higher proportions of moderate or moderately high habitat quality (Figure GPSallen B). As a result the relationship between habitat quality and RSFs for individual fishers showed high variability as well (Figure GPSallen). In some instances fisher selection was positively related to the habitat quality predicted by the Allen model whereas in other cases it was negative. The mean relationship, across the 4 collared fishers, was negative for the Allen model (Table GPSresults). This negative relationship, in part, relates to the strongly avoidance for habitat values in 0.8-0.9 ranges of predicted habitat quality. Additionally, fishers showed apparent indifference to habitat values that were very low. Fisher use of these areas in proportion to their availability is also related to the GPS data which collected points continuously through time. When fishers spend time stationary (perhaps resting for long periods) the collar continues collecting points. If the location of the fisher is in or near a boundary between low and high quality habitat the result is many locations occurring in poor habitat (Figure Femharvest). In future analyses we will identify areas where fishers stationary and use a mean value for that location and thus remove this bias.

Though harvest or logging activity is not considered a model of itself we decided to include the age when a unit was logged as a variable to test with other GPS data. Females appeared to have used areas that have not been logged in the last 50 years. The year a stand was logged explained fisher use better than did other models we tested. The beta-value for this model is somewhat arbitrary because we set the value for stands harvested before 1970 to 0. This decreased the magnitude of the beta-value because the explanatory variable had a range of over 2000 units. Nevertheless, though a small parameter estimate, harvest year and intensity may be a value metric to examine more closely in future analyses.

### Allen Overview

We emphasize for the Allen model that at every level of analysis the available habitat is biased toward the highest habitat quality bin. Yet, fishers use these areas disproportionately more than would be expected at random (Figure HR-compare). The fact that the Allen models predicts an abundance of high quality habitat but fishers use it preferentially suggests that something important to fishers is being captured by this part

of the model. Indeed, among all habitat models the Allen model shows among the strongest selection values for this top bin. Similarly, the strong avoidance of low habitat qualities also suggests the model captures something important about places fishers avoid. At moderate levels of habitat quality there may be confounding influences. In particular, the consistent avoidance of habitat values from 0.8 to 0.9 is interesting. Because we observed consistent avoidance of habitats within this range of values we explored the attributes of areas with those values compared to lower and higher habitat quality values (Figure AllenCompare).

We subdivided Stirling into three habitat types: habitat values  $< 0.79$ , habitat values  $\geq 0.80$  &  $\leq 0.90$ , and habitat values  $> 0.90$ . Within each of those three categories we calculated the mean values for each component of the Allen habitat model. The mean values for canopy, QMD, and canopy layers were all distributed as we would expect from the predictions of the Allen models (e.g., the highest canopy values occur in the highest predicted habitat quality). Yet, the percentage of hardwoods in a stand was lowest for habitats values from 0.80 – 0.90. The original Allen model considered stands dominated by hardwoods as relatively poor stands. Forests, or stands of forest, that have no hardwoods, but have high QMD and canopy, are classified relatively high habitat quality ( $> 0.80$ ). Thus, though not definitive, the results across the different Allen analyses indicate that fishers are avoiding stands with relatively high values for QMD, canopy and canopy layers, but with low proportions of hardwoods. Thomasma et al. (1994b) presented data suggesting the stand with low hardwoods were relatively poor habitat. In future refinements of the Allen model we will model the effect of hardwoods on the final habitat quality values similar to that of Thomasma et al. and evaluate differences between the two versions of the Allen model.

*Carroll 1999*

Stirling location

In contrast to the Allen model, the Carroll 1999 model predicted the highest amount of low quality habitat across Stirling. Mean available habitat quality on Stirling across all years was  $0.30 \pm 0.30$  SD. Mean available habitat quality increased steadily from the low in 2010 of  $0.29 \pm 0.35$  to  $0.31 \pm 0.36$  in 2014. The distribution of available habitat quality was skewed towards low values with the approximately 50% of Stirling occurring at the lowest predicted habitat quality (Figure CarrollRand). Habitat quality values above 0.9 comprised roughly 10% of Stirling in all years with a slight increase from 2010 to 2014. Habitat quality values from 0.2 to 0.8 were individually a relatively small proportion of the landscape, but were roughly equivalently distributed (Figure CarrollRand). Spatially, the areas with highest quality habitat were found along the lower portions of the West Branch of the Feather River, Butte Creek, and Big Chico creek (Figure Carroll).

The average habitat quality for locations fishers used was  $0.50 \pm 0.35$ . Mean habitat quality used by fishers consistent across years, but did show a trend towards increased values in later years (range = 0.50 – 0.52). The relationships between predicted habitat quality and both the Ivlev and modified Ivlev resource selection function demonstrated a positive relationship statistically different from 0 with  $R^2$  values over 0.50 (Table 3; Figure CarrollUsed). Both the Ivlev and modified-Ivlev RSFs indicate fishers avoided habitat quantified as low ( $< 0.20$ ), but selected habitat values greater than 0.90 (Figure AllenRSFalla). Additionally, habitat predicted by the Carroll model to be of moderate

value was selected more than expected by fishers. Habitats with the highest values were selected, on average, more than expected by chance. Nevertheless, the highest habitat values were not the most strongly selected by fishers.

Female and male fishers appear to have used habitat similarly based on the Carroll model. Mean used habitat for females ( $0.51 \pm 0.37$ ) and males ( $0.51 \pm 0.35$ ) was similar in pattern but did display differences across years. Mean female habitat use varied across years with the minimum value occurring in 2010 (0.31), but increased steadily to 0.60 by 2014. Mean male habitat use displayed a less obvious temporal trend with the lowest mean used values occurring in 2011 (0.37) and the highest in 2013 (0.61). Generally, male and female mean habitat use was similar with the exception of increased values for females in the latter years. The mean Ivlev and modified Ivlev resource selection functions showed similar patterns among females and males (Table 3). Both demonstrated positive relationships between predicted habitat quality and patterns of usage, but neither was significantly different from zero. As with the more general analysis, female and males both avoid habitat that is quantified below 0.1 and select habitat over 0.90.

#### Female Home ranges

The available habitat within female home ranges as quantified by the Carroll model was similar throughout most of the distribution to that observed for the entire study area. A notable exception occurred at the highest predicted habitat values. Within female home ranges the mean proportion of habitats with values from 0.9- 1.0 increased to 0.20 (range = 0.15 – 0.24). Across all years the highest proportions of available habitat were found in the lowest and highest habitat qualities. Thus, the distribution of available habitat was nearly bimodal with peaks at the ends of the range of habitat quality.

The mean habitat value selected by females within their home ranges was  $0.46 \pm 0.37$ . The mean habitat quality selected by females across years with their home ranges showed a similar pattern to mean values from all female locations with the highest mean values occurring in 2014 ( $0.54 \pm 0.35$ ). The relationship between female habitat selection (resource selection functions) and predicted habitat quality was highly variable across years (Figure CarrollHRbyyear). The pattern of female habitat selection we observed within home ranges was markedly different from that seen at the scale of locations (Table HRresults). Female's within their home ranges appear to have selected high quality habitat in proportions lower than expected. In fact, the mean relationship between predicted habitat quality and RSFs for the 25% and 50% isopleth of a female utilization distribution were negative (Table HRresults). Because the Carroll model indicated the lowest amount of high quality habitat this result is somewhat surprising. Yet, females apparently incorporated relatively high amounts of high quality habitat within home ranges and thus the proportions available within home ranges was different then the landscape generally.

#### GPS

The proportion of available habitat, as predicted by the Carroll model, within the minimum convex polygons of fishers with GPS collars was highly variable (Figure Carroll GPS). Similar to the Allen model the results of the Carroll analysis with GPS data were highly variable (Table GPSresults). The mean relationship between predicted habitat quality and fisher selection of habitat was positive though not significantly different from 1. In comparison to the Allen model analysis for GPS data we found no

strong results. Mean RSF values were intermittently high throughout the distribution and generally there appeared to be no actual pattern. Additionally, fishers showed apparent indifference to habitat values that were very low.

#### Carroll Overview

The Carroll model was the most restrictive with respect to predicting high quality habitat across Stirling (Figure Carroll). Thus, the Carroll model also predicted the highest proportion of low quality habitat of all models tested (that were built with SPI inventory data). The overall utility of the Carroll model is difficult to assess because of conflicting patterns seen through different analyses (Tables 3 and 4). At the scale of individual locations the Carroll model did a reasonable job of predicting locations that fishers avoided. Locations above a predicted habitat quality of 0.3 were used by fishers disproportionate to their availability (Figure CarrollUsed). Nevertheless, beyond the habitat value of 0.3 the Carroll model did not show strong selection at the highest habitat values compared to the moderate values. The Carroll model performed very poorly at the scale of home ranges and with data collected from GPS collared fishers (Figure CarrollhomerangebyYear). Within these analyses the predicted habitat quality was unrelated to the pattern of avoidance and selection by fishers. Spatially, we identify areas that the Carroll model predicted as low quality but used by fishers and in particular female fishers.

Because the Carroll model has many variables including two interaction terms we had difficulty understanding which, if any, variable, is consistently lacking or over-valued by this model. The Carroll model has the canopy closure QMD variables in common with the Allen model. Additionally, the Carroll model incorporates the percent of conifer in a stand and this metric is negatively linearly related to the percent hardwood (used in the Allen model). Nevertheless, the mathematical relationship among these variables to habitat quality is different from the Allen model and creates highly divergent results. The Carroll model was constructed as a descriptive model of fisher detection throughout California. Thus, Carroll et al. 1999 used variables such as precipitation, northing and northing<sup>2</sup> to explain fisher detection. The northing variables likely contributed to explaining fisher presence in the original model but reduce the generality of using the Carroll models (both 1999 and 2005) for predicting fisher habitat quality.

#### Carroll Index

##### Stirling locations

The Carroll Index, based on the Carroll 2005 model 3, had the second lowest predicted mean available habitat quality across Stirling. Mean available habitat quality on Stirling across all years was  $0.41 \pm 0.19$  SD. Mean available habitat quality was effectively constant from 2010 to 2014 (range = 0.41 – 0.42). The distribution of available habitat quality was skewed towards moderate values but very little of Stirling occurred in habitat values over 0.70 (Figure CarrollIndex). Habitat quality values above 0.7 comprised less than 1% in all years. Habitat quality values from 0.2 to 0.5 were roughly equivalently distributed (Figure CarrollRand). Because the Carroll index weighted terrain roughness and canopy cover equally the majority of high quality habitat occurred in location along drainages with steep terrain. Consequently, locations with relatively flat topography were predicted to have low quality habitat compared to areas with similar canopy cover but that were steep.

The average habitat quality for locations fishers used was  $0.52 \pm 0.15$ . Mean habitat

quality used by fishers was consistent across years, and did not show a trend towards increased through time (range = 0.51 – 0.52). The relationships between predicted habitat quality and the both the Ivlev and modified Ivlev resource selection function demonstrated a positive relationship that was statistically different from 0 with  $R^2$  values of 0.51 (modified-Ivlev) and 0.72 (Ivlev) (Table 3). Both the Ivlev and modified-Ivlev RSFs indicate fishers avoided habitat quantified below 0.50, but selected habitat values greater than 0.50 (Figure CarrollRSF). The pattern of avoidance and selection as stark with a clear divide at habitat values as 0.50. Habitat above 0.50 was not necessarily selected concordant with the predicted habitat quality. Nevertheless, those differences may emerge simply because of sampling error because few locations on Stirling were available with the highest values.

Female and male fishers used habitat similarly based on the Carroll index model. Mean used habitat for females ( $0.53 \pm 0.14$ ) and males ( $0.51 \pm 0.18$ ) and did not display differences across years. The mean Ivlev and modified Ivlev resource selection functions showed positive though beta estimates that were not significantly different from zero (Table 3).

#### Area locations

The Carroll index model, constructed using GNN data for the area on and around Stirling, had a mean available habitat value of  $0.29 \pm 0.21$  (Figure AllenGNN). The highest predicted habitats with GNN data were within the 0.4 – 0.70 value bins (71%). Habitat values less than 0.4 represented 27% of the total area whereas habitat with the highest values (0.9 – 1.0) comprised less than 2% of the area sampled. Moderate and high quality habitat was distributed along areas with steep terrain and thus major drainages (e.g., Feather River, and Butter creek).

Fishers selected moderate to high quality habitat ( $0.43 \pm 0.12$ ) on average than was available. Fishers also appeared to avoid areas with low predicted habitat quality and selected for the highest quality habitat (Figure Carrollin\_GNN). Fishers selected for locations in the area with predicted habitat values above 0.60. There were differences observed between the Ivlev and modified-Ivlev RSF (Figure Carrollin\_GNN). At habitat values above 0.80 the Ivlev RSF indicated avoidance by fishers whereas the modified-Ivlev RSF shows indifference. There were relatively few cells within these high habitat values and these results are likely due to sampling errors. The relationship between predicted habitat quality and both the Ivlev and modified-Ivlev RSF were not significantly different from zero (Table 3). Similar to the comparison with the Allen model, the two versions of the Carroll index were produced using different data and different scales (stand vs cell based). The Carroll index is different because it has fewer parameters (TRI and canopy). Canopy should be a relatively robust measure between data sets (data types) and TRI was the same in both models. Thus, the scale of the analysis (individual cells as well as a broader region) is likely the major contributor between the results of the two models.

#### Female Home ranges

The available habitat within female home ranges as quantified by the Carroll index model was similar throughout most of the distribution to that observed for the entire study area (Fig CarRand). The highest proportion of habitat occurred in the values from 0.5 to 0.6 with moderate amount at lower values. There were annual differences in the proportion of available habitat but minor in magnitude.

The mean habitat value selected by females within their home ranges was  $0.58 \pm 0.14$ . The mean habitat quality selected by females across years within their home ranges was relatively invariant (range = 0.51 – 0.53) with no trends through time. The relationship between female habitat selection (resource selection functions) and predicted habitat quality was variable across years but consistent with other analyses with this model (Figure CarrollHRbyyear). In all years, and for the mean across years, female fishers avoided areas with low predicted habitat quality but selected locations with high predicted habitat quality. The pattern of female habitat selection we observed within home ranges was similar to that seen at the scale of locations on Stirling (Table HRresults). Female's within their home ranges appear to have selected high quality habitat in proportions lower than expected. There was positive relationship between predicted habitat quality and RSFs for all isopleths of a female's utilization distribution (Table HRresults). Generally, the Carroll index model explained home range selection well at a broad scale of poor habitat (<0.50) and good habitat (>0.50). Additionally, the selection scores were among the highest of all models tested (Figure HR-compare). Similarly, selection scores for avoidance were also strong compared to other models with the exception of the Allen model at the 0.8 to 0.9 habitat quality range.

#### GPS

The proportion of available habitat, as predicted by the Carroll index model, within the minimum convex polygons of fishers with GPS collars was highly variable (Figure CarIndexGPS). The pattern of fisher response to the predicted habitat quality at the scale of GPS data was different from that seen at other levels (Table GPSresults). The mean relationship between predicted habitat quality and fisher selection of habitat was effectively zero ( $\beta = -0.010$ ), with no strong trend showing avoidance or selection. In comparison to the Allen model analysis for GPS data we found no strong results. Mean RSF values were generally low than expected, given the proportion of habitat, for high habitat values. As we noted with GPS data and the Allen model, these results may have something to do with more points collected at resting sites that border poor quality habitat. Additionally, because the GPS data is collected over a short amount of time the results are much more prone to sampling error than are other analyses. The nature of the Carroll index model may simply be too general to provide precision for the types of locations that are provided by GPS collars.

#### Carroll Index overview

The Carroll index model consisted of only 2 variables – TRI and canopy. Our index of the original model used a scaled mean value of both variables. TRI ranges from 0 to 160 and thus the highest values within our scaled TRI variable would occur at values of 160. Yet, the mean value for TRI on Stirling was  $22 \pm 13$  (Table TRI\_coor). Thus, the mean value for TRI in our model was only 0.14. The average for canopy and TRI would rarely approach 1.0 and hence there were few locations with predicted habitat value  $\geq 0.80$ . Consequently, the Carroll index cannot be thought of in the same way as other models we tested in terms of the values that represent good vs poor habitat. Nevertheless, the pattern of fisher use for this index was surprisingly consistent at the level of all locations across Stirling and within female home ranges (Tables 3 & HRresults). Fishers consistently avoided areas with low habitat quality values (low canopy and flat terrain). Locations with steeper terrain and more canopy appear favored which supports the earlier model of Carroll 2005 although we emphasize this is only an

index of that model. Regardless, the inclusion of only canopy and TRI demonstrated better resource selection values by fishers than most other models regardless of the data type or scale of analysis.

The canopy metric is nearly omnipresent in the models we tested and for fisher habitat models generally. Locations without canopy from trees appear avoided by fishers on average. Measurement of terrain ruggedness have appeared in other models (e.g, Davis et al. 2007). Nevertheless, terrain ruggedness, of itself, likely offers very little to fisher requirements. On Stirling TRI is correlated with several other variables that are potentially important for fishers (Table TRI\_coor). The percent hardwood is positively associated with TRI while percent conifer is negatively related. The results from the Allen model indicate that at Stirling, hardwoods may be important for fisher selection even when other attributes, such as QMD or canopy, are present. Additionally, canopy itself is correlated with TRI as are the number of logs per acre, tree diversity, and tree height (negative relationship). Obviously, many of these variables are themselves correlated. For example, areas with more hardwoods are likely to have high tree diversity; moreover, places with high tree diversity could be expected to have lower average tree height because of a greater proportion of sub-story trees. Steep terrain may reduce the amount of road building, logging and other management activities that alter many of the variables we mentioned. Thus, we hypothesize that TRI serves as an indicator of areas with low management, and high forest complexity (diversity) rather than being important itself. Within the Carroll index model TRI is likely accounting for many variables simultaneously that could be modeled individually. The inclusion of a terrain-related variable will likely always outperform models with the inclusion of multiple variables because terrain will explain similar variation with fewer estimated parameters. Nevertheless, future work should seek to understand which variables are truly important to fishers rather than relying on variables such as TRI that are unlikely directly related to the requirements of fishers. At broad scales identifying areas of steep terrain may be a way of refining early assessments of habitat. This, of course, is only viable if our hypotheses concerning management and terrain ruggedness are valid.

#### *CWHR*

##### Stirling locations

The CWHR model predicted modest, relative to other models, amounts of available habitat on Stirling. The mean available habitat quality on Stirling across all years was  $0.57 \pm 0.37$  SD. Importantly, the mean value for the CWHR model is not a value that is actually possible since this model allows for only 7 actual habitat values (Figure CWHR). There was almost no change in mean available habitat from 2010 (0.58) to 2014 (0.57) although 2012 was the lowest year of predicted available habitat at 0.56. The distribution of available habitat quality was skewed towards the highest values with > 50% occurring at the highest predicted habitat quality (Figure CWHRrand). No value higher than 0.89 was described on Stirling although a peak value of 1.0 is possible. Predicted values greater than 0.89 did not occur on Stirling because no stand has sufficient mean QMD to be classified in the 'medium/large' tree category needed for the top value in the CWHR system (Figure CWHR). Habitat quality for other habitat values was roughly uniformly distributed in most years. Spatially, areas with the highest quality habitat were found throughout most of Stirling. Low habitat quality occurred in recent clear cuts, areas with fires in the last 10 years and in some locations dominated by hardwoods.

The average habitat quality for locations fishers used was  $0.67 \pm 0.33$ . The mean CWHR habitat quality used by fishers was roughly equal across years (range = 0.67 – 0.68). The relationships between predicted habitat quality and both the Ivlev and modified Ivlev resource selection function demonstrated a positive relationship but statistically indifferent from zero (Table 3; Figure CWHR\_RSf). The Ivlev and modified-Ivlev resource selection functions indicated slightly different relationships between CWHR habitat quality and fisher selection. The Ivlev RSF showed fishers strongly avoiding habitats quantified as less 0.89 (the top value) whereas the modified-Ivlev showed avoidance at the lowest habitat values but relative indifference in moderate values. Both RSFs indicated selection for habitats predicted as the highest quality. Female and male fishers used habitat classified by the CWHR model virtually identically. Mean used habitat for females ( $0.68 \pm 0.33$ ) and males ( $0.68 \pm 0.34$ ) was indistinguishable as was mean habitat use across years (results not shown). Similarly, male and female selection and avoidance were similar to the pattern observed with the combined data set (Figure CWHR\_RSf)

#### Female Home ranges

The available habitat within female home ranges based on the CWHR habitat model tended was similar to that of habitat available across Stirling. Habitat in the highest quality interval was higher in each year within home ranges (range = 0.60-0.67) compared to across Stirling generally. Concordantly, the proportion of available habitat at lower values was reduced.

The mean CWHR habitat value selected by females within their home ranges was  $0.69 \pm 0.32$ . The mean habitat quality selected by females across years (range = 0.76 – 0.67) was generally similar with the lowest value occurring in 2012. The relationship between female habitat selection (resource selection functions) and predicted habitat quality showed a similar pattern of avoidance at low habitat quality values across years (Figure CWHR\_HR A). Similarly, fishers appeared to show selection for habitat in the highest quality habitats disproportionate to their availability (Figure CWHR\_HR). The RSFs functions were better explained by habitat quality values at low ( $\leq 50\%$ ) isopleths with highest R-squared values and significantly positive beta-values (Table HRresults). On average, female fishers appeared to avoid habitat with a CWHR value of 0.66 which are delineated as stands with trees 28 to 60 cm (11-24”) and canopy cover of 40-59%. In comparison to other habitat models at the home range scale, the CWHR showed a consistent pattern of selection by fishers. Nevertheless, fishers did not avoid areas with the lowest CWHR values as strongly as other models (Figure HR-compare). Moreover, fishers showed relatively weak selection for the highest CWHR habitat values compared to models such as the Allen, and Carroll index (Figure HR-compare).

#### GPS

The proportion of available habitat, as predicted by the CWHR fisher model of habitat, within the minimum convex polygons of fishers with GPS collars demonstrated similar variability as other habitat models (Figure CWHR\_GPS). Similar to the Allen model the results of the Carroll analysis with GPS data were highly variable (Table GPSresults). The mean relationship between predicted habitat quality and fisher selection of habitat was positive though not significantly different from 1. Additionally, a consistent pattern emerged among all models with the GPS data in which individuals that used poor habitat in high amounts did so across models (Table GPSresults).

## CWHR Overview

The conception of the CWHR model is straightforward and places the highest value on locations with large trees, of all types, and high canopy cover. Generally, this approach seems to predict roughly fisher selection and avoidance though not at all scales. The overall pattern of selection vs predicted habitat quality is positive across sexes, locations, and home ranges (Table 3 and 4). Nevertheless, in contrast to the Carroll index model and the Allen model the mean selection and avoidance scores are relatively weak (Figure HR-compare). Additionally, the available evidence suggests that fishers avoid areas with moderate habitat quality characterized by trees less than 60 cm (24'') and moderate canopy closure (<60%). The CWHR model does not incorporate attributes relative to the types or proportions of trees within a stand (e.g., deciduous). The Allen model suggested strong avoidance of areas with similar sized trees and canopy as those avoided at the CWHR 0.66 value but that lacked hardwoods. Thus, the attributes associated with size in the CWHR model may also reflect lack of other components such as hardwoods. Values for the CWHR model from 0.6-0.7 overlapped with the Allen model values of 0.8-0.9 on 10.4% of Stirling (Figure ModOverlap). These areas of overlap between the Allen and CWHR model had nearly no overlap with female utilization distributions at the 50% isopleth. These areas of moderate value occur primarily in the northern and eastern portions of Stirling where geology and elevation are different compared in comparison to much of Stirling. Future use and testing of the CWHR model may place added emphasis on understanding why fishers seem to avoid areas in classified by moderate values.

### *SPI Habitat Form*

#### Stirling locations

The SPI habitat form model predicted the second highest mean available habitat of all models tested on Stirling. The mean available habitat quality on Stirling across all years was  $0.59 \pm 0.37$  SD. The SPI habitat model was restricted to 4 values representing the four classes and thus the mean value is not directly comparable to other models. Available habitat was distributed roughly evenly across the 4 classes with the lowest values occurring at the 0.50 value (HF2; Figure SPIrand). Habitats in the two highest categories were roughly equivalent and represented the majority of predicted habitat in all years. There was almost no change in mean available habitat from 2010 (0.60) to 2014 (0.59). Low habitat quality occurred in recent clear cuts and areas with fires in the last 10 years.

The average SPI habitat fishers used (mean  $0.72 \pm 0.30$ ) was greater than that available. The mean SPI habitat quality used by fishers was roughly equal across years (range = 0.71 – 0.73). The relationships between predicted habitat quality and both the Ivlev and modified Ivlev resource selection function demonstrated a positive relationship that is statistically different from zero (Table 3; Figure SPI\_RSF). The Ivlev and modified-Ivlev resource selection functions showed very similar relationships between SPI habitat quality and fisher selection (Figure SPI\_RSF). Both functions indicated fishers avoided habitats classified as HF0 (0) but selected HF2hv and HF4 disproportionate to their availability. Nevertheless, the strength of the selection index was weaker than seen in the Allen and Carroll index and similar to that of the CWHR model.

Female and male fishers used habitat classified by the SPI habitat form model virtually identical (Figure Meanhab\_sex). Similarly, male and female selection and avoidance were similar to the pattern observed with the combined data set (Table 3) and showed positive relationships with relatively high r-squared values.

#### Female Home ranges

The available habitat within female home ranges based on the SPI habitat form model was similar to that of habitat available across Stirling. The distribution of available habitat was also similar across years from 2010 to 2014. Nonetheless, the proportion of habitat in HF1 increased slightly from 0.14 in 2010 to 0.16 in 2014. The highest proportion of habitat in the HF4 category occurred in 2012 (0.34) and was lowest in 2014 (0.30).

The mean SPI habitat value selected by females within their home ranges was  $0.73 \pm 0.28$ . The mean habitat quality selected by females across years (range = 0.72 – 0.79) was generally similar with the lowest value occurring in 2012. The relationship between female habitat selection (resource selection functions) and predicted habitat was positive in regardless of the isopleth where we evaluate selection (Figure HRresults). We observed an apparent avoidance of the HF2hv classification at the scale of the home range (Figure HRresults) within the SPI habitat form classification. Thus, indicating the females preferentially used only the highest classification habitat quality even with HF2hv was within their home ranges.

#### GPS

The proportion of available habitat, as predicted by the SPI fisher model of habitat, within the minimum convex polygons of fishers with GPS collars demonstrated similar variability as other habitat models (Figure SPI\_GPS). The mean relationship between predicted habitat quality and fisher selection of habitat was positive though not significantly different from 1. Additionally, a consistent pattern emerged among all models with the GPS data in which individuals that used poor habitat in high amounts did so across models (Table GPSresults). Additionally, fisher avoidance of areas classified as HF2hv was apparent in the GPS data as well as the home range analyses.

#### SPI Overview

The SPI habitat form model is similar to other models of fisher habitat in that it predicts areas the fishers use reasonably well. Additionally, it consistently predicts that fisher select areas of relatively high QMD and canopy closure. The SPI model performs similarly to the CWHR model and the Allen model for predicting the high class of fisher habitat (Figure HR-compare). At moderate values (specifically the HF2hv category) fishers appear to have weak selection for this class at the scale of the entire district. Within female home ranges this category was avoided consistently (Figure SPI\_HR, SPI\_GPS). Habitats described by the HF2hv are not identical to other values produced in other models, but is similar to that of the CWHR model values of 0.66-0.77. In both the CWHR and SPI model stand within this moderate and moderate-high values reflect medium sized tree QMD (>11" but often less than 24") and canopy closures below 60%. Additionally, we demonstrated overlap with these moderate values of the CWHR and the Allen models. Consequently, much overlap exists between the HF2hv classification and the Allen and CWHR models that were avoided by fishers over the period of observation.

#### *Mean model*

### Stirling locations

The Mean habitat model we created from other models tested predicted median available habitat value (Figure Mean\_rand) of all models tested on Stirling. The mean available habitat quality on Stirling across all years was  $0.54 \pm 0.29$  SD. The Mean habitat model showed peaks in available habitat at the lowest habitat values at those in range of 0.7-0.8 (Figure Mean\_rand). Generally, available habitat not at the lowest bin increased steadily until values of 0.75 and then declined again. Mean available habitat was invariant from 2010 to 2014 with a change of 0.004 seen among years.

The average Mean habitat fishers used (mean  $0.68 \pm 0.24$ ) was greater than that available. Indeed, across all the models used to calculate the mean model fishers always selected habitat value higher than available at random. The mean Mean habitat quality used by fishers was roughly equal across years (range = 0.67 – 0.69). The relationships between predicted habitat quality and both the Ivlev and modified Ivlev resource selection function demonstrated a strong positive relationship that was statistically different from zero (Table 3; Figure Mean\_RSf). The relationship between habitat predicted by the Mean model and the Ivlev function was nearly linear and exhibited high avoidance at low levels with high selection at high values. The relationship between predicted habitat and the modified-Ivlev resource selection functions appeared non-linear with relatively weak avoidance at low habitat values followed by relative neutrality at moderate values and then weak selection at high values. Nevertheless, both patterns are consistent with a model that explains fisher avoidance and selection as we predicted.

### Female Home ranges

There was little difference between the distributions of available habitat seen across Stirling compared to within female home ranges. Additionally, because we built the Mean model by taking a mean value from other models there was little change in the distribution of available habitat through time.

The mean SPI habitat value selected by females within their home ranges was  $0.73 \pm 0.28$ . The mean habitat quality selected by females across years (range = 0.65 – 0.70) was similar with the lowest value occurring in 2012. The relationship between female habitat selection (resource selection functions) and the predicted mean habitat was consistently positive but the magnitude of these relationships was weak and not statistically different from 0 (Table HRresults). We observed an apparent avoidance of areas with low predicted habitat qualities, but areas with habitat values  $>0.2$  were generally used in proportion to their availability.

### Mean Overview

There was strong agreement among models in quantifying very and very high habitat for fishers (Figure MeanSTD). Locations with habitat values near 0 or 1.0 showed the lowest amounts of variation (standard deviation). Indeed, the strongest disagreement among models in predicted habitat comes at the moderate values from 0.3-0.7 (Figure MeanSTD). Indeed, this is also where we observe high discrepancy among models in predicting fisher selection of habitats. Moreover, at this moderate values is also where the much contention concerning fisher and forest management converge. Among the models we have tested many of the moderate values for habitat are actually avoided consistently and often strongly. The reasons fishers chose to avoid such areas is not completely known, but most models rely on metric for only QMD and canopy closure. The Allen

Carroll (1999) model incorporate stand type more explicitly but still yield, but those parameters may need adjustment. In particular, we must retest the Allen model after incorporating a penalty for stands that lack all hardwoods.

The Mean habitat produced results that explained fisher habitat selection well at the landscape (Stirling) scale (Figure Mean\_RSf). Nevertheless, within home ranges Mean habitat provided poor explanatory power (Table HRresults). The Mean model may provide a good metric for identifying areas of poor habitat the fishers tend to avoid, but selection of the habitat may simply create home ranges that are already proportioned in ways that fishers will use that area. More work is needed to support this conjecture, but using Mean model outputs may be an appropriate way to identify important places across landscapes for fishers. We used a simple arithmetic mean value across a series of models, but more refined approaches may yield better results. We encourage additional work that incorporates consistency among models as a way to identify important areas for conservation and management.

### *Davis*

#### Area locations

The Davis models all were highly skewed towards low values of predicted available habitat in the area on and around Stirling (Figure DavisAvailable). Five the 6 models predicted the proportion available habitat as over 60% (Figure Davis Map). Because we used the models as initially developed we did not create models by years and thus do not account for changes through time or that occurred since the original model was published.

All the Davis models resulted produced low values for mean used habitat by fishers (range = 0.009 – 0.17). Further, the relationship between predicted habitat quality and fisher selection was consistently negative suggesting fishers studied from 2010 to 2014 used high quality habitat at rates lower than expected by random (Table 3). In all models fishers did avoid areas predicted as the lowest quality habitat (both Ivelv and modified-Ivelv). Yet, fishers used areas of moderately low habitat quality (0.2-0.6) at rates higher than expected by random (Figure Davis\_RSf).

#### Territory Opportunity

We evaluated 300 individual hexagons from 2010 to 2014 for overlap with female 50% utilization distributions (Figure TerritoryCore). Of these 300, 150 (50%) never overlapped with the utilization distribution of a female, 91 (30%) overlapped with 1 female utilization distribution, 28 (9%) with 2, 19 (6%) with 3 and 12 (4%) with 5. The total number of hexagons with at least one utilization distribution increased in each year with a slight increase in the number per hexagon (Table HexNum). Hexagons that never overlapped with a female utilization distribution were on average of lower quality than were hexagons with  $\geq 2$ , but with high variation (Figure MeanHexVal).

Female fishers had 50% utilization distributions that intersected with a diversity of hexagon types. The majority (86%) of females had utilization distributions with hexagons that were classified in all three categories. On average female utilization distributions were composed of 29% hexagons of the CBT, 34% SC and 36% TC (Figure Terr\_dist). Nevertheless, female utilization distributions were composed of a wide variety of different hexagon values. On average the 50% utilization distribution was composed of  $4.98 \pm 4.2 \text{ km}^2$  identified as a support core.

Our logistic regression analysis indicated that the value of a hexagon increased the

probability that a home range (utilization distribution) would occur within it (Table TerrOppResult). Models that incorporated the classification of the hexagon as an explanatory variable were more well supported ( $AIC_c \geq 10$ ) than models that incorporated yearly differences, location (easting and northing) or a random variable (Table TerrOppResult). The model that best explained the probability of a hexagon having a home range incorporated hexagon value as a discrete variable. A model treating hexagon value as a continuous variable was second best supported. Both models indicate a positive relationship between the likelihood of finding a home range within a hexagon and the assigned value of the hexagon. Nevertheless, the discrete model explained more variation and offers an important insight. A hexagon classified as below threshold (CBT) will be 0.3 (95% CI: 0.2-0.5) times less likely to have a female home range as will hexagons classified as SC or TC (Table TerrOppResult). Yet, a hexagon classified as TC is not statistically any more likely to have a home range than one classified as SC. The continuous model for hexagon value predicts an increased likelihood at all levels. Hexagons classified as CBT were have probability of holding a home range of 0.35, whereas one classified as TC had a probability of holding a home range of 0.66.

The polytomous logistic regression had very similar results to the logistic regression. The value, or classification, of a hexagon increased the likelihood that the hexagon would hold a female home range. This model better explained the probability of encountering a home range than did year effects, random effects or changes in direction east or north (results not shown). The probability of a hexagon having 1 (Odds ratio =  $1.8 \pm 1.49-2.34$  95%CI) or 2 (Odds ratio =  $2.37 \pm 1.6-3.5$ ) home ranges increased with hexagon value. Having 3 or 4 home ranges did not increase with hexagon value, but there were few hexagons with that many home ranges and thus we had little statistical power to detect an effect. Future analyses should bin all values over 2 home ranges together.

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Table 1. Tested models with variables and data type used during testing.

<b>ModelFamily</b>	<b>Model</b>	<b>DataType</b>	<b>Scale</b>	<b>Variables</b>
Allen	HSI	<sup>a</sup> SPI inv.	Stand	Canopy, QMD, Percent Hardwood, Canopy Layers
Allen	HSI	GNN/Lemma	30x30m	Canopy, QMD, Percent Hardwood, Canopy Layers
Carroll	Logistic Reg	<sup>a</sup> SPI inv.	Stand	Canopy, QMD, Percent Conifer, Annual Precip, UTM, UTM <sup>2</sup>
Carroll	Index	<sup>a</sup> SPI inv.	Stand	Canopy, Terrain Ruggedness Index (TRI)
Carroll	Index	GNN/Lemm	30x30m	Canopy, Terrain Ruggedness Index (TRI)
SPI	Index	<sup>a</sup> SPI inv.	Stand	Canopy, QMD, #trees >22"
CWHR	Expert Opinion	<sup>a</sup> SPI inv.	Stand	Canopy, Tree Size Category, Tree Type
Davis	GAM_norou	CWHR/Davis	1km <sup>2</sup>	Topographic Relief, CWHR fisher rating, Annual Precip
Davis	GAM_north	CWHR/Davis	1km <sup>2</sup>	Annual Precip, CWHR fisher rating, Canopy + Tree Size
Davis	GAM_south	CWHR/Davis	1km <sup>2</sup>	Annual Precip, Canopy + Tree Size, elevation
Davis	GAM_state	CWHR/Davis	1km <sup>2</sup>	Topographic Relief, Hardwood Ranking, Annual Precip, Prop. Canopy > 60%
Davis	MAX_nor	CWHR/Davis	2km <sup>2</sup>	Annual precip, Proportion Canopy > 60%, Topographic Relief
Davis	MAX_state	CWHR/Davis	2km <sup>2</sup>	Annual precip, Proportion Canopy > 60%, Topographic Relief

<sup>a</sup> Models were constructed for each year from 2010 to 2015.

Table 2. Number of females per year, the mean numbers of locations per female and the mean utilization distribution area.

<b>Year</b>	<b>NumFemales</b>	<b>Mean Locs</b>	<b>Mean UD (km<sup>2</sup>)</b>
2010	6	49±32	17±7
2011	7	44±23	28±20
2012	12	55±28	17±56
2013	13	87±32	15±46
2014	13	77±19	16±27

Table 3. Regression results for data on fisher habitat selection across Stirling (DataType = SPI\_inv) and surrounding areas (DataType = GNN).

<b>ModelType</b>	<b>DataType</b>	<b>Model</b>	<b>Dependent</b>	<b>Y_int</b>	<b>β</b>	<b>R<sup>2</sup></b>	<b>β-pval</b>
Allen	SPI_inv	meanHSI	Mean mIV	-0.13	0.14	0.06	0.50
Allen	GNN	HSI_GNN	tot mIV	-0.20	0.35	0.46	0.03
Allen	SPI_inv	HSI_Fem	Fem mIV	-0.07	0.11	0.07	0.45
Allen	SPI_inv	mMHSI	Male mIV	-0.09	0.15	0.17	0.23
Car index	SPI_inv	mCIavg	Mean mIV	-0.37	0.66	0.51	0.02
Car index	GNN	mCarIg	tot mIV	-0.18	0.30	0.21	0.18
Car index	SPI_inv	CarI Fem	Fem mIV	-0.19	0.23	0.30	0.10
Car index	SPI_inv	CarI Male	Male mIV	-0.22	0.45	0.21	0.18
Carroll	SPI_inv	mC9avg	Mean mIV	-0.21	0.49	0.60	0.01
Carroll	SPI_inv	fCari	Fem mIV	-0.12	0.23	0.30	0.10
Carroll	SPI_inv	mCari	Male mIV	-0.22	0.46	0.21	0.18
CWHR	SPI_inv	mCWHRavg	Mean mIV	-0.08	0.12	0.27	0.13
CWHR	SPI_inv	fCWHR	Fem mIV	-0.10	0.18	0.29	0.11
CWHR	SPI_inv	mCWHR	Male mIV	-0.09	0.17	0.37	0.06
Davis	CWHR/Davis	mMaxst	tot mIV	0.03	-0.03	0.00	0.85
Davis	CWHR/Davis	mMax_nor	tot mIV	0.04	-0.06	0.02	0.72
Davis	CWHR/Davis	mGstate	tot mIV	0.02	-0.03	0.04	0.60
Davis	CWHR/Davis	mGsouth	tot mIV	-0.03	0.00	0.00	1.00
Davis	CWHR/Davis	mGnorth	tot mIV	0.05	-0.07	0.12	0.32
Davis	CWHR/Davis	mGnorou	tot mIV	-0.07	0.08	0.02	0.73
Mean	SPI_inv	mMavg	Mean mIV	-0.09	0.16	0.58	0.01
SPI	SPI_inv	mSPIavg	Mean mIV	-0.09	0.16	0.49	0.02
SPI	SPI_inv	mFSPIavg	Fem mIV	-0.10	0.20	0.46	0.03
SPI	SPI_inv	mMSPI	Male mIV	-0.09	0.19	0.51	0.02

Table HRresults. Results of home range analysis where the mean modified-Ivlev resource selection function was regressed on predicted habitat quality by each model for female home ranges across Stirling from 2010 to 2014.

Model	Isopleth	Y-int	$\beta$	R <sup>2</sup>	Y-pval	$\beta$ -pval
Allen	0.25	-0.064	0.072	0.071	0.295	0.456
	0.50	-0.038	0.036	0.024	0.471	0.669
	0.75	-0.018	0.008	0.003	0.627	0.891
	0.90	-0.009	-0.002	0.000	0.786	0.969
	0.95	-0.014	0.008	0.003	0.665	0.876
	ALL	-0.026	0.025	0.017	0.475	0.718
Carroll	0.25	-0.015	-0.025	0.023	0.676	0.677
	0.50	-0.001	-0.036	0.096	0.955	0.384
	0.75	-0.038	0.046	0.191	0.100	0.207
	0.90	-0.022	0.022	0.102	0.156	0.368
	0.95	-0.026	0.024	0.152	0.070	0.266
	ALL	-0.020	0.006	0.005	0.245	0.845
Car index <sup>a</sup>	0.25	-0.153	0.234	0.433	0.031	0.038
	0.50	-0.122	0.187	0.446	0.028	0.035
	0.75	-0.117	0.178	0.413	0.036	0.045
	0.90	-0.103	0.161	0.389	0.048	0.054
	0.95	-0.110	0.170	0.440	0.031	0.037
	ALL	-0.103	0.186	0.437	0.033	0.037
CWHR <sup>b</sup>	0.25	-0.098	0.142	0.487	0.016	0.025
	0.50	-0.053	0.074	0.314	0.057	0.092
	0.75	-0.028	0.032	0.170	0.103	0.237
	0.90	-0.019	0.023	0.243	0.058	0.148
	0.95	-0.033	0.043	0.307	0.049	0.096
	ALL	-0.040	0.063	0.378	0.030	0.058
Mean	0.25	-0.067	0.074	0.157	0.110	0.257
	0.50	-0.035	0.023	0.029	0.258	0.635
	0.75	-0.027	0.019	0.063	0.133	0.484
	0.90	-0.020	0.014	0.057	0.155	0.507
	0.95	-0.028	0.022	0.095	0.097	0.386
	ALL	-0.033	0.030	0.120	0.070	0.327
SPI	0.25	-0.064	0.072	0.071	0.295	0.456
	0.50	-0.038	0.036	0.024	0.471	0.669
	0.75	-0.018	0.008	0.003	0.627	0.891
	0.90	-0.009	-0.002	0.000	0.786	0.969
	0.95	-0.014	0.008	0.003	0.665	0.876
	ALL	-0.110	0.135	0.773	0.087	0.121

Table GPSresults. Regression results for mean modified-Ivlev resource selection function for 4 fishers outfitted with GPS collars in fall of 2012, 2013, and 2015 (n=2) on Stirling district in northern California.

<b>Model</b>	<b>Y-int</b>	<b><math>\beta</math></b>	<b>R<sup>2</sup></b>	<b>Y-pval</b>	<b>B-pval</b>
Harvest Year	0.129	-0.0001	0.325	0.122	0.085
Allen	-0.004	-0.020	0.020	0.867	0.696
Carroll	-0.015	0.006	0.001	0.724	0.937
Carroll Index	0.010	-0.046	0.104	0.701	0.363
CWHR	-0.015	0.012	0.053	0.154	0.521
SPI	-0.023	0.033	0.028	0.551	0.646

Table TRI\_coor. Descriptive statistics for variables tested for correlations to terrain ruggedness index (TRI) using Spearman ranked correlation across Stirling district in northern California. Rho is the estimated relationship between TRI and the variable and the P-val is the probability of observing Rho at random with shaded areas those variables with P-val  $\leq$  0.05.

<b>Variable</b>	<b>Mean</b>	<b>Std Dev</b>	<b>Min</b>	<b>Max</b>	<b>Rho</b>	<b>P-val</b>
TRI	22.357	13.147	0.000	160.00	1.000	..
Percent Conifer	71.844	29.457	0.000	101.00	-0.291	<.0001
Percent Hardwood	24.191	26.077	0.000	100.00	0.374	<.0001
Tree Height (feet)	34.720	15.431	0.000	99.00	-0.061	<.0001
Tree Diversity	0.665	0.209	0.000	1.00	0.146	<.0001
Canopy	67.818	35.870	0.000	100.00	0.163	<.0001
Logs/Acre	1.649	1.501	0.000	11.43	0.014	0.0452
QMD	11.682	4.440	0.000	26.31	-0.013	0.0584
Num. Snags >24"	0.528	0.682	0.000	6.37	-0.005	0.4406
Basal Area	135.028	81.986	0.000	380.72	-0.003	0.6582

Table HexNum. The number of hexagons with 0 or at least 1 female fishers home ranges (at 0.50 isopleth level) by year. For hexagons with at least 1 female fisher home range the mean number, standard deviation, maximum and minimum found with the those hexagons.

<b>Year</b>	<b>0</b>	<b>1</b>	<b>Total</b>	<b>Mean Num</b>	<b>Stdev Num</b>	<b>Max Num</b>	<b>Min Num</b>
2010	57	67	124	1.4	0.61	3	1
2011	39	30	69	1.1	0.31	2	1
2012	52	47	99	1.1	0.28	2	1
2013	56	53	109	1.2	0.60	4	1
2014	64	55	119	1.4	0.71	4	1

Table TerrOppResult. Results from logistic regression analysis and the absence or occurrence of at least 1 female fisher home range at 50% isopleth within hexagon for all fishers located in northern California on Stirling from 2010 to 2014.

<b>Model</b>	<b>SubParam</b>	<b>AIC<sub>c</sub></b>	<b>R<sup>2</sup></b>	<b>Beta</b>	<b>OR</b>	<b>OR-low</b>	<b>OR-high</b>
HexHab	none	682.2	0.09	0.7	1.9	1.6	2.4
HexHab <sup>†</sup>	CBT vs TC	668.6	0.13	-0.9	0.3	0.2	0.5
HexHab <sup>†</sup>	SC vs TC	668.6	0.13	0.5	1.2	0.7	1.9
Random	none	718.7	0.00	0.0	1.0	1.0	1.0
Year	2010vs2014	717.9	0.01	0.2	1.4	0.8	2.3
Year	2011vs2014	717.9	0.01	-0.2	0.9	0.5	1.6
Year	2012vs2014	717.9	0.01	0.0	1.1	0.6	1.8
Year	2013vs2014	717.9	0.01	0.0	1.1	0.7	1.9
Year-cont	none	719.5	0.00	-0.1	0.9	0.8	1.1
East	none	706.6	0.04	0.0	1.0	1.0	1.0
North	none	712.5	0.02	0.0	1.0	1.0	1.0
East×North	none	700.1	0.05	0.0	1.0	1.0	1.0

<sup>†</sup> Modeled as discrete variable.

Figure Allen: The relationships between habitat suitability for fishers and percent canopy closure, mean diameter at breast height (DBH) of overstory trees, tree canopy diversity, and percent canopy closure.

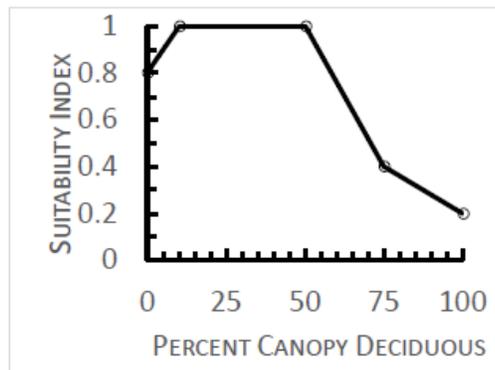
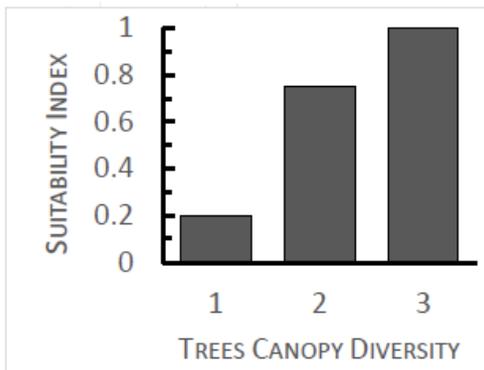
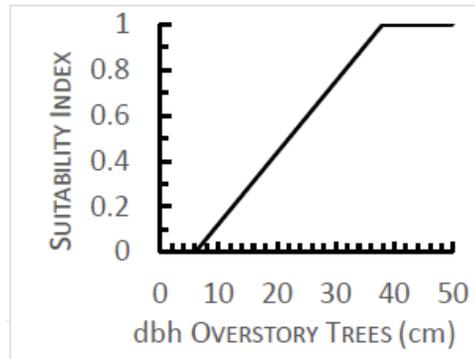
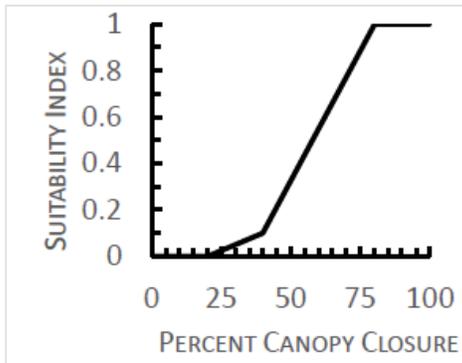


Figure AllenSPI. Distribution of habitat across Stirling as predicted by the Allen habitat suitability model.

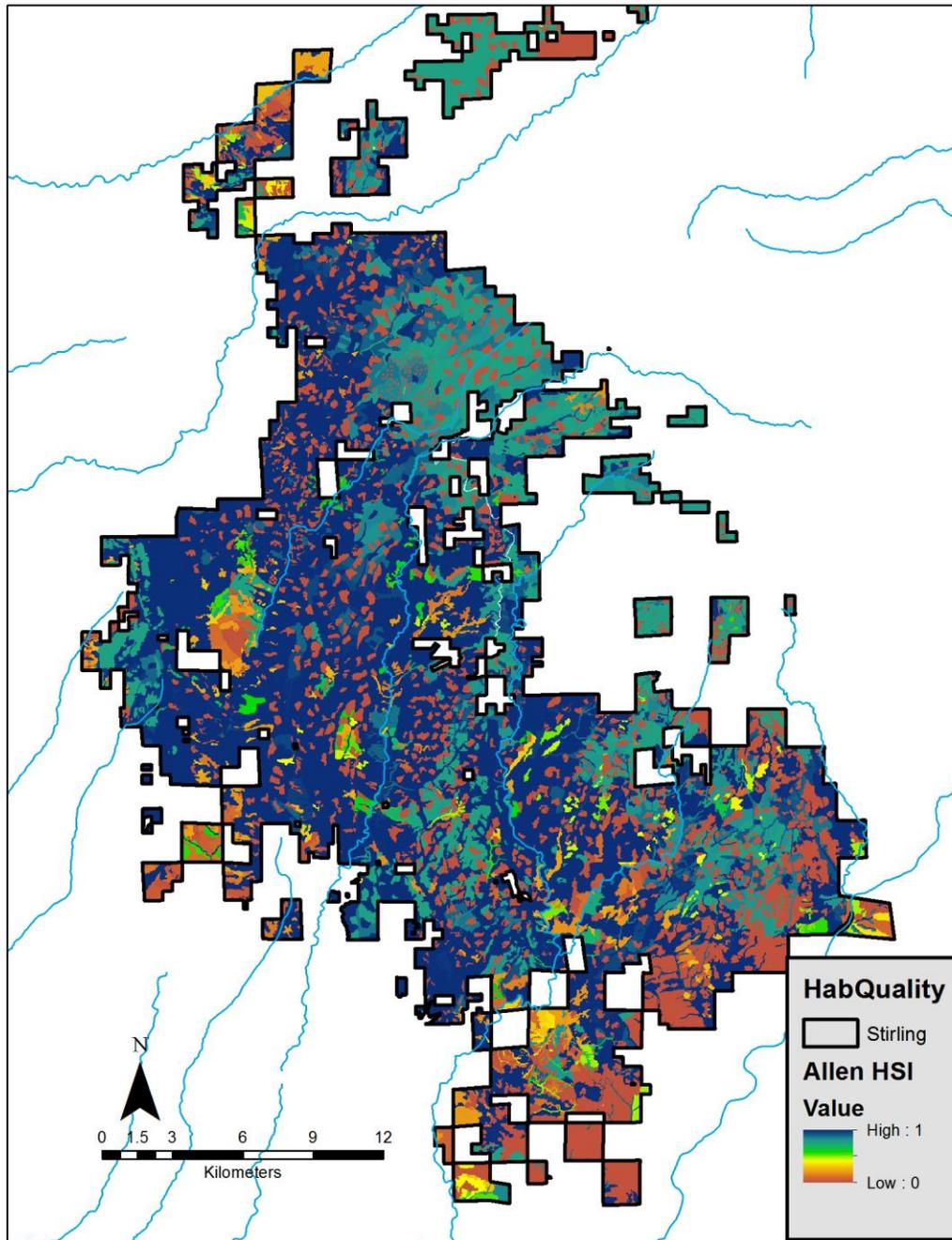


Figure Allen GNN. Distribution of habitat across Stirling and surrounding area as predicted by the Allen habitat suitability model (HSI) with underlying vegetation data taken from Gradient Nearest Neighbor (GNN) data (Lemma 2012).

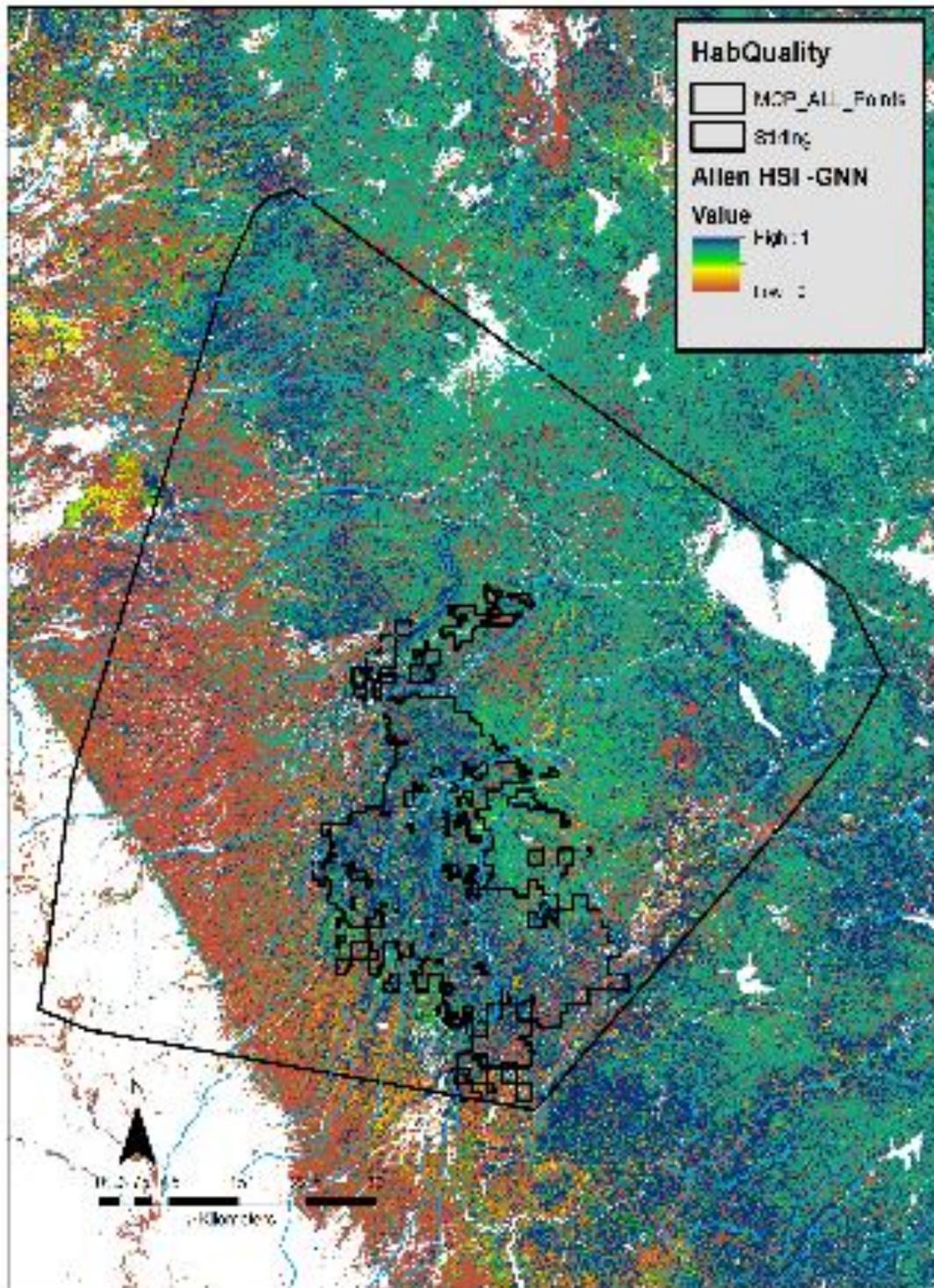


Figure Carroll. A) Distribution of habitat across Stirling implemented using parameters in logistic regression from Carroll et al. 2009. B) Distribution of habitat across Stirling from Carroll et al. 2009 after correction of stands with canopy < 10 and habitat quality > 0.90.

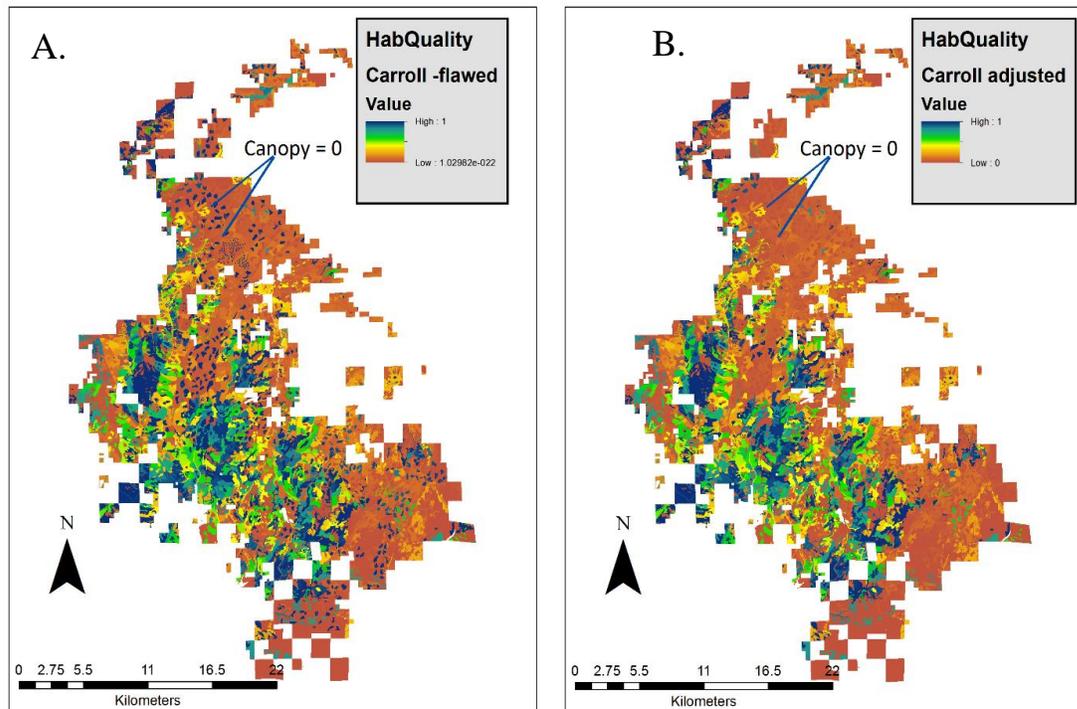


Figure CWHR. Screen capture from California Wildlife Habitat Relationships (CWHR) program 9.0 with habitat suitability information fishers in Sierran Mixed Conifer forests.

California Wildlife Habitat Relationships - Version 9.0

File Species Info Single Condition Two Condition Element Info Habitat Info BioView Window Help

Species Information

Habitat Suitability Information for FISHER

**FISHER**  
*Pekania pennanti*

CWHR ID Number: M155  
CNDDDB ID: AMAJF01020

Suitable Habitats	Size and Stage Classes	Rep.	Cov.	Feed	Suit. Value
JEFFREY PINE	1 Seedling Tree				
KLAMATH MIXED CONIFER	2S Sapling Tree Sparse				
LOGGED POLE PINE	2P Sapling Tree Open				
MONTANE HARDWOOD-CONIFER	2M Sapling Tree Moderate				
MONTANE RIPARIAN	2D Sapling Tree Dense				
PONDEROSA PINE	3S Pole Tree Sparse				
RED FIR	3P Pole Tree Open			L	0.11
REDWOOD	3M Pole Tree Moderate			L	0.11
SIERRAN MIXED CONIFER	3D Pole Tree Dense		L	L	0.22
SUBALPINE CONIFER	4S Small Tree Sparse			L	0.11
WHITE FIR	4P Small Tree Open			L M	0.33
	4M Small Tree Moderate	L	M	H	0.66
	4D Small Tree Dense	H	H	M	0.89
	5S Medium/Large Tree Sparse			M	0.22
	5P Medium/Large Tree Open		L	M	0.33
	5M Medium/Large Tree Moderate	M	M	H	0.77
	5D Medium/Large Tree Dense	H	H	H	1.00
	6 Multi-storied Tree	H	H	H	1.00

Arithmetic Average Suitability Value: 0.32

Calculation Method:  Arithmetic  Geometric

Calculation Scope:  Include all available classes  Include only classes with ratings

Figure LocYear. The number of locations for female and male fishers by year on and near Stirling study area in northern California.

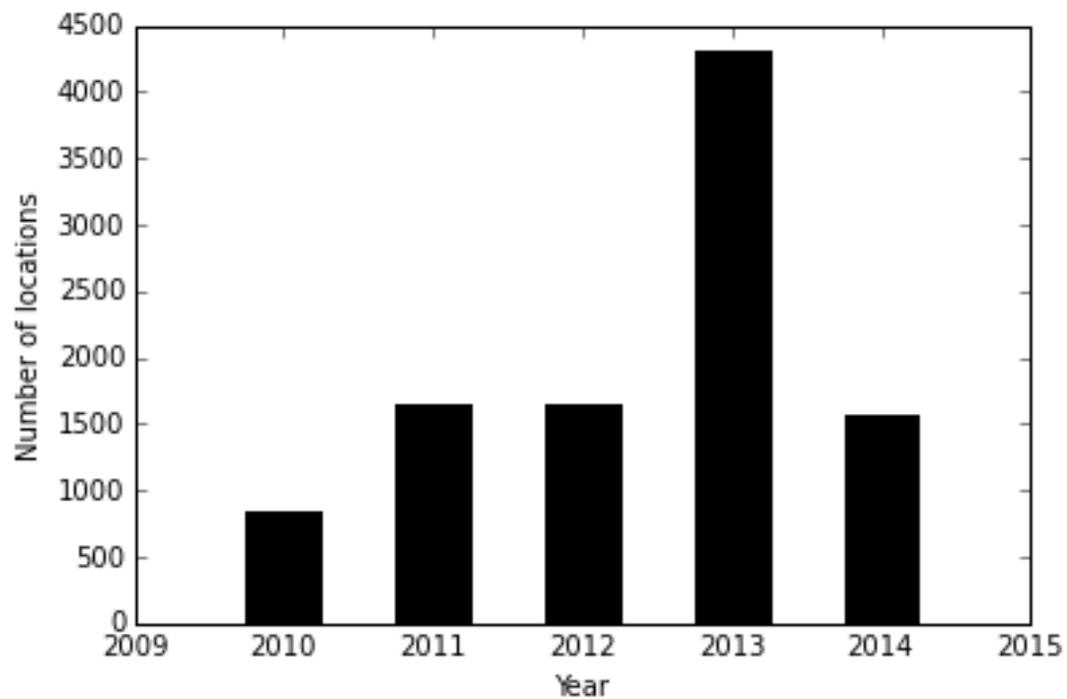


Figure AllenRandom. Distribution of available habitat as predicted by the Allen habitat suitability model for the Stirling district in northern California in study year 2010.

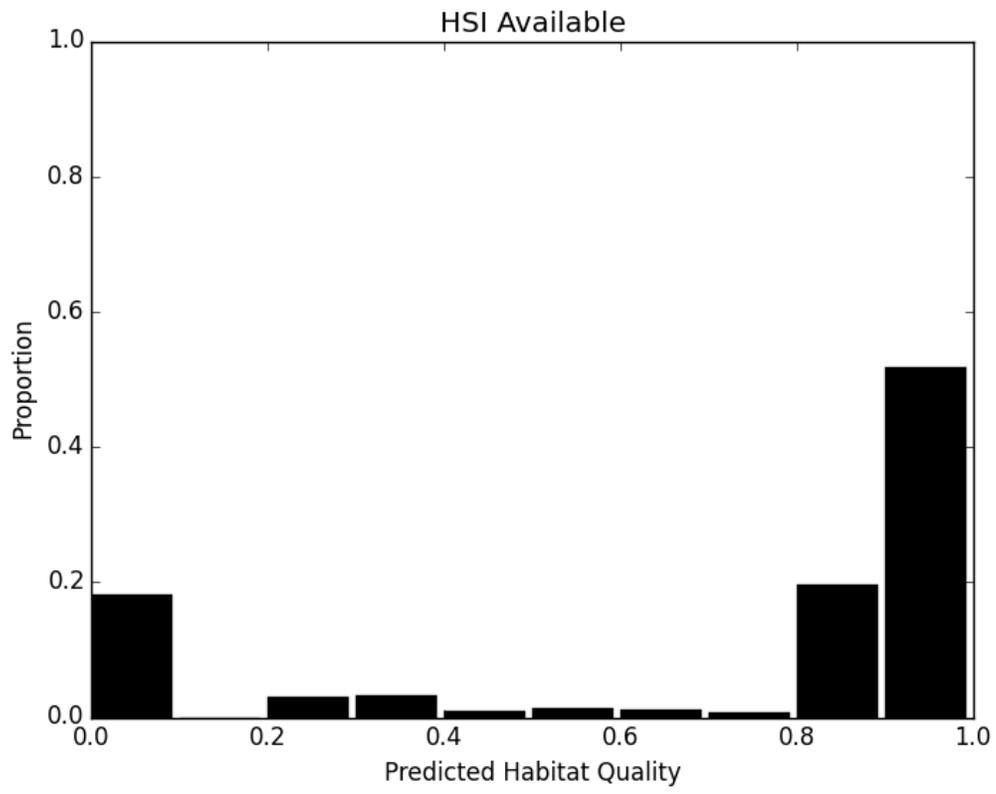


Figure AllenRSFall. Top) Mean Ivlev and modified-Ivlev resource selection functions for all fisher locations on Stirling and Bottom) Mean Ivlev and modified-Ivlev resource selection functions for all fisher locations on Stirling and surrounding areas from 2010 to 2014 in northern California.

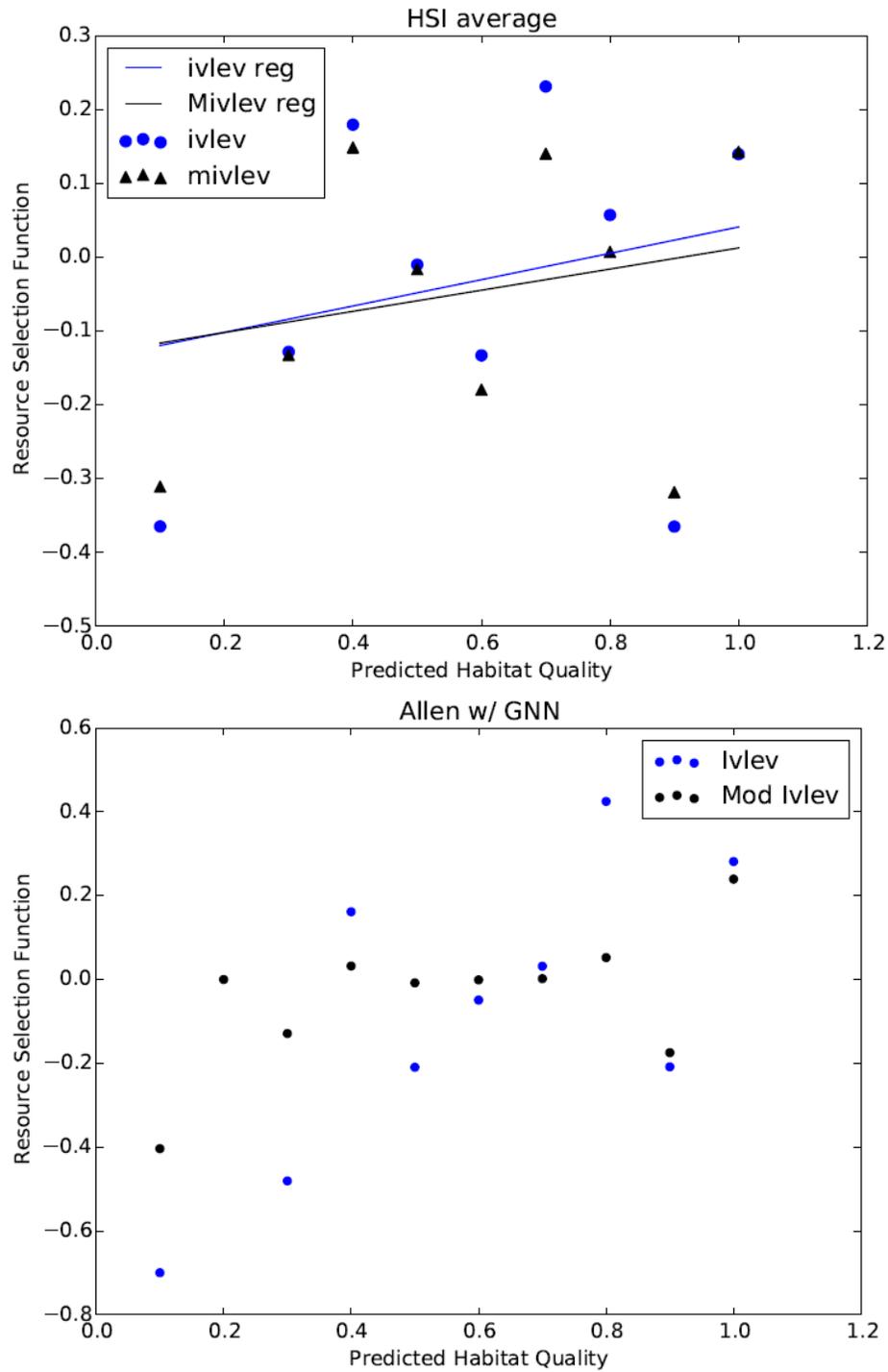


Figure Meanhab\_sex. Mean habitat quality used by male and female fishers based on 6 habitat models for all years from 2010-2014 on Stirling in northern California.

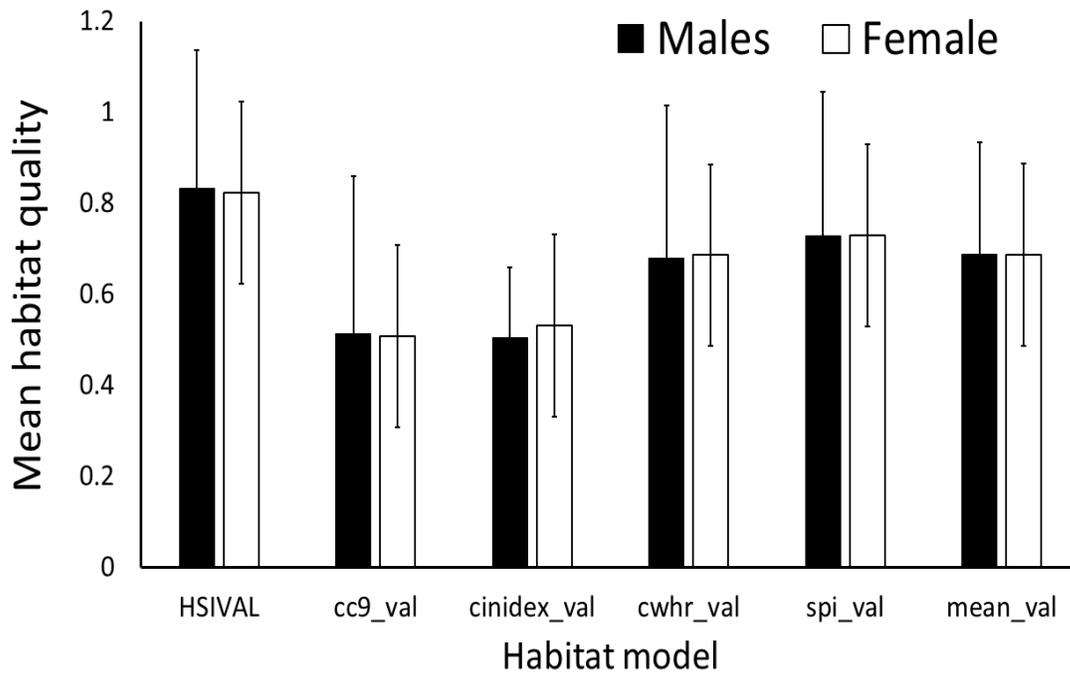


Figure Allensex. Mean modified-Ivlev resource selection function for male and female fisher locations on Stirling management area in Northern Sierra from 2010 to 2014.

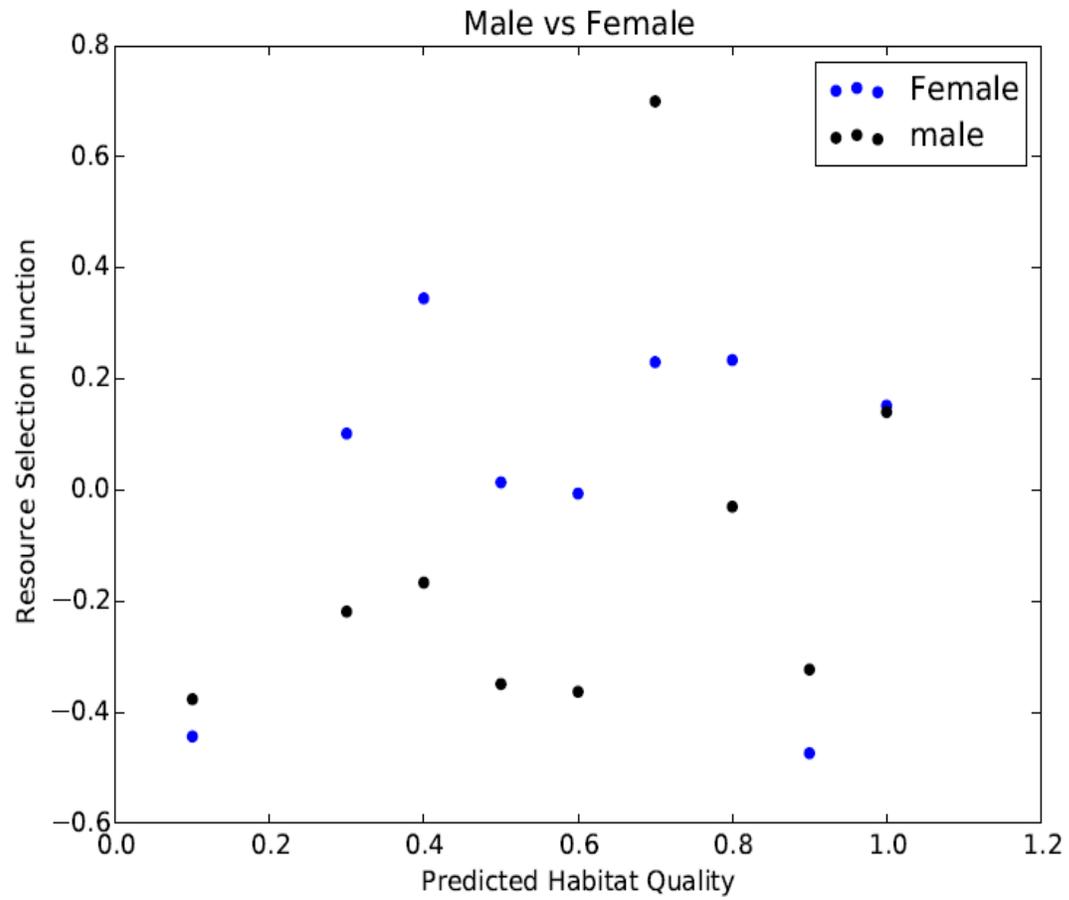


Figure. AllenHRbyyear. A. Mean modified-Ivlev resource selections female habitat selection for Allen habitat model for all female within the 50% isopleth of their home ranges for years 2010 to 2013 (error bars = 1 SD). B. Mean modified-Ivlev resource selection function for all females and years within 50% isopleth of their home ranges for years 2010 to 2014 on Stirling district in northern California.

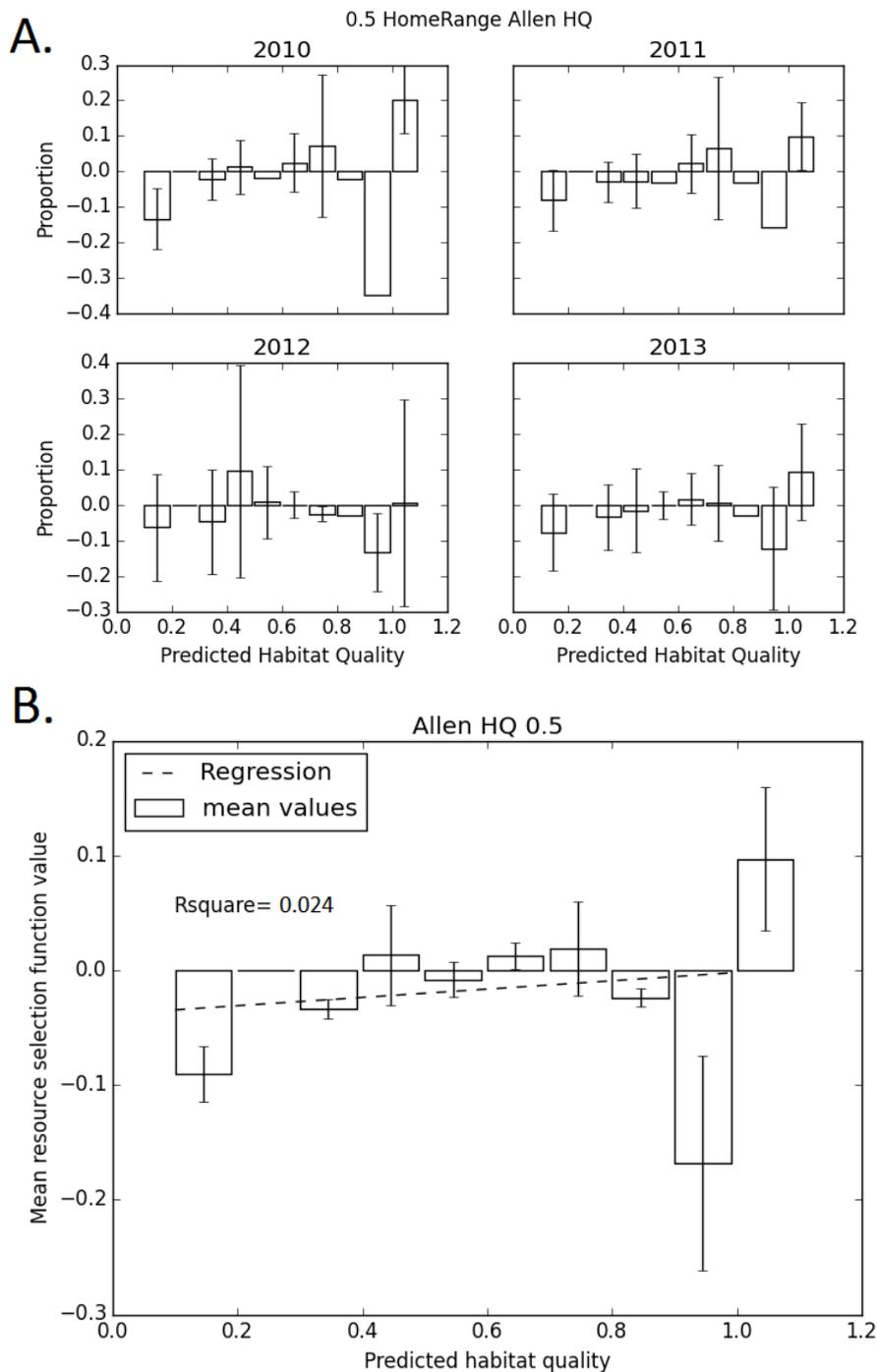


Figure GPSallen. Proportion of available and used habitat as predicted by the Allen habitat suitability model and resultant modified-Ivlev and Ivlev resource selection functions for A. data from a female fisher who wore a GPS collared 5 days in fall of 2015 and B) data from a second female fisher who wore a GPS collar for 6 days in fall of 2015, both data sets collected in northern California on the Stirling district owned by SPI.

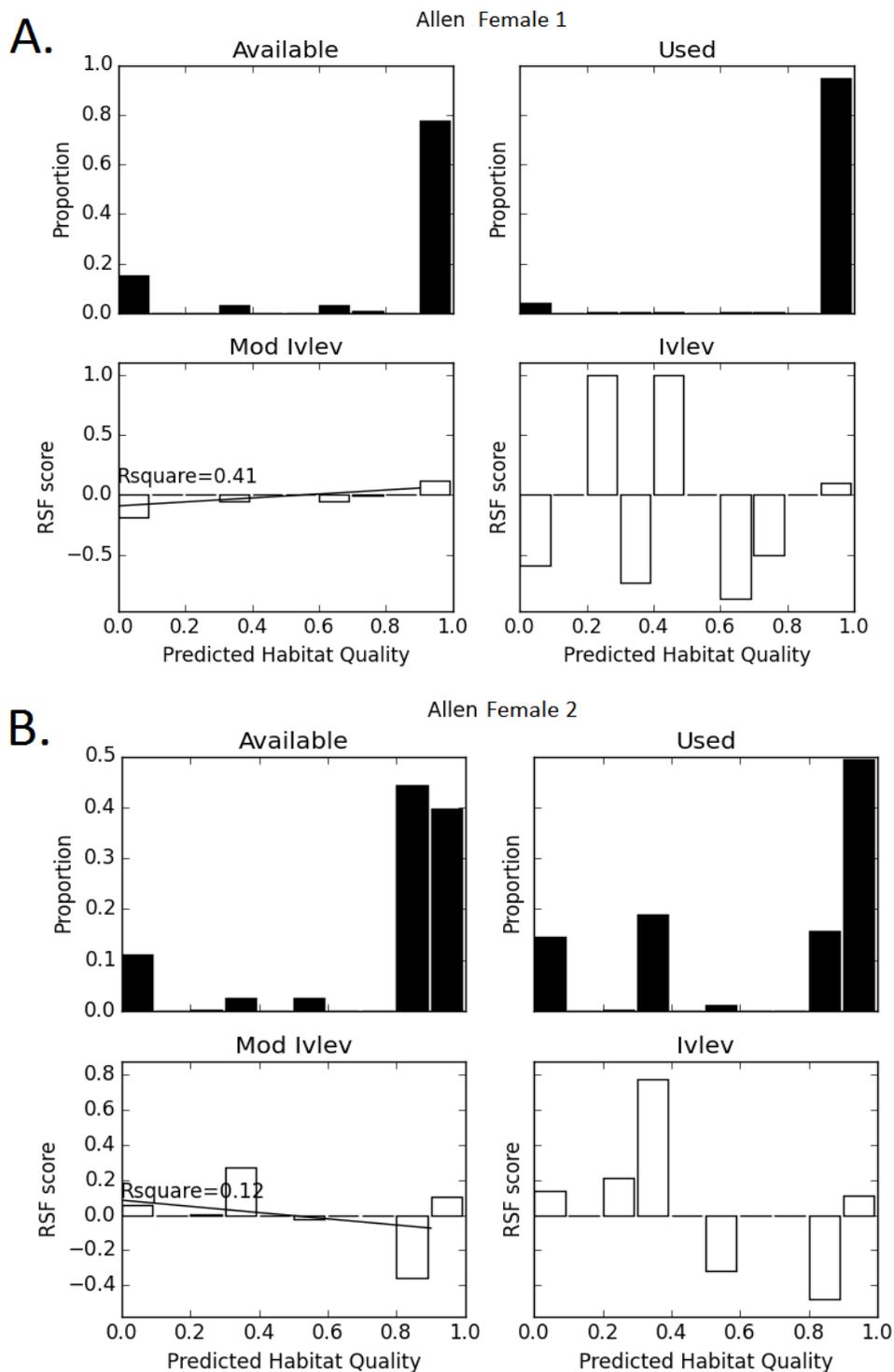


Figure FemHarvest. Estimated GPS locations (black dots) for a female fisher wearing an active collar for 6 days with collared polygons representing the year an area was logged. Areas with no color have not been clear-cut logged after 1950.

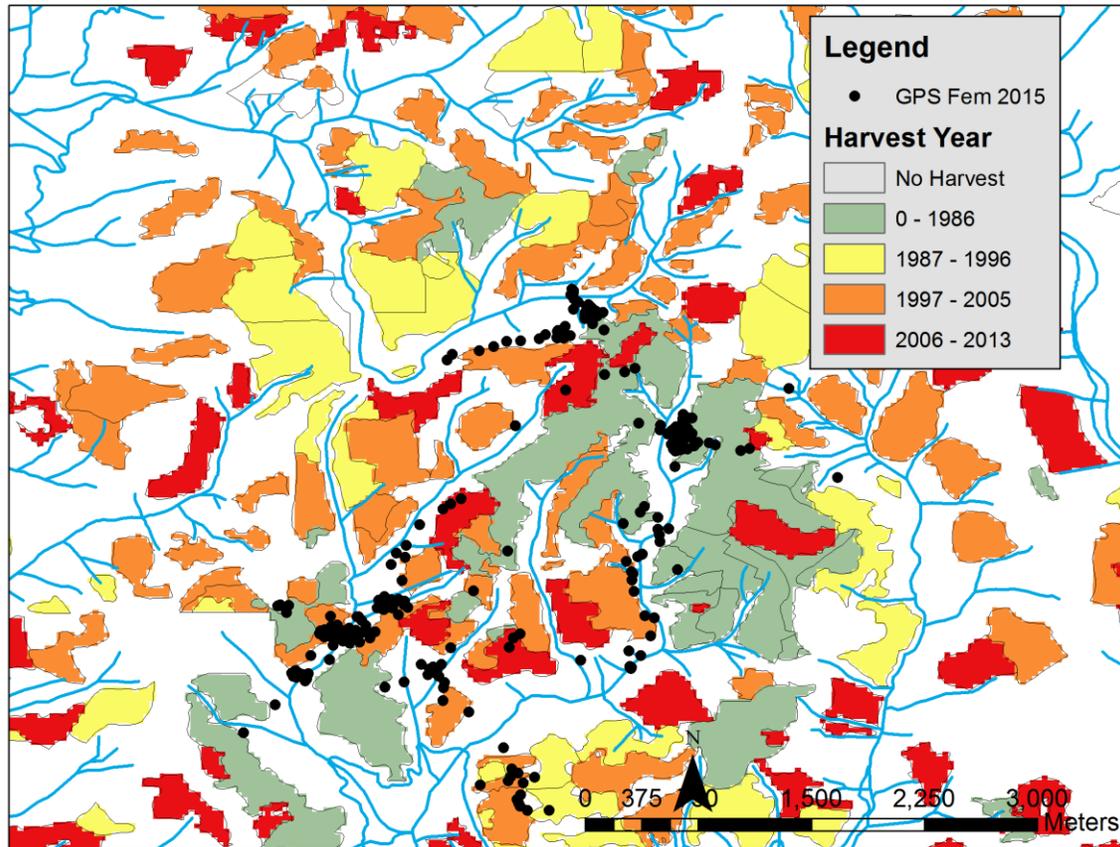


Figure HR-compare. Mean modified-Ivlev resource selection functions for female fishers within their home ranges for year 2010 to 2014 for the Allen habitat suitability model (upper left), Carroll et al. 1999 fisher detection model (upper middle), Carroll index model (upper right), California Wildlife Habitat Relationships model (lower left), SPI habitat form model (lower middle) and a composite (mean) model from the others presented (lower right).

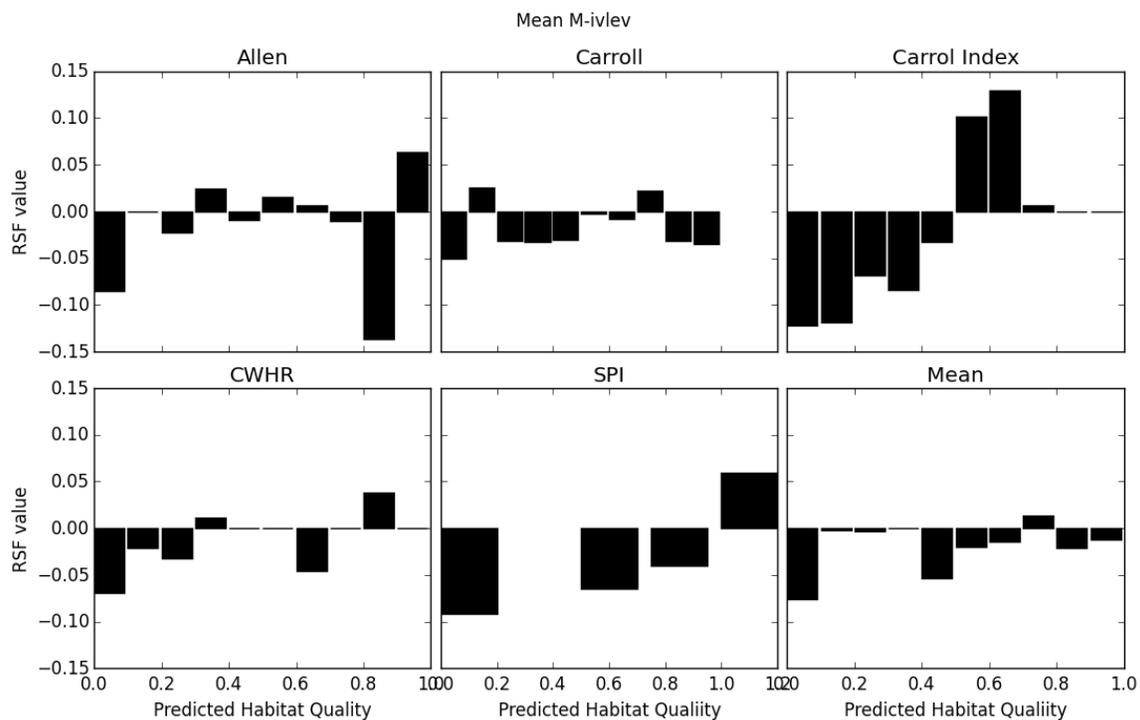


Figure AllenCompare. Distribution of fisher habitat as predicted by the Allen habitat suitability model classified into three discrete value ranges (<0.79, 0.80-0.90, and >0.90) for Stirling management district in northern California with A) no fisher locations and B) all fisher locations from 2010-2014 (red dots) overlaid on habitat distribution map.

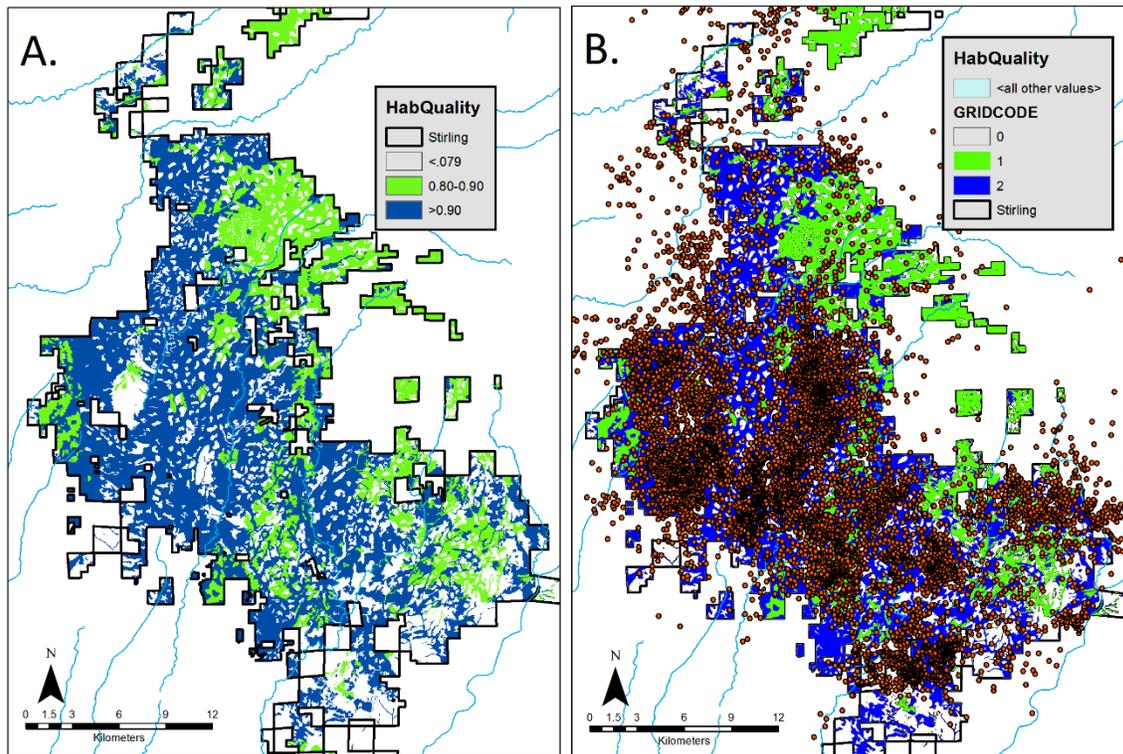


Figure AllenMean. Mean values for canopy closure, percent hardwoods, and quadratic mead diameter at breast height for all overstory trees (QMD) of the Allen habitat suitability index at 3 discrete habitat quality ranges (<0.80, 0.80-0.90, and >0.90). Error bars equal 1 standard deviation.

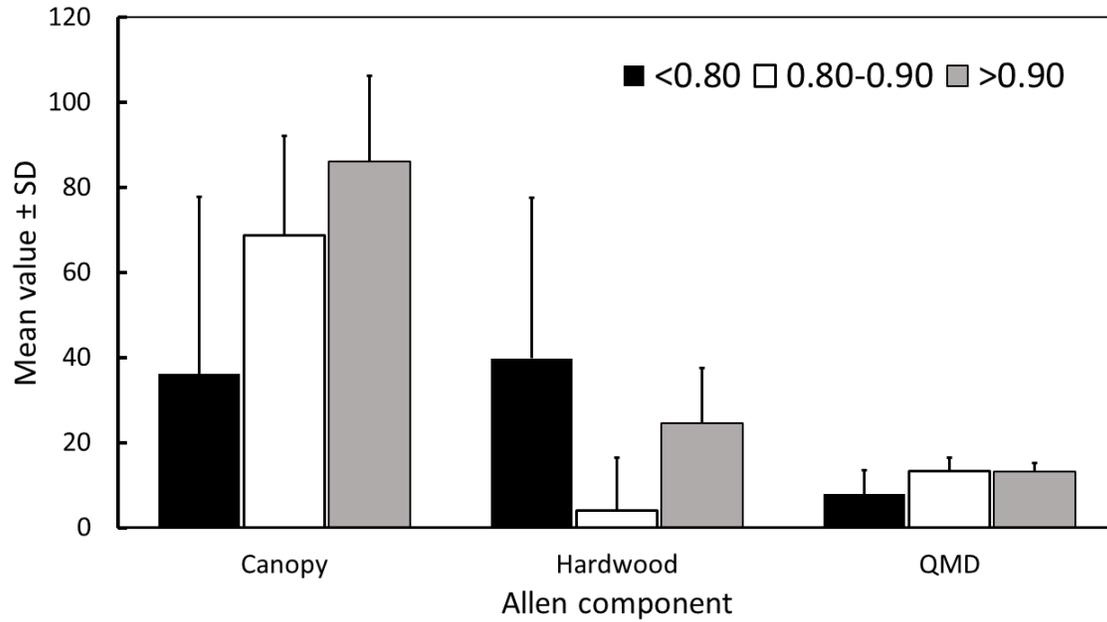


Figure Carroll Rand. Distribution of available habitat as predicted by the Carroll et al. 1999 habitat suitability model for the Stirling district in northern California in study year 2010.

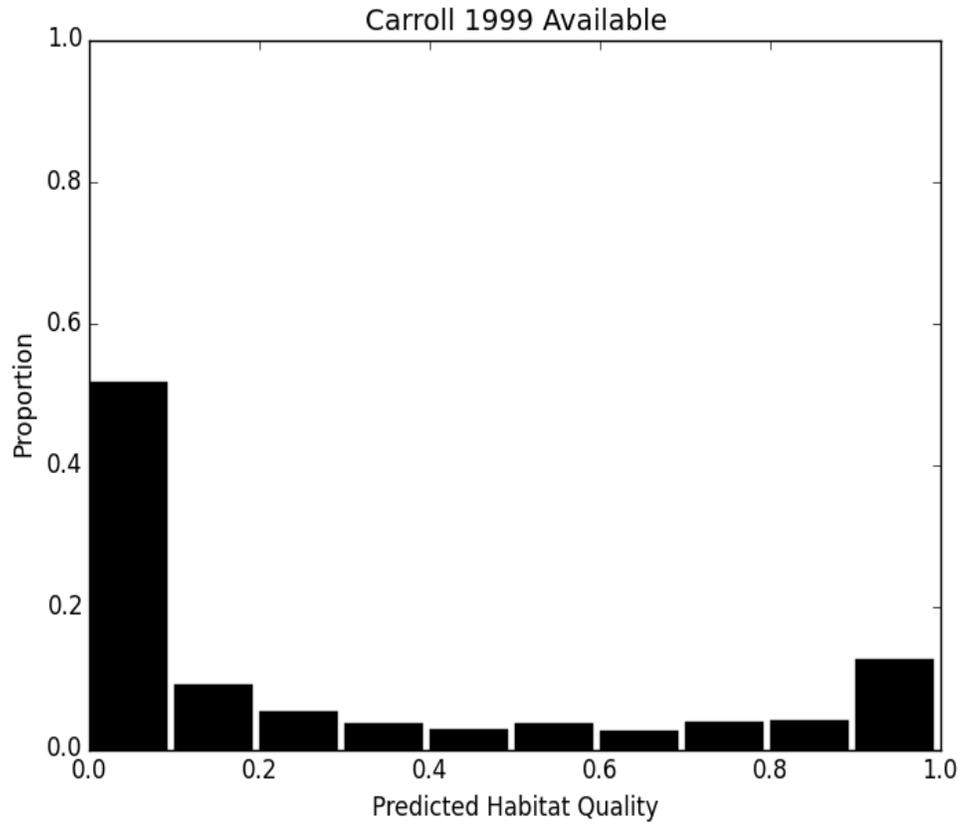


Figure CarrollUsed. Mean modified-Ivlev resource selection functions based on Carroll et al. 2009 habitat model for all fisher locations on Stirling from 2010 to 2014 in northern California.

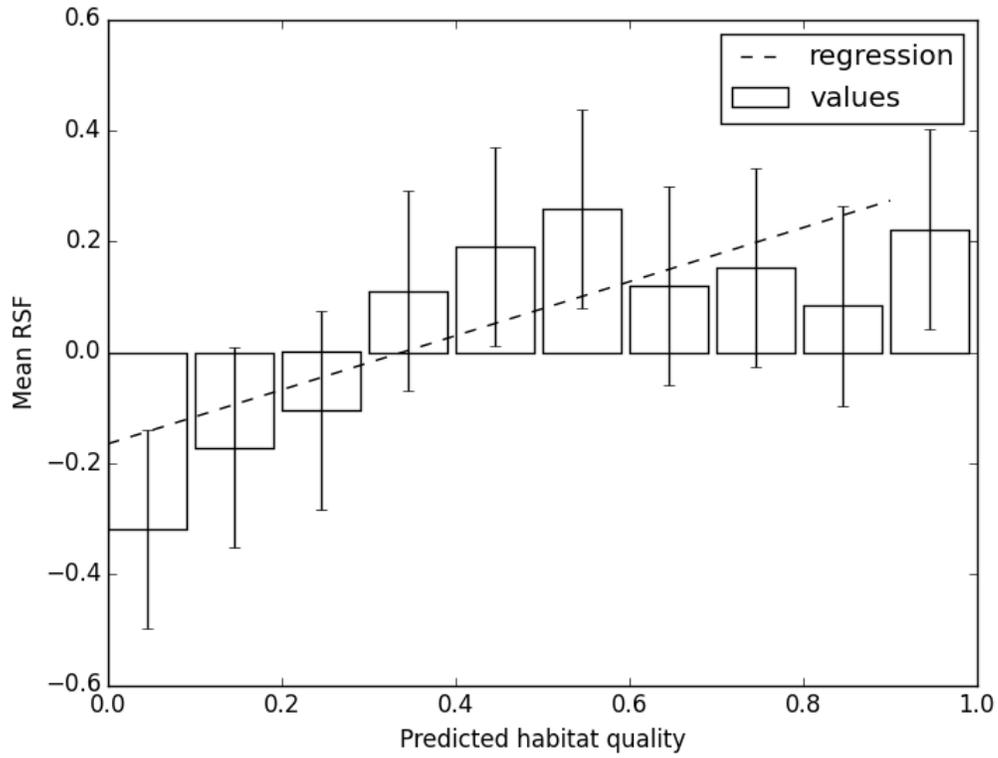


Figure Carrollhomerangebyyear. Mean modified-Ivlev resource selection functions for female habitat selection as predicted by the Carroll et al. 1999 model for all female within the 50% isopleth of their home ranges for years 2010 to 2013 (error bars = 1 SD). B. Mean modified-Ivlev resource selection function for all females and years within 50% isopleth of their home ranges for years 2010 to 2014 on Stirling district in northern California.

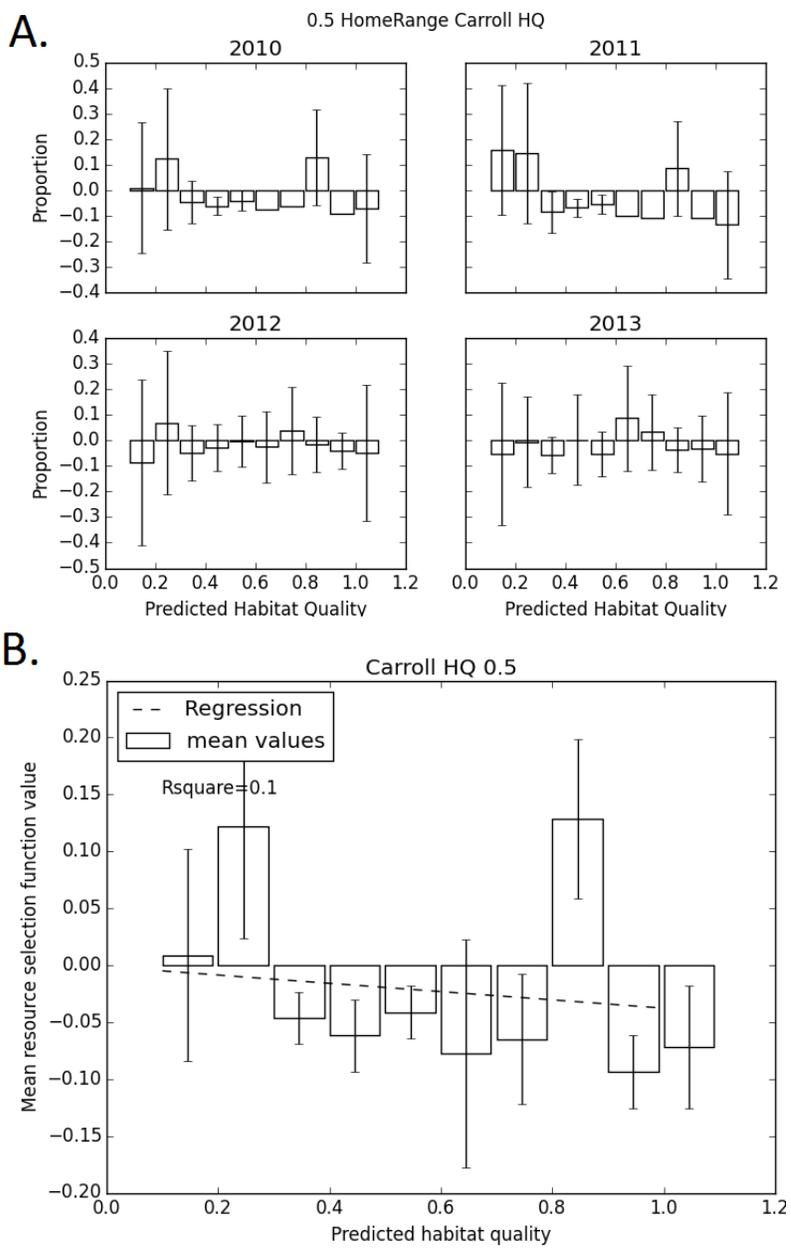


Figure Carroll GPS. Proportion of available and used habitat as predicted by the Carroll et al. 1999 fisher habitat model and the resultant modified-Ivlev and Ivlev resource selection functions for A. data from a female fisher who wore a GPS collared 5 days in fall of 2015 and B) data from a second female fisher who wore a GPS collar for 6 days in fall of 2015, both data sets collected in northern California on the Stirling district owned by SPI.

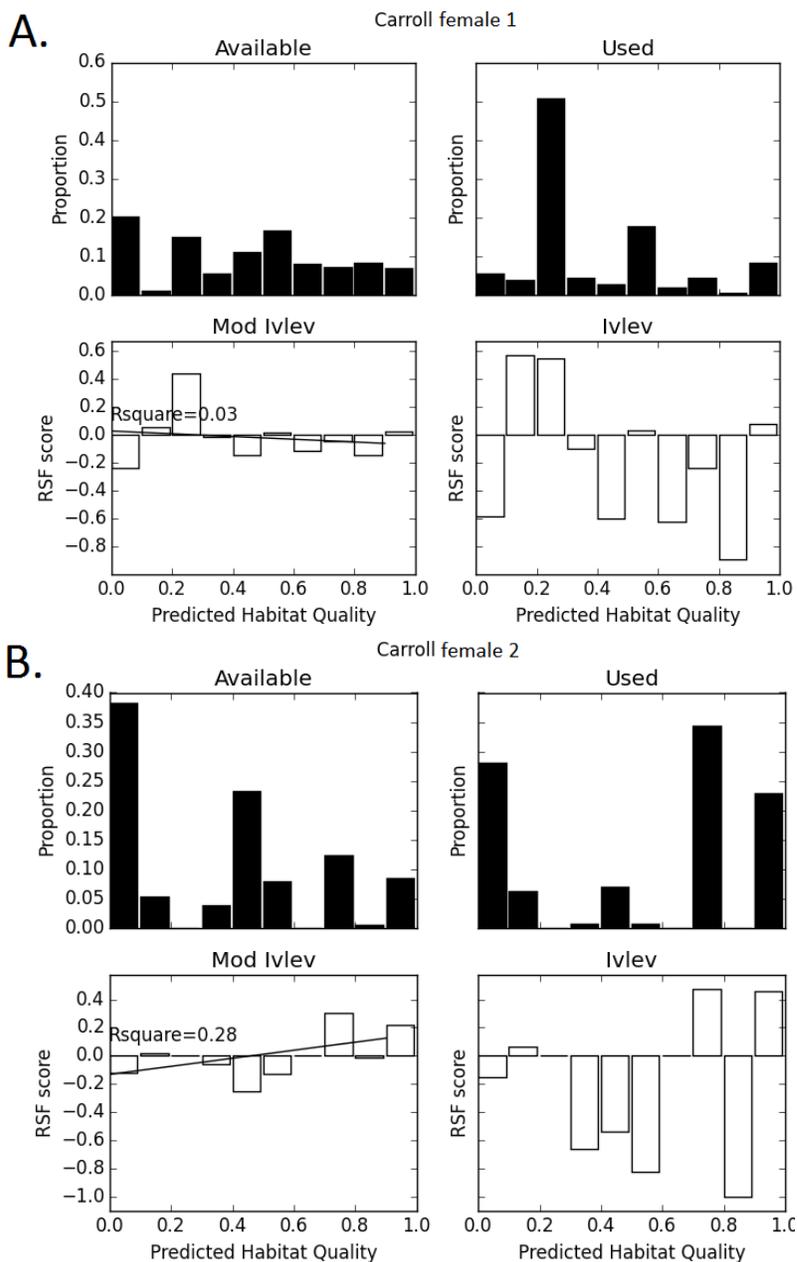


Figure CarrollIndex. Distribution of available habitat as predicted by the Carroll index model for fisher habitat for the Stirling district in northern California in study year 2010.

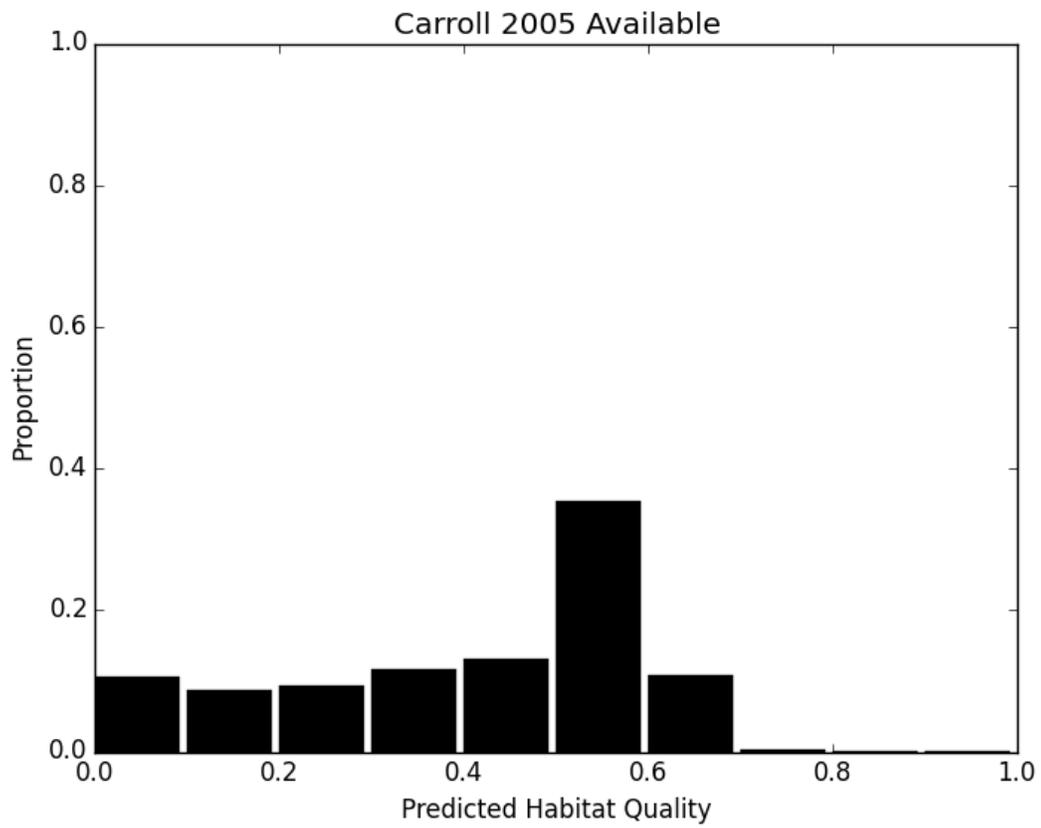


Figure CarrollRSF. Resource selection functions based on the Carroll Index fisher habitat model for Top) Mean Ivlev and modified-Ivlev resource selection functions for all fisher locations on Stirling and Bottom) Mean Ivlev and modified-Ivlev resource selection functions for all fisher locations on Stirling and surrounding areas from 2010 to 2014 in northern California.

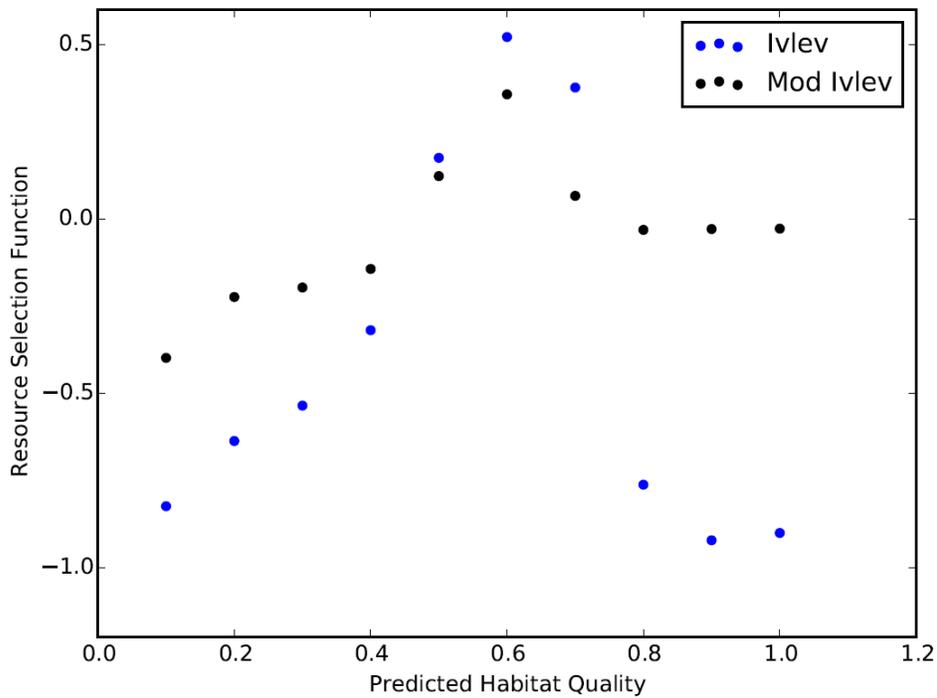
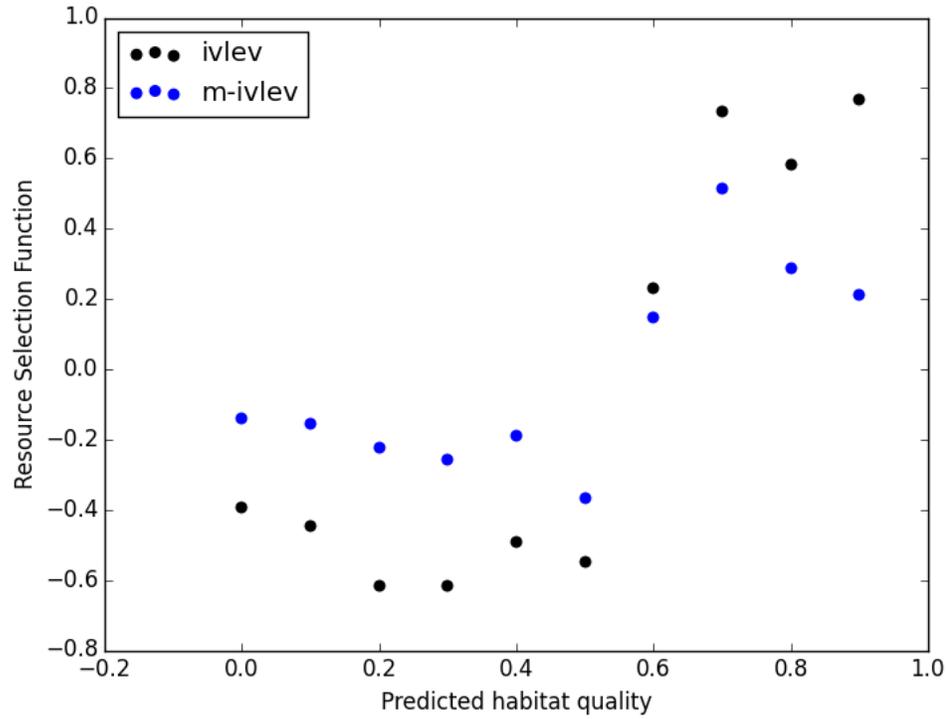


Figure CarRand. Distribution of mean available habitats as predicted by the Carroll Index fisher habitat model across years  $\pm$  SD for years from 2010 to 2014 on Stirling in northern California.

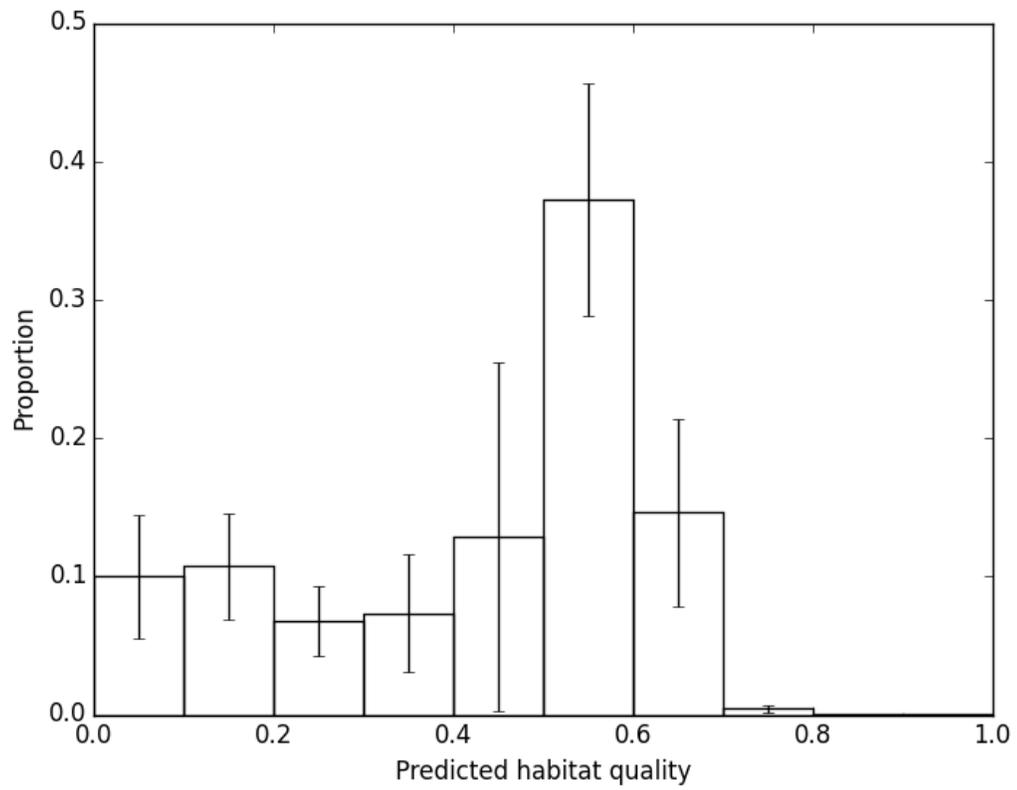


Figure CarIndex\_HR. A. Mean modified-Ivlev resource selections female habitat selection for the Carroll index habitat model for all female within the 50% isopleth of their home ranges for years 2010 to 2013 (error bars = 1 SD). B. Mean modified-Ivlev resource selection function for all females and years within 50% isopleth of their home ranges for years 2010 to 2014 on Stirling district in northern California.

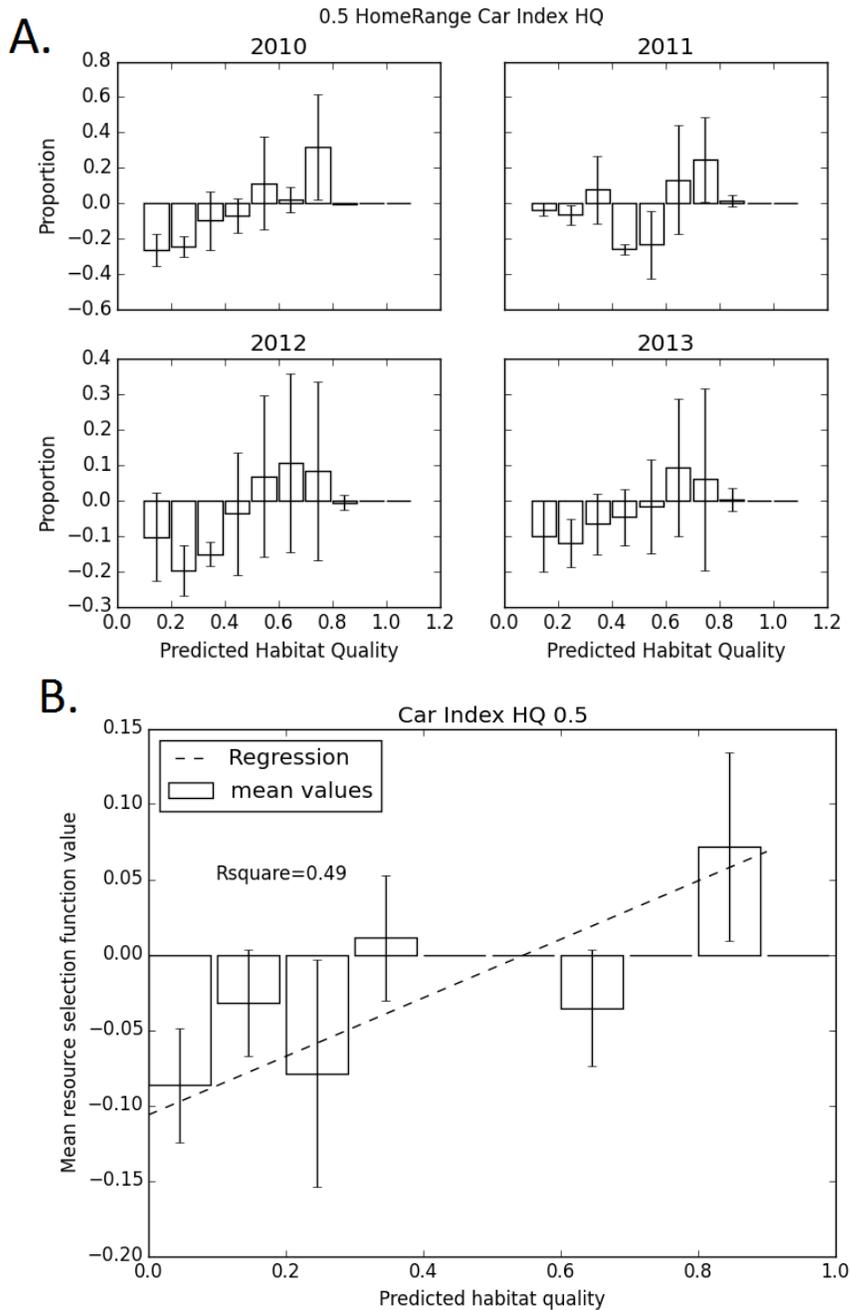


Figure CarIndexGPS. Proportion of available and used habitat as predicted by the Carroll index fisher habitat model and resultant modified-Ivlev and Ivlev resource selection functions for A. data from a female fisher who wore a GPS collared 5 days in fall of 2015 and B) data from a second female fisher who wore a GPS collar for 6 days in fall of 2015, both data sets collected in northern California on the Stirling district owned by SPI.

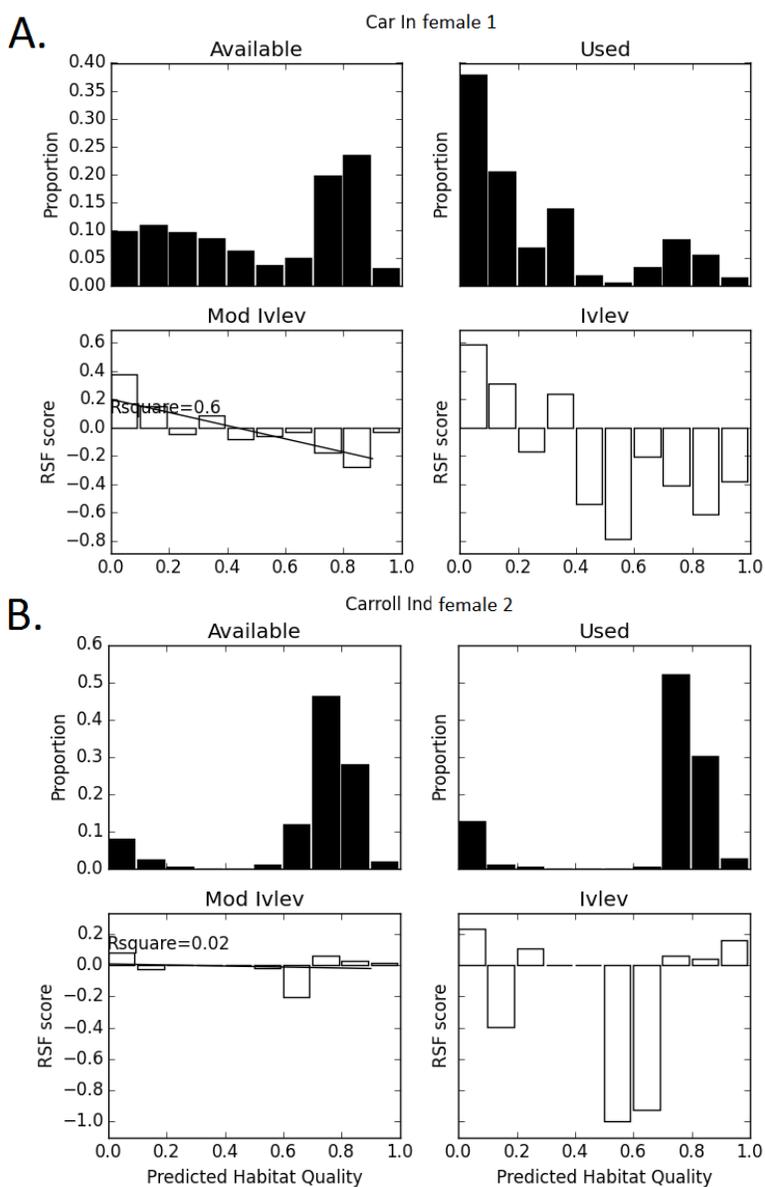


Figure CWHRrand. Distribution of available habitat as predicted by the CWHR habitat suitability model for the Stirling district in northern California in study year 2010.

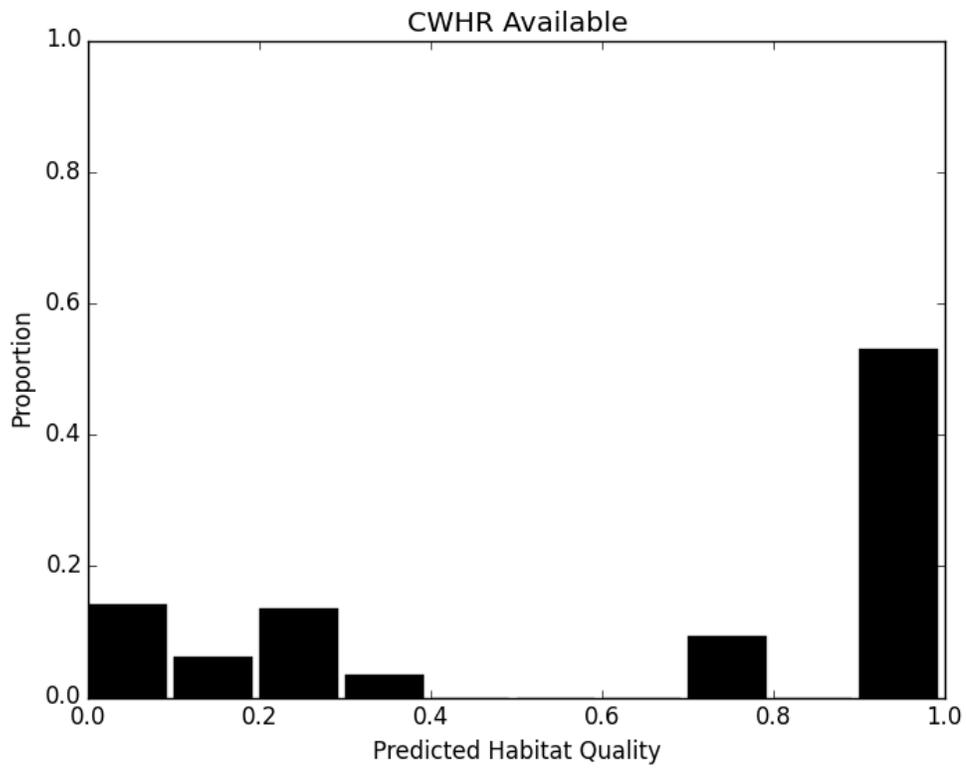


Fig CWHR\_RSF. The average Ivlev and modified-Ivlev resource selection functions based on the CWHR fisher habitat model values for all fisher locations on Stirling and surrounding areas from 2010 to 2014 in northern California

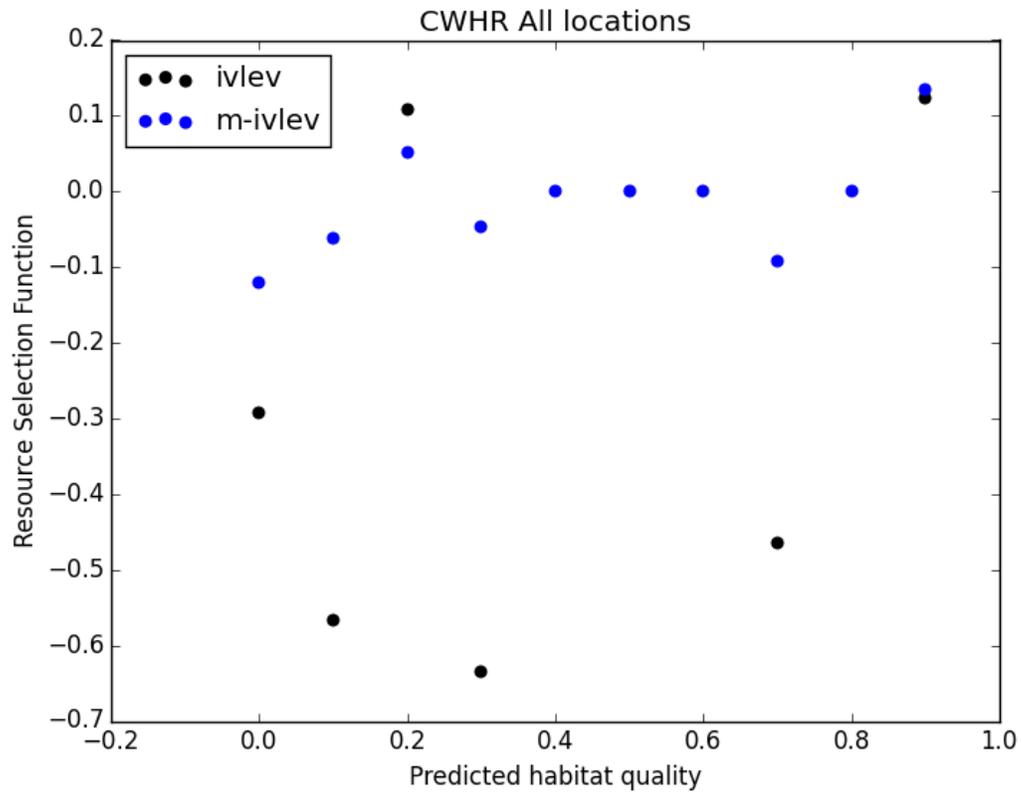


Figure CWHR\_HR. Mean modified-Ivlev resource selections female habitat selection for CWHR fisher habitat model for all female fishers within the 50% isopleth of their home ranges for years 2010 to 2013 (error bars = 1 SD). B. Mean modified-Ivlev resource selection function for all females and years within 50% isopleth of their home ranges for years 2010 to 2014 on Stirling district in northern California.

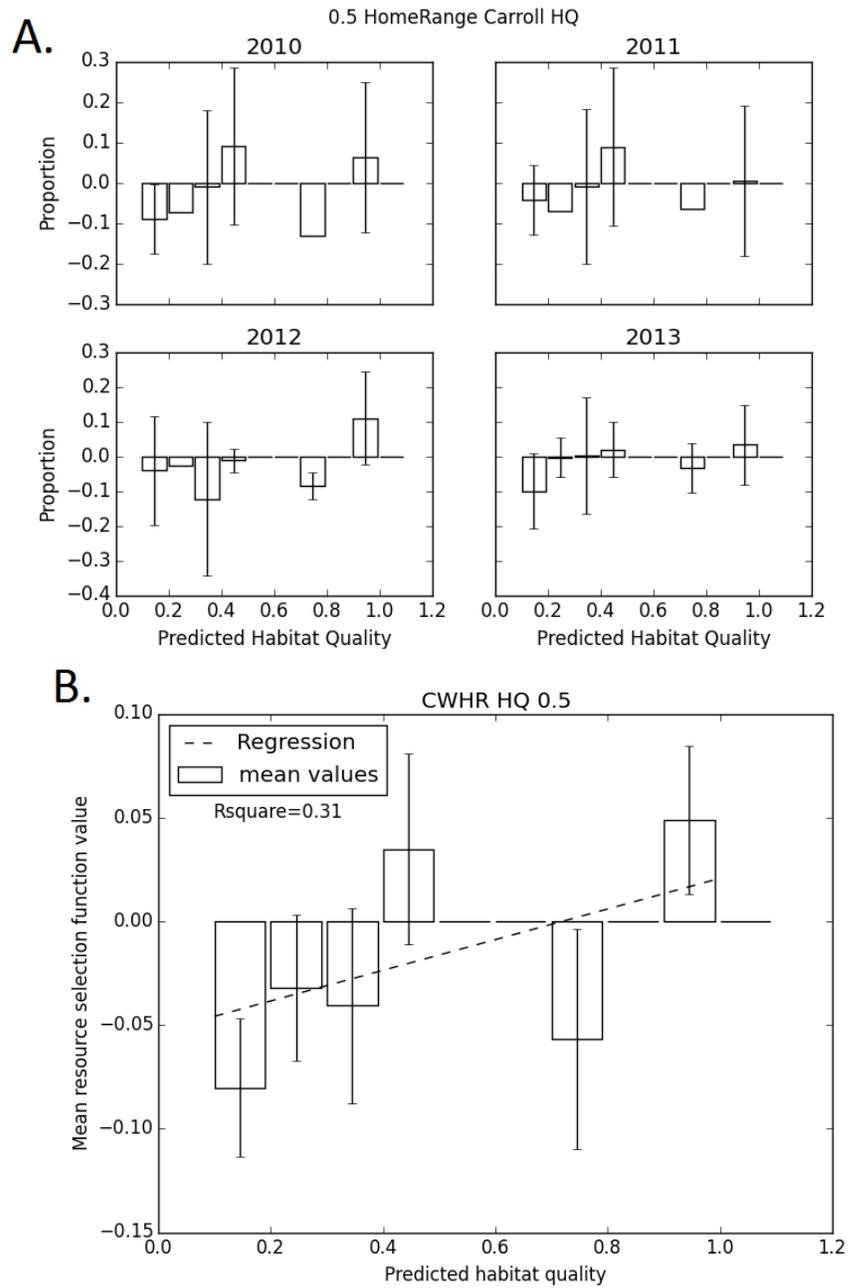


Figure CWHR\_GPS. Proportion of available and used habitat as predicted by the CWHR fisher habitat suitability model and resultant modified-Ivlev and Ivlev resource selection functions for A. data from a female fisher who wore a GPS collared 5 days in fall of 2015 and B) data from a second female fisher who wore a GPS collar for 6 days in fall of 2015, both data sets collected in northern California on the Stirling district owned by SPI.

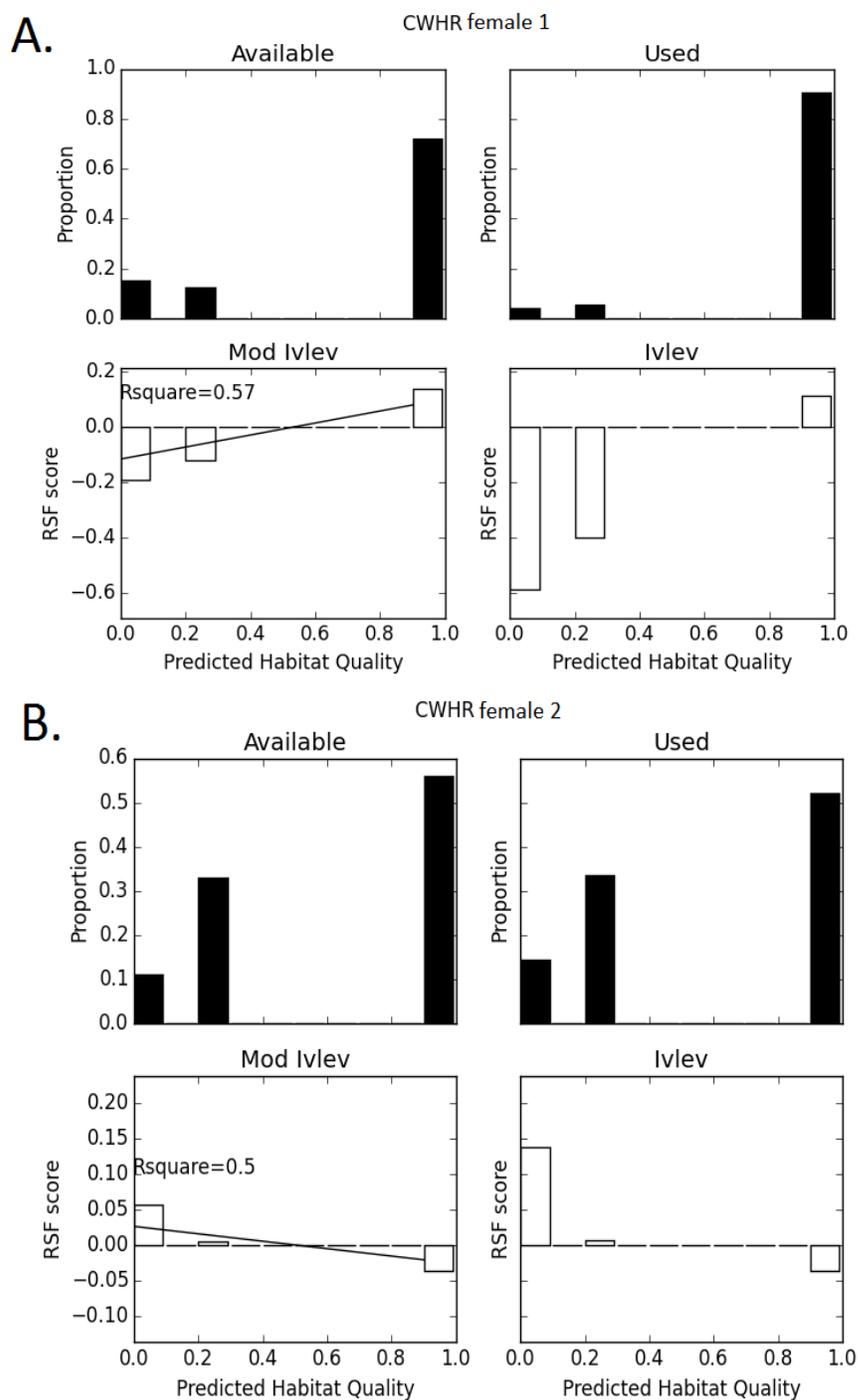


Figure ModOverlap. Areas on Stirling showing overlap between the Allen model (values 0.8-0.9 and the CWHR model (values 0.6-0.7) in green with all other value ranges in black) for year 2011. Colored lines are the 50% isopleths for female fishers in 2011, 2012, and 2013.

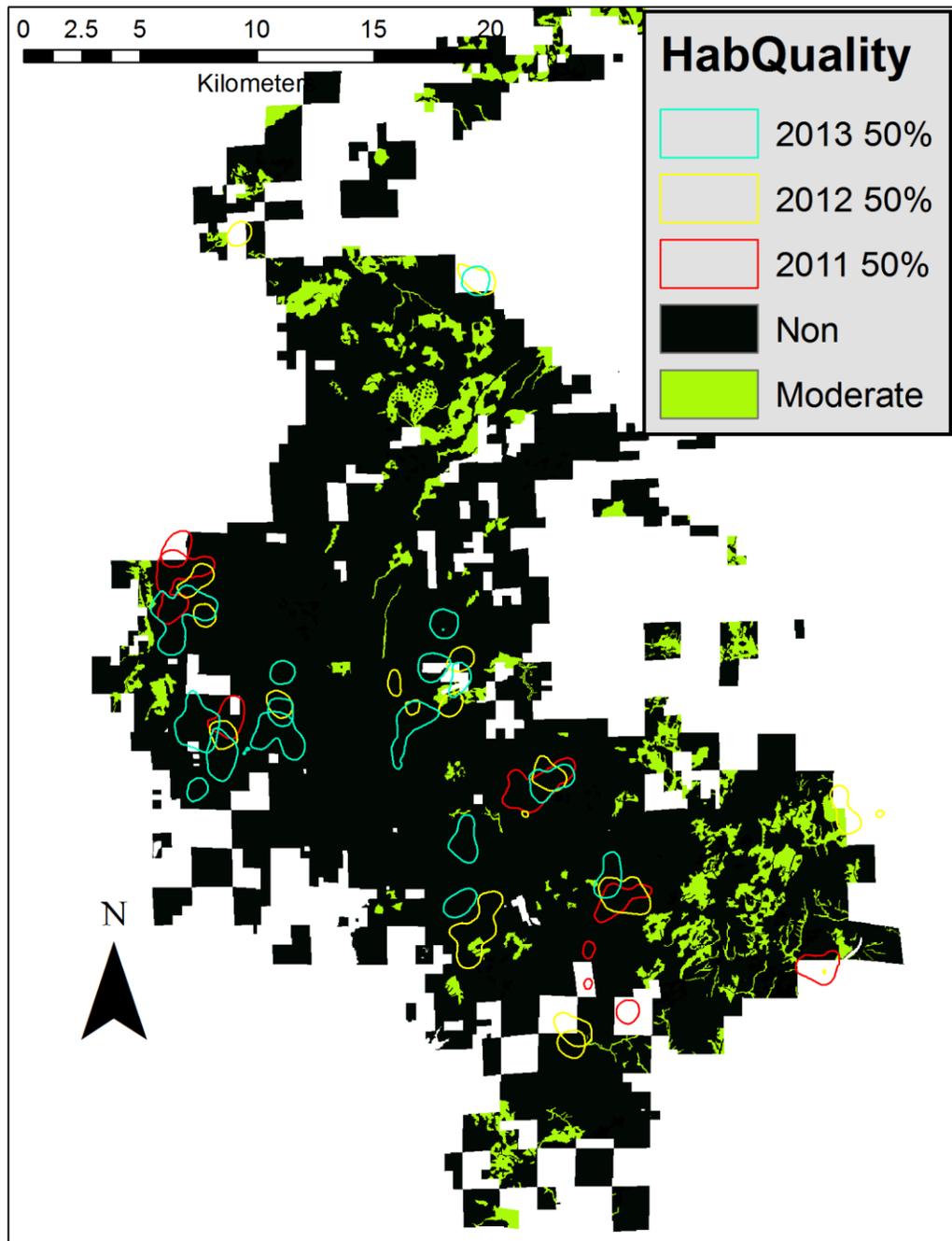


Figure SPIrand. Distribution of available habitat as predicted by the SPI habitat form model for fishers on the Stirling district in northern California in study year 2010.

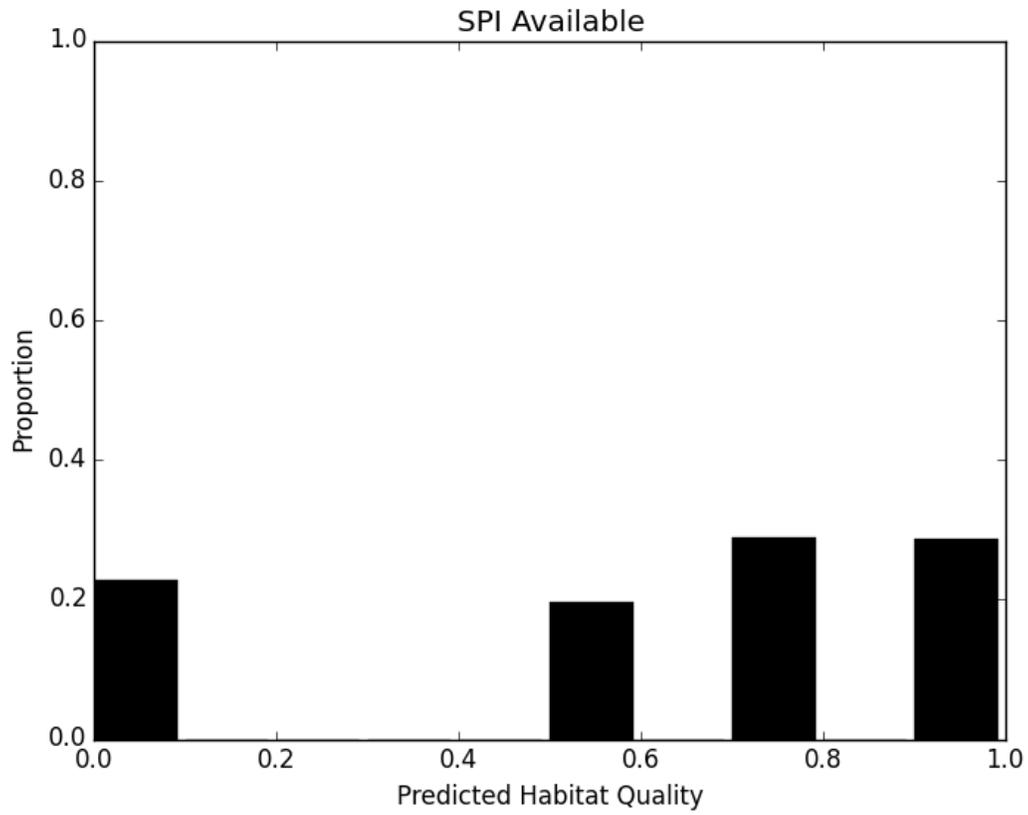


Figure SPI\_RSF. The average Ivlev and modified-Ivlev resource selection functions based on the SPI habitat form model values for all fisher locations on Stirling and surrounding areas from 2010 to 2014 in northern California.

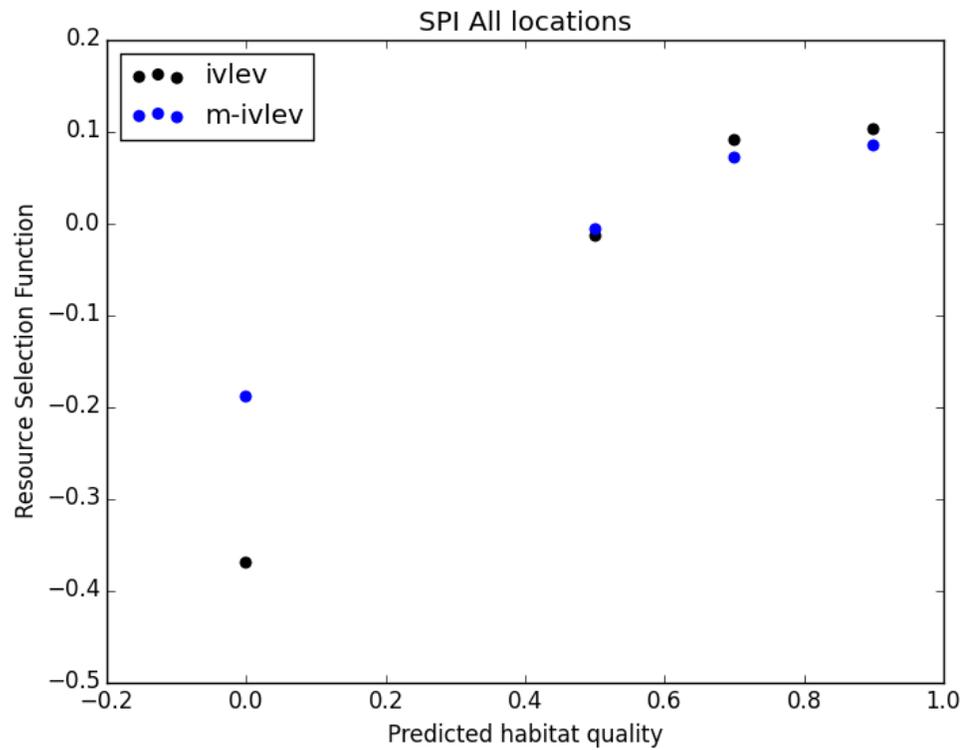


Figure SPI\_HR. A. Mean modified-Ivlev resource selections female habitat selection for Mean habitat for all female within the 50% isopleth of their home ranges for years 2010 to 2013 (error bars = 1 SD). B. Mean modified-Ivlev resource selection function for all females and years within 50% isopleth of their home ranges for years 2010 to 2014 on Stirling district in northern California.

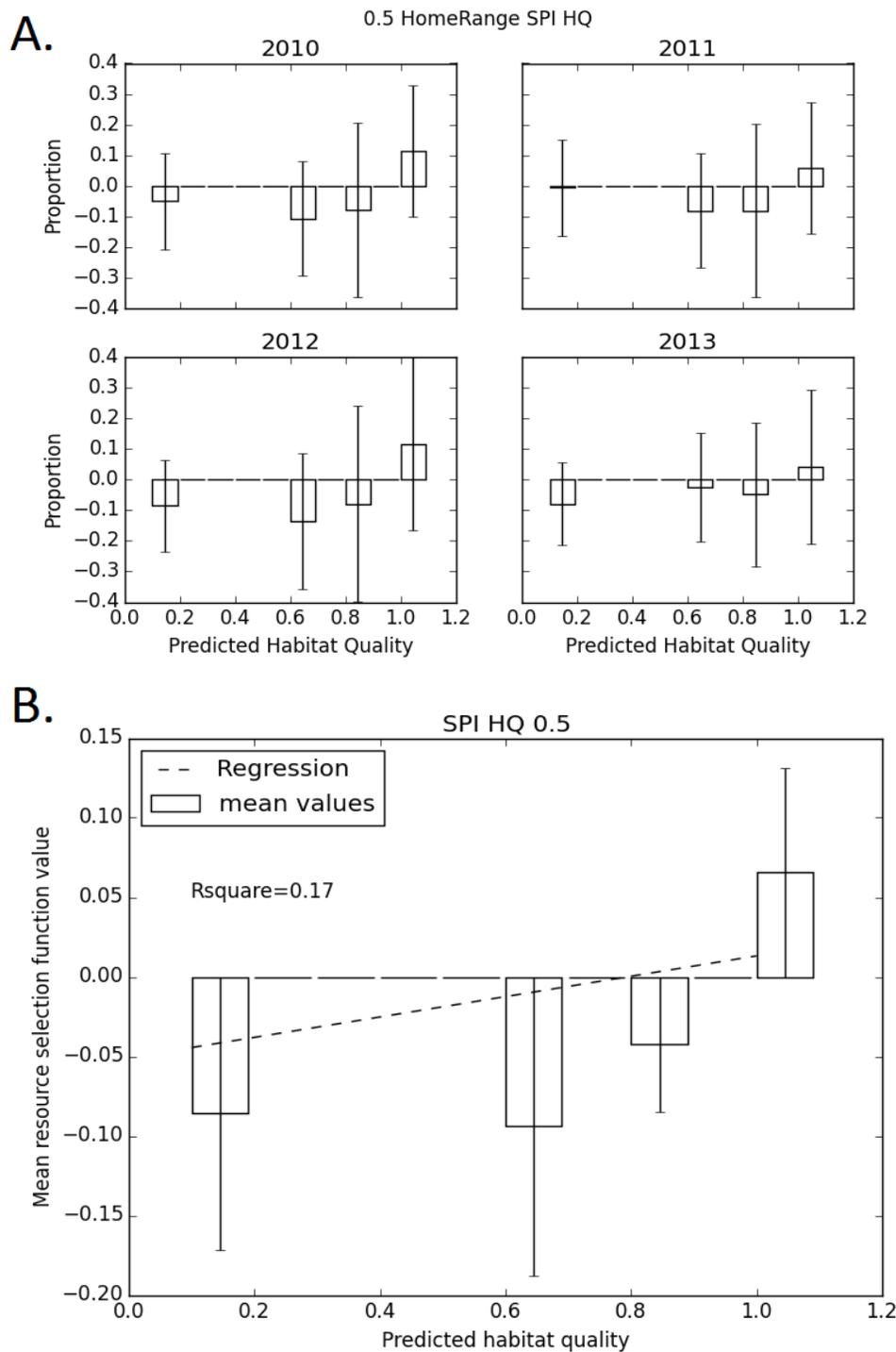


Figure SPI\_GPS. Proportion of available and used habitat as predicted by the Mean habitat suitability model and resultant modified-Ivlev and Ivlev resource selection functions for A. data from a female fisher who wore a GPS collared 5 days in fall of 2015 and B) data from a second female fisher who wore a GPS collar for 6 days in fall of 2015, both data sets collected in northern California on the Stirling district owned by SPI.

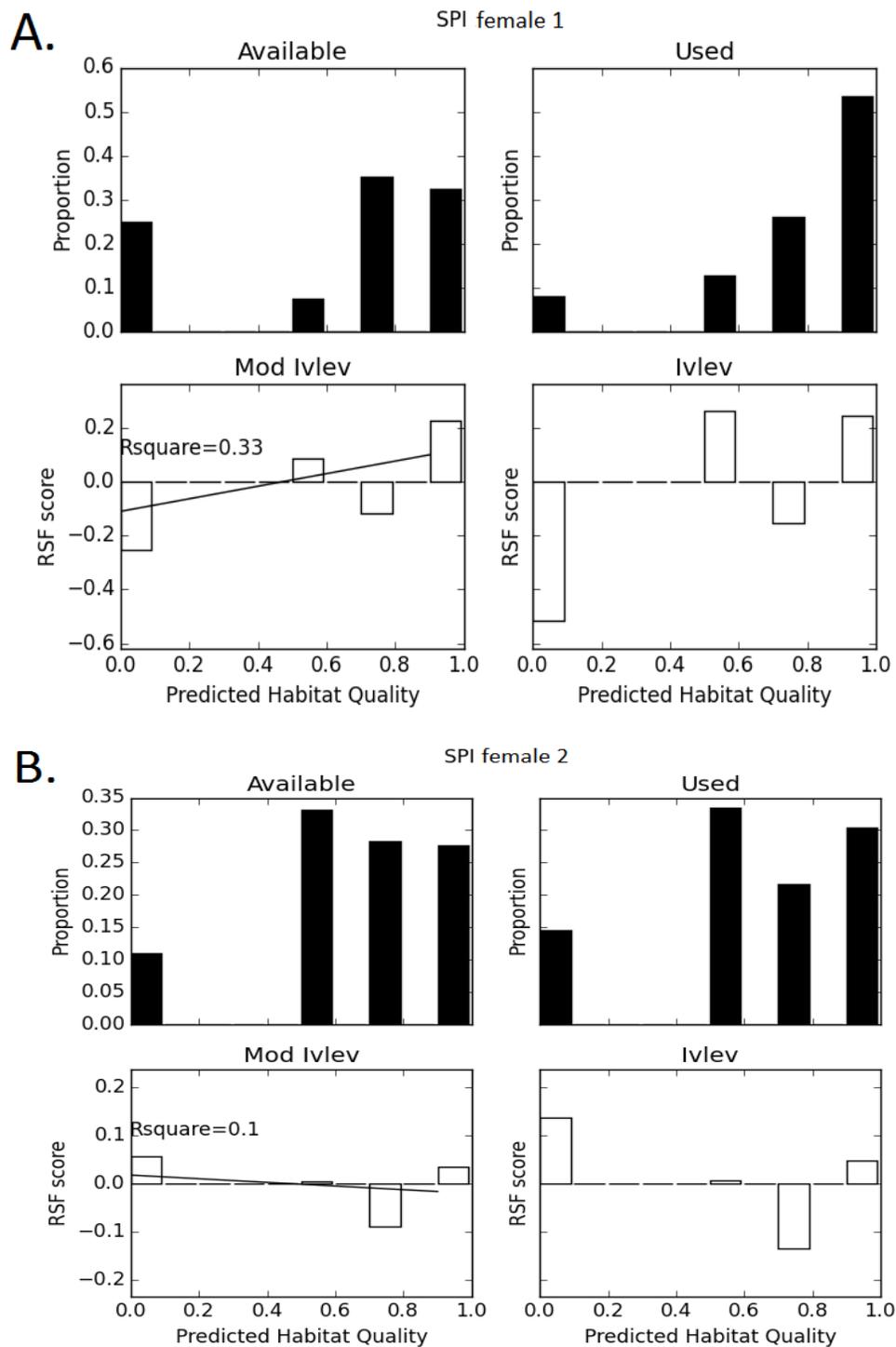


Figure Mean\_rand. Distribution of available habitat as predicted by the Mean habitat model for the Stirling district in northern California in study year 2010.

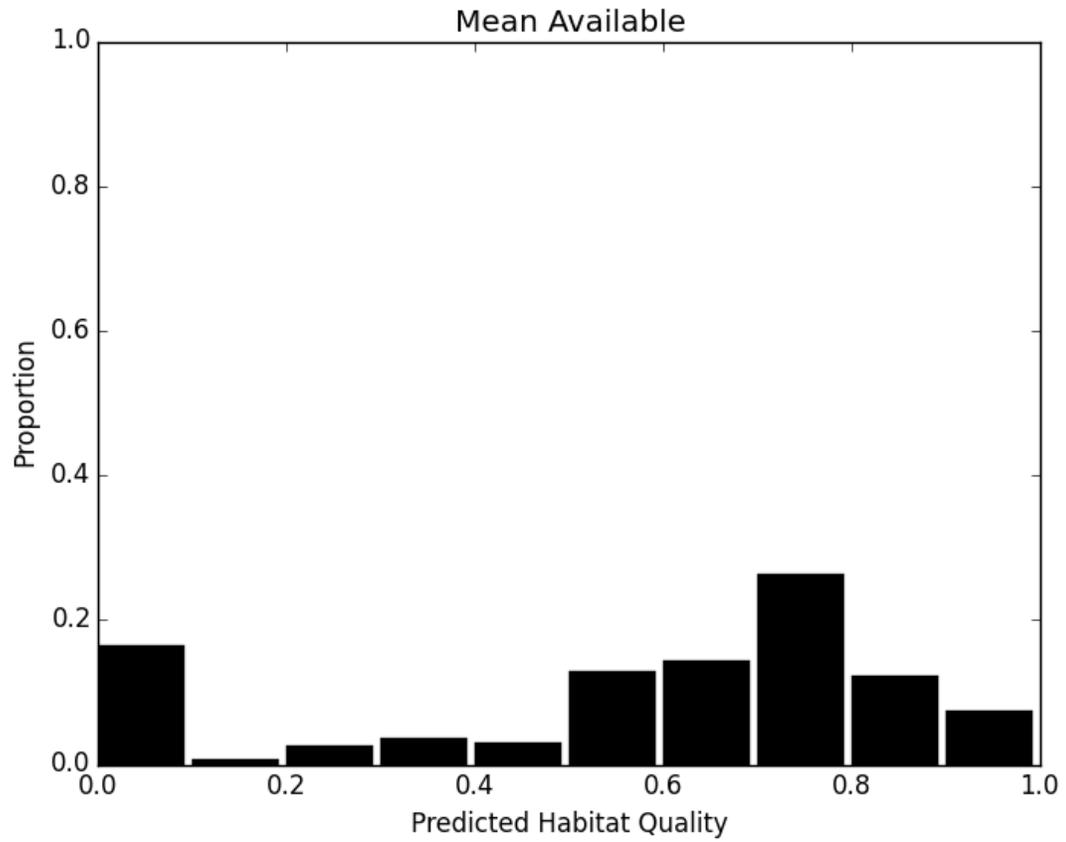


Figure Mean\_RSF. The average Ivlev and modified-Ivlev resource selection functions based on the Mean habitat model values for all fisher locations on Stirling and surrounding areas from 2010 to 2014 in northern California.

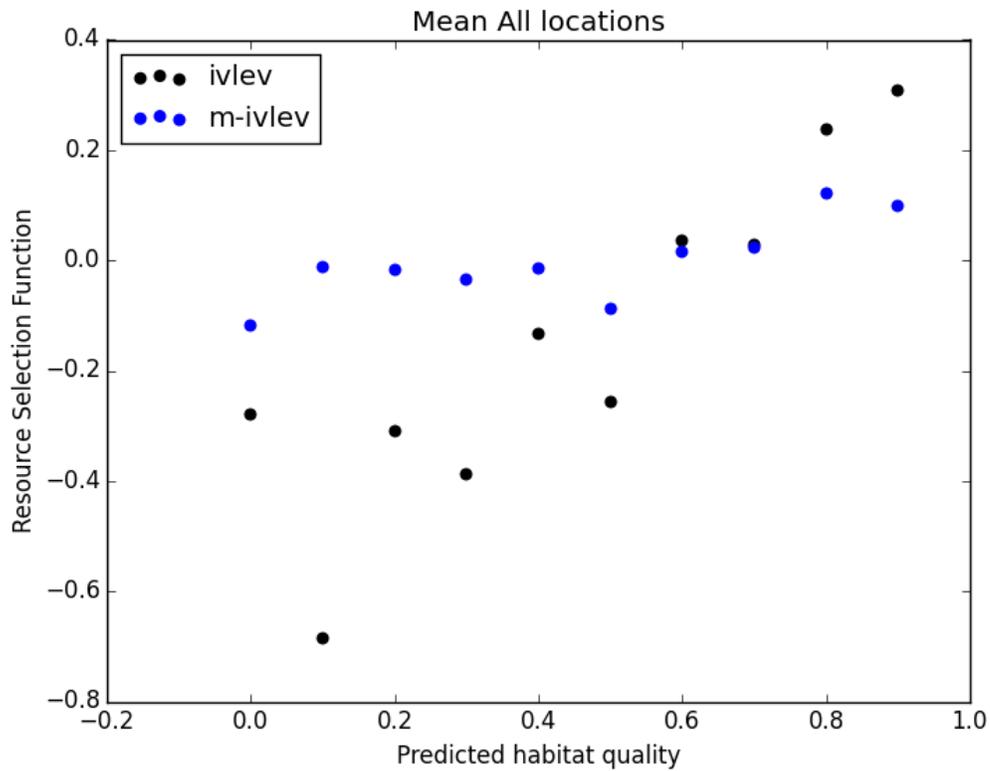


Figure Mean\_by\_year. The mean Modified-Ivlev resource selection function value (bars) at the 50% utilization distribution, and the estimated regression line (dashed line) for all female fishers on Stirling from 2010 to 2014.

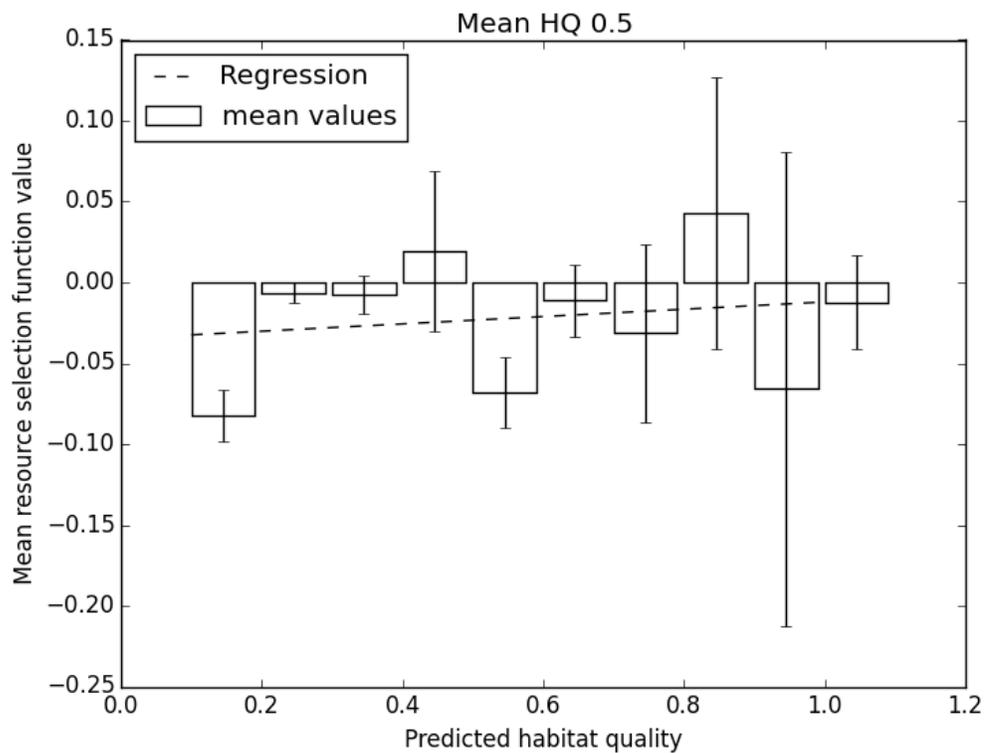


Figure MeanSTD. Plot of habitat values from the mean of 5 fisher habitat models (Allen, Carroll et al., Carroll Index, CWHR, and SPI) against the standard deviation from those same models.

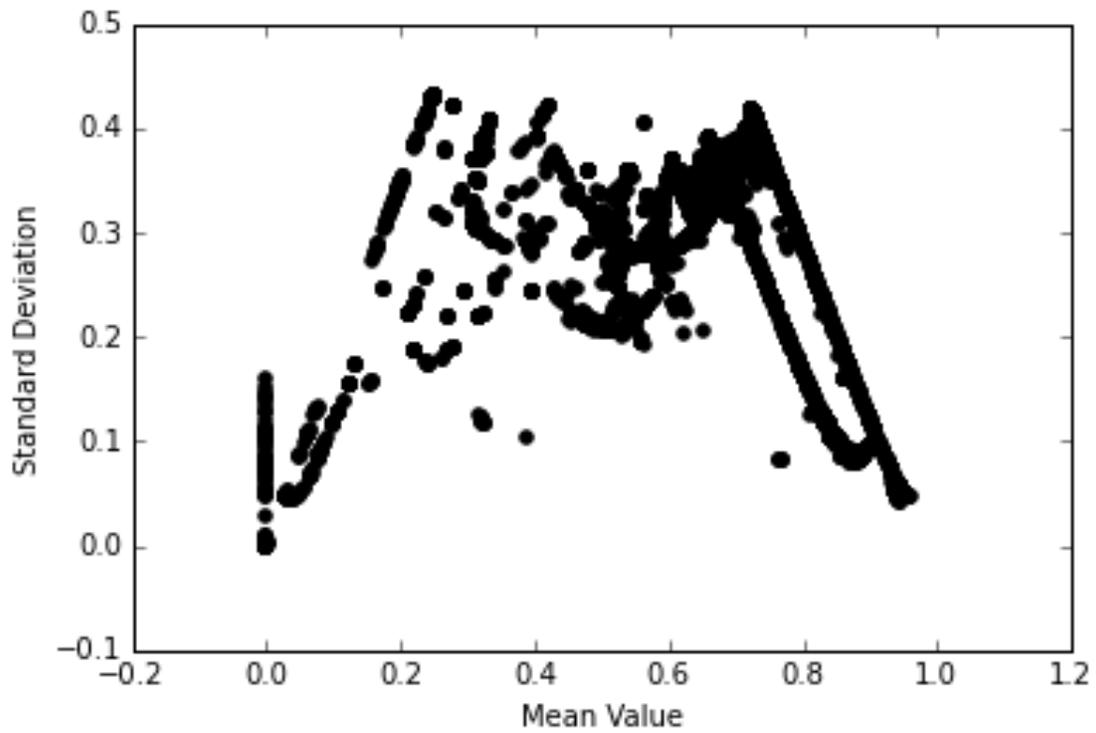


Figure DavisAvailable. Distribution of available habitat as predicted by 6 different fisher habitat models of Davis et al. 2007 for study area in northern California.

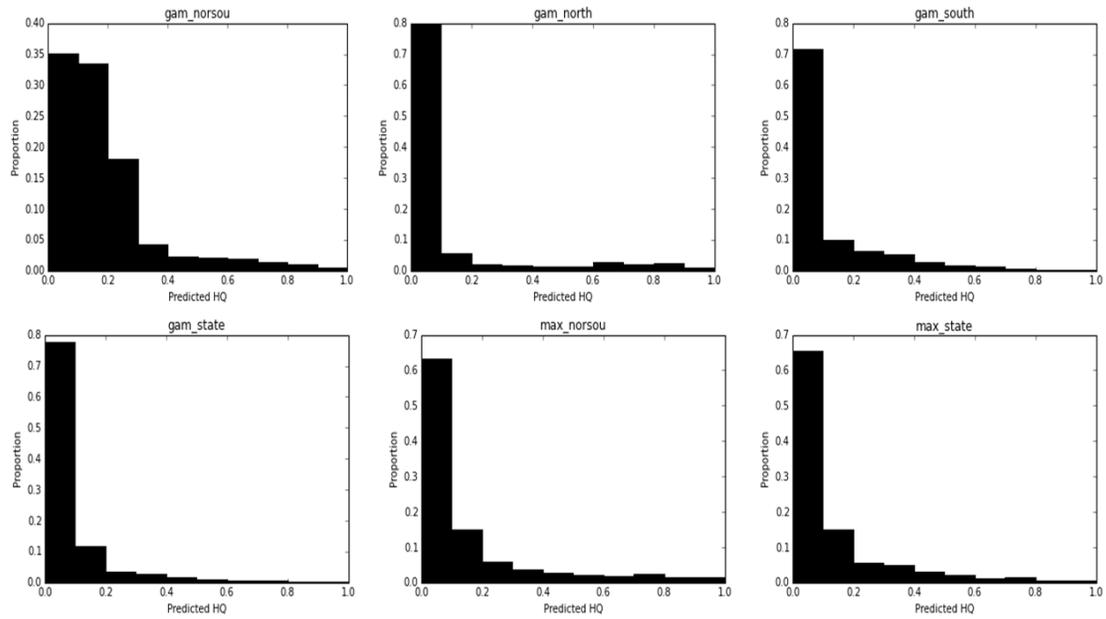


Figure Davis\_map. Spatial distribution of available habitat as predicted by the Generalized Additive Model of Davis et al. (2007) for northern California. Black outline (larger) represent the minimum convex polygon for all fisher locations from 2009-2014 whereas the smaller black polygon is the Stirling study site.

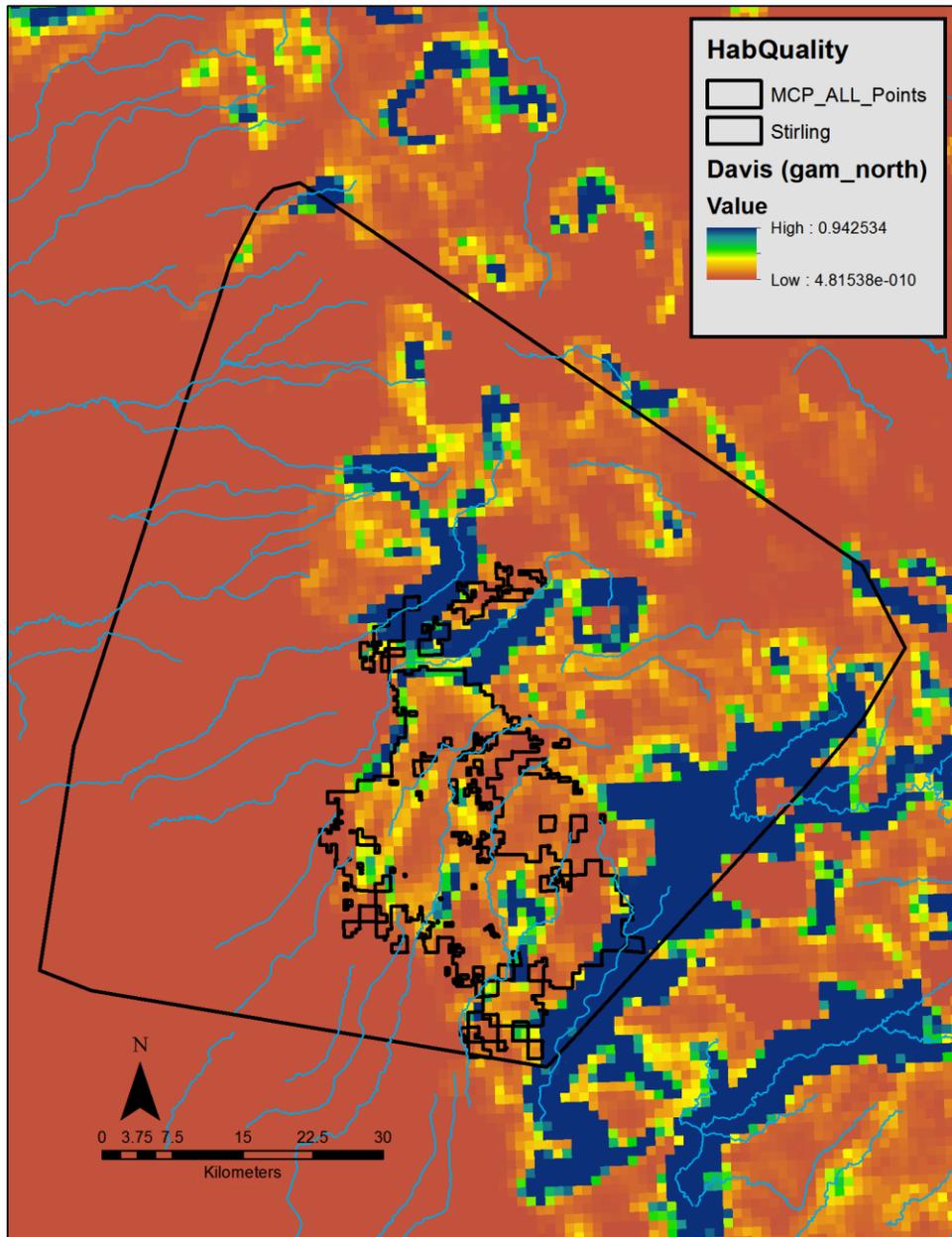


Figure Davis\_RSf. Mean Ivlev and modified-Ivlev resource selection functions based on the Davis et al. Generalized Additive Model for northern California all fisher locations on Stirling and surrounding area in Northern Sierra from 2010 to 2014.

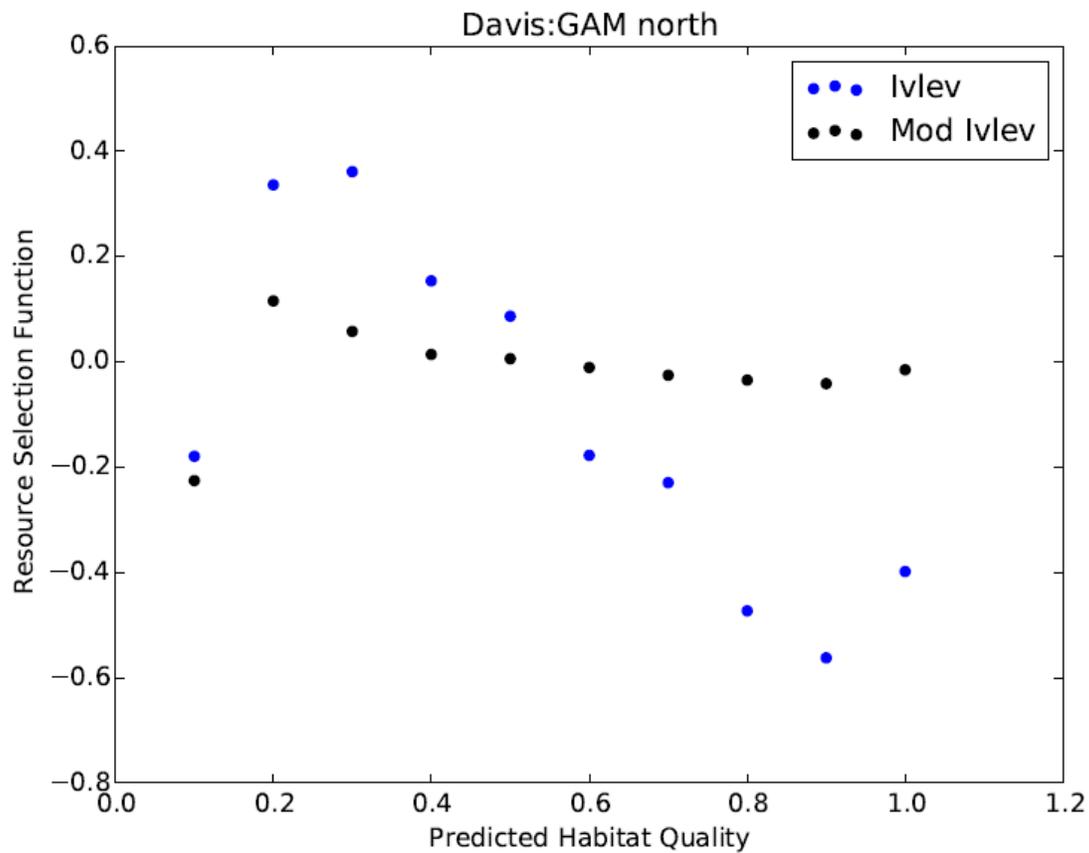


Figure TerritoryCore. Spatial distribution of hexagon categorized as low habitat value (CBT, yellow hexagons), moderate value (SC, green hexagons), and high habitat value (TC, blue hexagons). Hexagons with line fills have 1 (horizontal fill), 2 (diagonal fill), 3 (dotted diagonal fill) and 4 (with vertical dashed fill – a single cell) female 50% isopleth utilization distributions within them for fishers in northern California from 2010 to 2014.

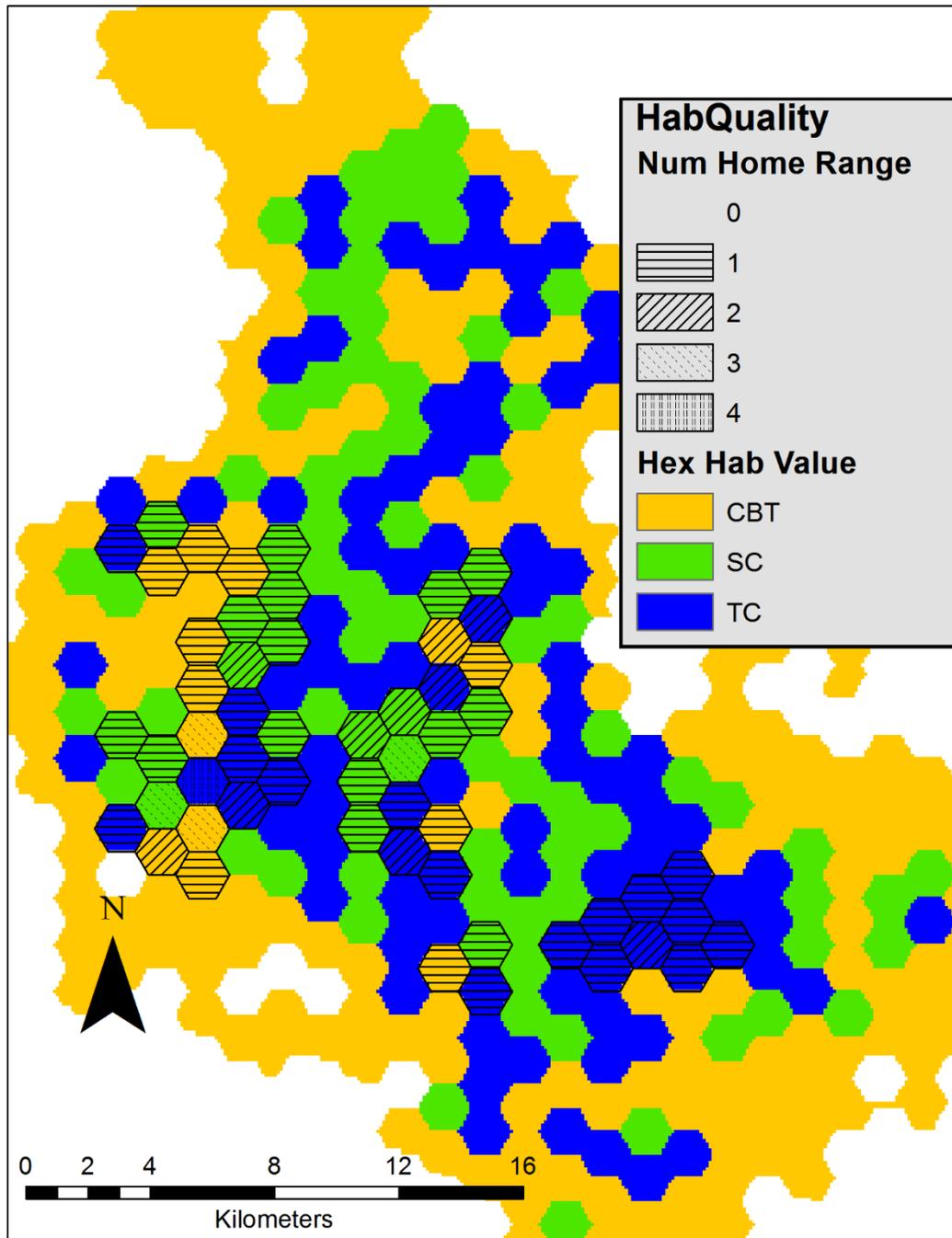


Figure MeanHexVal. The mean value of hexagons that had 1, 2, 3 or 4 female fisher home ranges within them from 2010 to 2014.

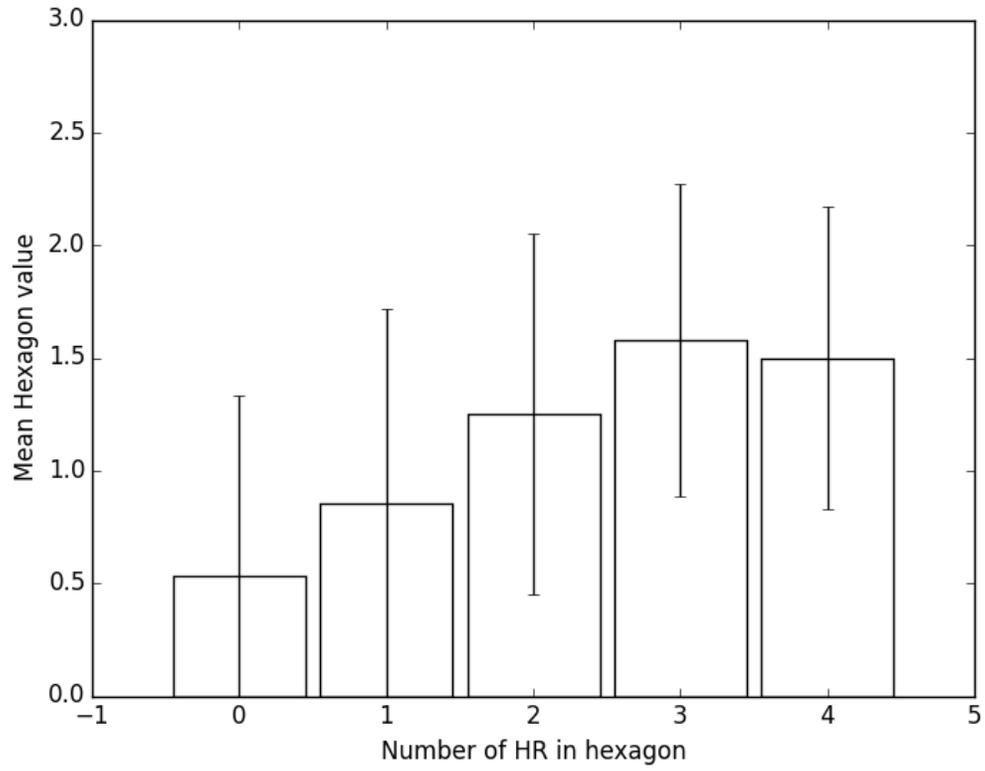


Figure Terr\_dist. Distribution of the proportion of female fisher utilization distributions that occurred in hexagons categorized as low habitat value (Currently Below Threshold [CBT]), moderate value (Support Core [SC]), and high habitat value (Territory Core [TC]) for fishers in northern California from 2010 to 2014.

