SEASONAL HOME RANGE VARIATION AND SPATIAL ECOLOGY OF PEREGRINE FALCONS (FALCO PEREGRINUS) IN COASTAL HUMBOLDT COUNTY, CA

By

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ABSTRACT

SEASONAL HOME RANGE VARIATION AND SPATIAL ECOLOGY OF PEREGRINE FALCONS (FALCO PEREGRINUS) IN COASTAL HUMBOLDT COUNTY, CA

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Peregrine falcons (*Falco peregrinus*) are renowned for their migratory habits, with ‘*peregrinus*’ often translated as ‘wanderer’ or ‘pilgrim’. However, their migratory habits may differ by population and some peregrine may falcons forgo migration when climate and resources remain stable. To examine peregrine falcon home range and space use, I fitted GPS-satellite transmitters to nine breeding adults in coastal northern California, an area with a mild climate and abundant waterbird populations. I used kernel density estimates and time-local convex hulls to examine seasonal home ranges and within-home range habitat use. All nine peregrine falcons remained resident in their territories year-round, and home ranges continued to center around the location of the nesting structure (i.e. bridge or cliff face) even during winter. Home range sizes were larger in the breeding season than in winter, indicating that peregrines did not need to travel farther to find food during the winter and that local conditions were conducive to year-round occupancy. Intensity of space use within the home range was influenced by several environmental covariates, including distance to water, distance to nest site, elevation, prey density, terrain ruggedness and habitat type. Peregrine falcons preferred habitat types associated with nest sites, where they remained year-round, and with open areas such as mud flats, beaches, some agricultural lands, and inland standing water. Intensity of use decreased with distance from bodies of water, distance from nest sites, and terrain ruggedness. Intensity of use was positively associated with elevation and an index of prey density. Our results demonstrate non-random space use within the home range and provide new information about previously unstudied non-migratory behaviors of coastal breeding peregrines in Humboldt County, California.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Describing animal home ranges and movement is a prerequisite for effective management and conservation and for understanding species behavior and ecology (Burt 1943, Cagnacci et al. 2010, Powell 2012, Powell and Mitchell 2012). While much focus within spatial ecology is often centered on estimates of home range size and boundaries (Powell 2012), examining the space use intensity and movement patterns that form home ranges may provide more information about how animals respond to and utilize their environment. Space use dynamics within the home range of peregrine falcons (*Falco peregrinus*) have received less attention compared to other aspects of their ecology (McGrady et al 2002, Ganusevich et al. 2004, but see Lapointe et al. 2013). Due to their migratory habits, most research investigating home range or space use in peregrine falcons focuses either on their breeding or wintering ranges (Jenkins and Benn 1998, McGrady et al. 2002, Ganusevich et al. 2004, Lapointe et al. 2013, Sokolov et al. 2014). To our knowledge, the changing aspects of seasonal home ranges throughout the year and within home range space use for peregrine falcons has not been evaluated.

Some peregrine falcons may make shorter migrations or completely forgo migration if the climate and prey availability permit (Jurek 1989, Ratcliffe 1993, White et al. 2002, Henny and Pagel 2003). Remaining resident on breeding territories throughout the year circumvents migration, which is a potentially dangerous and energy-intensive activity (Franke et al. 2011). It also allows breeding pairs or individuals to maintain their claim on valuable nesting sites typically found on rocky cliff faces, but more recently on suitable urban structures (Ratcliffe 1993, White et al. 2002). References to non-migratory peregrine falcons occur regularly within the literature, and they are generally referred to as inhabiting temperate, mid-latitude areas and areas of low elevation (Ratcliffe 1993, White et al. 2002, Henny and Pagel 2003). The spatial ecology of these non-migratory peregrine falcons has remained unstudied. Studying non-migratory segments of the general population may provide a valuable opportunity to examine the basic ecological relationship between individual peregrine falcons and their environment. It allows for the examination of home range and space use in the absence of migration, which is driven by seasonal fluctuations in climate conditions and prey availability (Newton 1979, Ratcliffe 1993). It also allows for comparison between migratory and non-migratory portions of the North American peregrine falcon population, which may differ in resource requirements, seasonal home range size, habitat utilization, survival, and reproductive success.

Selection of habitats or space within the home range (i.e. third order selection; Johnson 1980) is an important scale at which to study individual behaviors (Cagnacci et al. 2010, Benhamou and Riotte-Lambert 2012). Examining space use intensity at this scale can reveal important areas and habitats within the home range and improve our knowledge of how an animal utilizes resources and responds to changing environmental conditions (Behamou and Riotte-Lambert 2012, Lyons et al. 2013). For peregrine falcons, space use within the home range may be influenced by prey abundance or vulnerability, as well as the presence of habitats that provide hunting opportunities suitable for peregrine hunting tactics (Ratcliffe 1993, Dekker 2009). Habitats may influence space use by providing hunting opportunities through presence of prey, cover from which to launch surprise attacks, and open space in which to capture prey in open flight (Fox 1995, Dekker 2009, White et al. 2002). Although they are known for inhabiting a variety of habitats, peregrine falcons are heavily associated with wetlands, coastal habitats, and inland bodies of water where they can pursue alcids, shorebirds and waterfowl, which are some of the more commonly utilized prey groups (Ratcliffe 1993, Dekker 1999, White et al. 2002). Elevation and terrain ruggedness may also influence space use. Peregrine falcon hunting perches are frequently located on locally prominent landscape features that provide a wide vantage point over open space such as cliffs and ridgelines that overlook open habitats (Enderson and Craig 1997, Jenkins and Benn 1998). Searching for prey is done either in flight or, more frequently, from perches. Perch hunting is the more energy efficient (Ratcliffe 1993) and successful (Jenkins 2000) searching method, with a positive relationship between the height of cliffs from which attacks are launched and hunting success (Jenkins 2000). Shorebirds and waterfowl, common prey of peregrine falcons (White et al. 2002), are associated with coastal and inland bodies of water and can congregate in large numbers. Areas where prey habitually congregate may also influence intensity of space use within the home range. Peregrine falcons may actively seek out areas of higher prey concentration, or bodies of water where prey might congregate, in search of hunting opportunities or to increase hunting success. Determining what factors drive changes in home range size and within-home range space use in a potentially resident group of peregrine falcons ultimately has implications for understanding population-level ecology (Benhamou and Riotte-Lambert 2012, Powell 2012).

Another aim of my study was to confirm the occurrence of non-migratory behavior in peregrine falcons living in coastal northern California, where the climate is moderate and there is abundant potential prey (B. Walton personal communication in White et al. 2002). I also sought to quantify and compare home range characteristics during the breeding (March – August) and winter (September – February) periods for female and male peregrine falcons, as they may differ in seasonal behaviors (White et al. 2002). Possibly due to hunting activities after young have fledged, breeding females can have larger home range sizes than breeding male peregrines (Enderson and Craig 1997), although males have been observed to range more widely than females during the breeding season (Jenkins and Benn 1998). Males and females from the same breeding areas have also been seen to utilize different migratory paths and wintering areas (McGrady et al, 2002, White et al. 2002). Ratcliffe (1993) observed breeding pairs that appeared to remain resident on their territories during the winter in Britain. Some of these pairs appeared to stay together in their breeding territories, while others separated and roosted on different cliffs, and other pairs moved together to a different area within or near to their breeding territory. This is possibly a consequence of increased ranging during the winter in response to reduced prey availability or differences in prey distribution (Ratliffe 1993). In a coastal area with a moderate climate, peregrine falcons in Humboldt County may range more widely during the winter or shift their patterns of habitat use in response to seasonal changes in prey abundance or distribution.

I used third generation home range analysis methods to create seasonal utilization distributions and to generate seasonal indices of space use intensity within the home range for male and female peregrine falcons. I used generalized linear mixed models to examine the influence of selected environmental covariates and habitat types on the intensity of space use within the home range.

MATERIALS AND METHODS

Study Species

The peregrine falcon (*Falco peregrinus*) is a mid-sized falcon with a nearly global distribution, occurring on every continent except for Antarctica. Peregrine falcons exploit a wide range of habitats and prey species, (Ratcliffe 1993, White et al. 2002). Prey are primarily avian species which are generally selected in relation to their abundance or vulnerability, depending upon the geographic location and season. Peregrines may also may take bats, rodents and occasionally fish and invertebrates (White et al. 2002). It has been observed that certain individuals can specialize in hunting a few prey species, likely due to personal preference or acquired hunting skills, or both (Ratcliffe 1993, White et al. 2002). Three subspecies of peregrine falcon occur in California; the American (*anatum*), Peale's (*pealei*), and the Tundra (*tundrius*) (White et al. 2002). Only the American peregrine falcon (*F. p. anatum*) breeds in California (Comrack and Logsdon 2008). In North America regional populations generally follow a 'leap-frog' pattern of migration (McGrady et al. 2002). Northern breeding populations undergo the longest migrations, traveling farther south and passing over other populations that make shorter migrations. Peregrine falcons that breed at low elevations or in temperate areas may completely forgo migration if local climate and prey availability permit (White 1968, Jurek 1989, Henny and Pagel 2003).

Peregrine falcons occur in a wide variety of habitats, with habitat selection being driven by the availability of suitable nesting sites and proximity to prey (Newton 1979, Ratcliffe 1993). Nest site availability and prey density influence territoriality and territory size also influence breeding population densities (Newton 1979, Ratcliffe 1993). Within their seasonal home range areas, peregrine falcons of both sexes exhibit high fidelity to their nesting territories, and there is also evidence for fidelity to wintering areas (Varland et al. 2012). Many authors report large a variation of home range size estimates within their study population (Dobler 1993, McGrady et al. 2002, Ganusevich et al. 2004, Lapointe et al. 2013, Solokov et al. 2014), although some estimates may be difficult to compare across studies due to the use of different methods. Estimates from across the globe for females during the breeding season range from 23 – 1,251 km^2, whereas males range from 19.5 – 1,126 km^2, with the larger estimates and ranges of estimates occurring in northern areas or regions of high elevation (Enderson and Craig 1997, Jenkins and Benn 1998, Ganusevich et al. 2004, Lapointe et al. 2013, Solokov et al. 2014). Breeding and winter home range sizes are influenced by availability of suitable nesting sites in relation to prey availability and density and therefore range widely depending upon geographic locations (Newton 1979, Ratcliffe 1993). There are fewer winter home range estimates, and these also have a large range of reported values but are smaller than the breeding range size estimates with reported ranges varying from an average of 75.7 km^2 (harmonic mean) in Washington U.S.A, (Dobler 1993) to 169 km^2 (minimum convex polygon) in coastal Mexico (McGrady et al. 2002).

Study Area

I studied breeding peregrine falcons along the coastline of Humboldt County (N40° 44’ 59” to W124° 12’ 34”), California (Figure 1). Humboldt County forms part of the Pacific Flyway, and hosts migrant passerines, shorebirds, waterfowl and others. It is home to the second largest bay in California, Humboldt Bay, and several estuaries that serve as migratory stop-over or wintering sites for large numbers of shorebirds (Colwell 1994). and waterfowl (Monroe 1973). Colwell (1994) estimated that Humboldt Bay alone may host 10,000 – 100,000 migrating and wintering shorebirds, providing a seasonal source of prey during fall and spring migrations, and during the winter. 197 different species of bird breed within Humboldt County (Hunter et al. 2005), including many potential prey species such as shorebirds and medium-sized passerines. Humboldt County is home to an estimated 22 resident breeding pairs of peregrine falcons (Comrack and Logsdon 2008), one of the highest concentrations in California. The population is larger in the winter, when migratory peregrines winter or pass through Humboldt County’s coastal areas (Comrack and Logsdon 2008). Humboldt County provides nesting habitat for peregrine falcons in the form of coastal cliffs, riverine bluffs and other rocky outcroppings, as well as suitably large, old growth trees (Buchanan et al. 2014).

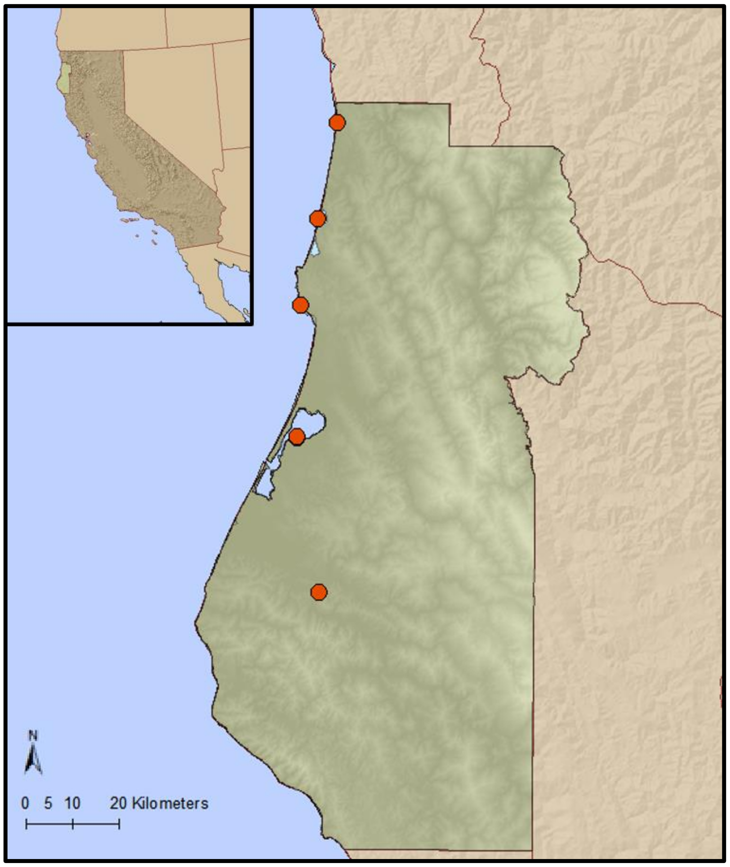


Figure 1. Map showing approximate peregrine falcon trapping locations in Humboldt County, California, USA.

Capture and Transmitter Attachment

We trapped, banded, and attached transmitters to five female and four male peregrine falcons from five locally breeding pairs during the 2014 and 2015 breeding seasons. We conducted this research under the Humboldt State University Institutional Animal Care and Use Protocol No. 13/14.W.87-A. Jeff Kidd and Scott Thomas performed trapping and transmitter attachment in accordance with federal and state permits (Federal Banding Permit #22951, California Fish and Wildlife MOU SC-

001408). Trapping occurred during the early and late phases of nesting to avoid disturbing incubating females during the 2014 and 2015 breeding seasons. We used dho-gaza nets with a live great horned owl (*Bubo virginianus*) lure, as well as bal-chatri traps and noose harnesses with domestic pigeon (*Columba livia domestica*), Eurasian collared dove (*Streptopelia decaocto*) or starling (*Sturnis vulgaris*) lures (Bloom et al. 2007, Boal et al. 2010) to trap target birds. We applied United States Geological Service (USGS) lock-on bands to the right or left leg of captured birds and applied color bands with an alphanumeric code to the other leg (black band with silver lettering) for visual identification. We took standard morphological measurements including culmen, wing cord, flat wing, tail length, hallux, tarsus width and weight. We collected feather and blood samples from three birds. We collected blood samples (0.5 – 1.0 ml) from the brachial vein of either wing using a 25-gauge needle attached to a 1-mL tuberculin syringe (Monoject, Tyco Heathcare Group, Mansfield, MA, USA) (Parga et al. 2001, Pond et al. 2012). Blood samples were given to the Institute for Wildlife Studies. Using a backpack style attachment with Teflon ribbon (Britten et al. 1999, J. Kidd personal communication), we equipped female peregrines falcons with 22g Argos/GPS Solar PTT-100 (Microwave Telemetry). We used 18g versions of the same PTTs for male peregrine falcons. These relative transmitter weights used for female and male birds ensured that we conformed to the common rule that tracking devices and attachment materials should not exceed more than 3% of an animal’s body weight.

Transmitter Data Collection

PTTs were set to collect GPS fixes (accuracy +/- 18 meters) every three hours for a total of five readings per day and one reading at night, with different hours specified for collection during spring (March – August) and winter (September – February). The actual GPS fix rate was dependent upon transmitter battery power, which was dependent upon the solar panels being sufficiently charged. Ancillary data collected concurrently with the GPS fixes included date, time, orientation (+/- 1 degree), speed (+/- 1 knot) and altitude (+/- 22 meters).

Home Range Analysis

There are numerous methods for constructing animal home range estimates. These vary from statistical or probabilistic methods such as kernel density estimators to mechanistic modeling methods (Kie et al. 2010, Cumming and Cornelius 2012, Demsar et al. 2015, Walter et al. 2015). Minimum Convex Polygons (MCPs) are polygons with convex vertices that encompass a certain percentage of animal location points (commonly 10%, 50% and 95%), different percentage levels are referred to as isopleths (Millspaugh et al. 2012). I used MCPs to create annual range estimates for each falcon at the 95% isopleth level for ease of comparison with previous studies. MCPs were created using Program R 2.12 (R Development Core Team 2014) and the adehabitatHR package (Calenge 2006).

I used Kernel Density Estimates (KDEs) to create 95% and 50% utilization distributions to estimate home range sizes and to compare areas of home range overlap between mated pairs. There are multiple ways of selecting a value for the bandwidth or ‘h’ parameter. The bandwidth affects the degree to which each density function affects the value of the neighboring density function, leading to peaks and valleys that reflect probability of occurrence within the utilization distribution (Worton 1989). I used the plug-in (h_{pi}) method for calculating the KDE bandwidth, which is more suitable for use with smaller geographic areas and highly clustered datasets (Gitzen et al. 2006), which are characteristics of my study’s dataset. I created KDE home ranges using the rhr package in R (Signer and Balkenhol 2015). I calculated a simple metric of seasonal area and proportion of 95% KDE and 50% KDE overlap for breeding using ArcMap 10.4 (ESRI 2015. ArcGIS Desktop: Release 10.4. Redlands, CA: Environmental Systems Research Institute). Home range maps were created in ArcMap 10.4 (see Appendix A).

Within Home Range Space Use

Time-local-convex-hull (T-LoCoH) is a nonparametric method to create utilization distributions based upon previous local-convex hull methods (Getz and Wilmers 2004). Utilization distributions are created by constructing what are essentially MCPs (i.e. local hulls) around each location point within the dataset and then merging the ‘local hulls’ from the smallest to the largest hulls to form the familiar 95% and 50% utilization distribution isopleths. Each location point with enough nearest-neighbor points (in this case nearest neighbors were selected using the *a*-method) is used to create a ‘local hull’ and is referred to as a ‘hull parent point’. I used the adaptive (*a*-LoCoH) method of nearest-neighbor selection, which is more suitable for data that include both sparse and highly clustered location densities, is generally robust to changes in the *a*-value and is less influenced by outlier locations (Getz and Wilmers 2004, Lyons et al. 2013). The *a*-value is based on the maximum theoretical velocity of the study animal, which is derived from the data (Lyons et al. 2013) and is a cumulative distance measure by which location points are selected for inclusion into a local hull. The *a* value is selected by using a graphical examination of *a* values and isopleth areas, and isopleth-edge-area ratios that minimize spurious holes within the utilization distribution. The same *a* value was used for all individuals (a = 10,000). The time-scaled distance (TSD) parameter *s* incorporates time (and therefore temporal autocorrelation) into the home range estimate by rescaling the Euclidean distance between two points in space into a time-scaled distance, when selecting nearest neighbors. I selected an *s* value (s = 0.001) which would differentiate points occurring more than 24 hours apart to highlight daily habitat use.

T-LoCoH also allows for sorting and merging local hulls based on features other than hull size such as hull eccentricity or elongation. Metrics of directionality of movement, re-visitation and duration of use for each local hull can be derived from the sorting hulls based on different hull features. These metrics can be used to derive information about the behavior of the individual being tracked and the resources it utilizes (Lyons et al. 2013). Metrics of re-visitation and duration of use are determined by specifying the inter-visit gap period (IVG), which is essentially how much time must occur between two points before they are considered separate visits to the same local hull. I were interested in daily habits as they change throughout the seasons, so I selected an IVG of 12 hours. Revisitation is defined as the number of separate visits to a local hull

(NSV), with separation determined by the IVG, and duration of use is defined as the mean number of locations per visit (MNLV), or the number of locations in the same hull within the IVG period.

Data Preparation

Peregrine falcon data

I calculated NSV and MNLV rates for all hull parent points for each bird's T-LoCoH utilization distribution for annual, breeding (March-August) and wintering (September-February) home ranges. I multiplied MNLV values by 100 to obtain integer results for use in statistical models. Breeding and non-breeding seasons were determined by behavioral observation of nest sites during 2014 and 2015. I then imported points into ArcMap 10.4 (ESRI 2015. ArcGIS Desktop: Release 10.4. Redlands, CA: Environmental Systems Research Institute).

Environmental Covariates

To evaluate space use within the home range, I obtained data for environmental factors that would likely affect peregrine falcon space use including: elevation, an index of terrain ruggedness, distance to water, an index of prey density, and habitat types.

During the non-breeding season, prey availability and suitable foraging areas are likely the most important factors for habitat utilization (Newton 1979, Ratcliffe 1993). When hunting, peregrine falcons often prefer open areas that lend themselves to initiation of attacks from a position of height, either in flight or from a perch (White and Nelson 1991, Dekker 2009). Both hunting perches and nest sites are often locally high elevation points that look out over an open terrain suitable for hunting (Enderson and Craig 1997, Jenkins 2000). Elevation and terrain ruggedness were selected as environmental covariates to reflect these preferences in habitat utilization within the home range area. Elevation data for Humboldt County were obtained from National Map (Nationalmap.gov, U.S. Geological Survey National Elevation Dataset; https://catalog.data.gov/dataset/usgs-national-elevation-dataset-ned) in the form of a 10 m resolution digital elevation model (DEM). I calculated a terrain ruggedness index was following Jenness (2002), to create a Relative Topographic Position (RTP) layer. The RTP layer is derived from the National Map DEM and is an integer index of each raster pixel’s relative position to its local neighborhood pixels, giving an indication of terrain roughness, on a scale from 0 – 10 from least to most rugged.

Prey availability is also a strong factor in habitat utilization (Newton 1979, Ratcliffe 1993, White et al. 2002). Unpublished data from a survey of plucking perches in Humboldt County showed that waterfowl and shorebirds comprised 86% of identifiable prey remains (unpublished data; Melberg 2004). Land cover or habitat types may play a role as both a predictor of prey occurrence and of vulnerability to attack (Dekker 2009). Land cover data was obtained from the California Department of Forestry and Fire Protection's CALFIRE Fire and Resource Assessment Program GIS Data website, in the form of rasters of statewide vegetation with Wildlife Habitat Relation (CWHR) types, CWHR size and CWHR density. These land cover rasters were created by CALFIRE in cooperation with the California Department of Fish and Wildlife’s VegCamp program using data from the United States Department of Agriculture (USDA) Forest Service Region 5 Remote Sensing Laboratory to create a standardized vegetation classification system for California. These data are in 30x30 m raster format and contain information about 59 different habitat type classes.

I created a spatial prey density index layer using eBird data (eBird. 2012. eBird Basic Dataset. Version: EBD_relNov-2015. Cornell Lab of Ornithology, Ithaca, New York. Available: <http://www.ebird.org>, Sullivan et al. 2009) to serve as a proxy for prey abundance. While citizen science data is often biased due to unstandardized levels of observation effort across non-random spatial extents (Dickinson et al. 2010), eBird data entered by observers is carefully vetted by regional data managers (Sullivan et al. 2017). In the absence of other spatial data relating to potential prey species, eBird provides spatially explicit data that includes vetted species occurrences and includes temporal and other ancillary information amenable for use in spatial analysis (Sullivan et al. 2017). This dataset is biased towards public lands and areas of human habitation, places where birders can easily access. It is also true that all but one pair of peregrines nested and remained resident on or near public lands and three pairs nested near or within areas of human habitat. I aggregated eBird data for numerous common prey species in the Humboldt County area (Beebe 1960, Dobler 1993, White et al. 2002, Mellberg 2004 unpublished data, Castellanos et al. 2006, Newsom et al 2010, see Table 1) into one dataset using records from the period of peregrine falcon data collection, and the total number of bird counts from birder observations was used to create a point density layer using ArcMap’s Point Density tool. This was then converted to a raster with a relatively coarse cell size of 1 km to account for spatial uncertainty and observer distance (see Appendix N).

Table 1. Prey species included in the prey density index raster, data obtained from eBird.

Common Name	**Scientific Name**	**Common Name**	**Scientific Name**
American Avocet	*Recurvirostra americana*	Northern Flicker	*Colaptes auratus*
American Coot	*Fulica americana*	Northern Pintail	*Anas acuta*
American Robin	*Turdus migratorius*	Northern Shoveler	*Spatula clypeata*
American Wigeon	*Anas americana*	Pacific Golden-Plover	*Pluvialis fulva*
American Golden Plover	*Pluvialis dominica*	Pigeon Guillemot	*Cepphus columba*
Ancient Murrelet	*Synthliboramphus antiquus*	Red Knot	*Calidris canutus*
Baird’s Sandpiper	*Calidris bairdii*	Red Phalarope	*Phalaropus fulicarius*
Band-tailed Pigeon	*Patagioenas fasciata*	Red-necked Phalarope	*Phalaropus lobatus*
Barrow's Goldeneye	*Bucephala islandica*	Red-winged Blackbird	*Agelaius phoeniceus*
Black Oystercatcher	*Haematopus bachmani*	Rhinoceros Auklet	*Cerorhinca monocerata*
Black Scoter	*Melanitta Americana*	Ring-necked Duck	*Aythya collaris*
Black-bellied Plover	*Pluvialis squatarola*	Rock Pigeon	*Columba livia*
Blue-winged Teal	*Spatula discors*	Rock Sandpiper	*Calidris ptilocnemis*
Cinnamon Teal	*Spatula cyanoptera*	Ruddy Duck	*Oxyura jamaicensis*
Brewer’s Blackbird	*Euphagus cyanocephalus*	Sanderling	*Calidris alba*
Bufflehead	*Bucephala albeola*	Semipalmated Plover	*Charadrius semipalmatus*
California Towhee	*Melozone crissalis*	Short-billed Dowitcher	*Limnodromus griseus*
Canvasback	*Aythya valisineria*	Snowy Plover	*Charadrius nivosus*
Cassin's Auklet	*Ptychoramphus aleuticus*	Spotted Sandpiper	*Actitis macularius*
Common Goldeneye	*Bucephala clangula*	Surf Scoter	*Melanitta perspicillata*
Common Murre	*Uria aalge*	Surfbird	*Calidris virgata*
Dunlin	*Caldris alpine*	Varied Thrush	*Ixoreus naevius*
Eurasian Collared-Dove	*Streptopelia decaocto*	Western Sandpiper	*Calidris mauri*
Eurasian wigeon	*Anas penelope*	Whimbrel	*Numenius phaeopus*
European starling	*Sturnus vulgaris*	White-winged Scoter	*Melanitta fusca*
Greater Yellowlegs	*Tringa melanoleuca*	Willet	*Tringa semipalmata*
Greater Scaup	*Aythya marila*	Wilson's Phalarope	*Phalaropus tricolor*
Lesser Scaup	*Aythya affinis*	Wilson's Snipe	*Gallinago delicate*
Green-winged Teal	*Anas crecca*		
Killdeer	*Charadrius vociferus*		

Least Sandpiper	*Calidris minutilla*		
Lesser Yellowlegs	*Tringa flavipes*		
Long-billed Curlew	*Numenius americanus*		
Long-billed Dowitcher	*Limnodromus scolopaceus*		
Mallard	*Anas platyrhynchos*		
Marbled Godwit	*Limosa fedoa*		
Marbled Murrelet	*Brachyramphus marmoratus*		

As shorebirds and waterfowl are an important component of peregrine falcon diets, I used ArcMap 10.4 and hydrologic data to create a distance to water (in meters) raster. The hydrologic data were obtained from Topologically Integrated Geographic Encoding and Referencing (TIGER) Database that was combined to include rivers, streams, ponds, lakes, bays and the coastal ocean (2015 TIGER/Line Shapefiles Technical Documentation prepared by the U.S. Census Bureau, 2015).

Peregrine falcons may range widely away from their core territories in response to prey abundance (Ratcliffe 1993, Enderson and Craig 1997). To maximize energy intake and reduce energy expended during travel, intensity of space use may also be influenced by distance from the nest site. To account for this, I created a distance-from nest site raster (in meters) for each bird, using the Euclidean Distance tool in ArcMap 10.2. All relevant spatial data layers were spatially joined to peregrine falcon T-LoCoH hulls in ArcMap 10.4 for use in statistical analysis in R.

Habitat Utilization Statistical Analysis

Data qualification for use in statistical models consisted of using Cleveland dot plots to examine the independent variable datasets for significant outliers. Pearson correlation values and pairwise plots were calculated between all independent variables to determine possible correlations, with a threshold of ≥ 0.5 indicating high collinearity between variables (Zuur et al. 2009). Variance inflation factor (VIF) values were also used to examine collinearity among the independent variables, with VIF > 3 used as a cut-off level for determining high collinearity (Zuur et al. 2007) in conjunction with correlation values. None of the predictor variables violated these criteria and all were retained.

I used non-parametric Mann-Whitney U-tests to test for significant differences between T-LoCoH and KDE home ranges size estimates (Dytham 2011). I also used Mann-Whitney U-tests to test for differences between male and female, and wintering and breeding KDE home range sizes (Dytham 2011).

Generalized linear models (GLM) were used to evaluate 95% KDE breeding and wintering home range size estimates in relation to season (breeding and wintering) and sex (male and female). To account for the repeated sampling of locations from individual birds, Generalized Linear Mixed Models (GLMM) were used to test the relationship between metrics of peregrine falcon intensity of use (NSV and MNLV) and environmental and spatial covariates, using individual peregrine falcon identity as the random effect in a random intercept model, while using season, sex, and environmental covariates as fixed effects (Bolker et al. 2000, Zuur et al. 2013) (R package: lme4; Bates et al. 2016). To help determine covariate inclusion into a GLMM model, I evaluated covariate importance in relation to NSV and MNLV rates using Random Forest (RF) modeling. Random forests are an extension of decision trees and are used for regression and exploring variable importance based on a response variable (Breiman 2001). Random forests are created by averaging many decision trees and can measure variable importance by estimating the loss of predictive power of a model when removing a variable or randomly reassigning the values of a variable within a training data set (Mean Decrease Accuracy). Random forests were selected to examine variable importance for their ability to handle large numbers of covariates and their ability to handle non-linear relationships (Breiman 2001). Random forests were implemented using the randomForest package in R (Liaw et al. 2015). For the GLMMs I used a Poisson distribution with a log-link function and Laplace approximation. Poisson GLMMs are appropriate for the NSV and MNLV values which are all positive integers. A set of *a priori* candidate models including a null model was created using the covariates that did not violate correlation value or VIF value cutoffs and were considered the most ecologically important. These models were then ranked using the Akaike information criterion scores corrected for small sample size (AICc) and AICc model weights, which evaluate each model's relative likelihood of occurrence given both the data and the set of candidate models (Burnham and Anderson 2002). Each candidate model's accuracy and fit were evaluated using conditional and marginal R^2 values as described by Nakagawa and Schielzeth (2013). Conditional and marginal R^2 values measure the amount of variation within a model that is explained by both the fixed and random effects, and by the fixed effects alone, respectively.

RESULTS

Home Range Analysis

A total of 14,084 GPS locations were obtained from nine peregrine falcons from June 2014 to August 2016 (Appendix B). One male peregrine falcon stopped transmitting approximately six months after transmitter attachment. That individual was included only in breeding season analyses and was not included in any analysis that required annual or wintering home range size estimates. Due to the consistently overcast conditions in coastal Humboldt County, more GPS locations were collected when transmitters had greater ability to recharge their solar batteries during the breeding season months, consequently breeding season home ranges have a larger number of GPS locations than for winter home ranges for all individuals (Appendix B).

MCP home range estimates varied widely among individuals with a mean of 487.63 km^2, a range of 22.2 – 3692.9 km^2 (SE = 400.9 km^2, see Appendix C). Male peregrine falcons had larger 95% MCP area than females (males = 765.94 km^2, females = 36.38 km^2, Mann-Whitney U-test, p = 0.056, w = 7). Breeding 95% KDEs ranged from 11.8 – 127.9 km^2 (mean = 38.6, SE = 11.6) and winter 95% KDEs ranged from 6.8 – 18.82 km^2 (mean = 12.6, SE = 1.5).

Breeding 95% KDEs were significantly larger than winter 95% KDEs (Mann-Whitney U-test p = 0.001, w = 67). Breeding 50% KDEs ranged from 0.7 – 4.88 km^2 (mean = 2.0, SE = 0.45) and winter 50% KDEs ranged from 0.2 – 1.44^2 (mean = 0.76, SE = 0.15).

Breeding KDEs were significantly larger than 50% wintering KDEs (Mann-Whitney U-test *p* = 0.002, *w* = 66, Figure 2, Appendix C). T-LoCoH and KDE methods produced significantly different home range estimates (Mann-Whitney U-test *p* = 0.006, *w* = 64) with T-LoCoH providing overall smaller home range size estimates than KDE methods (Appendix D). Core home ranges (50% UDs) were much smaller than 95% UDs for annual, breeding, and winter range estimates for both KDE and T-LoCoH home range estimates (Appendix D). There was no significant difference between annual 95% KDEs for male and female peregrines, although the sample size for comparisons between males and females was small ($n_{females}$ = 5, n_{males} = 4, Figure 2). Similarly, no significant difference was found between male and female breeding 95% KDEs (Mann-Whitney U-test *p* = 0.1, *w* = 3) or wintering 95% KDEs (Mann-Whitney U-test *p* = 0.1, *w* = 3), but males did have significantly larger 50% KDE breeding size estimates (Mann-Whitney U-test *p* = 0.01, *w* = 0). There was no significant difference between male and female 50% KDE wintering home range areas.

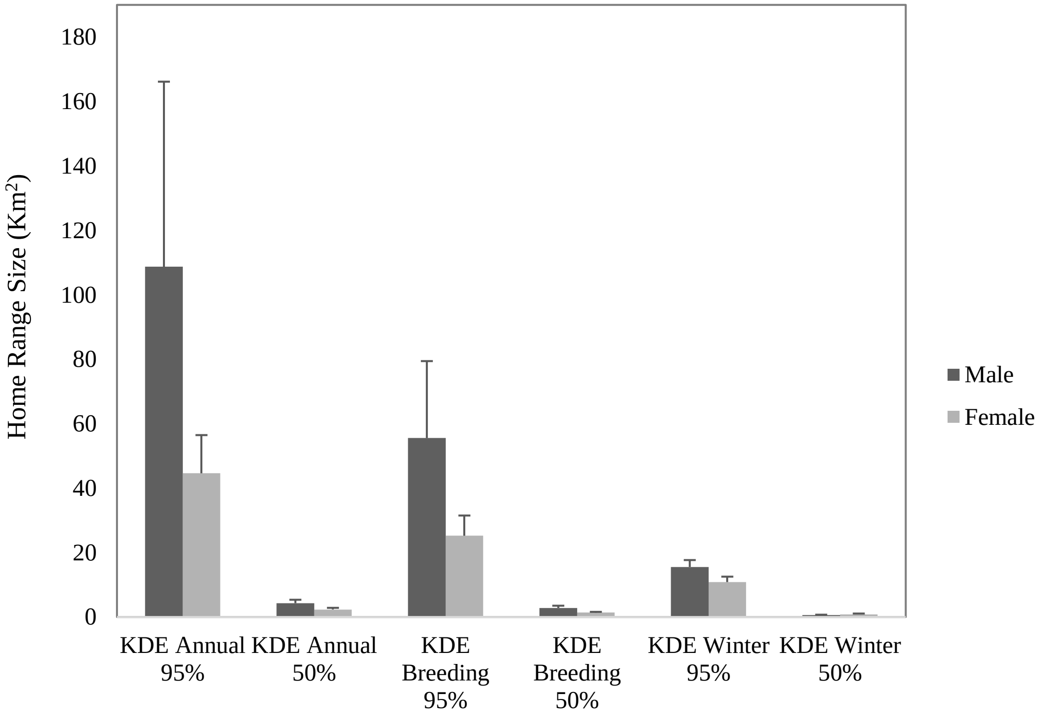


Figure 2. Mean kernel density estimates (+/- SE) for male (n = 4) and female (n = 5) peregrine falcons for annual, breeding season and wintering home ranges in km^2, from June 2014 to August 2016.

On average, female peregrine home ranges were almost completely overlapped by the territories of their male counterparts (Figure 3; also see Appendices E and F), although one female overlapped her male counterpart's home range significantly more during the breeding season than the other female falcons (Mann-Whitney U-test p = 0.039, w = 52). Male peregrine falcon home ranges were variably overlapped by their female counterparts (Figure 3; also see Appendices E and F) There was no significant difference in area of home range overlap for male and female peregrines during the winter season (Mann-Whitney U-test p = 0.574, w = 22).

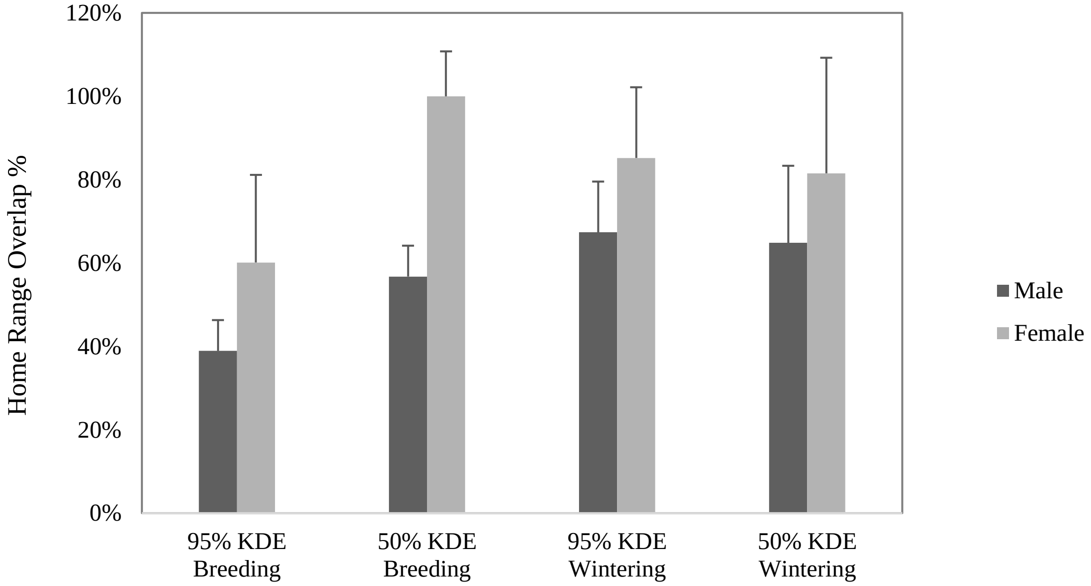


Figure 3. Average proportion of home range area (+/- SE) overlapped by each individual's mate for male (n = 4 breeding, n = 3 wintering) and female (n = 5) peregrine falcons for breeding and wintering home ranges, from June 2014 to August 2016.

Within Home Range Space Use and Habitat Utilization

Redwood, Montane Hardwood Conifer and Coastal Scrub habitat types comprised the largest percentage of land cover within the area of the combined peregrine falcon home ranges (Figure 4). NSV and MNLV rates for all peregrine falcons indicated that peregrines had higher revistitation rates and spent more time in CWHR types Barren, Coastal Scrub, Marine, Redwood and Riverine. NSV rates also show that peregrine falcons frequently revisited Lacustrine habitats (Figure 6). Seasonal differences in NSV and MNLV rates for the various habitat types show that use of some habitat types decreased or did not occur in the winter season, including Douglas fir, estuarine, irrigated hay field and perennial grasslands (Figure 5, Figure 6).

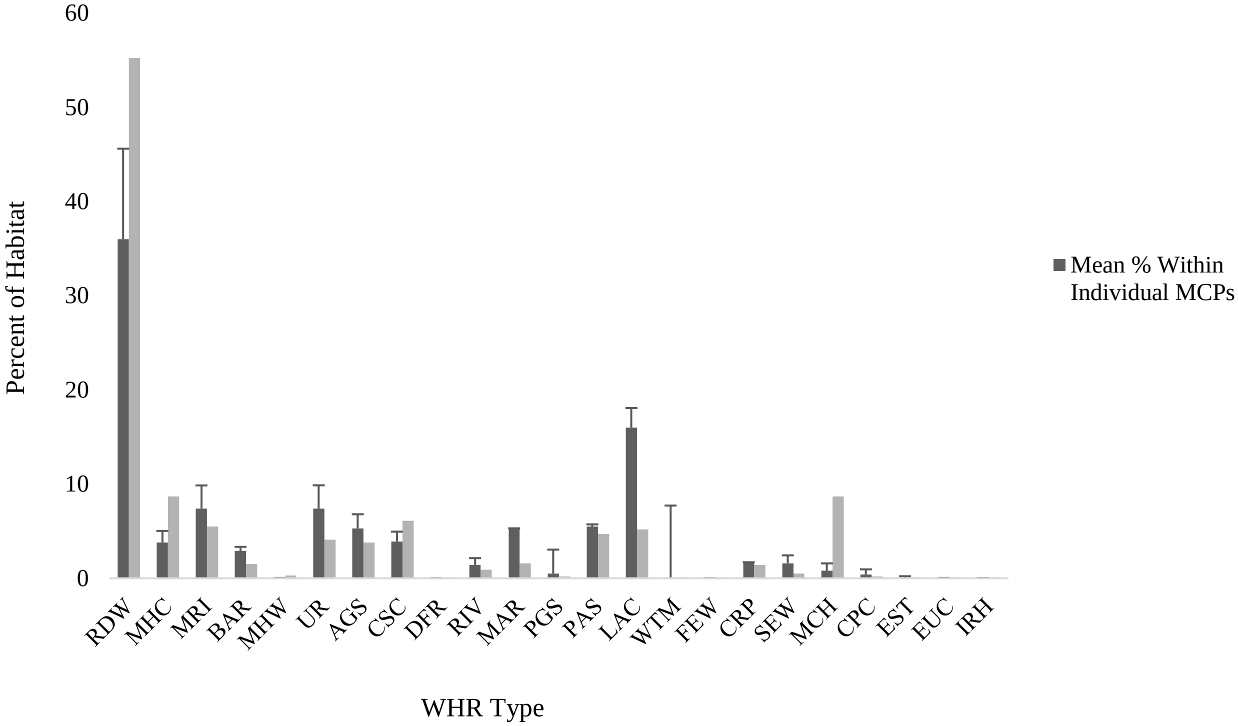
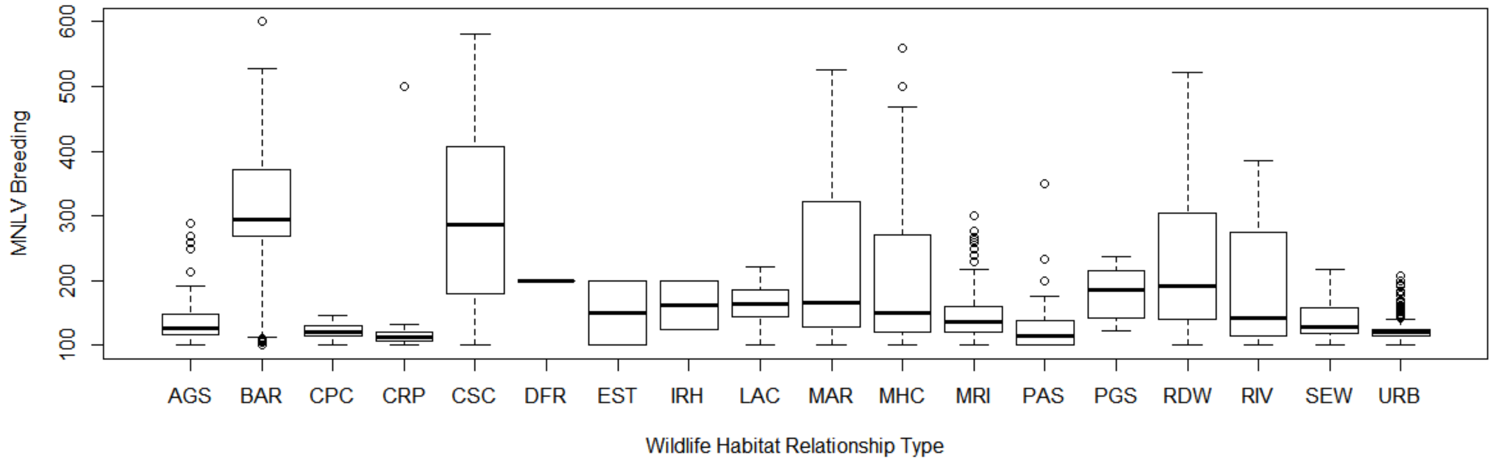


Figure 4. Percent composition of each California Wildlife Habitat Type (CWHR type) within the Boundary MCP created using all peregrine location data, and mean percent within individual peregrine MCP home ranges: RDW = Redwood, MHC = Montane Hardwood Conifer, MRI = Montane Riverine, BAR = Barren, MHW = Montane Hardwood, URB = Urban, AGS = Annual Grassland, CSC = Coastal Scrub, DFR = Douglas Fir, RIV = Riverine, MAR = Marine, PGS = Perennial Grassland, PAS = Pasture, LAC = Lacustrine, WTM = Wet Meadow, FEW = Fresh Emergent Wetland, CRP = Cropland, SEW = Saline Emergent Wetland, MCH = Mixed Chaparral, CPC = Closed-Cone Pine-Cypress, EST = Estuarine, EUC = Eucalyptus, IRH = Irrigated Hayfield.


MNLV Breeding
100
200
300
400
500
600
AGS
BAR
CPC
CRP
CSC
DFR
EST
IRH
LAC
MAR
MHC
MRI
PAS
PGS
RDW
RIV
SEW
URB
Wildlife Habitat Relationship Type

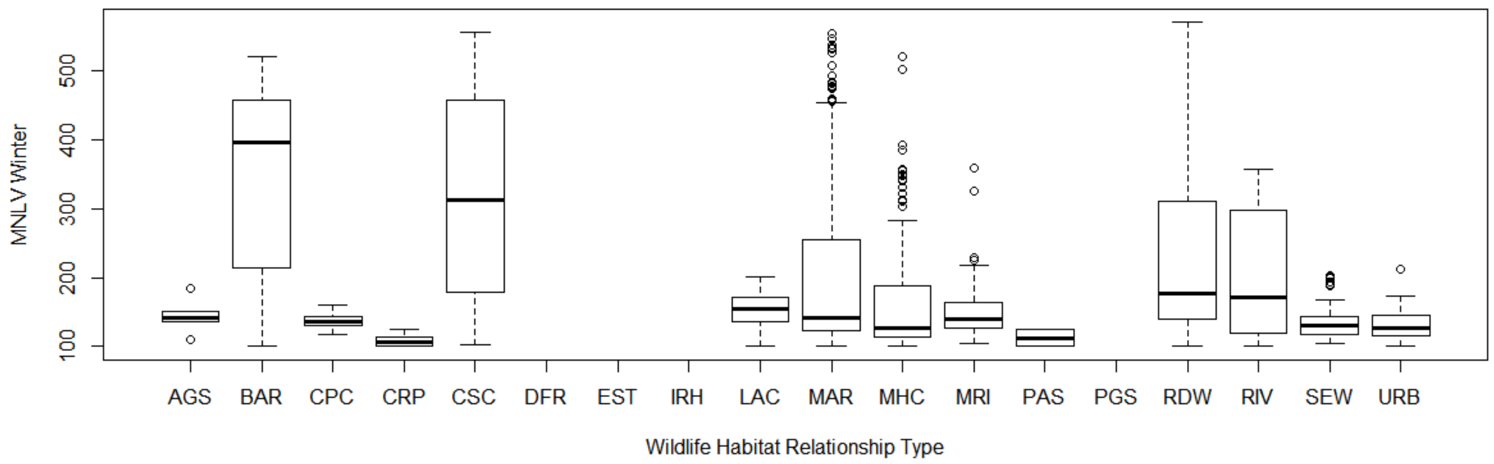
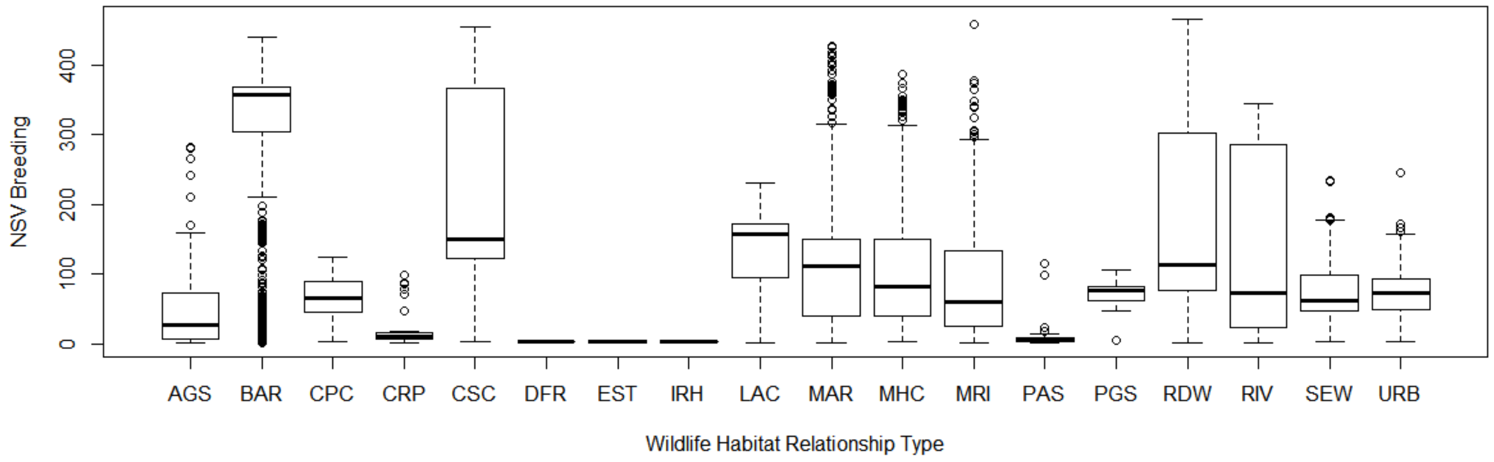

MNLV Winter
100
200
300
400
500
AGS
BAR
CPC
CRP
CSC
DFR
EST
IRH
LAC
MAR
MHC
MRI
PAS
PGS
RDW
RIV
SEW
URB
Wildlife Habitat Relationship Type

Figure 5. Comparison of seasonal MNLV rates against associated California Wildlife Habitat Types. The thicker lines in the center of boxes indicate median NSV values for each CWHR type, while boxes and error bars indicate the quantile range of NSV values values for each CWHR type, while boxes and error bars indicate the quantile range of NSV values. CRP = Cropland, URB = Urban, CPC = Closed-Cone Pine-Cypress, PAS = Pasture, AGS = Annual Grassland, SEW = Saline Emergent Wetland, MRI = Montane Riverine, EST = Estuarine, LAC = Lacustrine, IRH = Irrigated Hayfield, PGS = Perennial Grassland, MHC = Montane Hardwood Conifer, RIV = Riverine, DFR = Douglas Fir, MAR = Marine, RDW = Redwood, CSC = Coastal Scrub, BAR = Barren.


NSV Breeding
0
100
200
300
400
AGS
BAR
CPC
CRP
CSC
DFR
EST
IRH
LAC
MAR
MHC
MRI
PAS
PGS
RDW
RIV
SEW
URB
Wildlife Habitat Relationship Type

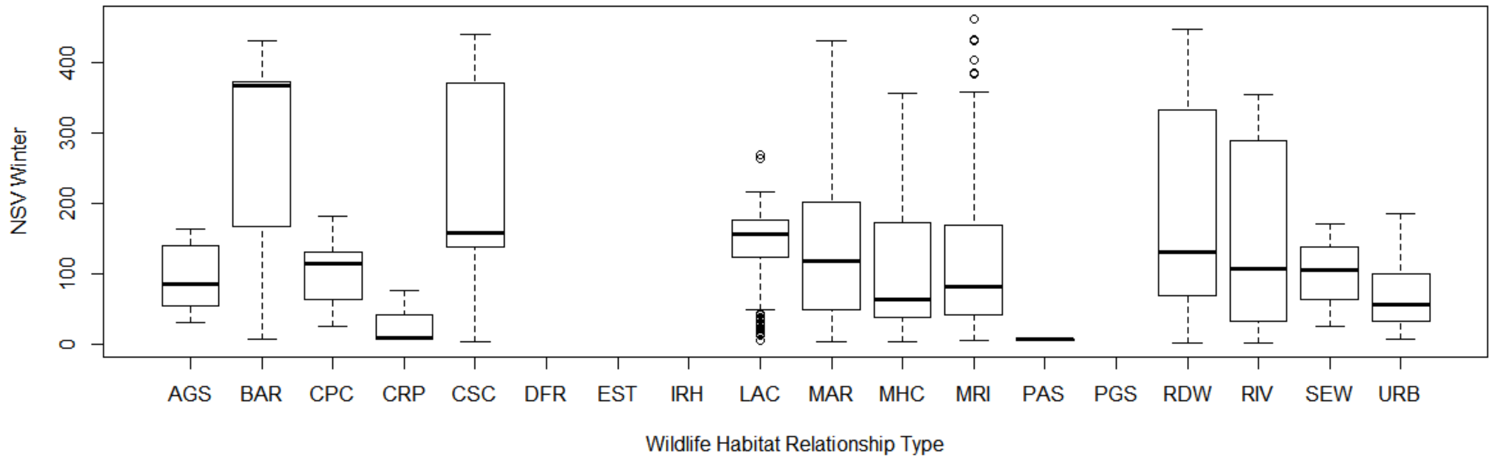

NSV Winter
0
100
200
300
400
AGS
BAR
CPC
CRP
CSC
DFR
EST
IRH
LAC
MAR
MHC
MRI
PAS
PGS
RDW
RIV
SEW
URB
Wildlife Habitat Relationship Type

Figure 6. Comparison of seasonal NSV rates against associated California Wildlife Habitat Types. The thicker lines in the center of boxes indicate median NSV values for each CWHR type, while boxes and error bars indicate the quantile range of NSV values. CRP = Cropland, URB = Urban, CPC = Closed-Cone Pine-Cypress, PAS = Pasture, AGS = Annual Grassland, SEW = Saline Emergent Wetland, MRI = Montane Riverine, EST = Estuarine, LAC = Lacustrine, IRH = Irrigated Hayfield, PGS = Perennial Grassland, MHC = Montane Hardwood Conifer, RIV = Riverine, DFR = Douglas Fir, MAR = Marine, RDW = Redwood, CSC = Coastal Scrub, BAR = Barren.

I used AICc (Burnham and Anderson 2002) to select the best model from a set of *a priori* selected generalized linear models (GLMs) using the 95% and 50% KDE home range size estimates with sex and season (breeding or winter) and an interaction term (sex* season) as covariates. Models for both 95% and 50% KDE estimates showed season alone as being the most important factor in determining 95% KDE and 50% KDE home range size (Table 2, Table 3). Seasonal home ranges were larger during the breeding season than during the winter season for all individuals with enough data to compare seasonal home ranges (n = 8, see Appendix C).

Table 2. Results of generalized linear models to determine the relationship between 95% KDE home range size (in km2) and sex and season (breeding or wintering).

Home Range Model	LogLik	AICc	Delta AICc	Weight
HR Size ~ Season	-78.168	164.2	0	0.606
HR Size ~ Sex * Season	-80.358	165.6	1.39	0.302
HR Size ~ Sex	-79.131	169.6	5.41	0.04
HR Size ~ Sex + Season + Sex * Season	-76.111	178.7	14.48	0

Table 3. Results of generalized linear models to determine the relationship between 50% KDE home range size (in km2) and sex and season (breeding or wintering).

Core Range Model	LogLik	AICc	Delta AICc	Weight
HR Size ~ Season	-21.676	51.2	0	0.791
HR Size ~ Sex * Season	-19.985	55.4	4.22	0.096
HR Size ~ Sex	-23.964	59.3	8.06	0.014
HR Size ~ Sex + Season + Sex * Season	-17.321	61.1	9.89	0.006

For both NSV and MNLV rates random forest results showed that distance to nest, individual identity and season were the most important variables in relation to model predictive performance. Random forest results obtained by randomly permuting each covariate’s values resulted in some loss of predictive power, so we included all covariates in the GLMM models (Figure 7).

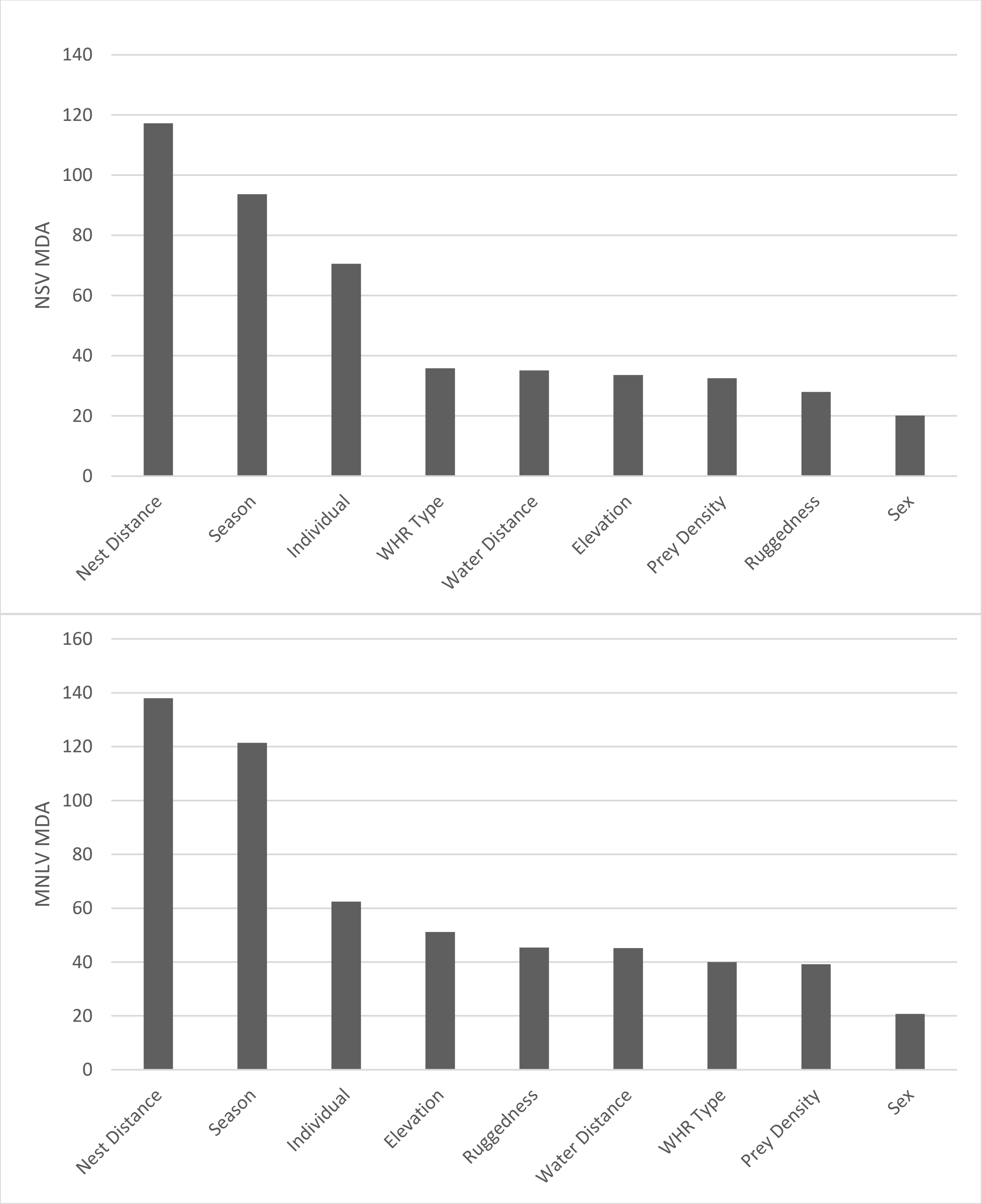


Figure 7. Random forest results ranking covariate importance in relation to NSV and MNLV rates, where MDA is the Mean Decrease in Accuracy in predictive performance for a model when a variable is left out or randomly permutated.

When modeling MNLV, models using both Poisson and negative binomial distributions models failed to converge. When modeling NSV rates I added an observation level random effect to the model, which effectively reduced problems with overdispersion. I also rescaled the continuous covariates due to large differences in range and scales. The global model that included all covariates and two interaction terms was selected as both the most parsimonious (as determined by AICc) and had the greatest model weight, as well as the highest Marginal and Conditional R^2 values (Table 4). No model averaging was considered since the second-best model was too different from the best model (ΔAICc = 9) and we were not attempting to use the model for predictive purposes. The null model containing none of the covariates had a much larger AIC than any of the models containing covariates and the lowest Marginal and Conditional R^2 values (Table 4).

Table 4. Results of generalized linear mixed models to determine the relationship between revistitation (Number of Separate Visits), distance from the nest site, terrain ruggedness, and land cover.

Model No.	**Space Use Models**	Log Likelihood	AICc	ΔAICc	Model weight	Marginal R^2	Conditional R^2
1	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist + CWHRtype + Sex + Season + Sex*Season + NestDist*PreyDens	-42250	84552	0	0.985	0.603	0.828
12	NSV ~ ELEV + WaterDist + PreyDens + NestDist + CWHRtype + Sex + Season + Sex*Season + NestDist*PreyDens	-42255	84561	9	0.008	0.603	0.828
3	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist + CWHRtype + Sex + Season + NestDist*PreyDens	-42256	84562	1	0.007	0.602	0.828
4	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist + CWHRtype + Season + Sex	-42297	84645	83	0	0.599	0.815
2	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist + CWHRtype + NestDist*PreyDens	-42321	84689	43	0	0.437	0.818
7	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist + CWHRtype	-42364	84772	83	0	0.302	0.744
6	NSV ~ NestDist + CWHRTYPE	-42795	85627	854	0	0.389	0.761

8	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist + Sex + Season + Sex*Season + NestDist*PreyDens	-42966	85956	328	0	0.581	0.757
11	NSV ~ ELEV + RUGGED + WaterDist + PreyDens + NestDist	-43082	86181	225	0	0.380	0.745
10	NSV ~ PreyDens + NestDist + Sex + Season + Sex*Season + NestDist*PreyDens	-43353	86727	546	0	0.546	0.711
5	NSV ~ WaterDist + PreyDens + NestDist + Sex + Season + Sex*Season + NestDist*PreyDens	-43408	86834	107	0	0.546	0.711
Null	NSV ~ Random Effects	-63323	126652	< 500	0	0.00	0.477

Parameter estimates of the effects of environmental covariates show that revistitation (Number of Separate Visits) was positively associated with elevation and prey density, and negatively associated with increasing distance from water, and increasing distance from the nest site (Table 5). Revisitation rates were also positively associated with several habitat types; closed cone pine cypress, coastal scrub, riverine, redwood, barren, and lacustrine. GLMM model coefficients indicate that these habitat types have a larger effect on revistitation rates than were indicated for CWHR types in general by the random forest model importance evaluation. Montane riverine, urban, and pasture habitat types were associated with lower NSV values, indicating that these habitat types were revisited less frequently. GLMM model coefficient 95% confidence intervals for croplands, perennial grasslands, and saline emergent wetland habitat types included zero and therefore should not be considered informative predictors of revistitation rates (Table 5).

Table 5. Summary of the highest-ranking model out of the candidate models explaining revistitation rates (NSV) within the home range by 9 peregrine falcons in Humboldt County, CA. GLMM coefficient estimates are log-counts.

			95% CI		
Model 1.	**Estimate**	**SE**	**Lower Limit**	**Upper Limit**	**Back-transformed Estimates**
Intercept	4.64	0.19	4.24	5.00	103.29
CWHR Closed cone pine cypress	0.52	0.08	0.25	0.55	1.68
CWHR Coastal scrub	0.46	0.05	0.33	0.54	1.59
CWHR Riverine	0.44	0.06	0.38	0.63	1.55
CWHR Redwood	0.42	0.05	0.25	0.46	1.52
CWHR Barren	0.40	0.05	0.28	0.50	1.49
CWHR Lacustrine	0.35	0.05	0.25	0.46	1.42
Elevation	0.18	0.01	0.20	0.23	1.20
Prey Density	0.16	0.01	0.07	0.11	1.18
CWHR Marine	0.13	0.05	0.02	0.23	1.14
CWHR Montane hardwood conifer	0.13	0.06	0.01	0.22	1.14
Season (W)	0.07	0.01	0.06	0.10	1.08
CWHR Cropland	0.00	0.15	-0.41	0.18	1.00
Ruggedness	-0.09	0.01	-0.07	-0.05	0.92
CWHR Perennial grassland	-0.10	0.10	-0.25	0.16	0.90
CWHR Montane riverine	-0.13	0.05	-0.24	-0.02	0.88
Prey Dens * Nest Dist	0.06	0.01	0.04	0.07	1.08
CWHR Urban	-0.16	0.06	-0.32	-0.11	0.85
CWHR Saline emergent wetland	-0.23	0.06	-0.18	0.04	0.80
Nest Distance	-0.30	0.01	-0.34	-0.32	0.74
CWHR Pasture	-0.40	0.20	-0.99	-0.20	0.67
Sex * Season	0.10	0.02	0.05	0.14	0.52
Sex (M)	-0.65	0.28	-1.16	-0.06	0.52

Although MNLV models failed to converge, looking at Figure 5 and Figure 6 we can see that the comparison of NSV and MNLV rates with difference habitat types reflect a similar intensity of use via revistitation and visit duration rates with the CWHR types barren, coastal scrub, marine, redwood and riverine, indicating that these habitats were frequently visited and were occupied for relatively longer periods of time. Additionally, habitat types estuarine, irrigated hayfield and pasture had very low NSV rates but had moderate MNLV rates during the breeding season, indicating that these habitat types were not visited as frequently as others but that individuals did spend more time in those habitats when they visited. Conversely, lacustrine, urban and closed cone pine cypress habitat types had relatively moderate NSV values but lower relative MNLV values, indicating that these habitat types were visited regularly but that peregrines did not spend a large amount of time in these habitats relative to other available habitats. Eucalyptus, fresh water emergent wetland, wet meadow and montane hardwood habitat types which comprised a very small percentage of the study area did not appear to be utilized by peregrine falcons.

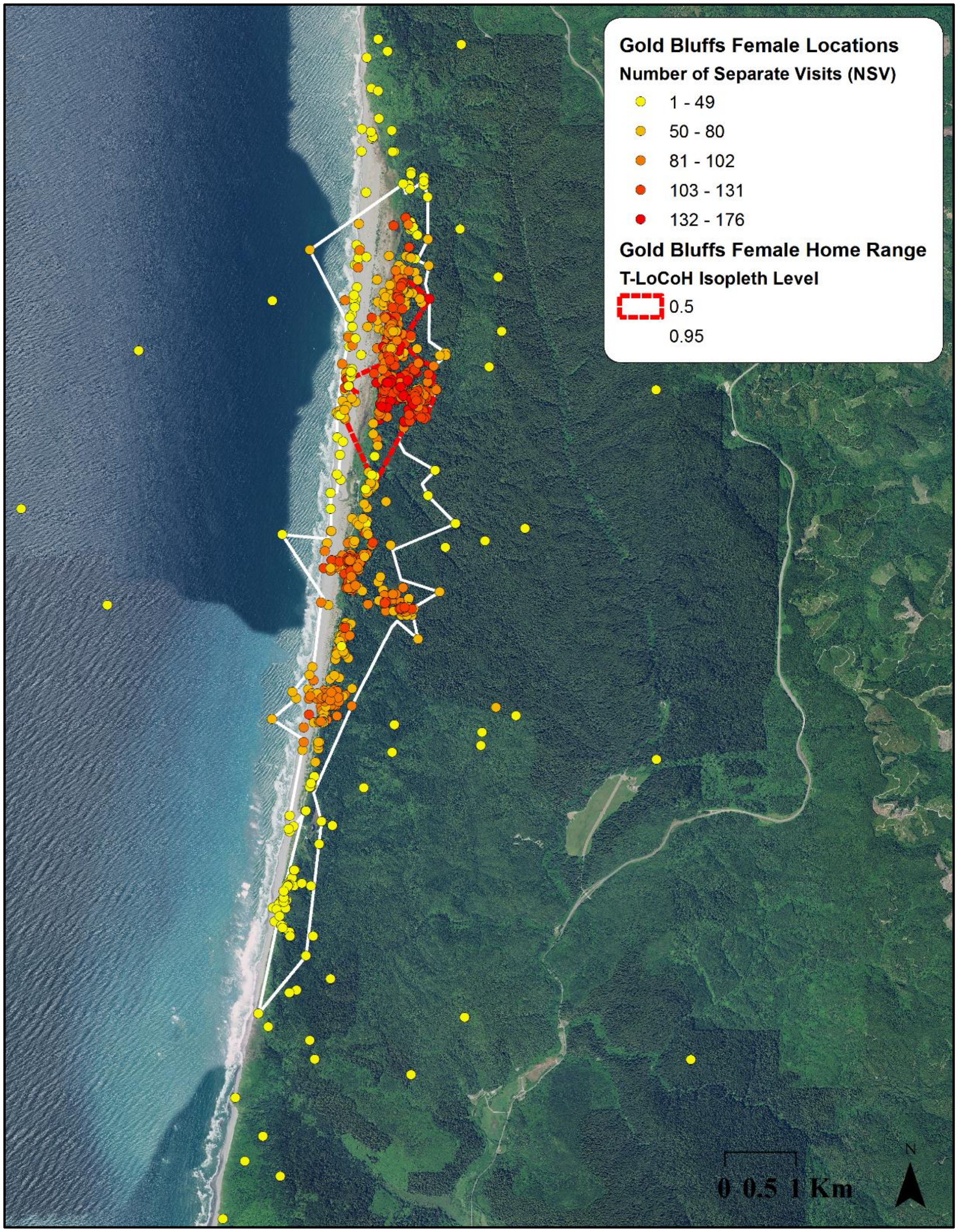


Figure 8. Gold Bluffs female peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from June 2014 to June 2016 in Humboldt County, California.

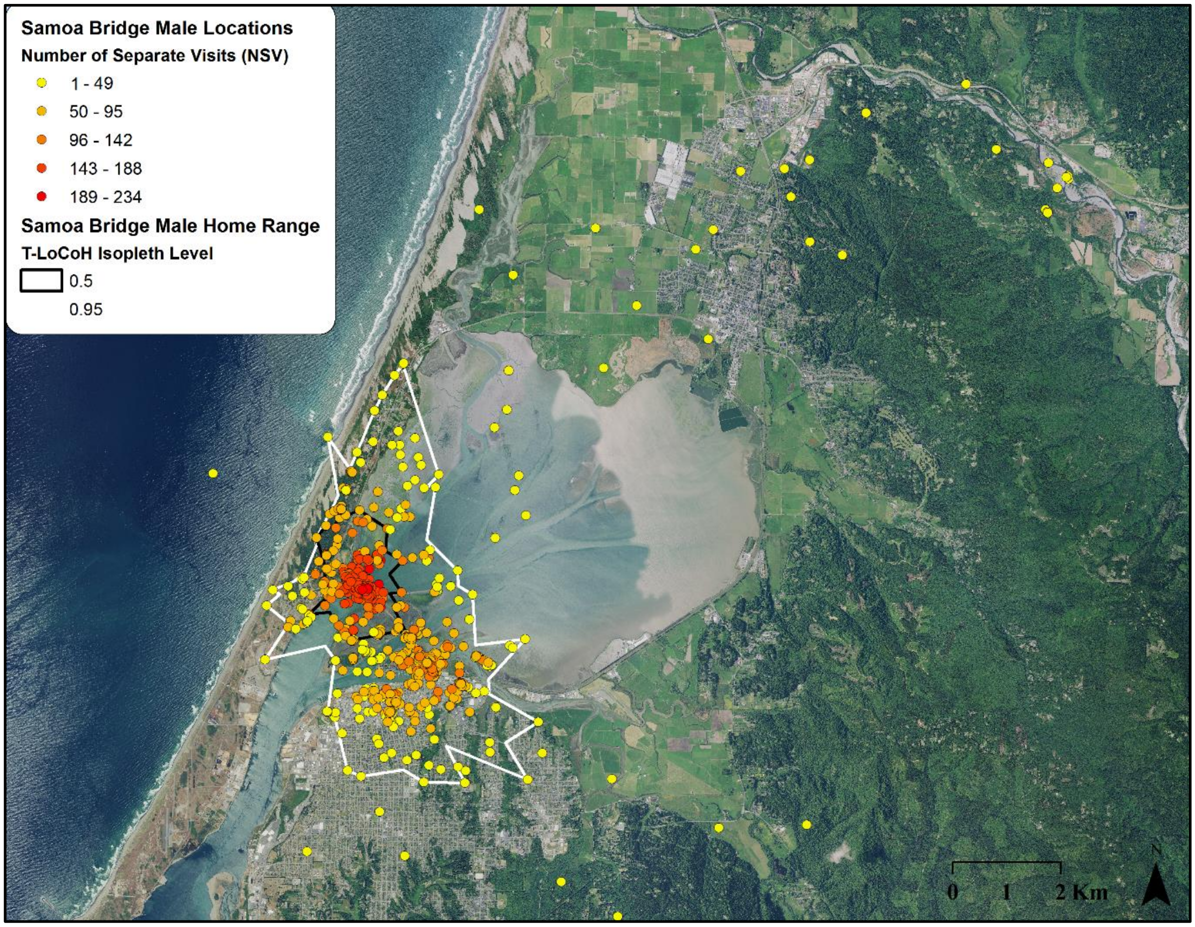


Figure 9. Samoa Bridge male peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from March 2015 to August 2016 in Humboldt County, California.

DISCUSSION

While most peregrine falcons are known to migrate vast distances between breeding and wintering locations (Ratcliffe 1993, McGrady et al. 2002, White et al. 2002), researchers have observed that in some areas peregrine falcons are non-migratory (Jurek 1989). This study confirmed that peregrine falcons nesting along the coast of Humboldt County in northern California occupied territories year-round. Annual MCP home range area estimates for peregrine falcons in Humboldt County ranged from 22.2 – 3692.9 km^2 (mean = 497.6 km^2, SE = 400 km^2, n = 9). Annual 95% KDE home range estimates ranged from 21.5 – 280.6 km^2 (mean = 108.7 km^2, SE = 26.7). To my knowledge, these are the first 12-month home range values determined for the species. The bird with the smallest home range was a female, living along a rocky area of coastline. The bird with the largest home range was a male, nesting along the coast at Humboldt Lagoons State Park. The mild climate and annual shorebird and waterfowl migrations that occurred in the coastal Humboldt County area seemed to provide adequate resources year-round, allowing peregrines to forego migration.

Eight previous studies have quantified the home range of peregrine falcons during the breeding (n = 5) or wintering (n = 3) ends of their migratory range, using a variety of indices allowing for comparisons with my study (Table 6). The studies from Table 6, which includes the estimates from this study for comparison, show a range of values for home range estimates within their study populations that are similar to ours, indicating a significant amount of individual variation within different geographical populations (see

Table 6; Enderson and Craig 1997, McGrady et al. 2002, Ganusavich et al. 2004, Lapointe et al. 2013, Sokolov et al 2014). In this study, the average home range values quantified during breeding and in winter were substantially smaller than all the other studies. For example, during breeding our coastal peregrines occupied an average home range of 38.6 km^2 (range = 11.8 – 127.9km^2, SE = 11.6) while in other studies the home range estimate averages for the breeding season ranged from 83.9 – 1200 km^2 (Table 6). A smaller estimate was also found for winter home ranges; the falcons in this study utilized an average area of 12.6 km^2 (range = 6.8 – 18.8 km^2, SE = 1.49) while home range averages in other wintering season studies ranged from 52.1 – 169.5 km^2 (Table 6).

The study with the most comparable data set and methods (i.e. similar number of locations fixes, location fix quality, and use of the same home range estimation methods to ours) was conducted on ten female falcons in southern Quebec, Canada (Lapointe et al. 2013). The falcons in their study occupied a region of lowlands and hilly terrain mixed with agriculture and wetlands. Female peregrines breeding in Quebec increased their breeding range sizes after young fledged from the nest (see Table 6). Lapointe et al. (2013) found that peregrine habitat use changed during nesting period, which is likely due to increasing fledgling food requirements. Lapointe et al. (2013) reported home range estimates for the breeding season that ranged from 0.3 - 811.1 km^2. While their smallest estimate is much smaller than those from coastal Humboldt county, peregrine falcon breeding range estimates had a smaller range of values, and the largest eastern Canadian peregrine home range was more than six times larger than the largest Humboldt peregrine range for the breeding season. This is possibly due to differences in habitat composition, with fewer agricultural lands in Humboldt County, and different prey densities and distributions along numerous smaller bodies of water in Quebec, whereas peregrines along the west coast may travel less widely to obtain food. Coastal Humboldt peregrine core breeding home range estimates (mean = 2.0 km^2, range = 0.7 – 4.8 km^2, SE = 0.15) were considerably smaller than those obtained by Sokolov et al. (2014) for peregrines breeding in the extreme north of Russia (mean = 13.5 km^2, range = 1.4 – 40.6 km^2) using fixed KDEs and ARGOS satellite data.

Table 6. Comparison of peregrine falcon home ranges estimates, where sample size refers to the number of transmittered birds in the study. For mean number of locations per bird, RT = radio telemetry, ARGOS = ARGOS satellite telemetry, GPS = GPS satellite telemetry, and Obs. Hrs. refers to observation hours during radio telemetry tracking when number of locations is not reported. Morata et al. refers to the data from this thesis.

Ref.	**Year**	**Location**	**Season**	**Mean HR Estimate (km^2)**	**HR Estimate Range (km^2)**	**Mean Core HR Estimate (km^2)**	**Core HR Estimate Range (km^2)**	**Estimation Method**	**Sample Size**	**Mean Locations Per Bird**
Enderson and Craig	1997	Colorado, U.S.A.	Breeding	880	358 - 1508	-	-	Harmonic Mean	5	209 (RT)
… cont.	1997		Breeding	1200	811 - 1440	-	-	MCP	5	-
Jenkins and Benn	1998	South Africa	Late breeding	86.3	52.6 - 140.4	4.7	0.1 - 13.8	Adaptive-KDE	4	184 (RT)
… cont.	1998		Late breeding	123	89.7 - 192.1	-	-	MCP	4	-
Ganusavich et al.	2004	Northern Russia	Breeding	1175	104 - 1556	-	-	MCP	4	131 (ARGOS)
Lapointe et al.	2013	Quebec, Canada	Nestling Period	83.9	0.3 - 392.5	-	-	Fixed-KDE	10	882 (ARGOS/GPS)
… cont.	2013		After Fledging	201.9	10.0 - 811.1	-	-	Fixed-KDE	10	-
Sokolov et al.	2014	Yamal, Russia	Breeding	98.1	19.7 - 221.6	-	-	MCP	10	453 (ARGOS)
… cont.	2014		Breeding	-	-	13.5	1.4 - 40.6	Fixed-KDE	10	-

Morata et al.*	2017	California, U.S.A.	Breeding	38.6	11.8 – 127.9	2.0	0.7 – 4.88	Fixed KDE	9	1327 (GPS)
Dobler and Spencer	1989	Washington, U.S.A.	Winter	77.9	-	19.7	-	Harmonic Mean	1	124 Obs. Hrs (RT)
Dobler	1993	Washington, U.S.A.	Winter	52.1	5.6 - 85.6	13.4	1.5 - 25.34	Harmonic Mean	3	62 Obs. Hrs (RT)
McGrady et al.	2002	Tamaulipas, Mexico	Winter	169.5	16.8 - 689.5	39.2	2.5 - 294.8	MCP	12	31 (ARGOS)
Morata et al.*	2017	California, U.S.A.	Winter	12.6	6.8 – 18.82	0.76	0.2 – 1.44	Fixed KDE	8	393 (GPS)

Interestingly, the home range estimates of all nine peregrine falcons in coastal Humboldt County were significantly larger during the breeding season than the winter season, at both the general and core levels (95% and 50% KDEs). Garrett et al. (1993) found that resident pairs of bald eagles (*Haliaeetus leucocephalus*) along the Columbia River Valley estuary in Washington remained near their nest territories year-round, and some pairs moved to other sites within the home range during winter. The authors noted that there was a large amount of variation among individuals; some mated pairs of eagles utilized larger home range areas during the breeding season, but some pairs utilized larger home range areas during the non-breeding season. Late summer and autumn movements away from the nesting territory to exploit foraging opportunities were a possible reason for this variation between breeding pairs of eagles (Garrett et al. 1993). Changes in home range size may be due to seasonal variation in prey abundance or distribution, where larger home ranges are required in situations of fewer available prey, or a patchy distribution of prey (Newton 1996, Peery 2000). Marzluff et al. (1997) found that prairie falcon (*Falco mexicanus*) increased foraging ranges in response to decreasing prey abundance. The smaller winter home range estimates for my study may indicate a smaller prey base during the summer compared to the fall, winter, and spring when migratory shorebirds and waterfowl move through the Humboldt Bay region (Monroe 1973, Colwell 1994). These migrations may provide increased hunting opportunities for young of the year and reduce traveling distances for resident adults seeking hunting opportunities. Another influence on winter home range sizes may be the presence of migrating and wintering peregrine falcons who would arrive in mid-latitude areas like

Humboldt County during September and October (McGrady et al. 2002, Worcester and Ydenberg 2008). Peregrine falcons that are temporary migrants or winter residents may utilize areas outside of the resident peregrines’ core home ranges. Territorial interactions with conspecifics near the eyrie were observed during winter, suggesting that defense of nest sites occurred year-round. A combination of territoriality at the core home range level (50% KDE) and simple avoidance of conspecifics may contribute to the contraction of home ranges during winter (*sensu* Newton 1979, Ratcliffe 1993, Enderson et al. 1995).

Extensive home range overlap between paired and neighboring male and female peregrines was observed in previous studies (Enderson et al. 1995, Enderson and Craig 1997, Jenkins and Benn 1998, Ganusavich et al. 2004). Among our breeding pairs, male coastal Humboldt peregrines had slightly larger core home range areas that completely overlapped the paired female’s core range, but not vice versa. This suggests that male peregrine falcons ranged more widely outside of the core home range on a more frequent basis than females (Figure 3, Appendices E and F).

While Enderson and Craig (1997) found that females had larger home ranges than males during the breeding season, we did not find a significant difference between annual, breeding or wintering 95% KDEs for male and female falcons. However, we found that male falcons had a significantly larger core range size (50% KDE) than females during the breeding season. Jenkins and Benn (1998) also found that, at least during the early breeding season in South Africa, male peregrines ranged more widely than females and spent less time at the nest site. Although the nest site is the center of activity for both members of the pair year-round, the tendency for female peregrine falcons to remain closer to the nest site than males may indicate that, in the absence of migration, females are the main territory holders and defenders.

Coastal Humboldt County peregrine falcons did not utilize the landscape within their home range randomly. Home range maps with GPS locations classified by NSV rate show high revistitation rates to a select few areas within home range, demonstrating preferential use of certain habitat types (Figures 8, Figure 9, Appendices G-L). Jenkins and Benn (1998) concluded that space use for peregrine falcons in South Africa during the late summer was not associated with land use or habitat types. However, Lapointe et al. (2013) found that breeding female peregrines in Quebec used certain agricultural habitat types more than others during the early breeding season, and that those habitat preferences changed as the breeding season progressed. Coastal Humboldt County peregrine falcons utilized certain habitat types more intensively than others within their home ranges areas, which were largely comprised of redwood, montane hardwood conifer, mixed chaparral, and coastal scrub habitat types. (Figure 4). Barren, lacustrine, marine, and riverine habitat types were visited more frequently within the home range than the montane hardwood conifer and mixed chaparral habitat types that covered larger proportions of the study area (Figure 4, Figure 5). The redwood habitat type comprised over 50% of the total study area, but had lower NSV and MNLV rates than barren, coastal scrub, and lacustrine habitat types (Figure 4, Figures 5 and 6). Some habitat types showed some seasonal differences in intensity of use. The use of Douglas fir, estuarine, irrigated hay field and perennial grassland habitats decreased or did not occur in the winter season (Figure 5, Figure 6). This likely reflects the contraction of home range sizes during the winter, and possibly the reduced need to range widely in search of hunting opportunities, since each nest site was placed in a position of height over an area utilized by potential prey, including a river, tidal mud flats, beaches and open water. Although there were some seasonal differences in intensity of habitat use, the core home range areas and most frequently visited areas within the home range changed little throughout the year.

Barren and lacustrine habitat types were positively associated with NSV rates (Figure 6). In coastal areas, the barren habitat type indicates rocky intertidal and subtidal zones, mudflats and sandy beaches. Inland barren habitat types include river banks, canyon walls, and large rocky areas. Three of our nest sites occurred directly along the coastline on ocean-facing cliffs. Thus, barren habitat types would be highly associated with nesting areas. Barren habitat types are also associated with potential hunting areas such as intertidal zones, mudflats, and beaches. Lacustrine habitats consist of areas of inland standing water, including small ponds, lakes, reservoirs and lagoons. Both lacustrine and barren habitat types are potential hunting areas for peregrine falcons along the coast where prey species would congregate to feed or roost (Colwell 1994, Colwell and Sundeen 2000), and where open space would allow for typical peregrine hunting tactics (Beebe 1960, Dobler 1993, Enderson et al. 1995, Dekker 2009, White et al. 2002).

Similarly, the marine habitat type includes areas from the open ocean to the intertidal zone and barren lands between the shore and terrestrial vegetation, where surprise hunting attempts may be aided by the concealing vegetation (Dekker 2009). High revistation rates for open space is also reflected in GLMM results which indicate that terrain ruggedness is negatively related to NSV rates, but NSV is positively associated with elevation (Table 5). Both males and females of each pair were observed actively hunting from or nearby the nest site. These hunting attempts, initiated from the nesting cliff and sometimes from the eyrie itself, frequently took place in habitats such as beaches, river bars and intertidal mudflats. Beaches were frequently targeted from positions of height on the nesting cliff and from off shore rocks.

Northern coastal scrub consists of moderate-sized shrubs and perennial herbs, and at low elevations is associated with grasslands, croplands and pasture lands. These habitat types are potential foraging areas for peregrines hunting starlings and other passerines (Brambilla et al. 2006). Coastal scrub is also associated with coastal dunes, which often include seasonal wetlands that may be utilized by migrating shorebirds and waterfowl.

Wetlands areas are highly associated with shorebirds and waterfowl, which are prey groups commonly taken by peregrine falcons (Ratcliffe 1993, Dekker 2009). We expected wetland areas to have a higher intensity of space use, as the migrating and resident shorebirds and waterfowl may congregate around the Humboldt Bay area (Monroe 1973). While prey density was positively associated with intensity of use in our GLMM, and some of the highest prey densities in our index occurred around Humboldt Bay, wetlands were surprisingly underutilized compared to the other habitat types. This may be because none of the peregrines in this study nested close to the main wetlands in the area and remained tied to their nesting cliffs year-round. Peregrines may also be utilizing other habitats also associated with congregating shorebirds and waterfowl, such as foraging areas like tidal flats and pasture lands (Dekker 2009). Many hunting attempts observed during this study appeared to be opportunistic in nature, initiated from a habitual perch or the nesting cliff. However, some were repeated, active attempts targeting areas of high prey concentration in habitats other than wetlands. A favored technique of the male nesting at Trinidad Head was to circle up above the coastal landmass and gain sufficient height before diving directly towards a series of large off-shore rocks. One of these rocks hosted large numbers of breeding sea birds such as pigeon guillemots. Another individual frequently targeted flocks of pigeons in a parking lot near the nest site, perching directly on powerlines in the parking lot in a buteo-like manner, showing that local areas of high prey concentration were known and actively utilized.

Closed-cone pine-cypress, coastal scrub, riverine and redwood habitat types are the most positively related to revisitation rates (Table 5). High revistitation rates for closed-cone pine-cypress and redwood habitat types are attributable to two coastal nesting sites and one riverine nesting site being associated with large conifer and redwood stands. High revistitation rates for riparian areas (Table 5) was influenced by the riverine nesting pair, but three of the coastal females and two male peregrines also visited riparian areas, each bird repeatedly visiting either the same general area or the same body of water. Use of riparian or riverine areas was similarly noted by Enderson and Craig (1997) for female peregrines in Colorado during the nesting season. GLMM model coefficient 95% confidence intervals for saline emergent wetlands included zero, and therefore was not an informative predictor of revisitation rates (Table 5).

The three birds with the largest annual home ranges, two coastal males and one female that nested more inland along the Eel Rivier, did range far outside the 95% home range area. Even when looking at MCP ranges which often overestimate home range sizes compared to KDE or T-LoCoH estimates. Similar ranging behavior was also noted by White and Nelson (1991), Enderson and Craig (1997), Jenkins and Benn (1998) and Ganusavich et al. (2004) where peregrines moved up to 80 km away from nesting sites during the summer. These behaviors seem unlikely to be driven by the need to find prey or suitable hunting areas. These trips were not regular enough to coincide with the need to find food, particularly during the breeding season. Such ranging trips may serve as prospecting trips, which may provide individuals with opportunities for discovering new, profitable hunting areas or gleaning other information about the environment. It is possible that such excursions are for checking on certain areas that are good for hunting only during a part of the annual cycle. Alternatively, visits to different areas may provide indications of the start of certain important phases of the annual cycle such as the beginning of waterbird and passerine migrations. The long-range movements exhibited by peregrines in Humboldt County (up to 70 km away but typically within 30 km of the nest site) were not restricted to certain hours during the day and were not restricted by seasons. Only two birds showed evidence of wide ranging events that resulted in roosting outside of the home range area and one of these birds, a male, had several roosting events outside the 95% KDE home range area throughout the annual cycle.

During the study period three male peregrine falcons ceased to transmit data due to bird mortality. The first peregrine stopped transmitting six months after transmitter attachment and the next two both occurred more than a year after transmitter attachment. Despite searching, and an attempt to climb a cliff for retrieval, these birds were not located and were assumed deceased. Due to the length of time after transmitter attachment, it is unlikely that the transmitters were the direct cause of mortality. Two of the three males were replaced by new individuals less than two weeks after their transmitters stopped working. These new individuals were observed in close association with the transmittered, resident females. The rapid replacement of male peregrines during the breeding season implies that there was a steady population of non-breeding adult birds in the area ready to quickly fill vacancies at nesting territories.

Peregrine falcons are impressive, apex predators capable of traveling thousands of miles during seasonal migrations (Fuller et al. 1998, White et al. 2002). Peregrines that live along the northern California coast experience environmental conditions that are favorable throughout the year; resident birds do not have to migrate, and in fact occupy smaller home ranges during the winter. In a study group less constrained by prey availability and the rigors of long distance migration, a large amount of individual variation was evident in the home range size estimates and in individual space use patterns. Resident peregrine falcons utilized different habitat types more intensively than others within their home ranges, showing higher intensity of use for habitats associated with nest sites, and for open areas associated with water. The data presented here provides new information on home range sizes and seasonal differences in home range size, augmenting previous findings about breeding and winter home ranges and providing new insights about movement behaviors and habitat use. Further research investigating the breeding and wintering ranges of migratory peregrine falcons would improve our understanding of this flexible species' response to different environmental conditions. Examining migratory stopover and winter site fidelity in migratory peregrines is another important future endeavor to determine winter habitat, space, and food requirements, and to identify potential areas of conservation.

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APPENDICES

APPENDIX A. Geographic boundary and imagery data used for creating study area and home range maps, and data sources.

Data	**Source**
Humboldt County Boundary	Humboldt County webpage (http://www.humboldtgov.org/1357/Web-GIS)
California Satellite Imagery	USDA Natural Resources Conservation Science (https://gdg.sc.egov.usda.gov/GDGOrder.aspx)
Ocean Imagery	ESRI World Imagery (ESRI, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstop, and the GIS user community)
California Boundary	United States Census Bureau TIGER/Line Shapefile (https://catalog.data.gov/dataset/tiger-line-shapefile-2013-state-california-current-place)

APPENDIX B. Number of GPS locations collected and data collection dates for nine peregrine falcons in Humboldt County, CA.

Bird ID	Data Collection Date Ranges	No. of GPS Locations	No. of GPS Breeding Season Locations	No. of GPS Wintering Locations
Dry Lagoon Female	6/28/2014 - 8/22/2016	2750	2035	716
Dry Lagoon Male	5/22/2015 - 6/17/2016	1075	777	299
Gold Bluffs Female	6/26/2014 - 6/17/2016	1782	1372	411
Samoa Female	6/22/2014 - 8/22/2016	1409	1372	228
Samoa Male	3/06/2015 - 8/21/2016	1303	1047	257
Scotia Female	6/24/2014 - 8/22/2016	2823	2202	622
Scotia Male	5/20/2015 - 3/26/2016	956	594	363
Trinidad Female	2/26/2015 - 8/22/2016	1644	1392	253
Trinidad Male	3/13/2015 - 9/9/2015	344	344	NA

APPENDIX C. Home range estimate sizes in km^2 for minimum convex polygons (MCP) and kernel density estimates (KDE) from June 2014 to August 2016 for nine peregrine falcons in Humboldt County, CA.

Bird ID	**MCP Size**	**Annual 95% KDE**	**Annual 50% KDE**	**Breeding 95% KDE**	**Breeding 50% KDE**	**Winter 95% KDE**	**Winter 50% KDE**
Dry Lagoon Female	85.07	33.48	2.00	19.13	0.76	6.85	0.25
Dry Lagoon Male	3692.87	280.64	7.17	127.19	4.88	18.82	0.78
Gold Bluffs Female	65.87	36.36	2.17	21.63	1.57	13.80	1.34
Samoa Female	123.45	41.44	2.85	24.57	1.69	14.65	1.44
Samoa Male	61.49	44.97	3.38	29.36	1.97	11.49	0.64
Scotia Female	140.85	90.20	3.87	48.89	1.92	12.03	0.30
Scotia Male	45.38	46.37	4.44	34.07	2.37	16.26	0.48
Trinidad Female	22.24	21.59	0.82	11.87	0.94	6.87	0.81
Trinidad Male	151.46	x	x	62.80	2.18	x	x

APPENDIX D. Mean, range and standard deviation in km^2 for KDE and T-LoCoH 95% home range estimates from June 2014 to August 2016 for nine peregrine falcons in Humboldt County, CA.

	T-LoCoH			**KDE**		
	Mean	Range	St.Dev	Mean	Range	St.Dev
All Annual	31.0	5.08 - 140.17	41.9	73.1	21.59 - 280.64	80.3
Annual Male	51.3	18.24 - 140.17	59.3	108.7	44.97 - 280.64	114.9
Annual Female	14.7	5.08 - 31.93	11.4	44.6	21.59 - 90.20	26.5
All Winter	10.0	1.95 - 21.30	6.3	12.6	6.85 - 18.82	4.2
Winter Male	13.6	7.41 - 21.30	6.9	15.5	11.49 - 18.82	3.7
Winter Female	7.1	1.95 - 11.71	4.3	10.8	6.85 - 14.65	3.8
All Breeding	28.7	5.04 - 129.25	20.7	38.7	11.87 - 127.19	34.8
Breeding Male	48.2	19.05 - 129.25	22.5	55.5	29.36 - 127.19	47.8
Breeding Female	8.6	5.04 - 26.18	22.2	25.2	11.87 - 48.89	14.0

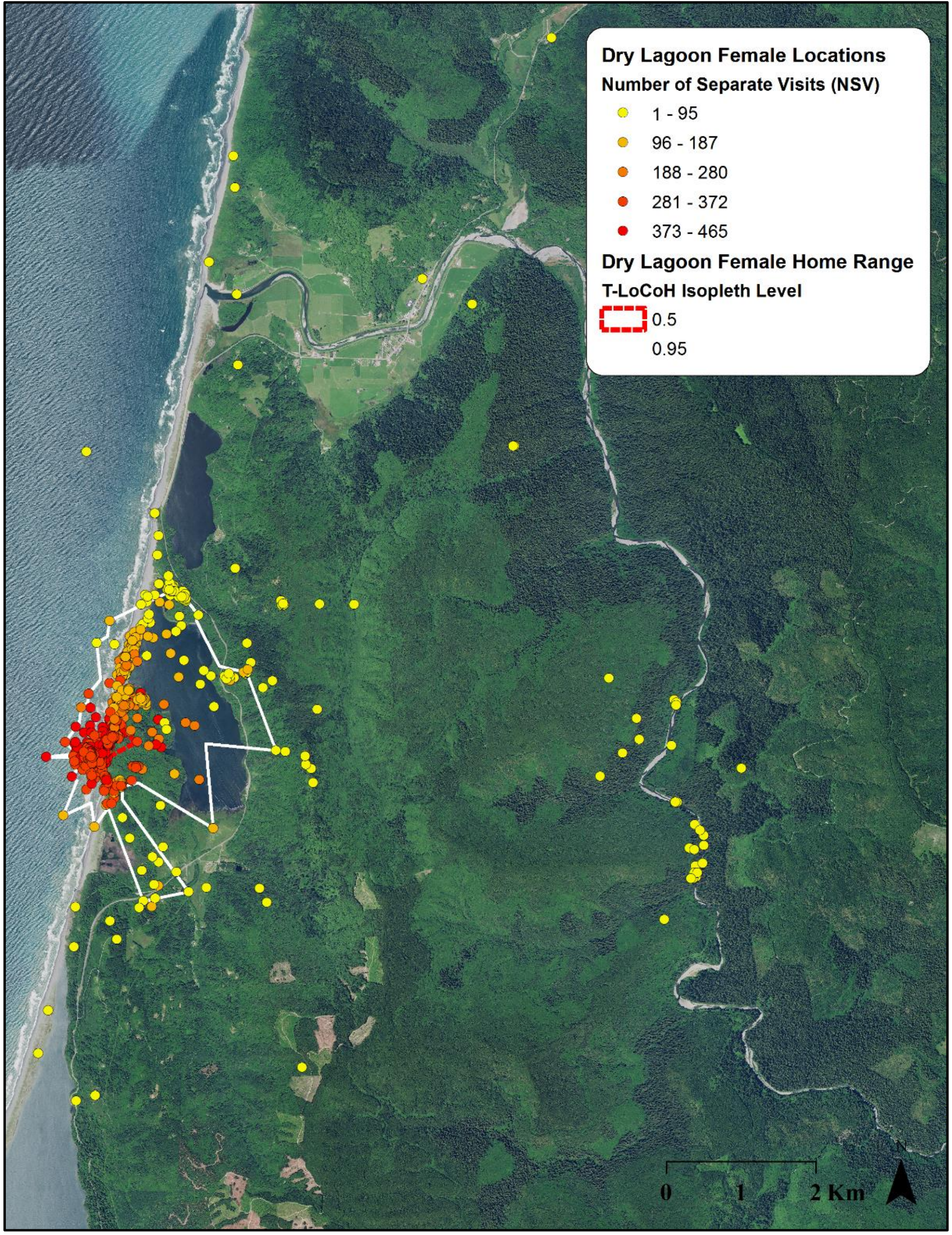
APPENDIX E. Area and proportion of overlap in km^2 for breeding season 95% KDEs for breeding pairs of peregrine falcons in Humboldt County, CA.

Breeding	95% KDE		50% KDE	
Bird ID	Area of Overlap	Proportion of Overlap	Area of Overlap	Proportion of Overlap
Dry Lagoon Female	9.21	48%	0.76	100%
Dry Lagoon Male	9.21	7%	0.76	16%
Samoa Female	16.11	66%	1.69	100%
Samoa Male	16.11	55%	1.69	85%
Scotia Female	21.12	43%	1.92	100%
Scotia Male	21.12	62%	1.92	81%
Trinidad Female	9.92	84%	0.94	100%
Trinidad Male	9.92	31%	0.94	45%

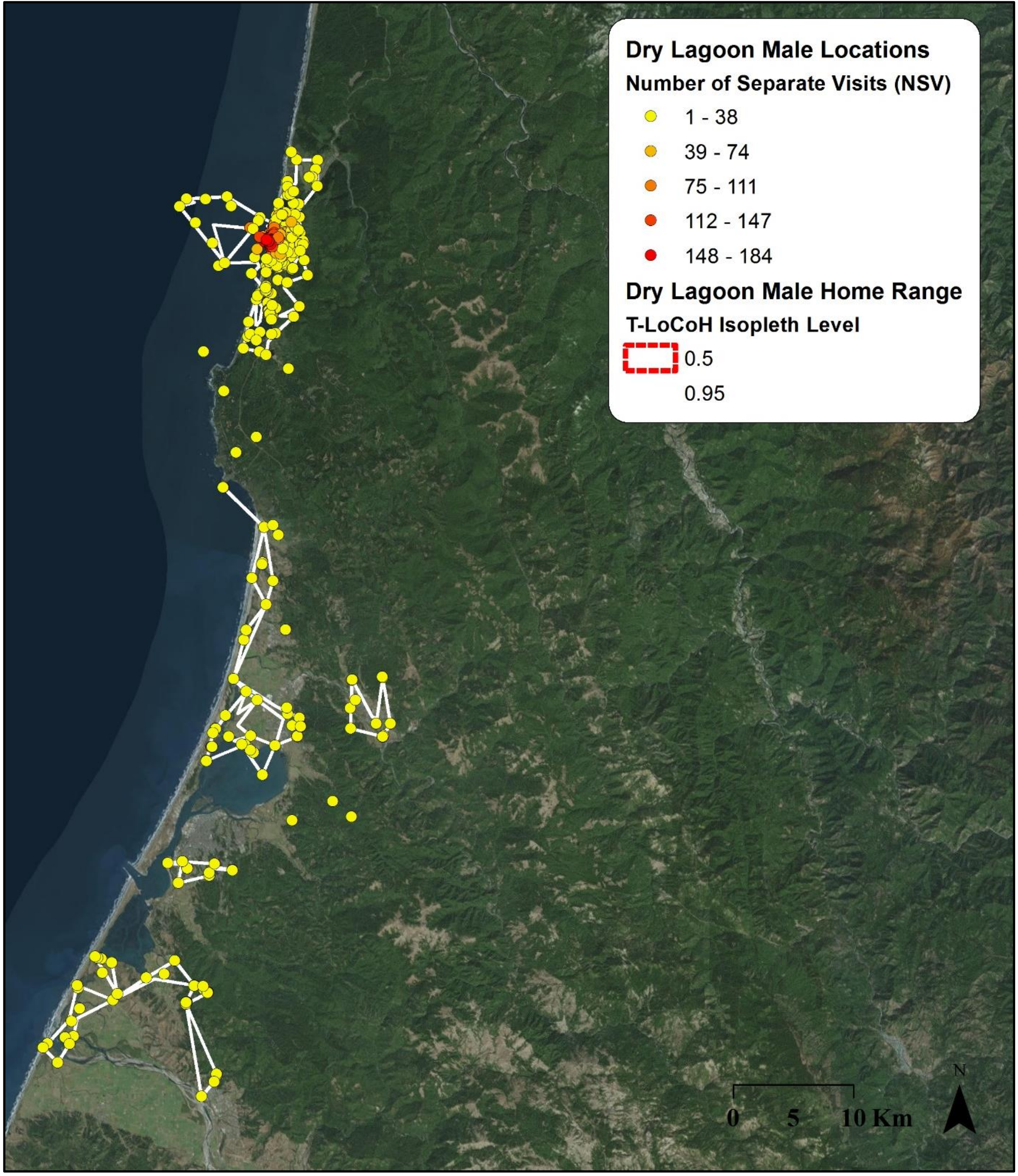
APPENDIX F. Area and proportion of overlap in km^2 for winter 95% KDEs for breeding pairs of peregrine falcons in Humboldt County, CA.

Wintering	**95% KDE**		**50% KDE**	
Bird ID	**Area of Overlap**	**Proportion of Overlap**	**Area of Overlap**	**Proportion of Overlap**
Dry Lagoon Female	5.29	77%	0.25	100%
Dry Lagoon Male	5.29	28%	0.25	32%
Samoa Female	11.49	78%	0.64	45%
Samoa Male	11.49	100%	0.64	100%
Scotia Female	12.03	100%	0.30	100%
Scotia Male	12.03	74%	0.30	62%

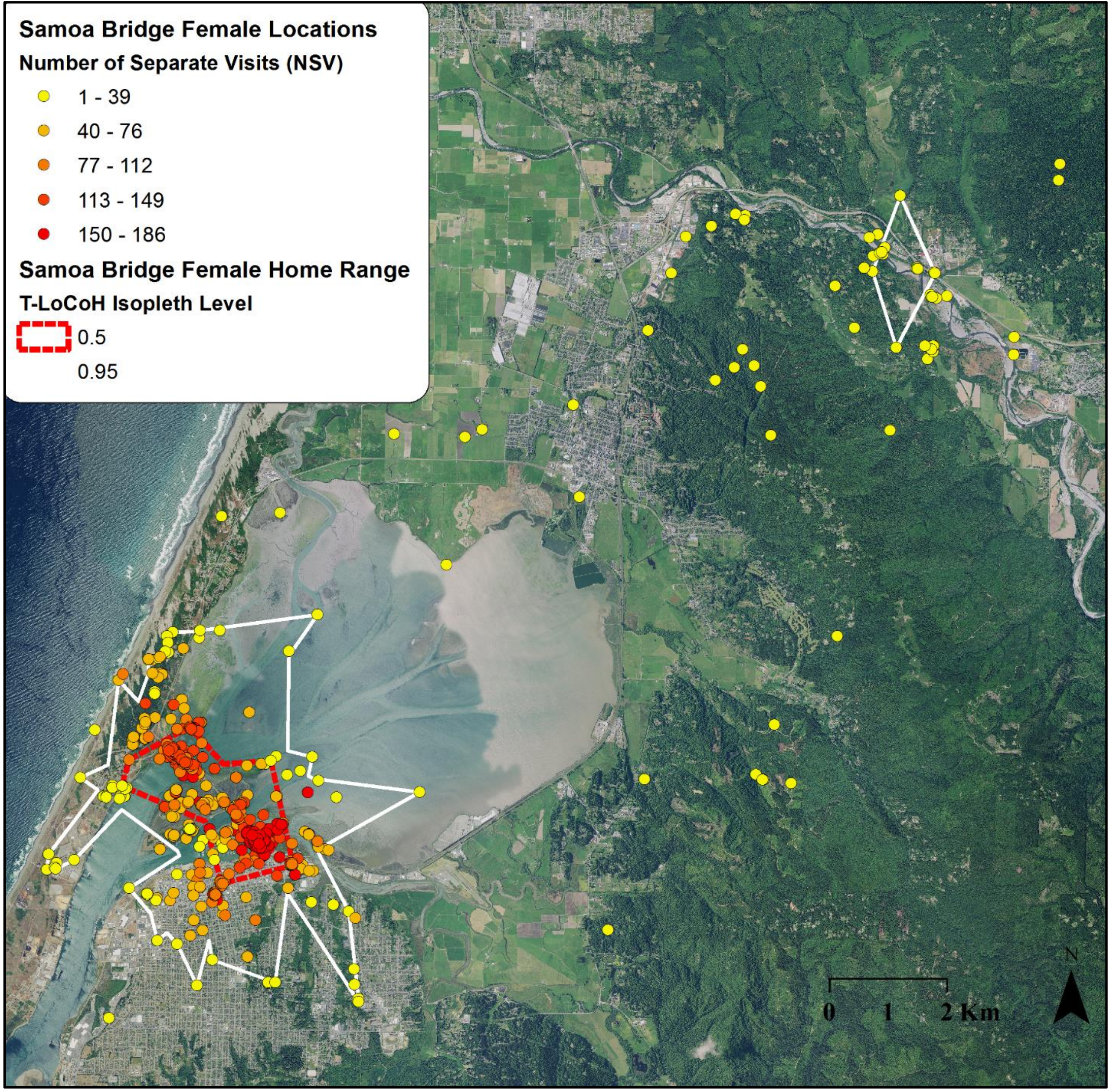
APPENDIX G. Dry Lagoon female peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from June 2014 to August 2016 in Humboldt County, California.



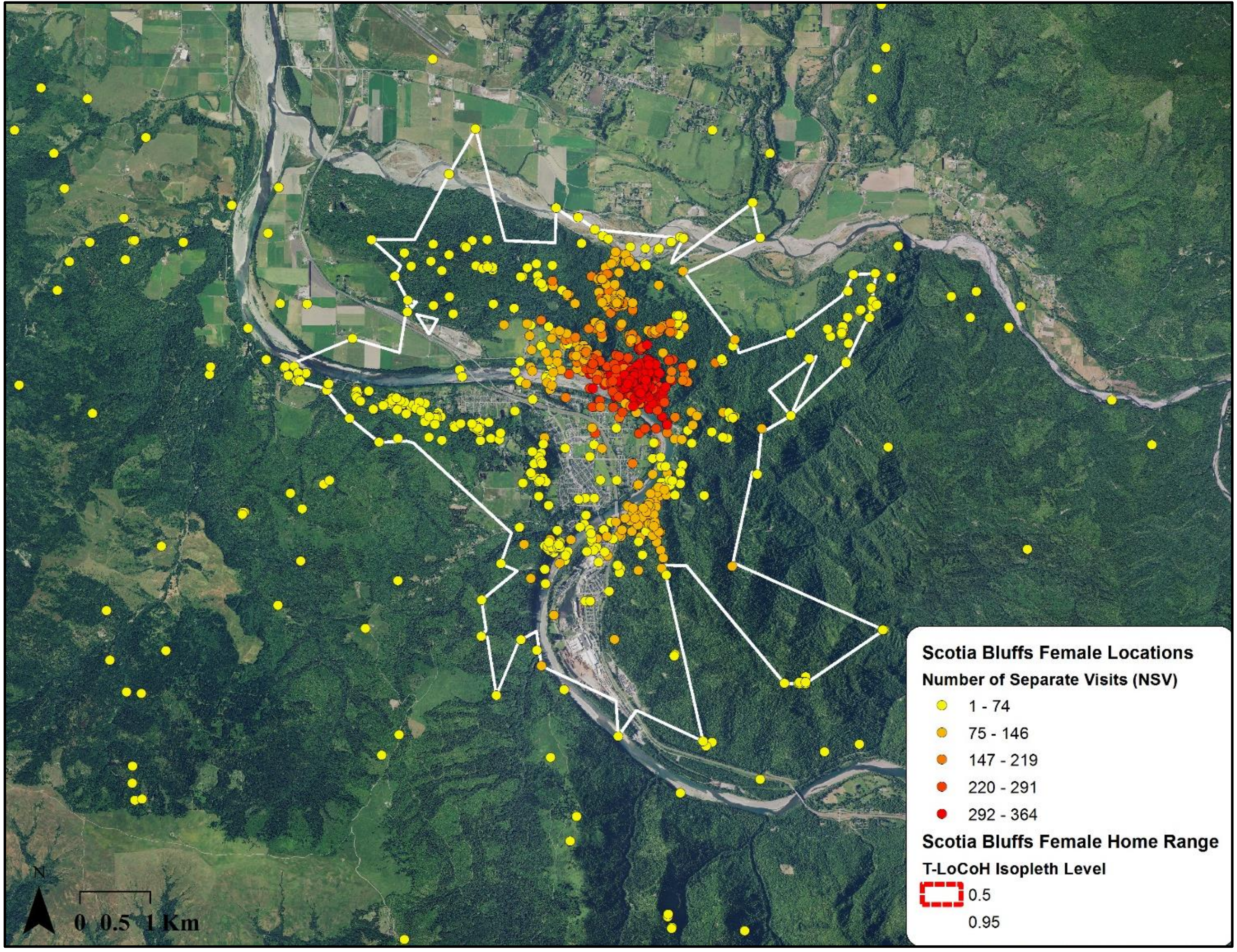
APPENDIX H. Dry Lagoon male peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from May 2014 to June 2016 in Humboldt County, California



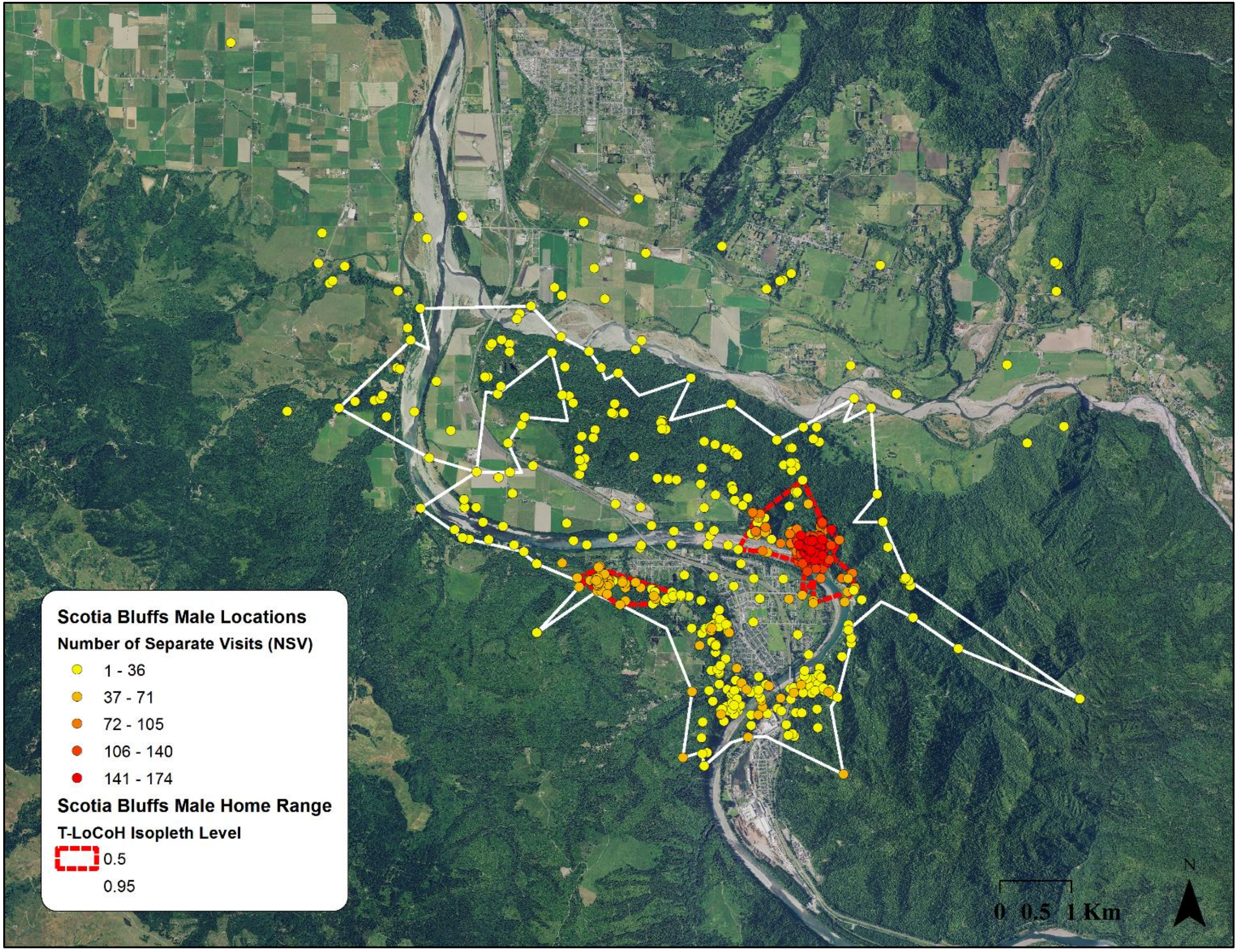
APPENDIX I. Samoa Bridge female peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from June 2014 to August 2016 in Humboldt County, California.



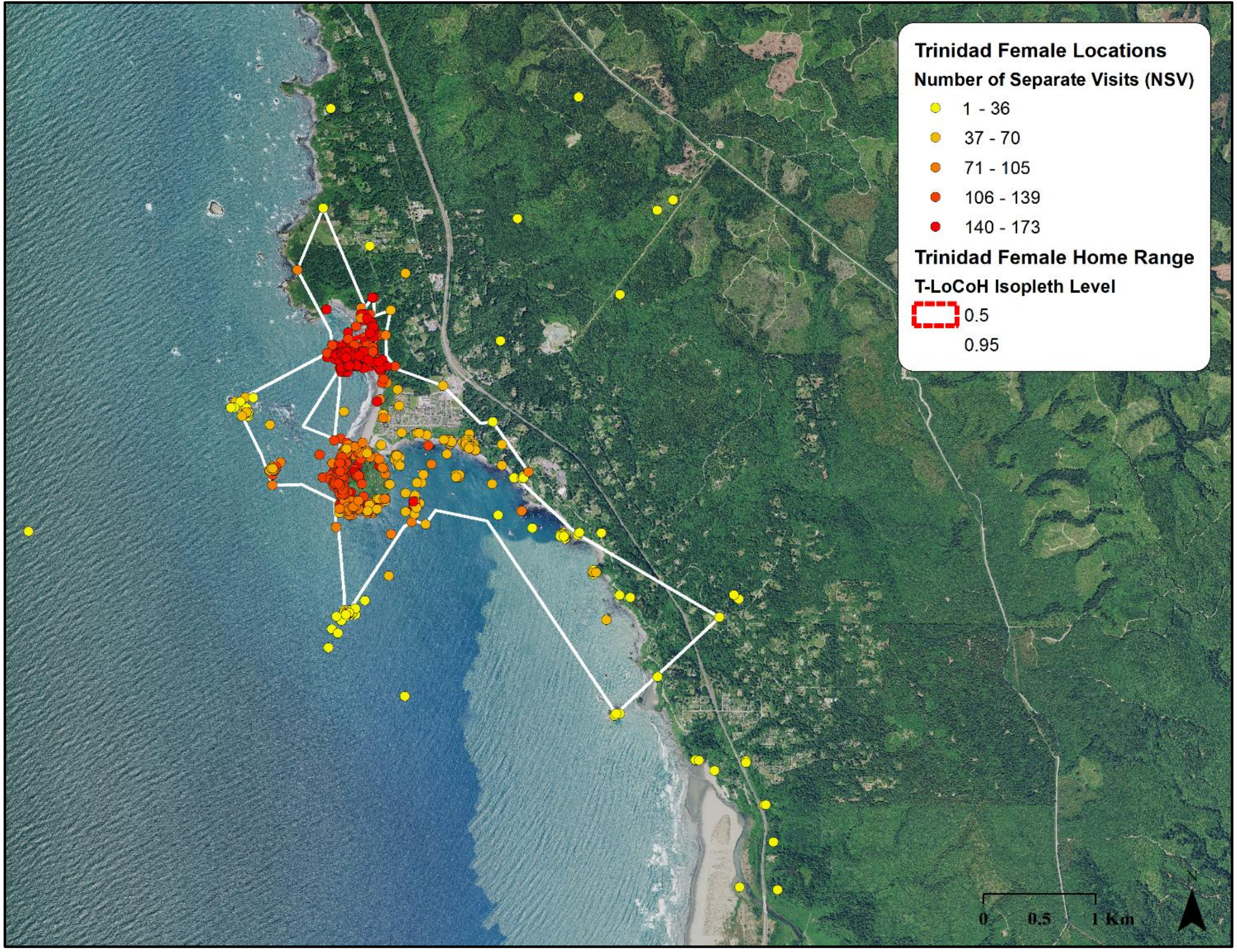
APPENDIX J. Scotia Bluffs female peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from June 2014 to August 2016 in Humboldt County, California.



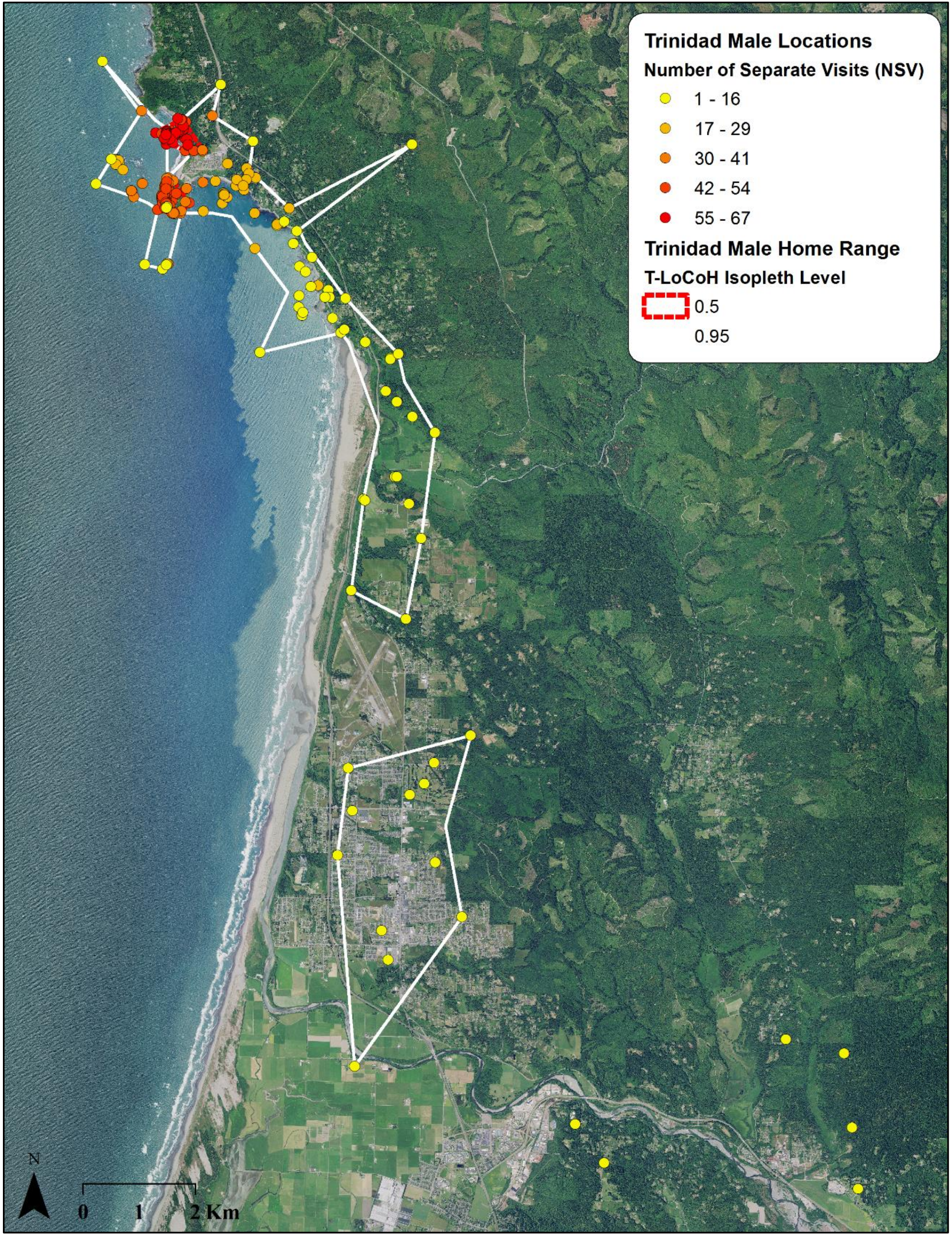
APPENDIX K. Scotia Bluffs male peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from June 2014 to August 2016 in Humboldt County, California



APPENDIX L. Trinidad female peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from February 2015 to August 2016 in Humboldt County, California.



APPENDIX M. Trinidad male peregrine falcon T-LoCoH home range estimate, showing parent hull points colored by Number of Separate Visits (NSV) values, from March 2015 to September 2015 in Humboldt County, California.



APPENDIX N. Spatial data used in GLMMs; digital elevation model (a.), terrain ruggedness index (b.), eBird prey density index showing prey hotspots (c.) and California Wildlife Habitat Relation types (d.).