

MOVING RIGHT ALONG: THE EFFECT OF HABITAT TYPE ON RANGING
PATTERNS IN WHITE-HANDED GIBBONS (*HYLOBATES LAR*) IN WESTERN
THAILAND

by

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ABSTRACT

MARGARET SOBASZEK. Moving right along: The effect of habitat type on ranging patterns in white-handed gibbons (*Hylobates lar*) in Western Thailand. (Under the direction of DR. LYDIA EOLIGHT)

White-handed gibbons are found through Southeast Asia, but little is known about how they adapt to lower quality resources. At Huai Kha Khaeng Wildlife Sanctuary in Western Thailand, these gibbons inhabit a heterogeneous landscape that encompasses evergreen forest, dry dipterocarp forest, and mixed deciduous forest. The population of gibbons at this site are relatively understudied compared to gibbon habitats elsewhere. My research focuses on whether habitat type affects the ways in which they range by estimating home range and core areas. I use my data to compare to a previous study at the same habitat on the same groups, examining home range areas and site fidelity at a short time scale. Using six different methods of range estimation, I found varying results and degrees of biological relevance for this project. Addressing habitat type and ranging behaviors will allow for the comparison of the diverse needs of populations inhabiting different habitats. Improved knowledge on ranging patterns will allow for an improvement in management practices with better conservation designs. The preservation of species can be effectively managed by determining home ranges which are affected by the distribution of their resources, the areas used for travel, and areas that are otherwise managed socially.

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LIST OF ABBREVIATIONS

CHP	Characteristic hull polygons
FP	Fixed percent
HKK	Huai Kha Khaeng Wildlife Sanctuary
KNR	Khao Nang Rum Research Station
KDE	Kernel density estimates
LSCV	Least squares cross validation
MCP	Minimum convex polygon
REF	Reference bandwidth

INTRODUCTION

The goal of the proposed research is to examine the effects habitat type has on the ranging behavior of white-handed gibbons (*Hylobates lar*) at Huai Kha Khaeng Wildlife Sanctuary (HKK) in Western Thailand. The white-handed gibbons in this area reside in a heterogeneous habitat that is characterized as being at the extreme edge of their range (Light 2016). As a clear majority of research on white-handed gibbons has been done in resource abundant evergreen habitats that have low levels of seasonality (Brockelman 2009), more research needs to be done to understand how gibbons adapt to different ecological conditions.

Landscape ecology and spatial ecology are the fundamental drivers to animal movement. Therefore, I will be examining the effects that ranging patterns have on core areas and home ranges because they are the result of animal movement and the landscape that they reside in. To give this some context, I will briefly examine landscape ecology and spatial ecology, the concepts that lead up to what influences animal movement, home range use, and core area use. I will investigate the role of habitat quality on animal movement through an analysis of home ranges and core areas in white-handed gibbons living in two types of habitat, the evergreen habitat and the savannah habitat, in western Thailand.

Although animal movement is one of the most basic functions of many animals, a thorough understanding of it is still limited because it requires consideration of many different factors. The factors that influence behavior and movement in animals in the wild are subject to temporal and spatial change, within and between species. Animal movement studies have important applications in conservation management and

behavioral ecology studies that deal with group living, finding mates, disease transmission, and predator-prey interactions.

Ranging behavior is important because it is one of the most essential behavioral patterns that can inform us on the nature of the habitat. Home ranges can be used to properly manage a species for conservation because an animal will get at least 95% of its resources from this area (Downs *et al.* 2018, Worton 1987). Core areas are a much smaller portion of their range that are subject to frequent temporal and spatial shifts due to the changing nature of the environment. The frequent shifts in core area location is likely not enough to create an effective conservation plan, although there does need to be more work done on understanding the complexities of core areas (Asensio *et al.* 2014). Methodological choices will result in different estimations of ranging patterns. An integration of multiple types of home range estimations will allow for analyses of different aspects of range use and implications for future directions.

The most notable factor that impacts ranging is the environment in which they live. The way in which gibbons use home ranges, use core areas, and maintain site fidelity are likely to be dependent on the habitat they occupy. However, there are few studies examining ranging patterns in white-handed gibbons living in low quality landscapes. The results of this study will contribute to evaluating impacts of ecological factors that alter ranging patterns especially in white-handed gibbon populations living in sub-optimal habitat.

BACKGROUND

SPATIAL ECOLOGY AND LANDSCAPE ECOLOGY

Spatial ecology focuses on the fundamental effects of space on individual species and on the structure, dynamics, diversity, and stability of communities that contain many different kinds of species (Tilman and Kareiva 1997). The spatial structure of the landscape is aggregated in patches or gradients that will affect how populations and communities of individuals use space and may be indicative of species interactions such as competition, predation, and reproduction (Legendre and Fortin 1989, Perry *et al.* 2002). My research looks at spatial ecology through the lens of landscape ecology, which focuses on the broader spatial scales as well as the ecological effects of the patterns of space use and interactions within ecosystems (Turner 1989, Wiens *et al.* 1993). Spatial pattern influences important ecological processes and the effects of these need to be considered in ecological studies and resource management decisions (Turner 1989). The study of spatial patterns is used to infer the existence of underlying processes in ecology such as movement (Perry *et al.* 2002). An individual's ability to move in space is variable within and between species due to the reactions of the individuals to one another and to the environment (White and Harris 1994). Animal movement and ranging behavior is "the glue that binds together both behavior at a lower scale of organization and population dynamics at a higher scale of organization" (Nams 2014, 1228).

Animal space use pattern, or movement, "in geographic space emerges from all its relocation events" (Van Moorter *et al.* 2016, 22). Elucidation of the proximate and ultimate causes that are responsible for the movement of organisms is the basic motivation for the research done in the fields of spatial, landscape, and behavioral

ecology. Movement plays an important role in the fate of individuals, the structure and dynamics of populations, communities, and ecosystems as well as the evolution and diversity of life (Nathan 2008, Avgar *et al.* 2013, Roshier *et al.* 2008, Westcott and Graham 2000). Understanding movement patterns is important not just in furthering our understanding of animal behavior, but also in managing and restoring degraded landscapes, controlling the spread of pests, invasive alien species, allergens, toxins, and infectious diseases (Nathan 2008).

Movement patterns are often dependent upon both spatial and temporal scales. Habitat type (Raynor *et al.* 2017), encounters with other animals (Wartmann *et al.* 2014, White and Harris 1994) and resource availability (Roshier *et al.* 2008) are ecological conditions that affect animal movement. Certain behaviors may only be displayed for specific situations. Animals may respond as specific spatial scales change and likewise, some behaviors may only be available for specific temporal scales (Avgar *et al.* 2013). Demographic information is likely to change over time and affect movement (Tao *et al.* 2016). Other time dependent encounters may involve predator-prey interaction (Coleman and Hill 2014), intergroup conflicts (Strong *et al.* 2017) or mating availabilities (Fagan *et al.* 2013) that may only be available at a specific spatiotemporal scale (Gudmundsson *et al.* 2008). The variable nature of these conditions means that they can and often do change and conclusions or inferences regarding these patterns and processes need to take into account the importance of these scales (Turner 1989).

The relationship between animal behavior and movement creates a particular ecological phenomena that is extremely sensitive to variations in space (Wiens *et al.* 1993). When quantifying the spatio-temporal dynamics of the distributions in populations

it is crucial to pay attention to the relationships that exist within the moving individuals as well as the analysis of the individual movement paths (Mueller *et al.* 2011). Individual movement studies are affected by interactions between life history, physiology, behavior, and habitat (Patterson *et al.* 2008). Animal movement may be altered by territorial aggression, which is an act of defending the resources of an individual or group (Getty 1981) or by predator avoidance (Fortin *et al.* 2005, Coleman and Hill 2014), which causes a shift in the movement of the prey (Turner and Montgomery 2003). Factors that affect movement such as community structures, predator-prey interactions, mating probabilities, and territoriality are all affected by the landscape (Wiens *et al.* 1993).

Movement is a complex behavior that involves many variables (Roshier *et al.* 2008). Variation in movement patterns can be a result of differential experiences of individual encounters (Roshier *et al.* 2008). While many studies suggest movement is in response to mate distribution (Nathan *et al.* 2008), availability of food (Reyna-Hurtado *et al.* 2017), occurrence of barriers (Beyer *et al.* 2016), knowing the habitat (Fagan *et al.* 2013), avoiding predators (Raynor *et al.* 2017, Coleman and Hill 2014), defending territories (Mitani and Rodman 1979), range of movement (Clutton-Brock and Harvey 1976), and dietary preferences (Milton and May 1976), the structure of the landscape is an external and underlying factor that greatly affects the way an individual or a group moves throughout the habitat.

Animal movement throughout a landscape is the result of the interaction between the organism and its environment (Raynor *et al.* 2017). In order to understand this interaction, knowledge of the temporally dynamic nature of these environments is crucial (Avgar *et al.* 2013). Due to seasonality, which affects the abundance and type of

resources available as well as permeability through an area, this structure may change through time. The distribution of species is affected by the way the landscape is composed and consists of characteristics such as type of habitat, resource-patch size, edge length, configuration, disturbance or human made landscape structure (Saïd and Servanty 2005).

One influential factor of spatial ecology is landscape heterogeneity, which is important for understanding population dynamics of organisms living in complex landscapes. Heterogeneous landscapes are described as landscapes that have more than one, often multiple, different types of cover that gives the habitat a more complex spatial patterning (Fahrig *et al.* 2011). Different parts of the habitat may vary in their use by an individual based on resource availability, predation, mating opportunities, and probabilities of reproductive success (Johnson *et al.* 1992). The ability for organisms to move freely in their habitat is affected by how much the environment impedes or facilitates movement (Beyer *et al.* 2016). Obstacles or barriers that obstruct an animal's movement can have profound effects on their home range, social activity, and mating opportunities.

HOME RANGES

The home range is the area used by the individual in normal activities of food gathering, mating, and child care, excluding occasional excursions (Burt 1943, Powell 2000). Home ranges “link the movement of animals to the distribution of resources necessary for survival and reproduction” (Börger *et al.* 2008, 644). The location and size of home ranges do not necessarily cover the same area during the entire life of an individual or group (Burt 1943). They may vary with sex, age, and in response to seasonal change (Börger *et al.* 2006). Population density variations (Burt 1943), the fluctuation in availability of resources (Powell 2000) and social factors may also influence long-term variation in home ranges (Ramos-Fernandez *et al.* 2013, Bermejo 2004).

Home ranges are generally heterogeneous landscapes where resources are distributed unevenly within the boundary where certain areas are abundant in resources while others are not (Samuel *et al.* 1985). These areas are subject to change in habitats that have seasonal variation. Home ranges are generally smaller when areas are more abundant in necessary resources. Low food densities allow for larger ranges that often overlap with neighboring home ranges (Börger *et al.* 2008). Landscape heterogeneity is an important variable that helps assess which habitats are used by different species and the density in which species can occur across many different environments (Riley 1999). Animals often respond to spatial and temporal heterogeneity by altering their movement patterns (Frair *et al.* 2005) which affects the size and location of their home ranges. Depending on the taxa, the distribution of vegetation, and the spatial scale, species abundance can either decrease or increase along with habitat heterogeneity (Tews *et al.*

2004) which is important to consider when assessing the distribution of home ranges in a habitat.

The area that an animal inhabits must be large enough that it contains an adequate amount of resources necessary to survive (Grant *et al.* 1992). Home ranges are fundamental products of animal behavior that are essential in understanding how to manage a species (Burt 1943). Two different populations of the same species can use their home ranges differently because of variations in their habitat type. Animals should move in a way that minimizes costs such as energy (Mathot and Dingemanse 2015), predation risk (Coleman and Hill 2014), or competition for resources, whilst maximizing the benefits they derive from the way they move (José-Domínguez *et al.* 2015). When defining home ranges, time is a critical component because the measure of space used is a function of the temporal scale and will vary at different scales (Spencer *et al.* 1990). The factors that need to be considered when undertaking a study are dependent on the location, demographic information of the species (Tao *et al.* 2016), and time scale (Campioni *et al.* 2013, Gudmundsson *et al.* 2008).

There are 15-20 gibbon species and 4 genera that are generally characterized as small, diurnal, and arboreal apes that live in social groups of 2-7 individuals and are mostly believed to occur in socially monogamous groups with associated offspring (Bartlett 2003, Bartlett and Light 2017, Fan *et al.* 2017). They move arboreally through the canopy of the forest using brachiation, bipedal running, and leaping (Fleagle 1976). Gibbons are characterized as primarily frugivorous (Clutton-Brock and Harvey 1976) and as more territorial than most other primate species (Bartlett 2009, Raemaekers *et al.* 1984, Reichard and Sommer 1997). White-handed gibbons are found in southeast Asia

and have their largest population density in Thailand (Brockelman and Geissmann 2008). Most of our knowledge on these gibbons are from sites high in resources with less variation in seasonality (Brockelman 2009) because they are found most often in wet forests with an array of floristic diversity (Bartlett 2009). But they are also found in habitats that are uncharacteristic of their usual evergreen abundance (Light 2016). In areas with lower resource availability, gibbons are observed as having larger home ranges (Savini *et al.* 2009). White-handed gibbons were observed, on average, to use most of their range when fruit was most abundant and less of their range when fruit was scarce (Bartlett 2009). Their home ranges are relatively small averaging around 40 hectares (Bartlett 2011). However, research on white-handed gibbons living in suboptimal habitats shows an increase in home range size, ranging from 31-60 hectares (Light 2016). Though there is variation in home range size between sites, these gibbons are known to maintain stable home ranges over extended periods of time (Asensio *et al.* 2014).

Site fidelity is an animal's tendency to use the same geographical area over time (Asensio, Schaffner, *et al.* 2012, José-Domínguez *et al.* 2015). Site fidelity and regular use of certain areas are common characteristics of animal movement (Börger *et al.* 2006). The importance of how well the animals are familiar with an area is a relevant concept in site fidelity because it is beneficial to know the habitat in order to find high quality foods (Brockelman 2009), which is particularly advantageous when an animal lives in a heterogeneous environment (Ramos-Fernandez *et al.* 2013). Strong site fidelity may reflect stability in an area in response to the availability of resources and temporal shifts result in weak site fidelity (José-Domínguez *et al.* 2015). Site fidelity could be due to the resources available or social factors. One possible benefit of site fidelity is knowing

where important resources are located. These can include sleeping sites, feeding trees, or efficient travel routes (Wartmann *et al.* 2014).

Site fidelity in territorial animals may be related to defense of the home range or a portion of the range (Ramos-Fernandez *et al.* 2013). Individuals that exhibit aggressive behavior that is spatially oriented are defined as territorial (Börger *et al.* 2008). Home ranges are often divided into a more intensively used area that is defended as their territory “by means of systematical patrol and aggressive evictions, and an external area, which is used primarily during their foraging bouts” (Tao *et al.* 2016, 460). Range size in territorial animals must be negotiated between having an optimal strategy for movement, foraging beyond an individual’s territory, and protecting their territory from outside conspecifics (Tao *et al.* 2016). Group living primates have different factors that affect their home range use such as defending their partners, offspring, or food resources from neighboring groups (Wartmann *et al.* 2014). The protected part of the home range is the territory and can consist of the entire home range, a portion of the home range, or a smaller core area (Burt 1943, Hayne 1949).

CORE AREAS

Core areas are regions of the home range that are used more intensively than any other part of the home range (Hayne 1949, Samuel *et al.* 1985). They are considered by some to be the minimum area needed for an individual or group to live and reproduce as it has the most important resources for a group or individual (José-Domínguez *et al.* 2015, Asensio, Lusseau, *et al.* 2012). While home ranges often overlap, core areas should not (Samuel *et al.* 1985, Ewer 1968). Core areas should be more ecologically relevant to the resident animals than the non-core areas (Asensio, Lusseau, *et al.* 2012). Addressing large scale movements such as the home range and small scale areas such as resource patches or core areas help in delineating space use (Benhamou and Riotte-Lambert 2011). Each animal uses their core area differently whether it is in regards to neighboring conspecifics, availability of food, sleeping sites, or mating areas, which explains the difference in sizes of the core areas (Powell 2000).

Core areas within the home range identify areas selected by the animal. They are determined by comparing the observed pattern of space use with the expected uniform pattern of use and by finding the areas where use exceeds expected uniform distribution (Samuel *et al.* 1985). Food resources, sleeping sites, or refuges are some of the preferred features of the habitat that are relative to the animal that the core area may contain (Ramos-Fernandez *et al.* 2013). Examination of environmental and behavioral processes are necessary in order to understand the disproportionate use of the core areas (Samuel *et al.* 1985). More quantitative analysis on core areas will tell us more information on the importance of their role in conservation (Asensio, Lusseau, *et al.* 2012). Because any changes in the size, shape, and location of home ranges will directly affect core areas,

home ranges must be taken into account when identifying core areas (Samuel *et al.* 1985).

Unlike home ranges that have high site fidelity, core areas may, and frequently do, shift over time (Asensio *et al.* 2014). Within the home range, individuals may restrict their movement to smaller core areas that are less than expected from their locomotion capacities (Benhamou and Riotte-Lambert 2011). Generally, core areas are centralized and high quality (Powell 2000). Core areas may be visited in varying degrees of intensity depending on the depletion of resources (Benhamou and Riotte-Lambert 2011), the presence of predators (Turner and Montgomery 2003), or the change in habitat. The shift in core areas suggests that different areas meet the requirements of an animal at different temporal scales (Asensio *et al.* 2014).

The objective of this research is to investigate the variations in ranging patterns of white-handed gibbons in two types of habitat. I test the hypothesis that habitat type will affect ranging behaviors in these gibbons by altering their home range use. In testing this hypothesis, I expect that ranging patterns will be different, with the group in the savannah habitat having a larger overall home range and core area because of the lower quality habitat compared to the evergreen habitat. I also examine site fidelity and my expectations are that the savannah group would travel through less of their overall range each week and maintain higher levels of site fidelity than the evergreen group. In order to see the changes over time in the ranging patterns of gibbons, I compare my data to the data from Light (2016). I expect that my overall home range will fall within Light's overall home range.

METHODS

In order to do this, I measure ranging using a few different methods, so I'll be discussing home range, core area, site fidelity. Home ranges are generally thought as 95% of their observed ranging behavior while core areas are constructed as being 50% of their ranging behavior. I calculated range estimates using three major methods kernel density estimates (KDE), minimum convex polygons (MCP), and characteristic-hull polygons (CHPs) (Light 2016, José-Domínguez *et al.* 2015). I use Minta Index to determine site fidelity.

STUDY SITE

Huai Kha Khaeng Wildlife Sanctuary is located in Western Thailand and is a 278,000 hectare reserve (Bunyavejchewin *et al.* 2004). It is an ideal location for this project because it is an excellent example of an undisturbed, healthy forest that is home to different habitat types. The landscape of the sanctuary is a mosaic of several forest types including dry dipterocarp seasonal dry evergreen, mixed deciduous, and dry montane forests (Bunyavejchewin *et al.* 2004, Ratnam *et al.* 2011). The savannah habitat is characterized by a mixture of discontinuous tree canopy and a continuous C4 grass-dominated understory (Ratnam *et al.* 2011, House *et al.* 2003). The study site at Khao Nang Rum Wildlife Research Station (KNR) (15°25'-15°31'N, 99°15'-99°20'E) is located in the northeast portion of HKK (Light 2016). The combination of forest types has previously been described as creating two distinct habitat types, evergreen forest habitat, primarily evergreen forest with small patches of mixed deciduous forest, and savannah habitat, with a combination of dry dipterocarp and mixed deciduous forests

with small patches of evergreen forest (Walker and Rabinowitz 1992). These different habitat types are not bounded, but are combined in a patchwork configuration which allows for the opportunity to study the effects that habitat type has on gibbon behavior (Light 2016). The wet season lasts from May to October (Walker and Rabinowitz 1992) with peak rainfall occurring during May-June and September-October (Light 2016).

STUDY GROUPS

There are several groups of white-handed gibbons found at this field site. Groups have previously been habituated starting in 2012 by Light (2016). My research focused on two groups of white-handed gibbons, one from each habitat. Group B is located in the evergreen habitat and group D is in the savannah habitat (see Figure 2) (Light 2016). Group B consisted of one adult female (Belle), one adult male (Balasz), one subadult male (Bailey), one juvenile (Brooklyn), and one infant (Boots). All individuals in this group were buff colored with the exception of the Belle and Brooklyn who were brown colored. In group D, there was one adult female (Daisy), two adult males (Darwin and Downey), and one infant (Dexter). Darwin and Dexter were brown and the adult female and the other adult male were buff.

DATA COLLECTION PERIOD

I collected data for 27 days between August 12 and October 1. During my observations of the gibbons, I used 10 x binoculars (Brockelman *et al.* 1998) because of their arboreal nature and tendency to stay higher in the tree tops (Bartlett 2009). I followed the two groups alternating every week for six weeks. My goal was to follow

each group from night tree to night tree for at least five consecutive days per week. With the help of my field assistants, I began the day at 6:00 a.m. to find the gibbons and ended at 3:00 p.m. My focal animal for location data was the adult female because they are known to lead group movements more often than other individuals within the group (Barelli *et al.* 2008). I collected spatial data every five minutes at the base of the tree in which the focal subject is located (Light 2016). I recorded location data using a Garmin eTrex Summit® handheld GPS device (<10 m 95% accuracy).

HOME RANGE AND CORE AREA ESTIMATIONS

I imported my location data into ArcGIS 10.6 (Environmental Systems Research Institute, Redlands, CA, USA), QGIS 2.18 (Open Source Geospatial Foundation), and Ranges version 9 (Anatrack Ltd, United Kingdom) to analyze ranging patterns. The size and location of core areas are dependent on home range size because they are often calculated as a percentage of the home range (Samuel *et al.* 1985). I calculated home range estimates using kernel density estimates (KDE), minimum convex polygons (MCP), and a relatively newly developed and underutilized method called characteristic-hull polygons (CHPs) (Light 2016, José-Domínguez *et al.* 2015). I chose to do three methods of ranging analysis to provide a larger comparative scope to my project that has a small sample size. Within each method, I chose two different ways to calculate home range estimations.

I used KDE to define home ranges at 95% (Laver and Kelly 2008, Downs *et al.* 2011). I used reference bandwidth (REF) KDE with a cell size of 1. I then used least squares cross validation (LSCV) KDE methods as recommended by Downs *et al.* (2011)

with a cell size of 10. MCP construct home ranges by connecting different recorded locations with straight lines to form a polygon (Kernohan *et al.* 2001, Mohr 1947). I calculated home ranges as MCP enclosing 100% and 95% of the group locations (José-Domínguez *et al.* 2015). CHPs are created in GIS by using the Delaunay triangulation of a set of points where the small triangles represent areas of high ranging activity and the larger triangles, which represent unused or less frequently used areas, are removed (Downs and Horner 2009, José-Domínguez *et al.* 2015). I calculated home ranges as 95% of the smallest triangles for the CHPs methods (Downs and Horner 2009). For fixed percent (FP), I classified Delaunay triangles based on their perimeter size, then CHPs were generated for 95% home ranges by taking out 5% of the largest triangles. In the statistical CHP method, I excluded all triangles with Z-scores of more than 2 to get the home range estimation (José-Domínguez *et al.* 2015).

I used Prism 8 (Graphpad, San Diego, CA, USA) for all statistical analyses. I used a one-way ANOVA test with an alpha level set at 0.05 to compare the different home range and core area estimates from each method. I calculated the average weeks for both groups and used Welch's *t* test to test the difference between group B and D for each method used.

I calculated KDE core areas as 50% isopleths of relative intensity (Downs *et al.* 2011). For the MCP core areas I calculated the ranges as being 50% of the group locations (José-Domínguez *et al.* 2015). For FP CHPs, I calculated core areas by removing 50% of the largest triangles. The statistical method of CHPs estimation is composed of all triangles with Z-values ≤ 2 and core areas values < -2 (José-Domínguez *et al.* 2015, Downs *et al.* 2011).

SITE FIDELITY

To determine what areas are used most consistently, I calculated overlap between weeks of the same group and between each week and the overall group home range by using the Minta Index (1992). Minta Index calculates site fidelity as a measure of overlap of space, or shared area. I calculated site fidelity using the Minta Index as used by Bartlett *et al.* (2016) and Asensio, Schaffner, *et al.* (2012):

$$\frac{\bigcap_{i=1}^n a_i}{\sqrt[n]{\prod_{i=1}^n a_i}}$$

The numerator is the shared area covered by the ranges and the denominator is the geographic mean of the intersected areas (Bartlett *et al.* 2016, Asensio, Schaffner, *et al.* 2012). I compared each week with the overall home range of the corresponding group for each of the six methods. I also used the Minta Index to compare my overall data to the data from the overall home ranges and the summer home ranges of Light (2016). A percentage of the Minta index of 100 indicates complete overlap between areas, whereas 0 signifies that the areas do not overlap at all (Asensio, Schaffner, *et al.* 2012).

RESULTS

TEMPERATURE AND PRECIPITATION

Rainfall and temperature were recorded by the staff at KNR (Table 1).

Temperatures ranged from 22°C to 30°C in August and from 21°C to 31°C in September.

Rainfall for the month of August was 126 mm and 179 mm in September.

HOME RANGE AND CORE AREA ESTIMATION

Using REF KDE, LSCV KDE, 100% MCP, 95% MCP, FP CHPs, and statistical CHPs, I created overall and weekly home range estimates for groups B and D (Figures 1-14), core area estimates for the overall range and weekly range (Figures 15-26) and home ranges comparing my data with the data from Light (2016) (Figures 27-34). I looked at home ranges and core areas of two groups of gibbons using six different methods. Different methods for range estimation produced varying estimations of range sizes (Table 2). Overall home range area for group B ranged from 14.57 ha (REF KDE) to 4.82 ha (FP CHPs) and for group D ranged from 49.16 ha (REF KDE) to 12.27 ha (fixed percent CHP) (Table 2).

Average weekly home ranges varied between $3.17 \pm \text{SD } 1.50$ ha (FP CHPs) and $15.42 \pm \text{SD } 7.62$ ha (REF KDE) for group B and between $8.50 \pm \text{SD } 6.01$ ha (FP CHPs) and $37.01 \pm \text{SD } 27.25$ ha (REF KDE) for group D (Table 2).

Using a one-way ANOVA, I compared each group's weekly ranges. There were no significant differences between the methods for group D ($P = 0.3989$). However, in comparing the different home range methods for group B, there were significant

differences ($P = 0.0199$) with 95% MCP method resulting in the smallest home range area (1.65 ha) and REF KDE methods the largest (23.37 ha).

To compare the difference in weekly home range area between group B and group D, I used an unequal variance t test, or Welch's t test. I did this for comparison between the weekly ranges of the two groups for each method that I used. There was no significant difference in home ranges between the two groups using any method (REF KDE: $P = 0.3158$; LSCV KDE: $P = 0.1991$; MCP 100: $P = 0.2225$; MCP 95: $P = 0.2236$; FP CHPs: $P = 0.2747$; statistical CHPs: $P = 0.2562$).

Across all methods, weekly core areas ranged from 0.25 ha (FP CHPs) to 5.69 ha (LCSV KDE) for group B and 0.31 ha (FP CHPs) to 23.91 ha (REF KDE). Overall core areas ranged from 0.74 ha (FP CHPs) to 5.69 ha (LSCV KDE) for group B and the range in group D was from 1.73 ha (FP CHPs) to 24.09 ha (50% MCP) (Table 3). There was no significant difference in core areas between the two groups using any method (REF KDE: $P = 0.25.97$; LSCV KDE: $P = 0.1583$; MCP 50: $P = 0.2416$; FP CHPs: $P = 0.3692$; statistical CHPs: $P = 0.4543$).

SITE FIDELITY

Weekly Minta Index values measuring the similarity between the overall home range and each weekly range varied from 58.67% to 75.40% (Tables 4-6). Group B had higher average Minta Index values (0.6376 ± 0.0487 SD) than group D (0.6461 ± 0.072 SD).

The average weekly Minta Index values for all of the methods was used to compare amount of range overlap between groups B and D using an unequal variance t

test. There were no significant differences in the Minta Index values between the two groups for any of the methods (REF KDE: $P = 0.8895$; LSCV KDE: $P = 0.8667$; MCP 100: $P = 0.9303$; MCP 95: $P = 0.6744$; FP CHPs: $P = 0.9624$; CHPs statistical: $P = 0.6874$).

COMPARISON WITH A PREVIOUS STUDY

I recreated the home ranges of Light's (2016) research using slightly different methods which I then compared to my data. I used the largest estimation from all three methods (REF KDE, 100% MCP, and statistical CHPs) to broadly estimate the site fidelity between the two datasets. I used the Minta index to calculate the degree of overlap between our data. Comparing my overall data to Light's overall data using REF KDE resulted in a Minta Index of 59.25% for group B and 23.65% for group D. Using the REF KDE to compare the summer data between our two sets resulted in a Minta Index of 89.15% for group B and 52.50% for group D. Using 100% MCP estimates for overall, the Minta Index for Light's overall range with my overall range was 66.98% for group B and 77.21% for group D. For the summer data using 100% MCP, Minta Index for group B was 56.75% and for group D at 28.30%. The Minta Index for group B's overall home range is 53.26% and 61.19% for the overall home range of group D using the statistical CHPs method (Table 7). For her summer data compared to my overall data, the Minta Index was 34.08% and 31.16% for groups B and D, respectively (Table 8).

DISCUSSION

This research adds valuable information to an understudied population of white-handed gibbons living in a unique environment. However, due to the limited scope of the project, these results do not address questions requiring long-term datasets or a large number of study groups.

METHODOLOGICAL CONSIDERATIONS

My results showed the variation in range estimation between core areas and home ranges in all methods. Overall home range area for group B ranged from 14.57 ha (REF KDE) to 7.04 ha (statistical CHPs) to 4.82 ha (FP CHPs). Group D ranged from 49.16 ha (REF KDE) to 29.49 ha (LSCV KDE) to 12.27 ha (fixed percent CHPs) (Table 2). No range estimation was consistent in any of the methods. While REF KDE were most often the largest and FP CHPs were most often the smallest, this was not consistent through all of the range estimations.

A consensus on the best home range estimation is not established, and likely will vary based on the organism under research considerations. A more realistic treatment of behavior in movement models is necessary in the study of ranging behaviors (Schick *et al.* 2008). The type of habitat an individual inhabits will factor into how to analyze data and how to consider external pressures on one's own research. Mitchell and Powell (2004) suggest that animals inhabiting landscapes with patchily distributed resources will have home ranges with selected resource-bearing patches embedded within unimportant patches that are used primarily for travel. The behavior of species or populations will also affect the methods or statistical models used in obtaining accurate information on animal

range and distribution in an area. Therefore, studies concerning animal movement should use study- and site-specific methods that take into consideration the environment, organism being studied, behavior, and other factors which will provide more accurate data for determining home range and core area analysis.

Home range estimation delineates the spatial extent that an animal occupies, as well as identifying core areas of more intense activity (Downs *et al.* 2011). A major debate in home range estimation is in deciding on the method that is most appropriate. Kernel density estimation and minimum convex polygon have traditionally been favored although there has been much criticism and debate over the use of them (Downs and Horner 2009). I used KDE because they are the most prevalent method that calculates core areas and home ranges (Laver and Kelly 2008) that provides a probabilistic measure of how animals use their space and also distinguishes between areas of different intensities of use (Horne and Garton 2006). In home range analysis, the density at any location is an estimate of the amount of time spent there (Seaman and Powell 1996). KDE-based results have been criticized as being affected by the method of bandwidth selection (Horne and Garton 2006), sensitive to sample size (Seaman and Powell 1996), and not being robust to the shape of the point patterns of locations (Mitchell and Powell 2008). KDE generate a continuous intensity surface of the distribution of an animal by smoothing the point pattern so the home range is more rounded (Downs and Horner 2008). LSCV KDE is seen as being too variable in terms of undersmoothing the data, making it difficult to understand the structure of the data (Jones *et al.* 1996). REF KDE may result in undersmoothing in areas where there are sparse observations and

oversmoothing in other parts (Van Kerm 2003) resulting in an overestimation of home ranges and core areas (Downs *et al.* 2011).

A bounding hull is a polygon that encloses some number of points, lines, or other polygon features in its interior and MCP is the most used hull, which creates the smallest area polygon that contains all points of a distribution where the internal angles are less than 180 degrees (Downs and Horner 2009). MCP-based results are also criticized as being inaccurate, inconsistent, highly sensitive to sample size and point pattern shape (Worton 1987, Downs and Horner 2009). The MCP method is criticized for overestimating home-range size because it is sensitive to outliers and sample size (Seaman and Powell 1996). The MCP method is not sensitive to the use of a location multiple times, unlike KDE and CHPs. It does not take into consideration the frequency of use that an animal spends in a location and the frequency which an area is revisited and the intervals at which the area is revisited vary and are important to note when looking at home range characteristics (Benhamou and Riotte-Lambert 2011). However, because both KDE and MCP are widely used and for comparison purposes, I have used them as well.

Characteristic hull polygons are a relatively recent non-probabilistic method of home range estimation (José-Domínguez *et al.* 2015, Downs and Horner 2009). They are also bounding hulls like MCP, but unlike MCP, they can have non-convex edges and empty holes within the polygons (Downs and Horner 2009). CHPs can be composed of disjoint regions, concave edges, and empty portions of unused space within hull interiors which allows for a more accurate way to distinguish more frequently used areas (Downs *et al.* 2011). Core areas of fixed percent and statistical estimates are criticized as

underestimating core areas but produce higher spatial accuracy in home ranges (Downs *et al.* 2011). Both CHPs methods are more robust to different sample sizes compared to KDE and MCP estimates (Downs *et al.* 2011). While the results of Downs *et al.* (2011) conclude that fixed percent CHPs performed best overall, I found that statistical CHPs provided the most accurate representation of the construction of core areas because it shows the areas the gibbons used the most due to the location of important resources. The 100% MCP method of home range estimation was the best for my data set because it encompassed most of my data while not overestimating the range to the degree where it would interfere with neighboring groups.

COMPARING THE METHODS USING MY DATA

For home range analysis, both KDE methods provided results that did not accurately portray my data. I found that REF KDE were consistently the largest range estimate and overestimated and oversmoothed the results, although the ranges that were constructed contained all of my data (Figures 5, 15, and 16). The LSCV KDE frequently dissected the range into two or more parts and excluded parts of the range that were notable for both groups (Figures 6, 17, and 18). The 100% MCP had encompassed most of my data, even if the ranges were an overestimation (Figures 7, 19, and 20). The 95% MCP were almost exactly the same as 100% MCP but, like the LSCV KDE, excluded important areas that the gibbons used (Figures 8, 21, and 22). Fixed percent CHPs are extremely angular and a very literal outline of the outermost points used by the gibbons (Figures 9, 23, and 24). The statistical CHPs, while they dissected the home range into two separate regions for each group, provided more accurate estimates on area used (10,

25, and 26). Overall, I found that the statistical CHPs and 100% MCP methods for home range estimation has the most biological relevance for my dataset compared to the KDE methods. Therefore, in my discussion, I will be referring to these two methods to explain my results.

HOME RANGE ESTIMATIONS

I expected group D to have larger overall home ranges and core areas because of evidence from a previous study (Light 2016) as well as the location of their home range in a lower quality habitat compared to the other habitat in my research. Home ranges need to cover an adequate amount of resources (Grant *et al.* 1992). Animals living in stable and/or productive environments often have smaller scale movements and form territories that they defend and home ranges in which they occupy (Roshier *et al.* 2008). In areas with lower resource availability, like group D, groups or individuals will need larger home ranges to cover an area that contains the necessary amount of resources to survive (Börger *et al.* 2008).

The weekly home range average using statistical CHPs for group B was $4.29 \pm$ SD 2.26 ha with the overall range at 7.04 ha and the weekly home range average for group D was $12.53 \pm$ SD 8.79 ha with the overall range at 15.97 ha. Using 100% MCP group B's weekly range average was $6.64 \pm$ SD 2.99 ha and group D had a weekly range average of $23.78 \text{ ha} \pm$ SD 16.71 ha. The 100% MCP method is much larger than the home range estimations using statistical CHPs because it is an inclusive method that incorporates most of the points from the data into the construction of the polygon and does not allow for empty portions or unused space within the home range. There were no

statistically significant differences in the different methods for home range group D, but there was for group B. This could be the result of the smaller overall home range or the small sample size. Using Welch's *t* test in comparing the weekly ranges between groups for each method, no method showed a statistically significant difference.

The overall core area of group B using statistical CHPs was 0.75 ha and 2.49 ha for group D. Using the 50% MCP method, group B's overall core area was 3.74 ha and group B's overall core area was 24.09 ha. The overall core areas for statistical CHPs accurately reflected the areas in which the gibbons frequented the most and the longest. These areas generally had the most food resources that the gibbons exploited. Core areas using MCP were less accurate than the statistical CHPs. The 50% MCP method was more accurate in depicting the overall core areas for group B than group D. Group D's core area was extremely overestimated because MCP does not take into consideration frequency of use. Because the areas in which they were recorded in most often are spread further apart than in group B, the MCP method is not as accurate because it does not allow for empty areas within the range estimation like CHPs do.

SITE FIDELITY

Due to the overall lower resource availability, I expected that group D would traverse less of their overall range each week and maintain higher levels of site fidelity than group B. My expectation was, while they might have to travel further, they would also have larger and more stable weekly ranges than group B. I expected that group D's home range would contain larger core areas with fewer resources in them than the evergreen habitat but that those resources would be exploited more because of the lower

resource abundance elsewhere in their habitat. I thought because group B has a higher quality habitat, would have more resources to choose from and therefore the ability to move around more with less limiting factors on ranging patterns.

Weekly ranging patterns did vary with both groups each week, but the difference does not appear to be habitat specific. The mean Minta Index values for statistical CHPs estimations were higher in group B (66.3%) compared to group D (58.75%). Group D had less overlap and lower site fidelity than group B but this was not statistically significant ($P = 0.6874$). Using the 100% MCP estimations, Minta Index values were higher in group D (75.4%) than group B (70.19%) but was also not significant ($P = 0.9303$). While speculative, higher Minta values for MCP could be due to the overestimation that is so frequent in this method. It allows for more area in a range to overlap with another range. Group D ranges were generally, much larger than group B's ranges, thus using 100% MCP instead of statistical CHPs would provide a higher Minta Index. Resource availability at HKK is lowest during the rainy season from May to October, which suggests that both groups had fewer resources that they could exploit across their ranges at this time, so they maintained higher site fidelity than maybe other times of the year.

COMPARISON TO PREVIOUS DATA

I used the data from Light (2016) in order to see how this compares to a more robust dataset. I used the largest estimation from all methods and to compare between her summer data and my overall data. The results varied for each method. Comparing my overall data to Light's summer data using 100% MCP estimates, the Minta Index was

higher for group B (89.15%) than group D (52.50%). The Minta Index was relatively similar at 34.08% and 31.16% for groups B and D, respectively, using the statistical CHPs method.

The high overlap using the 100% MCP between Light's summer data with my overall data in group B shows that the gibbons overall summer home range did not change much since 2012-2013 when Light collected her data (Figure 29). However, the Minta Index was relatively low using the statistical CHPs method which might indicate that location of resources used by the gibbons had changed between our data collection periods for groups B and D. The difference between our results could be due to the sampling schedules that might result in missing important ranging behavior in one of our data collections. I had three weeks: one week of data collection in August and two weeks in September for both groups. To compare to these three weeks, I selected her points from three weeks of a close time frame (July-September).

It does appear that my group B ranges shifted from what was previously observed in Light's study. Home range estimations for both 100% MCP (figure 29) and statistical CHPs (figure 32) show an area frequently used by gibbons outside of Light's overall home range which may suggest that important resources are available in this area that were not there before. It could also mean that gibbons home ranges can shift more frequently in lower quality habitats. This could be the result of a loss of preferred resources for the gibbons at this time and they had to adjust their ranging accordingly.

Group D's 100% MCP Minta Index was low and is likely due to size difference of the observed ranges between my research study and Light's (Figure 29). My overall home range overlaps less with her overall because it is much smaller. Another reason for

the shift in ranging patterns could be the difference in temperature and precipitation during data collection periods or the change in group membership. When Light (2016) did her study, the group membership consisted of Daisy, Darwin, Downey, and Denison along with a juvenile female but at the end of her study Darwin was no longer observed with group D and there was an infant. During my study, group D consisted of Daisy, Darwin, Downey, and Dexter. My group had an infant and Light's study did not have an infant during the summer, but her study did contain a juvenile which I did not have. Light's group B consisted of Belle, Bailey, Balazs, and another female, while I had Belle, Bailey, Balazs, as well as Brooklyn who was a juvenile and Boots who was an infant.

Choosing an appropriate temporal scale is crucial to the success of animal movement studies as varied temporal scales can result in differences in size and shape of the home range (Saïd and Servanty 2005). My overall data would not be enough to address the minimum area requirement needed by the gibbons because it only covered part of the ecological cycle.

FUTURE DIRECTIONS

There has not been much work done on gibbon core areas. The importance of this research allows for insight that may help future studies in the methodological choices. The integration of more than one method will allow for the researcher to choose the most efficient and biologically relevant methods for their own research. This could also be applied to research on similar primates, particularly those that are also arboreal, territorial, and frugivorous as well as broader implications for methodological home range estimation. The previous (and currently only) study on gibbon core areas by Asensio *et al.* (2014) uses only one method, MCP, with a 100% MCP to calculate home

ranges and 50% MCP for core areas. I found that statistical CHPs were the most accurate at providing estimates for overall core areas for both groups in terms of resources used. Using 50% MCP to delineate core areas providing more realistic results for group B than group D. This study highlights the shortcomings of MCP core areas and identifies more appropriate methods.

Home ranges and core areas in primates are not necessarily distinct from those of other animals. Instead of looking at primate core areas as separate from those of other taxa, it is important to consider the specifics of each population that is being studied. Habitat type, social structure, mating system, diet, and size of any animal should be reflected in the design of the research on core areas. The importance of the core areas to the individual(s) using them varies across species and populations. White-handed gibbons are recorded as having low fidelity to core areas (Asensio *et al.* 2014), which suggests that they change more often and a shorter temporal scale is necessary in order to assess that change. While Asensio (2014) posits that white-handed gibbon core areas are related to the spatial distribution of food resources over a short temporal scale, the study did not consider effects of sociality, interspecific competition, or behavior. For future studies, conspecific encounters should also be noted in reference to core areas because interaction in white-handed gibbons often occur near or in food trees (Reichard and Sommer 1997) which should effect territorial defense and core area locations. Just as home ranges are affected by external factors such as encounters from members of another group, core areas should also be expected to be affected.

Instead of calculating weekly core areas as 50% of their weekly range as done by Asensio *et al.* (2014), I suggest that weekly ranges should be considered more important

than weekly core areas. Weekly home ranges are already a smaller portion of their overall home range and using those smaller ranges to define core areas as 50% or as a Z-score of < -2 is not biologically relevant. These weekly home ranges will, over time, represent the most important areas of the overall home range, and the minimum area that an individual needs to survive. This allows for the study of weekly ranges as important for conservation over longer periods of time. Asensio *et al.* (2014) concludes with the advisement of using weekly core areas on a fixed temporal scale as an insufficient basis for conservation management. He posits that the superposition of all weekly core areas could define a region that theoretically reaches the minimum area needed for survival with most resources being within but this approach will result in a region that reflects the shape of the long-term home range because all parts of the home-range (short-term core areas) are likely to be important at some point in the life of the animals. I would argue that not all parts of the home range will be considered core areas, but that does not mean they are any less important. The use of MCP will overestimate core areas and home ranges and it is likely that using this method for weekly core areas would, over a longer period of time, define the long-term home range. The statistical CHPs method would provide core area estimation that is a more accurate representation of resources and areas used by the gibbons the most. Because home ranges are often heterogeneous areas that has an unequal distribution of resources, there will be parts of the home range that may just be used to travel from one area to another and not necessarily contain any important food resources.

Many different factors need to be considered when looking at what is affecting animal behavior. Population dynamics, animal movement, mating strategies, foraging

strategies, home ranges, and core areas are all affected by habitat type. The most notable factor is the environment in which they live. The way in which gibbons interact with one another, use home ranges, travel daily path lengths, and use core areas are likely to be dependent on the habitat in which they occupy. However, there are few studies examining ranging patterns in white-handed gibbons living in sub-optimal habitat. Future studies at this site should therefore integrate investigate ranging in relation to social behaviors and focus more on lower qualities habitats.

A more comprehensive approach to analyzing data is necessary to provide comparison and a better understanding of space use in primate ranging behavior. Using several different methods together will provide a way to compare the results to one another and use them in conjunction with one another to best manage a species. I was able to find home range and core area estimations that were best suited for my data by applying several different methods for analysis. An integrative approach is necessary in order to adequately study temporal and spatial variation in home range behavior, because it is impacted by both behavioral and ecological processes (Campioni *et al.* 2013). While animal home range use should be part of conservation strategies, the use of them in management plans is a relatively new idea (Fauvelle *et al.* 2017).

When delineating home range areas, it is imperative to consider the necessary area required by the gibbons to survive, which includes resource patches as well as travel patches. For a home range estimation method that considers this, I would suggest the 100% MCP are better at providing a more encompassing estimation of gibbon home range areas. Using observation points in FP CHPs will probably underestimate the area an individual needs but may be better suited for telemetry data because they provide a

very literal outline to the outermost data points. Using location data from observation only will likely underestimate the area used for FP CHPs. My data show that statistical CHPs are a more accurate estimation for the location and use of resources that are important for gibbons. However, they do not provide an accurate estimation of the necessary area that an animal needs to survive. The use of CHPs might underestimate the area that the gibbons defend or the areas needed to travel in between resource important patches. The dissection of the home ranges into two separate parts does not allow for an accurate depiction that allows for an understanding of home ranges.

A long-term study would be better able to elucidate some of the questions that I was unable to answer in my discussion. Understanding core areas and assessing their importance needs to be done on a longer time scale. The overall core areas for my groups were not as informative as my weekly home ranges. Overall core area would be more important with a longer term study and a more robust dataset. Weekly home ranges are likely to continue to change and shift, not just from month to month, but from year to year. There are myriad factors that shape core areas which, unlike home ranges, are expected to change more frequently. It is expected that gibbons should have low site fidelity to core areas because they are using them for shorter temporal intervals than home ranges.

A more robust sample size, demographic information, changes in group membership, and social behavior should also be considered when trying to understand animal ranging patterns. The amount of rainfall during the study period is also likely to have an effect on movement and therefore should be considered in relation to ranging patterns. Overall fruit availability associated with temperature and rainfall at lower

quality gibbon sites may cause seasonal shifts in the ranging patterns of gibbons (Kim *et al.* 2011). Phenology data would also be useful in determining how gibbons structure their movements according to available food resources. The nutritional quality of food and their locations in the home range would provide interesting insights into understanding factors relating to ranging. An integrative approach to studying ranging and analyzing the results will allow for more biologically relevant home range estimations in the future.

CONCLUSION

Because white-handed gibbons are classified as Endangered (IUCN 2017), it is important to understand more about how they alter their activities according to lower quality habitat type. Gibbons generally have a preference for less seasonal, lowland evergreen forests and because of this, most gibbon studies are conducted in these habitats. But because of the “behavioral flexibility that gibbons display, especially under variable ecological conditions, further research is necessary before accurate evolutionary models of hylobatid social organization can be developed. A realization that our current understanding is incomplete may have important implications for the conservation of these organisms” (Malone and Fuentes 2009, 253). The landscape at my research site consists of seasonal habitats in a heterogeneous landscape (Light 2016) which allowed for the study of ranging patterns of white-handed gibbons that differed from other habitats and differences between two groups with distinct habitats.

The most inclusive methods for home range delineation in my dataset were REF KDE and 100% MCP, with MCP being more biologically relevant to home range area. Moving forward, gibbon home range and core area estimation should be done using several different methods. When doing analyses, it is imperative to consider the necessary area required by the gibbons to survive, which includes resource patches as well as travel paths. Range use is not just an ecological factor, so many different social factors should be included to get a thorough understanding of the results that different methods may present.

Gibbons are thought to maintain a stable home range over time (Asensio *et al.* 2014), but perhaps this is more common in areas with more stable and higher quality

resources. Animal movement is continuously changing. Shorter term studies on home range over long periods of time can inform us on the nature of those changes. Weekly, monthly, and seasonal range use when compared over multiple years can inform us on changes in the nature of the habitat. The difference between my overall home range and Light's overall home range tells us that, while white-handed gibbons remain in the same general area over time, there are expansions of the overall home range. Comparing species that are located in different habitat types will allow for a broader understanding of range use differences and the variation in overall shape and size. Studies on minimum area requirements explicitly address the necessary amount of space needed by an organism and can therefore be highly useful in determining conservation management plans (Pe'er *et al.* 2014). Conservation practices should not assume that all groups or populations of a species will range similarly, especially if the habitat types differ.

Movement studies need not only focus on movement, but often need to consider population ecology, phenological patterns, habitat type, social systems, intergroup encounters, and changing climate. Therefore, understanding both the state of the organisms and the environment in which they move is necessary when assessing interactions between the two. Intraspecific variation can inform management programs when assessing both the vulnerability and the resilience of populations when anthropogenic effects are so prevalent on primates and their habitats (Strier 2017). With ongoing habitat change due to degradation, fragmentation, and deforestation, learning how these gibbons cope with suboptimal habitats can help inform future conservation practices on the management of forests and preservation of white-handed gibbons. Understanding intraspecific variation is the most urgent scientific challenge for the field

of primate behavioral ecology today because it reflects a combination of factors ranging from decisions about data, disparities in data quality, standardization of cross-sectional and longitudinal data, and the integration of new dynamic theoretical frameworks (Strier 2017).

The study and understanding of spatial ecology on animal movement is useful in determining the spread of diseases and invasive species, home range characterization, reserve design as well as understanding population ecology and dynamics (Patterson *et al.* 2008). Landscape ecologists have focused on the interaction between individuals and their movement in an effort to understand future impacts from habitat loss and climate change (Schick *et al.* 2008). The sub-optimal habitat that my study groups occupies allows us to infer what type of future landscape gibbons will inhabit due to anthropogenic effects on higher quality gibbon habitats. While these gibbons were able to live in this environment, they needed overall larger home range areas to ensure a sufficient amount of resources.

The selection, design, and management of protected areas and species requires knowledge about how much area is necessary for long-term maintenance of biodiversity (Pe'er *et al.* 2014). Home ranges are an essential part in understanding animal movement because it is a common pattern of space use and as such, has fundamental consequences for ecological processes (Börger *et al.* 2008). Because home ranges are considered the minimum area necessary for animals to survive, they are the foundation in our understanding of conservation matters. However, an understanding of other important factors are needed in relation to home ranges. The concept of core areas are widely used across animal studies, but more understanding on the nature and relationships between

the use of core areas, home ranges, and animal conservation are still not understood (Asensio *et al.* 2014). Core areas are likely to shift in time and space based on the abundance of resources and more studies on core area use will inform us of their importance in management plans.

This study demonstrates that there are many factors that, when studied under different combinations, can affect the results of data analysis. Deconstructing mechanisms of home range size into components of variation in temporal, spatial, and individual-level processes will result in more reliable inferences (Börger *et al.* 2006). Using multiple home range estimation methods will allow for a more comprehensive understanding of range use. Explicit reports of details on home range estimates from studies should be used more broadly in order to improve reproducibility and credibility of spatial ecology studies (Fauvelle *et al.* 2017). The study of ranging behaviors can illuminate aspects of space use including territoriality, population density, and longer-term measures of space use such as home ranges (Jetz *et al.* 2004, Carbone *et al.* 2004). Accurately estimating home ranges and core areas is necessary for characterizing ranging patterns and species requirements for the creation of more effective guidelines and policy implementations in the future (Downs *et al.* 2018). An increase of knowledge of primates in the wild will allow the design and management of protected areas, rehabilitation, captive breeding, and reintroduction of primates to be most effective (Malone and Fuentes 2009).

The increasingly anthropogenic context in which primate populations live has resulted in an expanding theoretical in anthropological primatology and a concern with the human-environment interface (Riley 2013). In a world of growing human needs as

well as human impacts, social-ecological research will work to benefit all and ensure a more certain future for conservation (Ban *et al.* 2013). Practicing applied primatology allows for a broader approach to primate studies by embracing emerging opportunities for interdisciplinary work and expanding the realm of applied anthropology by engaging in primate conservation (Riley 2013). When working with primates, conservation issues are now always relevant because it's no longer possible to study nonhuman primates without coming into contact with human interaction, manipulation, and/or habitat destruction (Fuentes and Wolfe 2002).

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APPENDIX A: TABLES

Table 1: Temperature and precipitation during August and September at the KNR research station

August				September			
Date	Temp (°C)		Rainfall (mm)	Date	Temp (°C)		Rainfall (mm)
	6:00 am	1:00 pm			6:00 am	1:00 pm	
1	23	29	0	1	24	30	0
2	24	28	10	2	24	30	0
3	24	28	0	3	23	29	13
4	24	29	0	4	23	29	0
5	24	29	19	5	23	25	0
6	22	29	5	6	23	29	0
7	23	29	20	7	24	29	0
8	22	28	0	8	24	28	0
9	24	28	0	9	23	25	0
10	24	29	0	10	23	30	6
11	24	28	0	11	23	28	0
12	23	29	0	12	22	28	0
13	24	29	0	13	23	28	50
14	23	28	0	14	23	28	0
15	23	28	0	15	22	25	50
16	24	26	0	16	23	30	5
17	24	26	5	17	24	30	0
18	23	26	0	18	23	28	0
19	23	29	0	19	23	29	0
20	24	28	0	20	22	28	0
21	23	29	0	21	23	30	0
22	23	29	0	22	22	30	0
23	23	28	0	23	23	30	0
24	23	29	0	24	23	31	6
25	24	28	0	25	21	31	0
26	23	29	31	26	22	30	0
27	22	29	0	27	22	31	10
28	23	30	26	28	23	31	33
29	22	27	0	29	23	31	0
30	23	27	0	30	23	32	6
31	23	29	0				

Table 2: Overall home ranges for all data sets

Home ranges	REF KDE	LSCV KDE	100% MCP	95% MCP	FP CHPs	Statistical CHPs
B all	14.57	14.03	12.01	11.29	4.82	7.04
B week 1	14.69	10.78	9.94	7.83	4.75	6.68
B week 2	8.19	8.00	5.88	5.31	2.99	4.00
B week 3	23.37	7.80	4.12	1.65	1.77	2.19
D all	49.16	29.49	36.59	35.01	12.27	15.97
D week 1	49.74	42.82	33.16	31.40	10.51	17.47
D week 2	5.84	9.69	4.49	2.73	1.74	2.39
D week 3	55.46	28.84	33.69	32.07	13.25	17.74
Light 2016 B all	10.91	10.72	17.86	13.56	10.03	12.37
Light 2016 B summer	12.54	10.39	7.74	6.73	6.21	5.59
Light D 2016 all	46.20	41.25	60.84	57.20	31.57	37.83
Light 2016 D summer	31.04	24.50	38.92	28.95	22.14	20.99

Table 3: Core areas for weekly and overall ranges

Core areas	REF KDE	LCSV KDE	50% MCP	FP CHPs	Statistical CHPs
B all	5.24	5.69	3.74	0.74	0.75
B week 1	5.18	4.57	3.10	0.66	0.63
B week 2	3.10	3.61	2.00	0.72	0.62
B week 3	5.35	2.70	0.55	0.25	0.99
D all	12.36	10.85	24.09	1.73	2.49
D week 1	23.91	11.07	19.47	1.08	2.41
D week 2	2.36	4.34	0.82	0.31	0.33
D week 3	17.34	12.53	12.45	2.22	1.20
Light 2016 B all	3.89	4.47	3.083838	1.57	3.22
Light 2016 B summer	4.18	4.13	1.732212	0.99	1.24
Light 2016 D all	20.53	16.05	22.085994	3.30	3.30
Light 2016 D summer	8.33	5.46	2.962125	2.07	6.32

Table 4: Minta Index for overlap between weekly ranges and overall ranges

	REF KDE			LSCV KDE		
	Area (ha)	Overlap (ha)	Minta	Area (ha)	Overlap (ha)	Minta
B all	14.57			14.03		
B week 1	14.69	14.32	.9788	10.78	8.95	.7274
B week 2	8.19	8.20	.7504	8.00	6.90	.6510
B week 3	23.37	4.91	.2661	7.80	5.42	.5183
B mean			.6651			.6322
D all	49.16			29.49		
D week 1	49.74	42.00	.8494	42.82	23.72	.6672
D week 2	5.84	5.09	.3006	9.69	6.11	.3613
D week 3	55.46	37.78	.7239	28.84	22.98	.7878
D mean			.6246			.6054

Table 5: Minta Index for overlap between weekly ranges and overall ranges

	MCP 100%			MCP 95%		
	Area (ha)	Overlap (ha)	Minta	Area (ha)	Overlap (ha)	Minta
B all	12.01			11.29		
B week 1	9.94	9.94	.9097	7.83	7.83	.8328
B week 2	5.88	5.88	.6997	5.32	5.32	.6864
B week 3	4.13	4.13	.5864	1.66	1.05	.2425
B mean			.7019			.5872
D all	36.59			35.01		
D week 1	33.16	33.16	.9520	31.41	31.41	.9472
D week 2	4.49	4.49	.3503	2.73	2.73	.2792
D week 3	33.69	33.69	.9596	32.07	31.10	.9281
D mean			.7540			.7182

Table 6: Minta Index for overlap between weekly ranges and overall ranges

	FP CHPs			Statistical CHPs		
	Area (ha)	Overlap (ha)	Minta	Area (ha)	Overlap (ha)	Minta
B all	4.82			7.04		
B week 1	4.75	3.61	.7546	6.68	5.69	.8303
B week 2	2.99	2.76	.7260	4.00	3.98	.7502
B week 3	1.77	0.73	.2482	2.19	1.60	.4078
B mean			.5763			.6628
D all	12.27			15.97		
D week 1	10.51	6.67	.5868	17.47	10.21	.6112
D week 2	1.74	1.73	.3760	2.39	2.39	.3872
D week 3	13.25	10.17	.7974	17.73	12.86	.7642
D mean			.5867			.5875

Table 7: Minta Index for overlap between my overall data and Light's data

	REF KDE			MCP 100			Statistical CHPs		
	Area (ha)	Overlap (ha)	Minta Index	Area (ha)	Overlap (ha)	Minta Index	Area (ha)	Overlap (ha)	Minta Index
B all	14.47	7.47	.5925	12.01	9.81	.6698	7.04	4.97	.5326
Light 2016 B all	10.91			17.86			12.37		
D all	49.16	11.27	.2365	36.59	36.43	.7721	15.97	15.04	.6119
Light 2016 D all	46.20			60.84			37.83		

Table 8: Minta Index for overlap between my overall data and Light's summer data

	REF KDE			MCP 100			Statistical CHPs		
	Area (ha)	Overlap (ha)	Minta Index	Area (ha)	Overlap (ha)	Minta Index	Area (ha)	Overlap (ha)	Minta Index
B all	14.57	11.24	.8915	12.01	9.81	.6698	7.04	3.18	.3408
Light 2016 B sum	10.91			17.86			12.37		
D all	49.16	25.02	.5250	36.59	36.43	.7721	15.97	7.66	.3116
Light 2016 D sum	46.20			60.84			37.83		

APPENDIX B: FIGURES

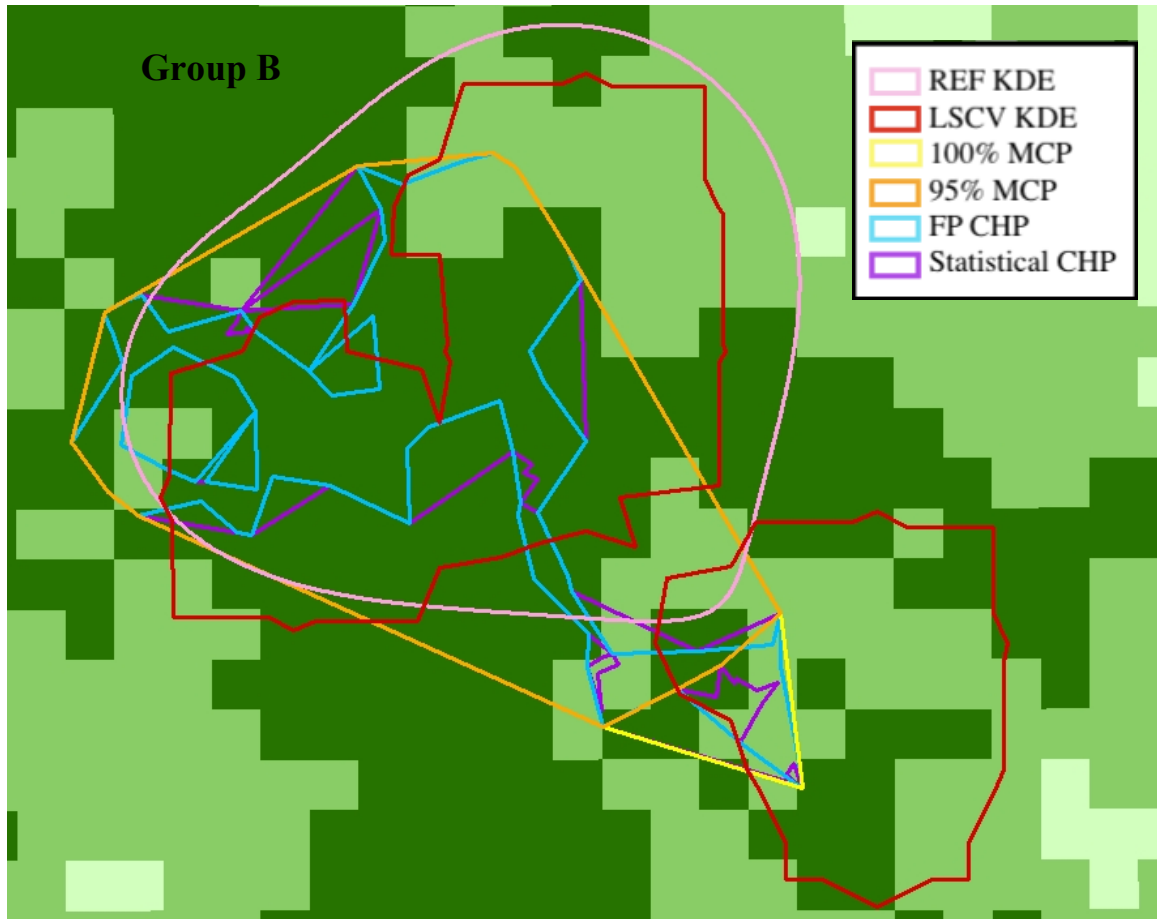


Figure 1. Group B home range using all methods. Dark green represents evergreen areas, medium green represents mixed deciduous areas, and light green represents dry dipterocarp areas.

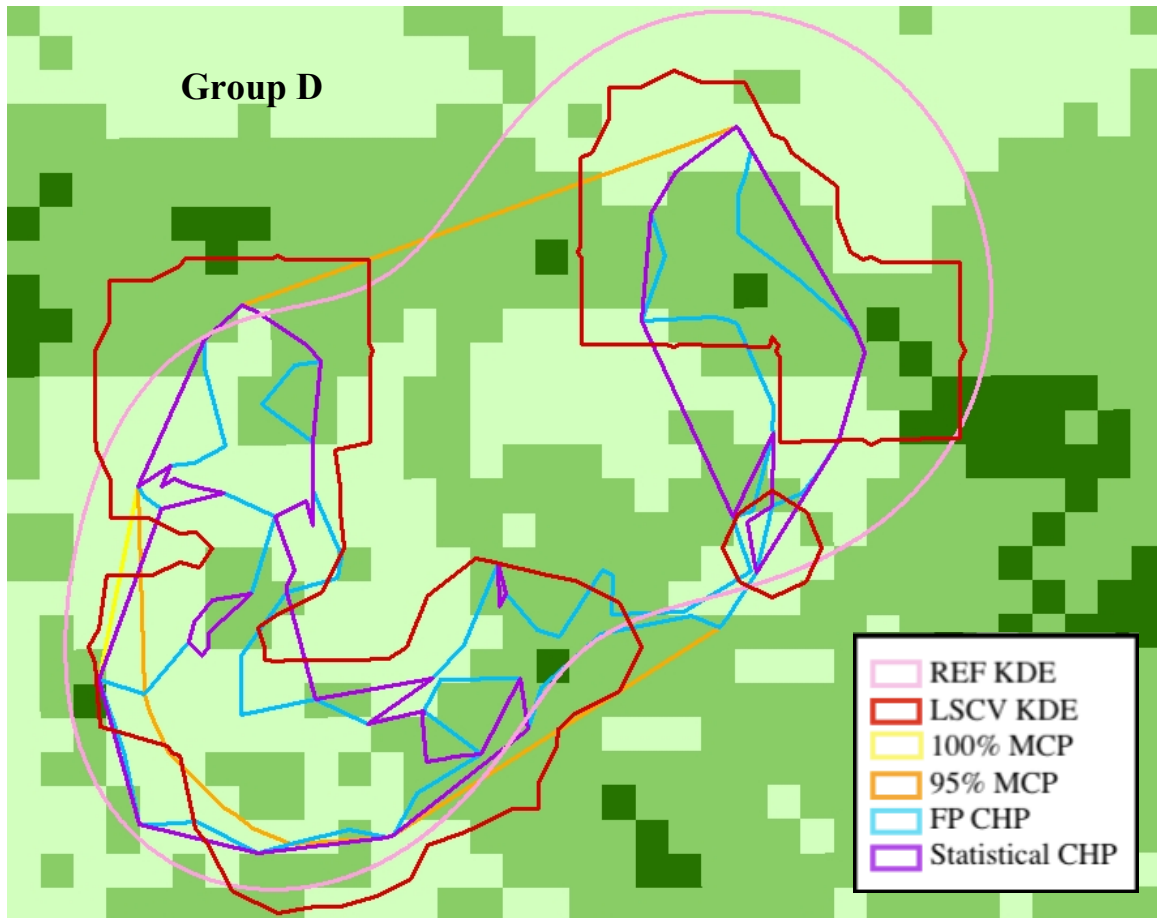


Figure 2. Group D home ranges using all methods.

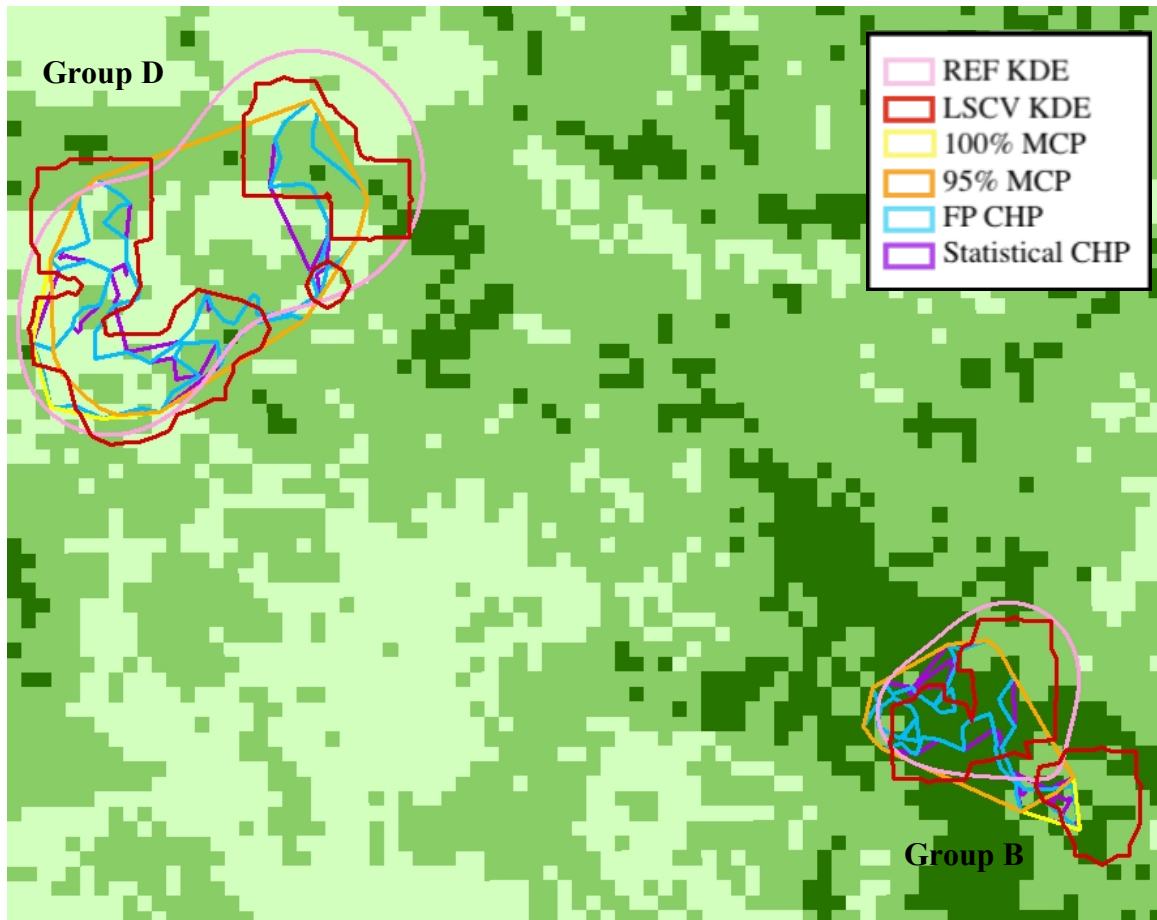


Figure 3. Group B and group D home ranges.

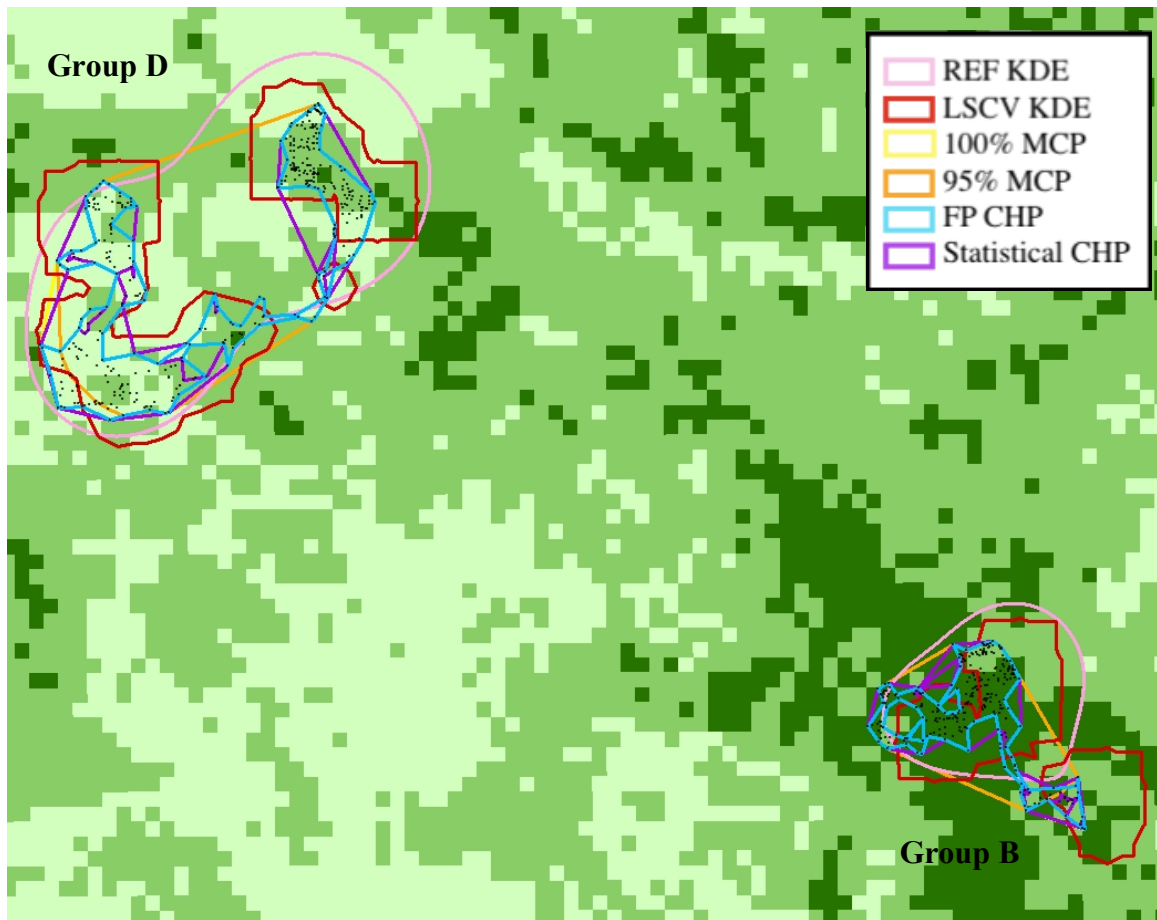


Figure 4. Group B and group D home range using all methods with GPS points included.

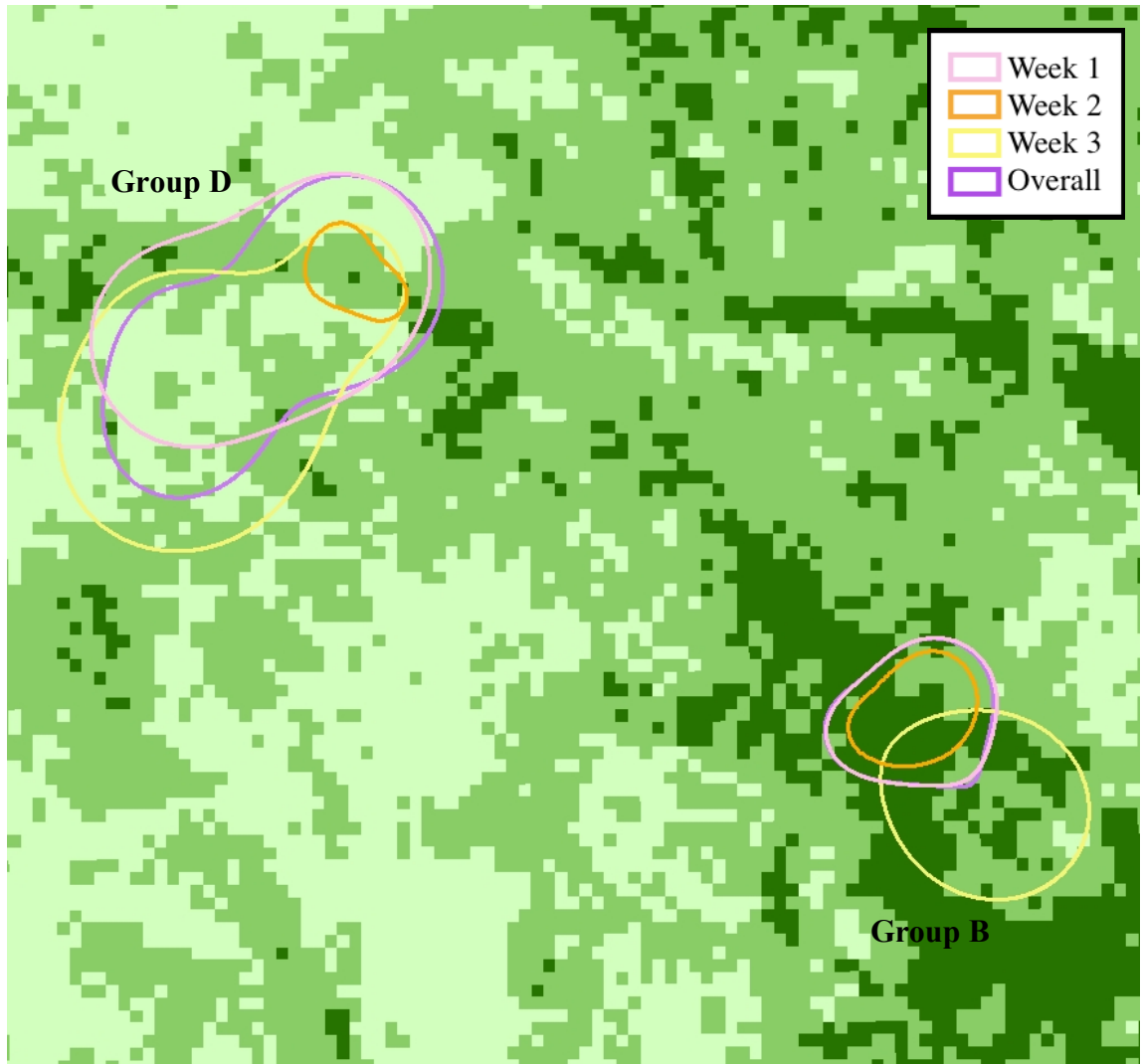


Figure 5. Group B and D overall home range with weekly ranges using the REF KDE method.

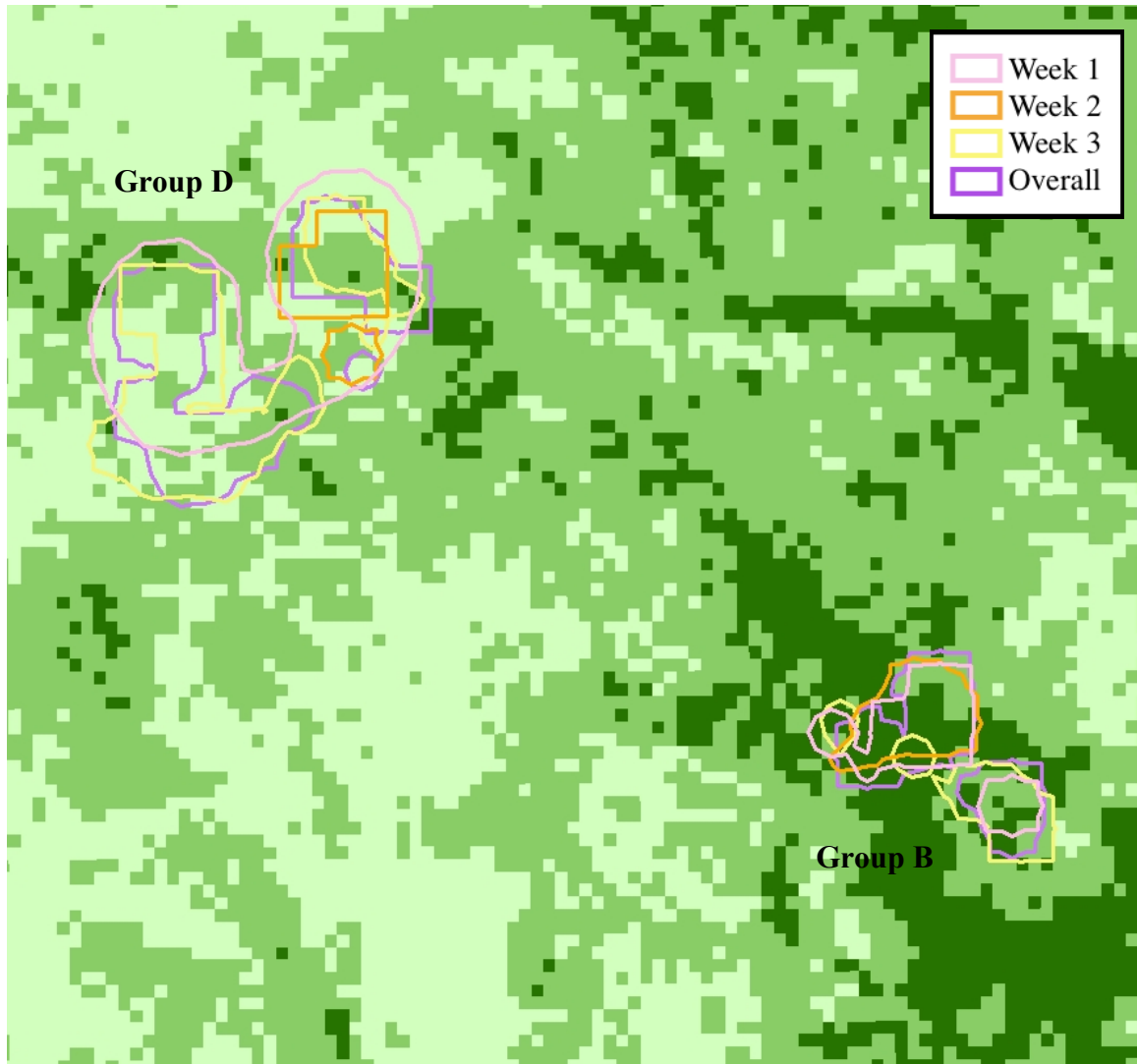


Figure 6. Group B and D overall home range with weekly ranges using the LSCV KDE method.

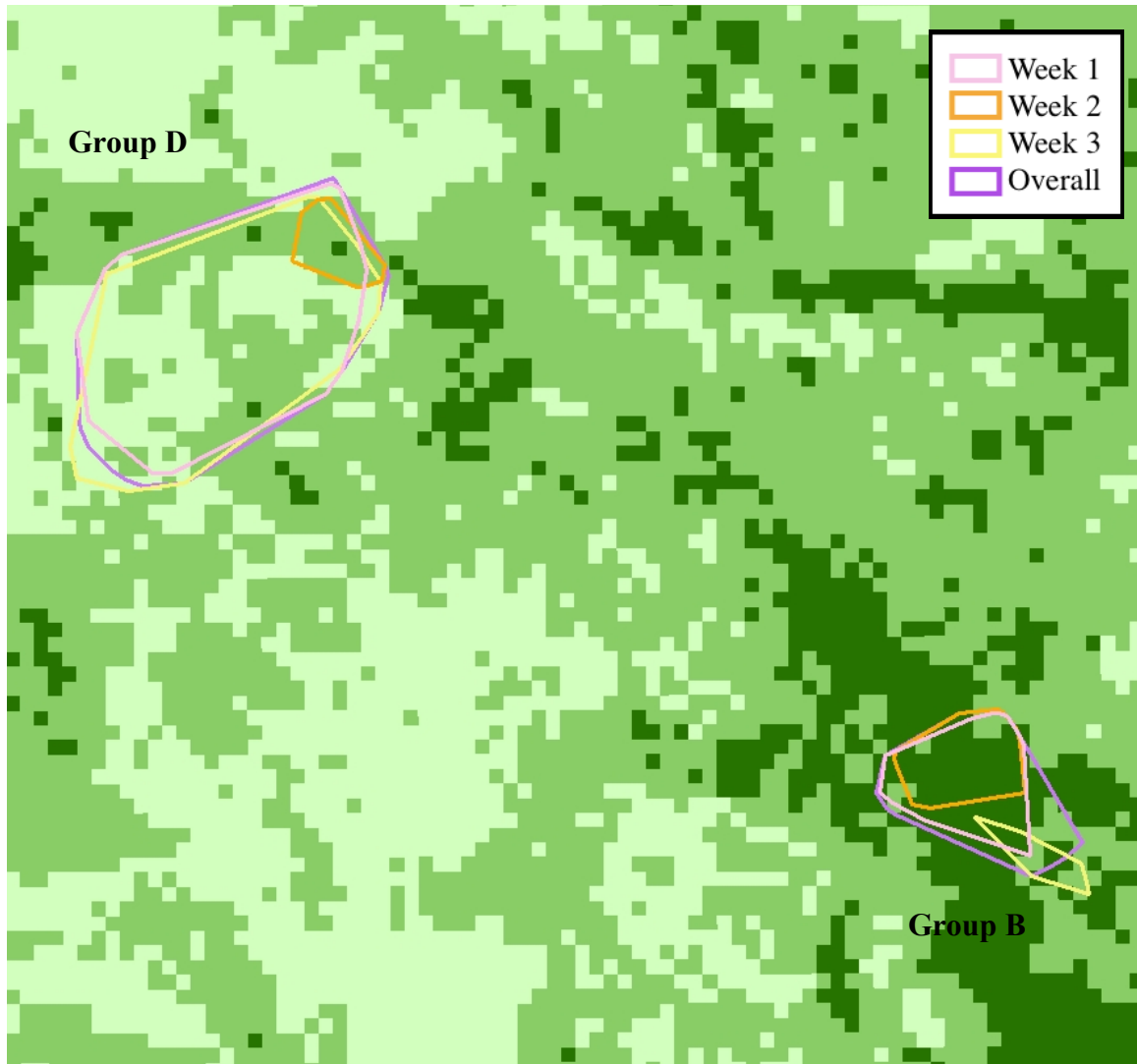


Figure 7. Group B and D overall home range with weekly ranges using the 100% MCP method.

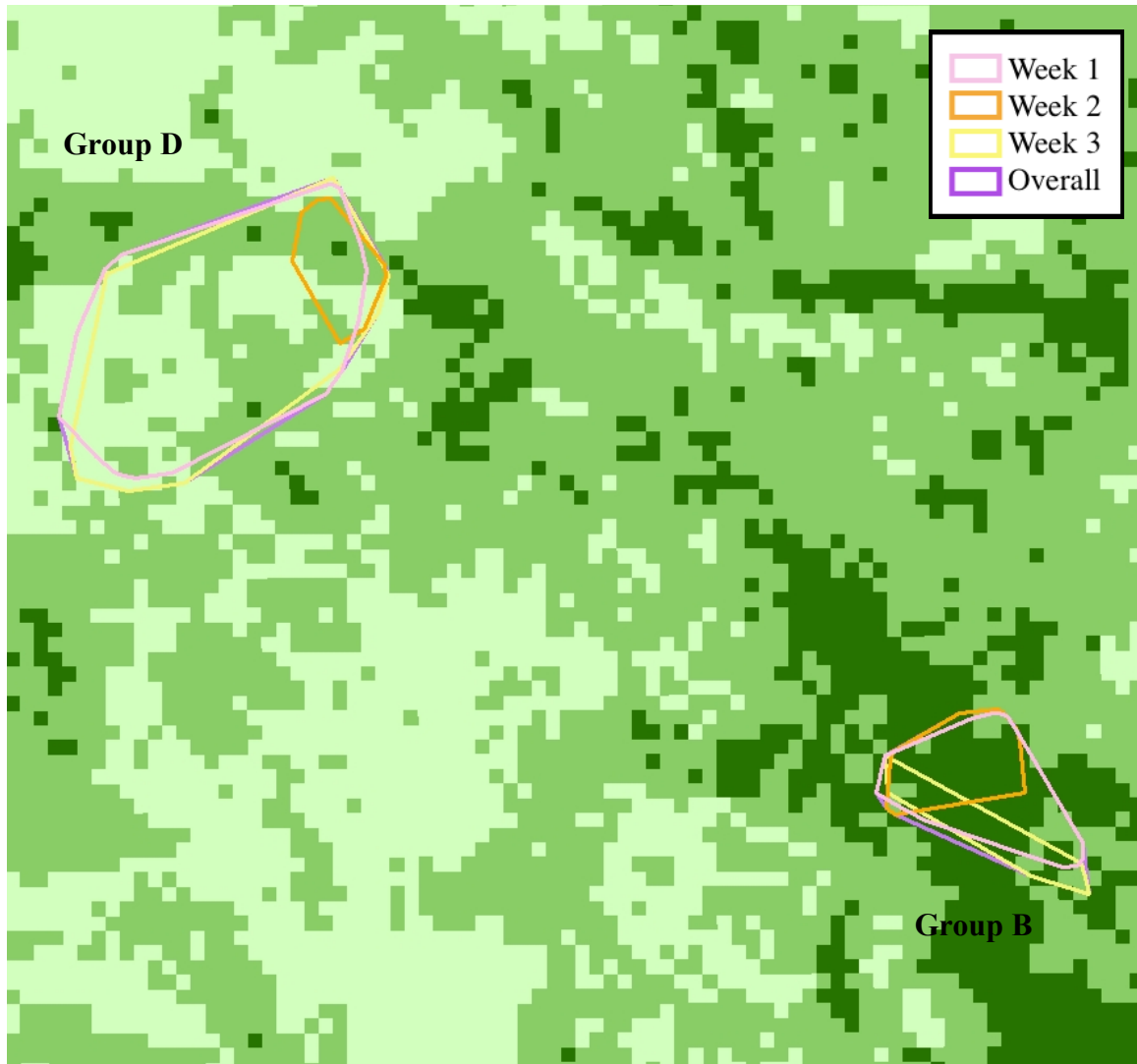


Figure 8. Group B and D overall home range with weekly ranges using the 95% MCP method.

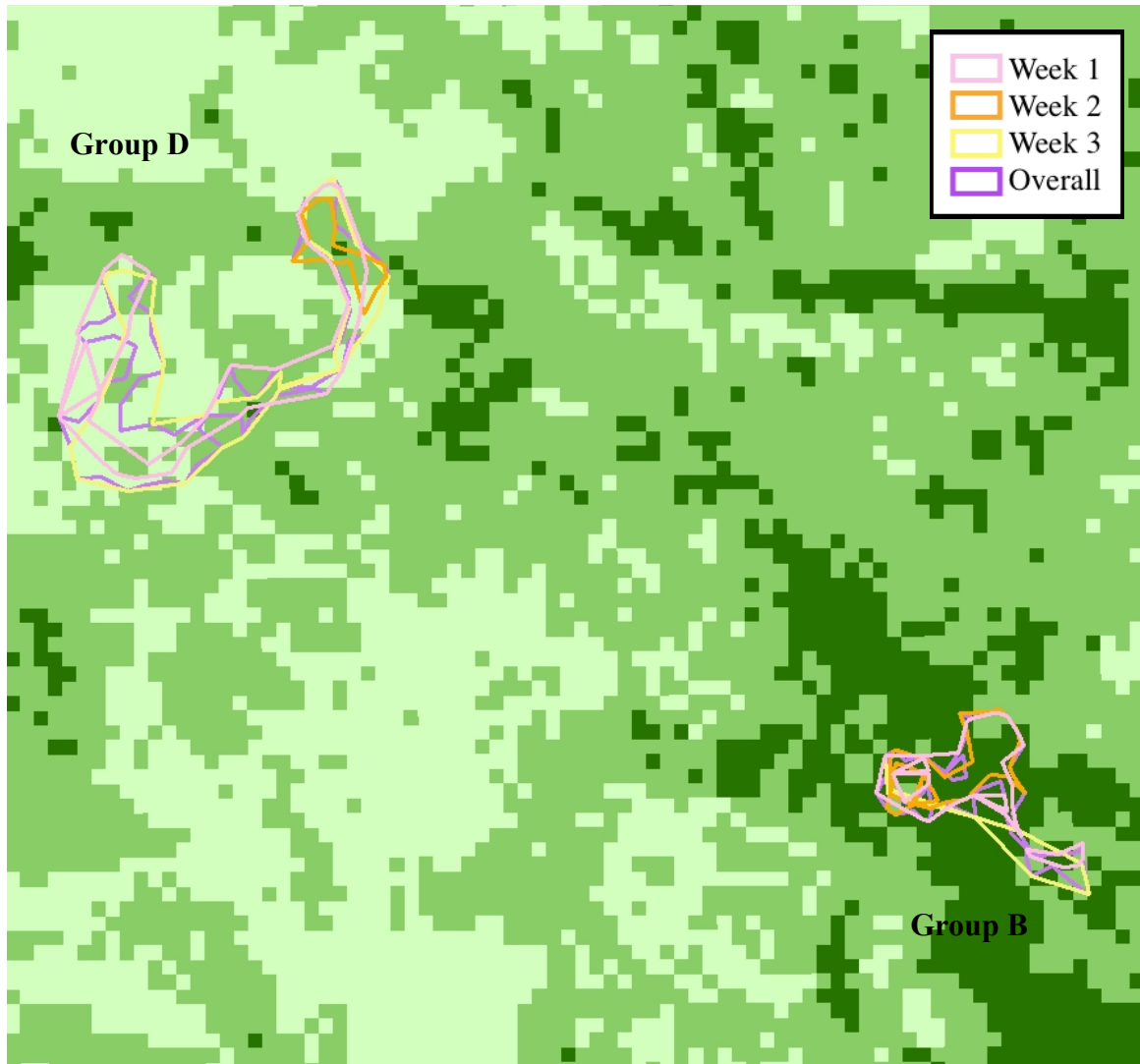


Figure 9. Group B and D overall home range with weekly ranges using the FP CHP.

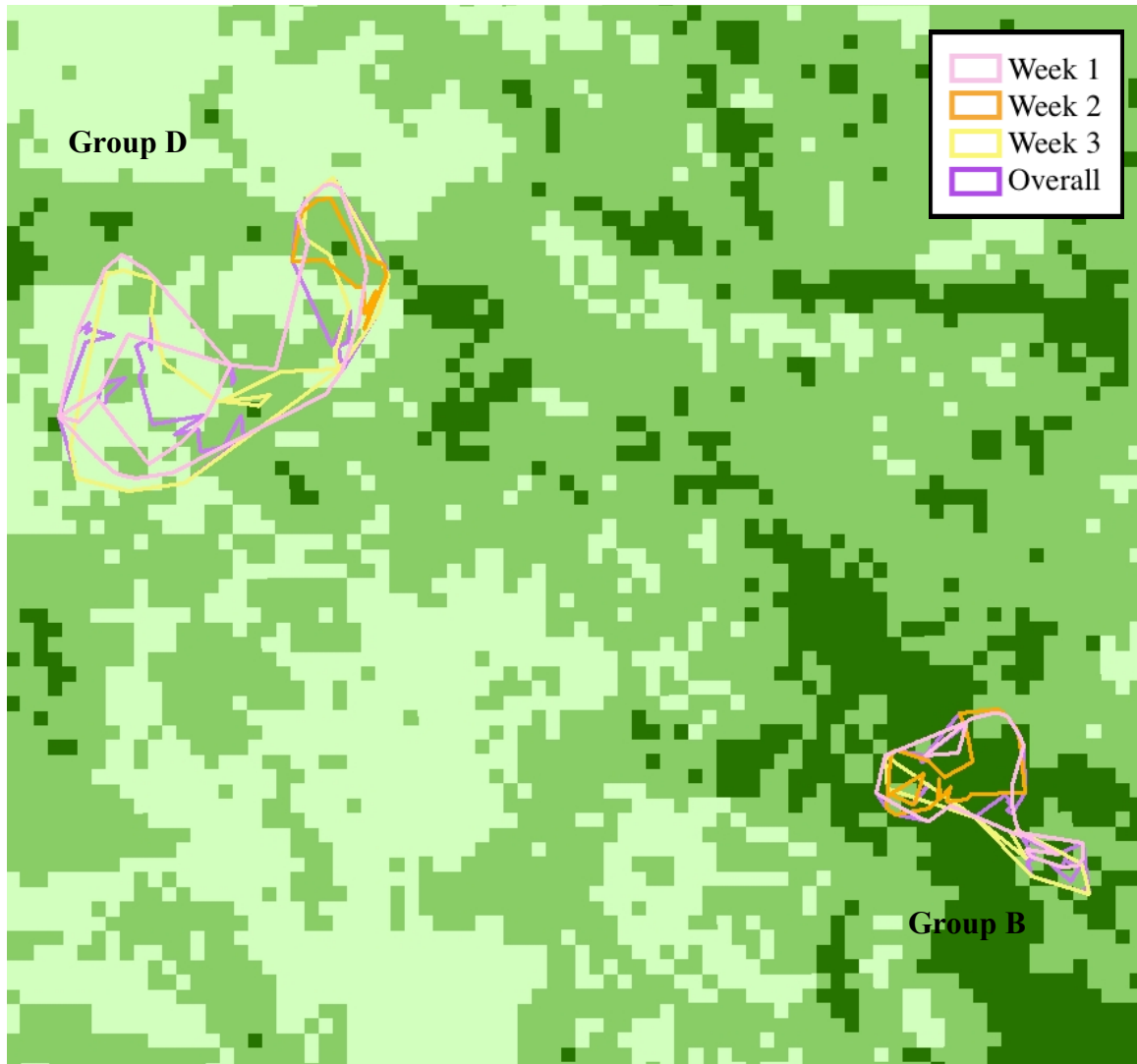


Figure 10. Group B and D overall home range with weekly ranges using the statistical CHP method.

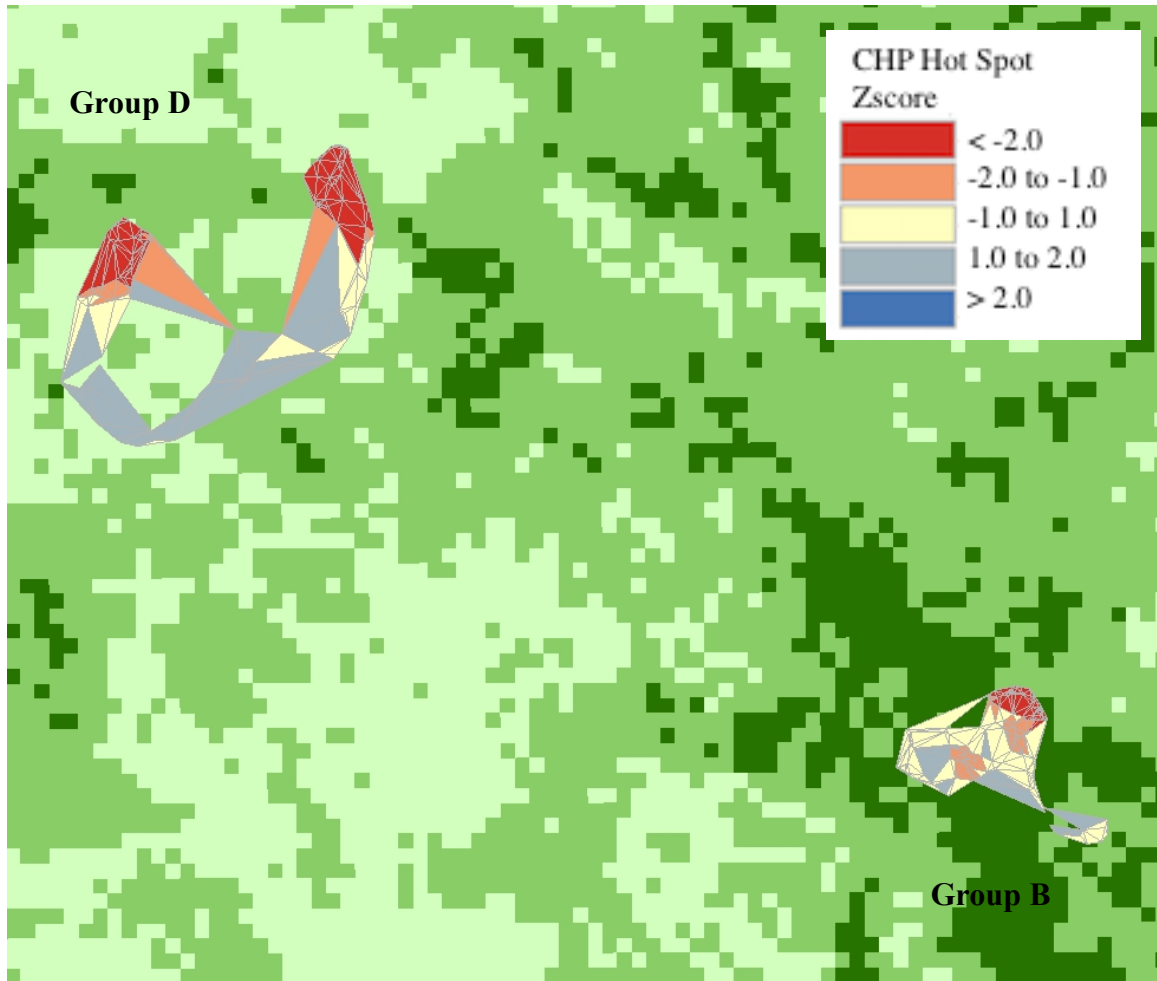


Figure 11. Week 1 ranges for groups B and D using statistical CHP with hot spot analysis.

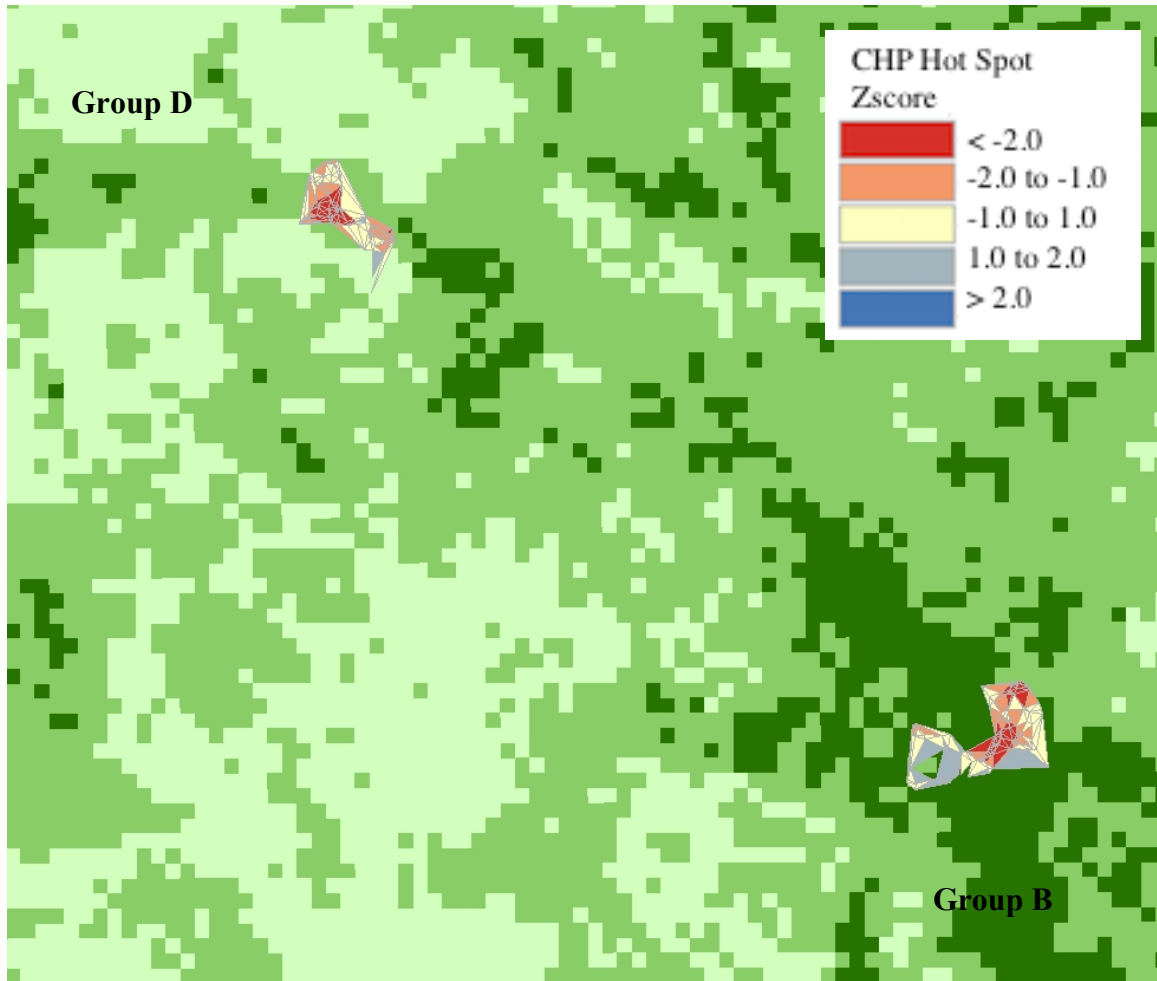


Figure 12. Week 2 ranges for groups B and D using statistical CHP with hot spot analysis.

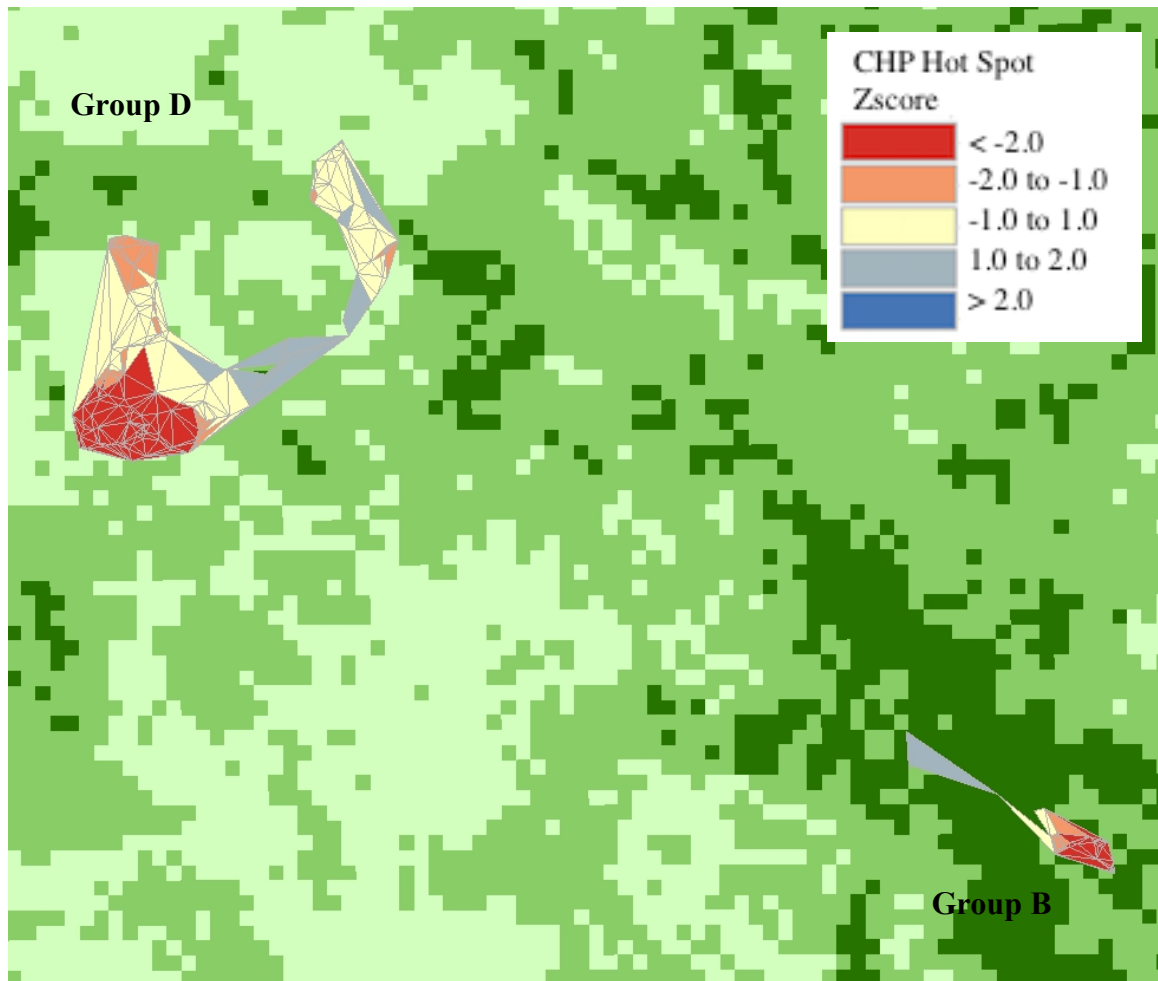


Figure 13. Week 3 ranges for groups B and D using the statistical CHPs for hot spot analysis.

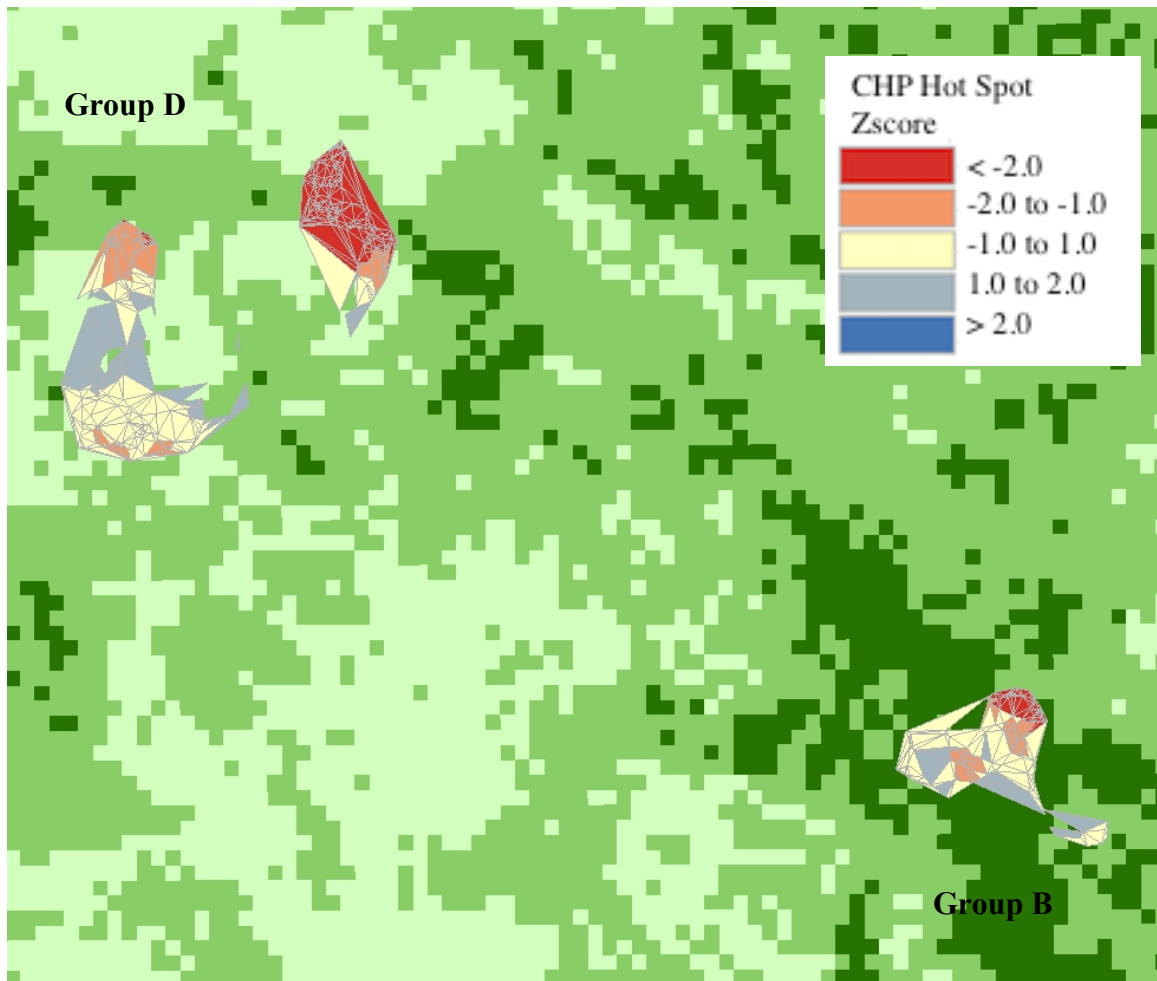


Figure 14. Overall ranges for groups B and D using statistical CHPs with hot spot analysis.

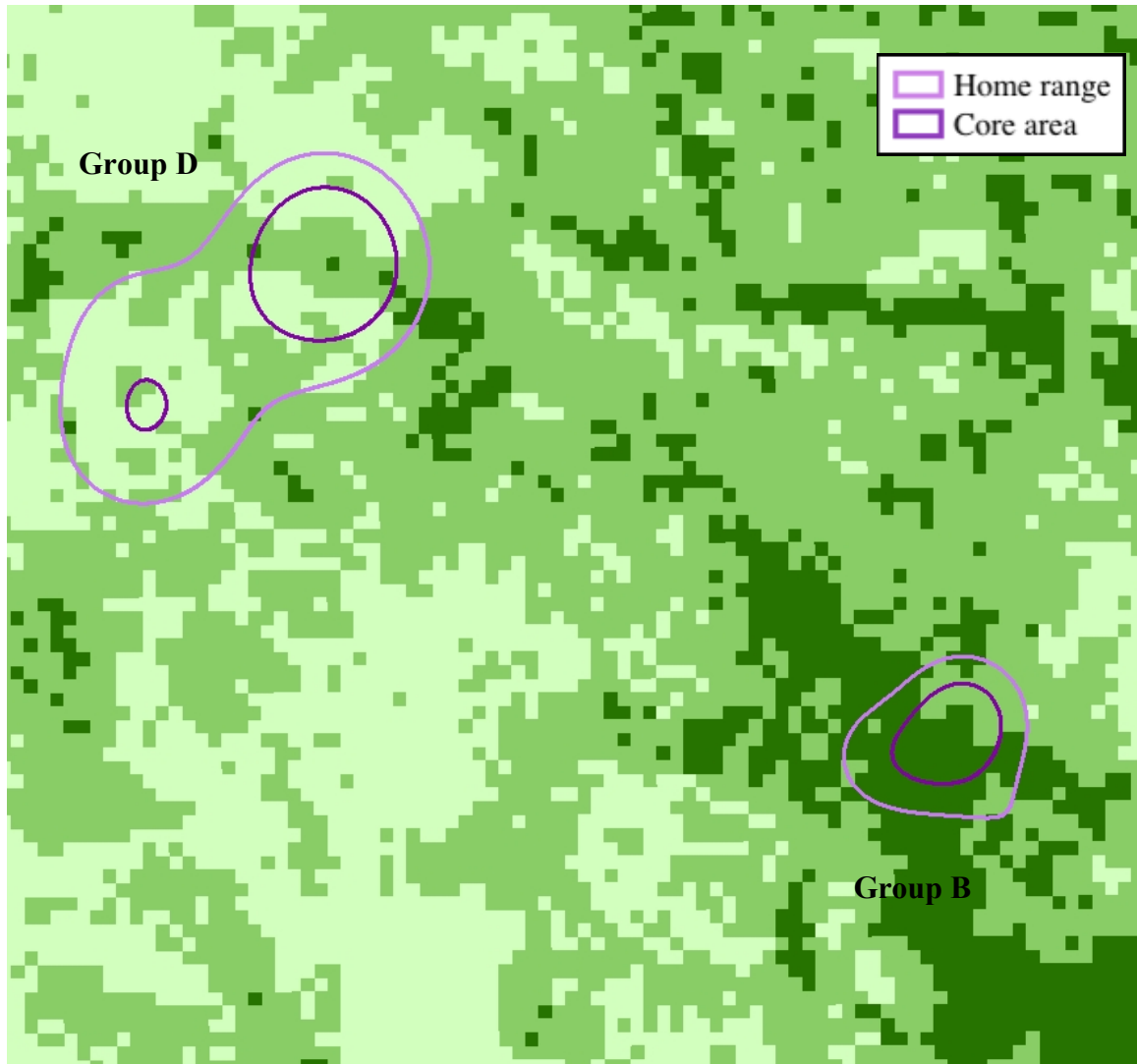


Figure 15. Overall home ranges and overall core areas for groups B and D using the REF KDE method.

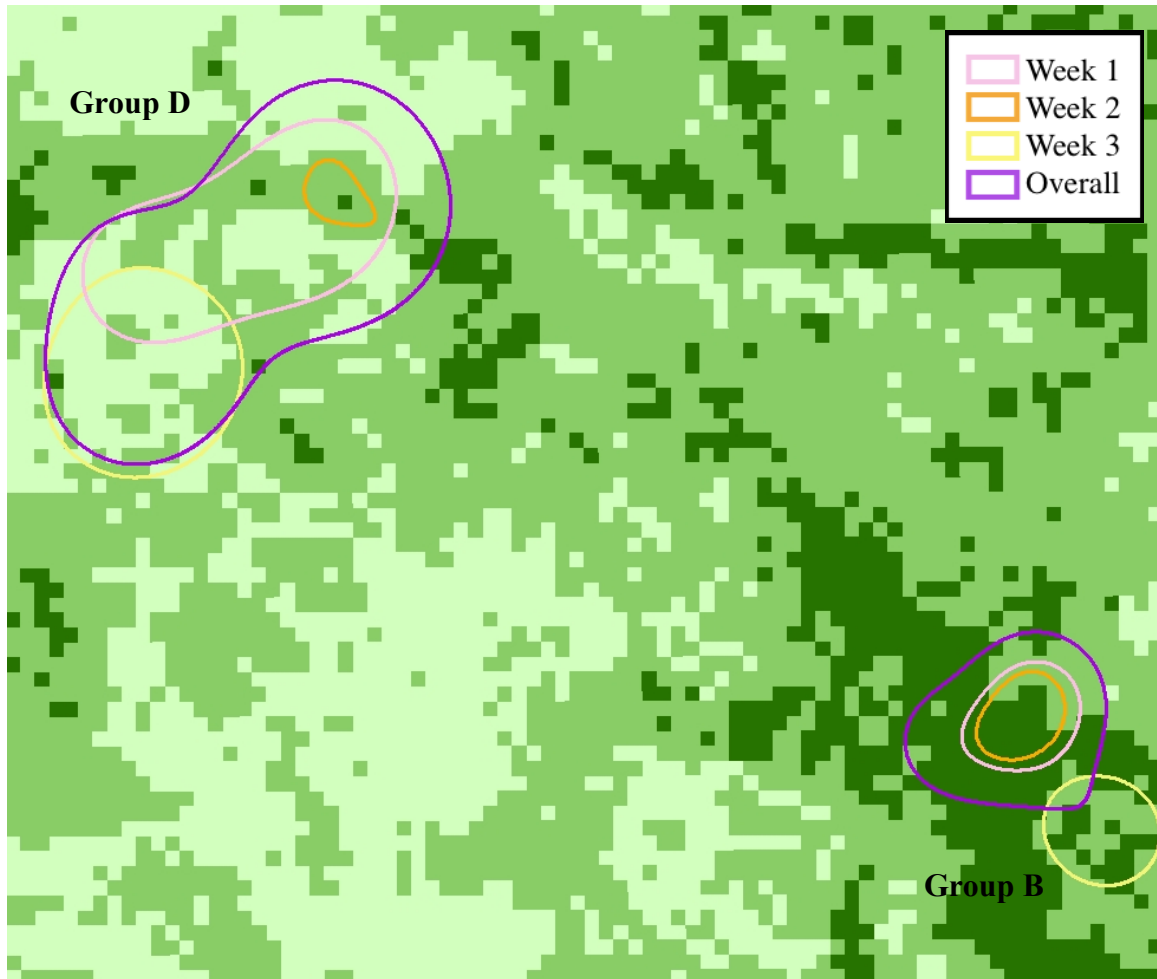


Figure 16. Overall home range with weekly core areas for groups B and D using the REF KDE methods.

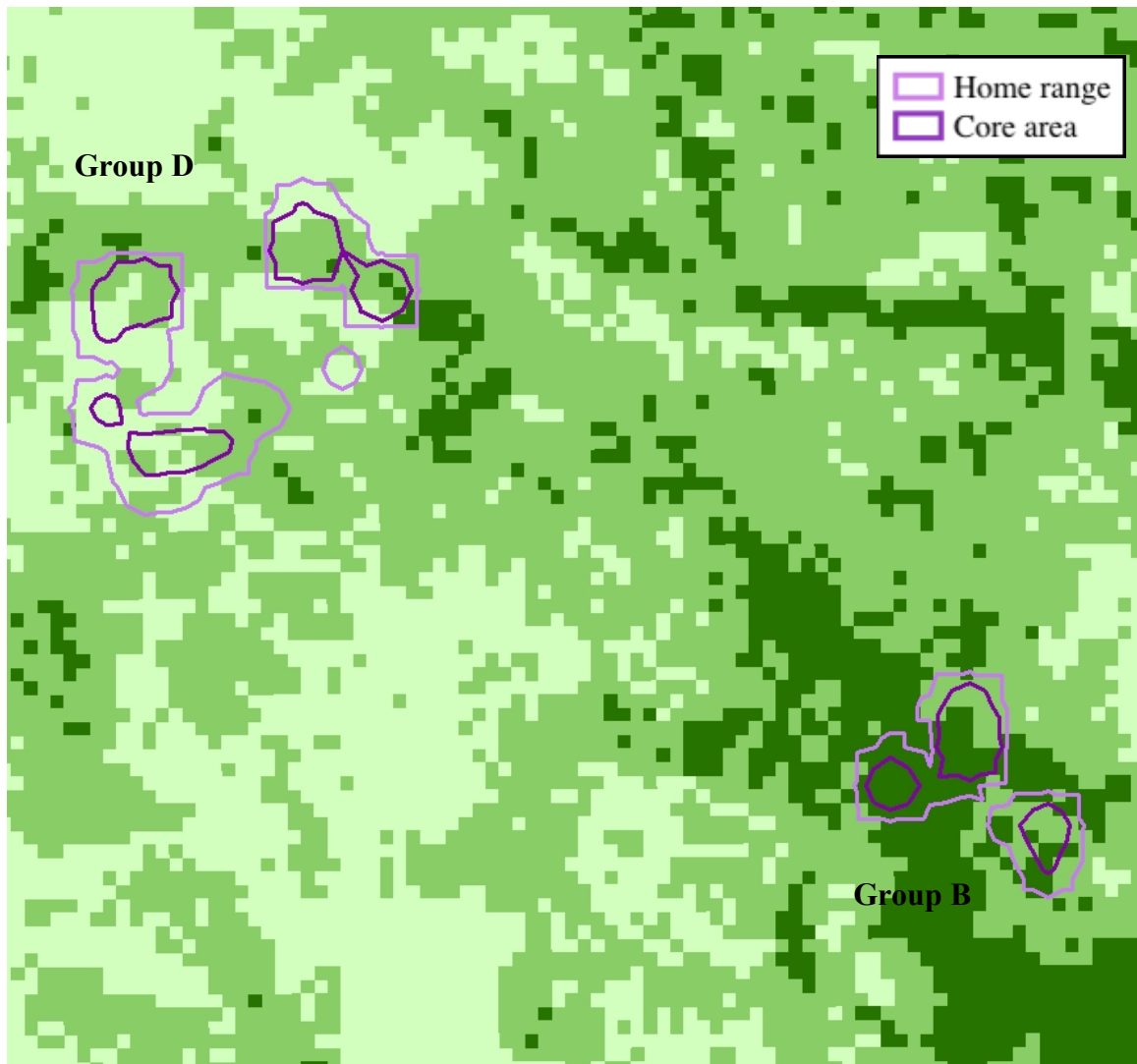


Figure 17. Overall home ranges and overall core areas for groups B and D using the LSCV KDE method.

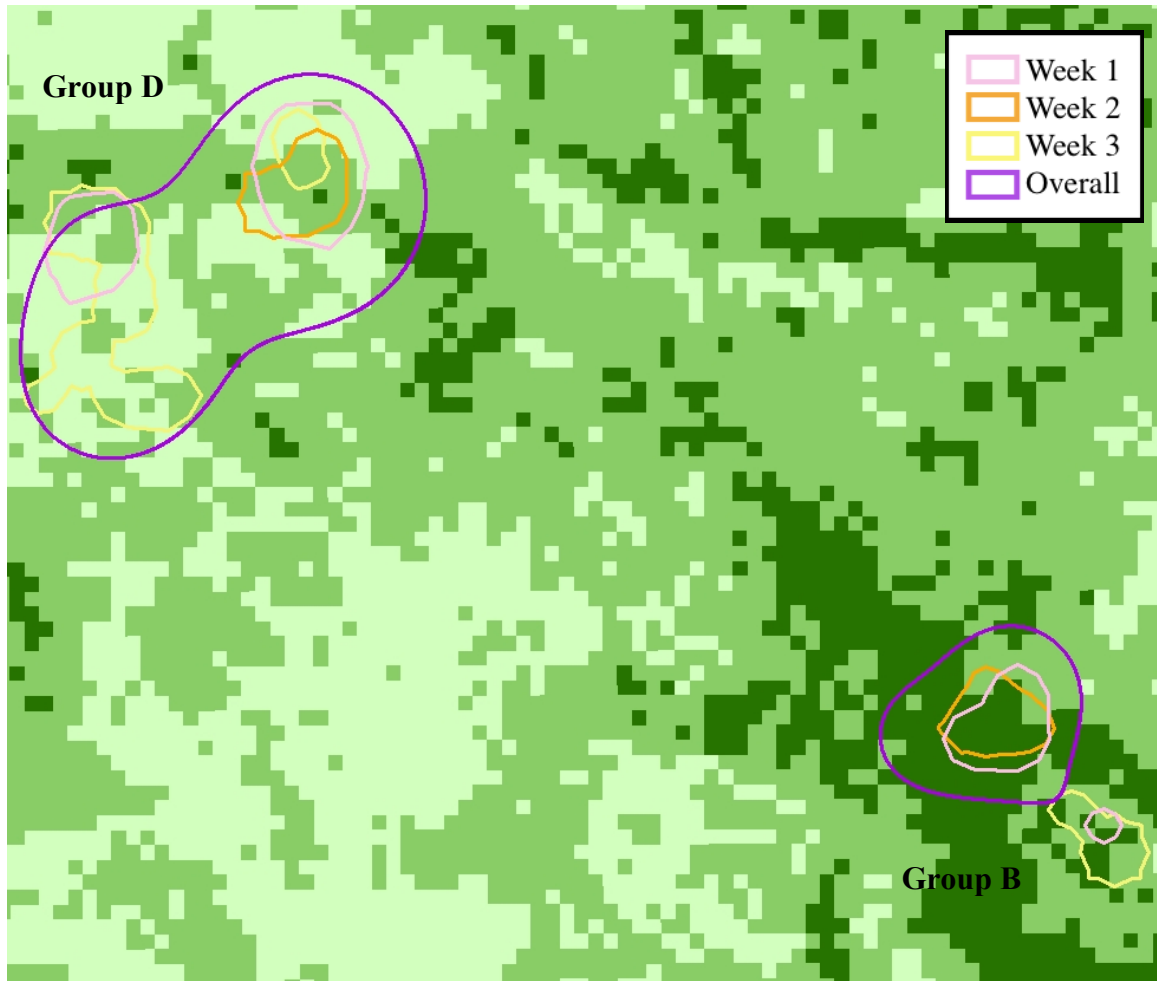


Figure 18. Overall home range with weekly core areas for groups B and D using the LSCV KDE method.

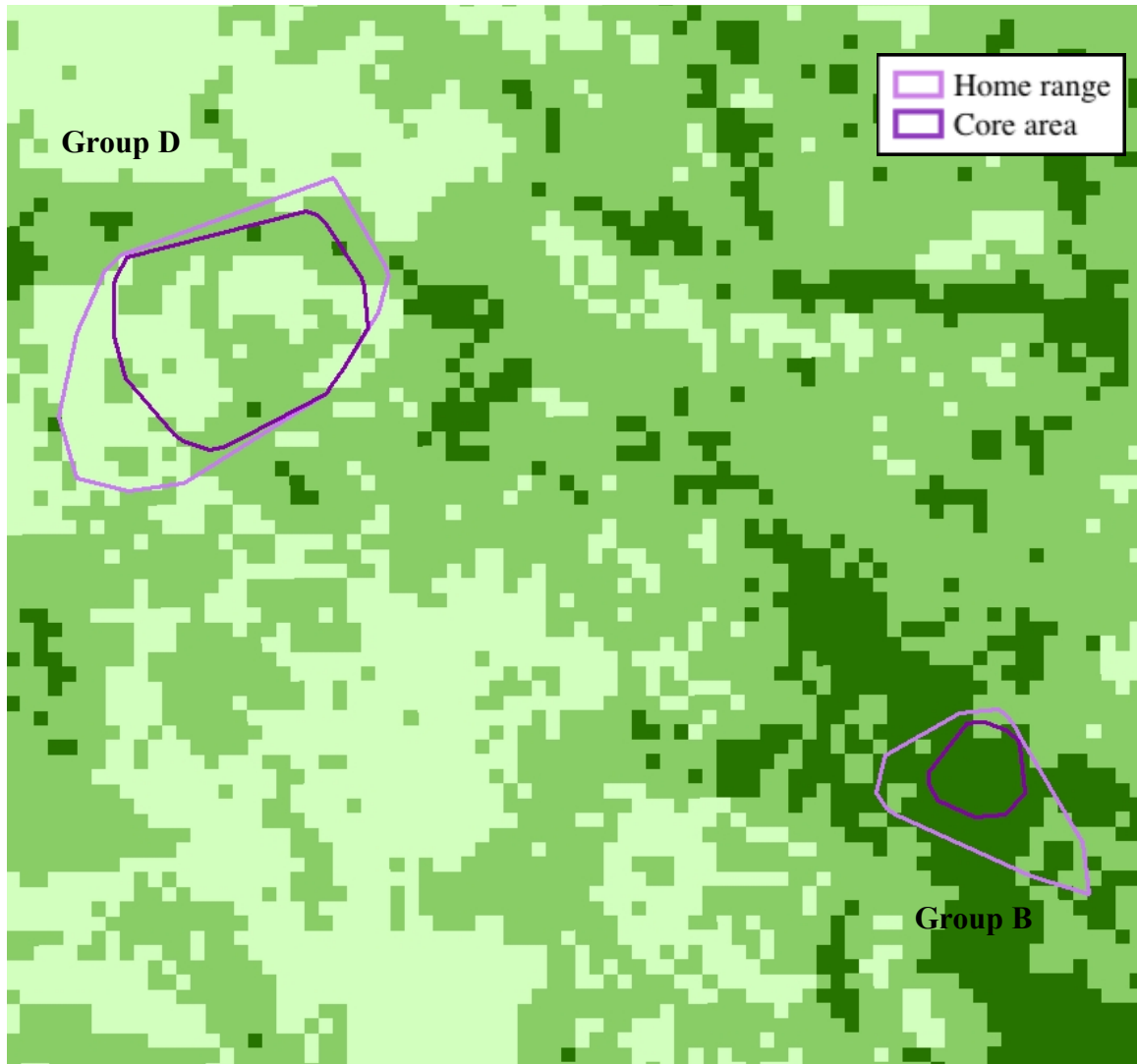


Figure 19. Overall home ranges and overall core areas for groups B and D using the 100% MCP method for home ranges and 50% MCP for core areas.

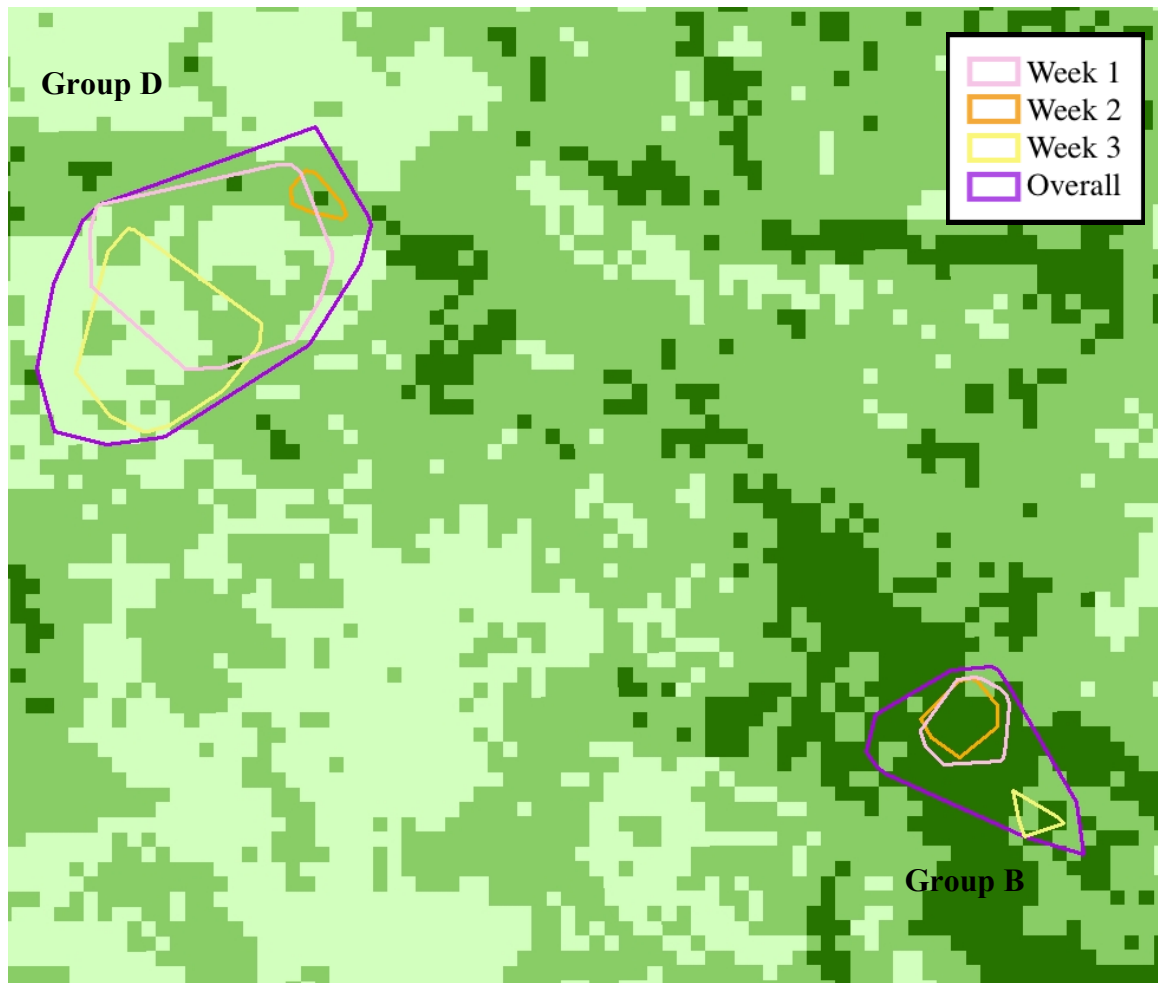


Figure 20. Overall home range with weekly core areas for groups B and D using the 100% MCP for home ranges and 50% MCP method for core areas.

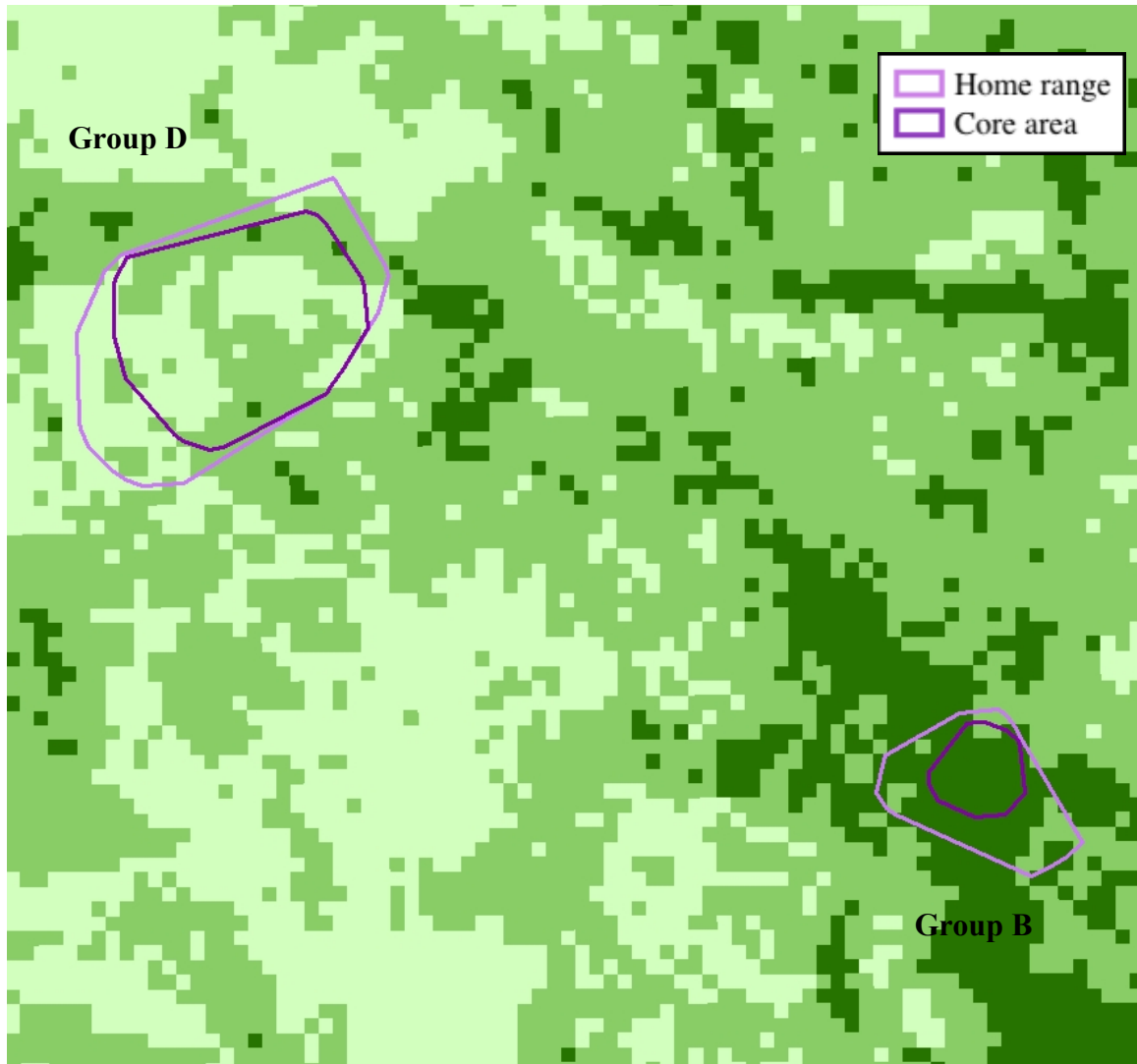


Figure 21. Overall home ranges and overall core areas for groups B and D using the 95% MCP method for home ranges and 50% MCP method for core areas.

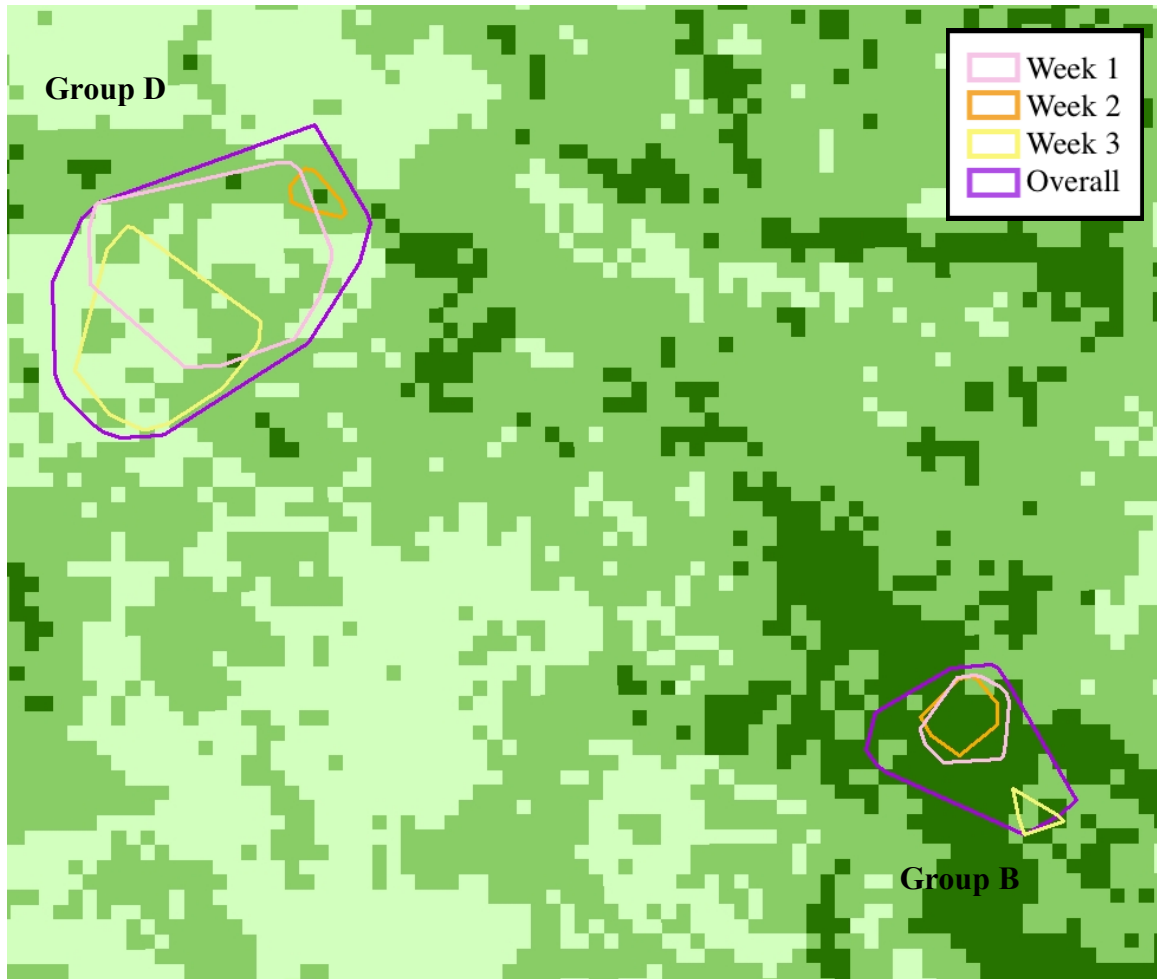


Figure 22. Overall home range with weekly core areas for groups B and D using the 95% MCP method for home ranges and 50% MCP method for core areas.

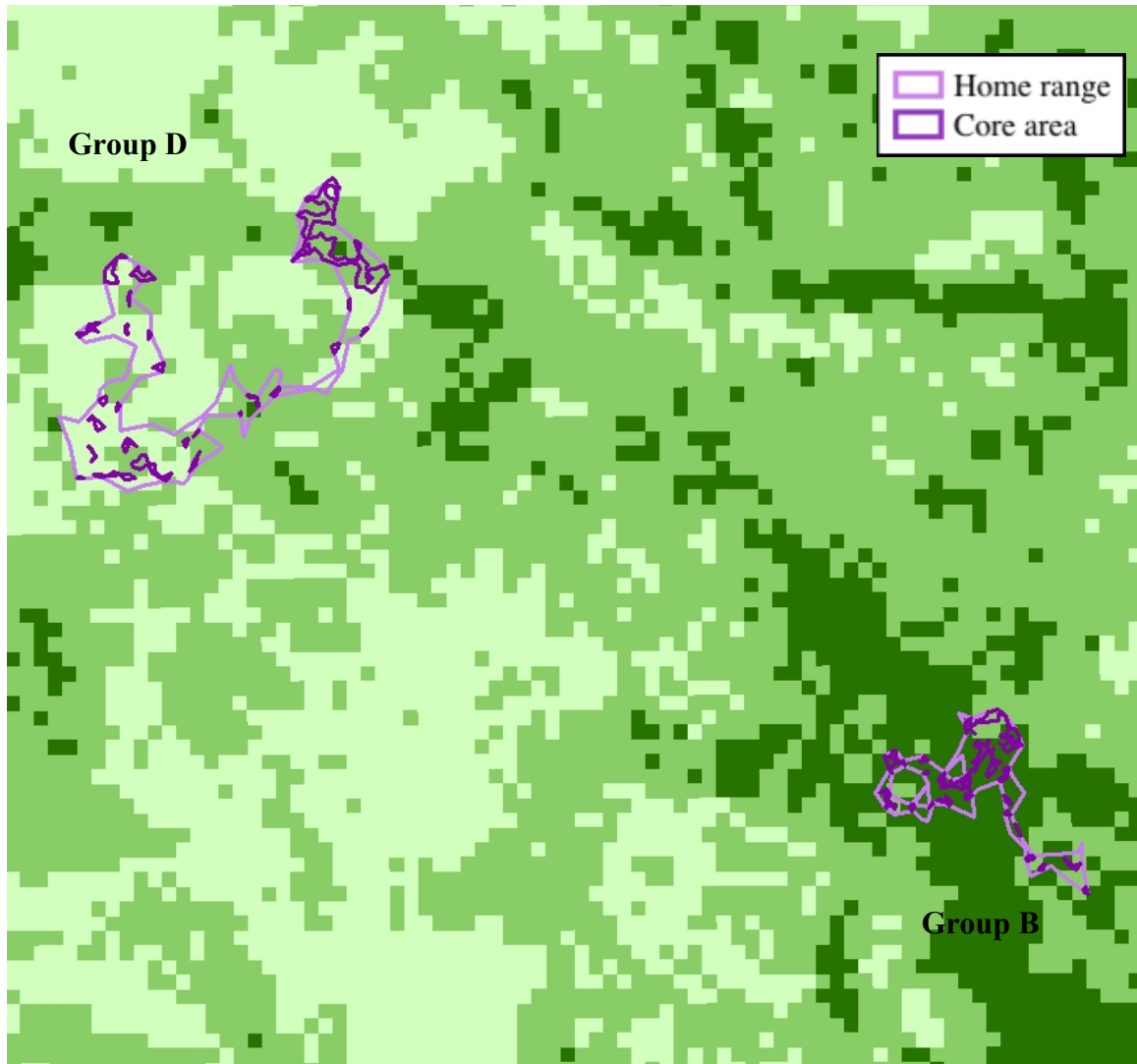


Figure 23. Overall home ranges and overall core areas for groups B and D using the FP CHP method.

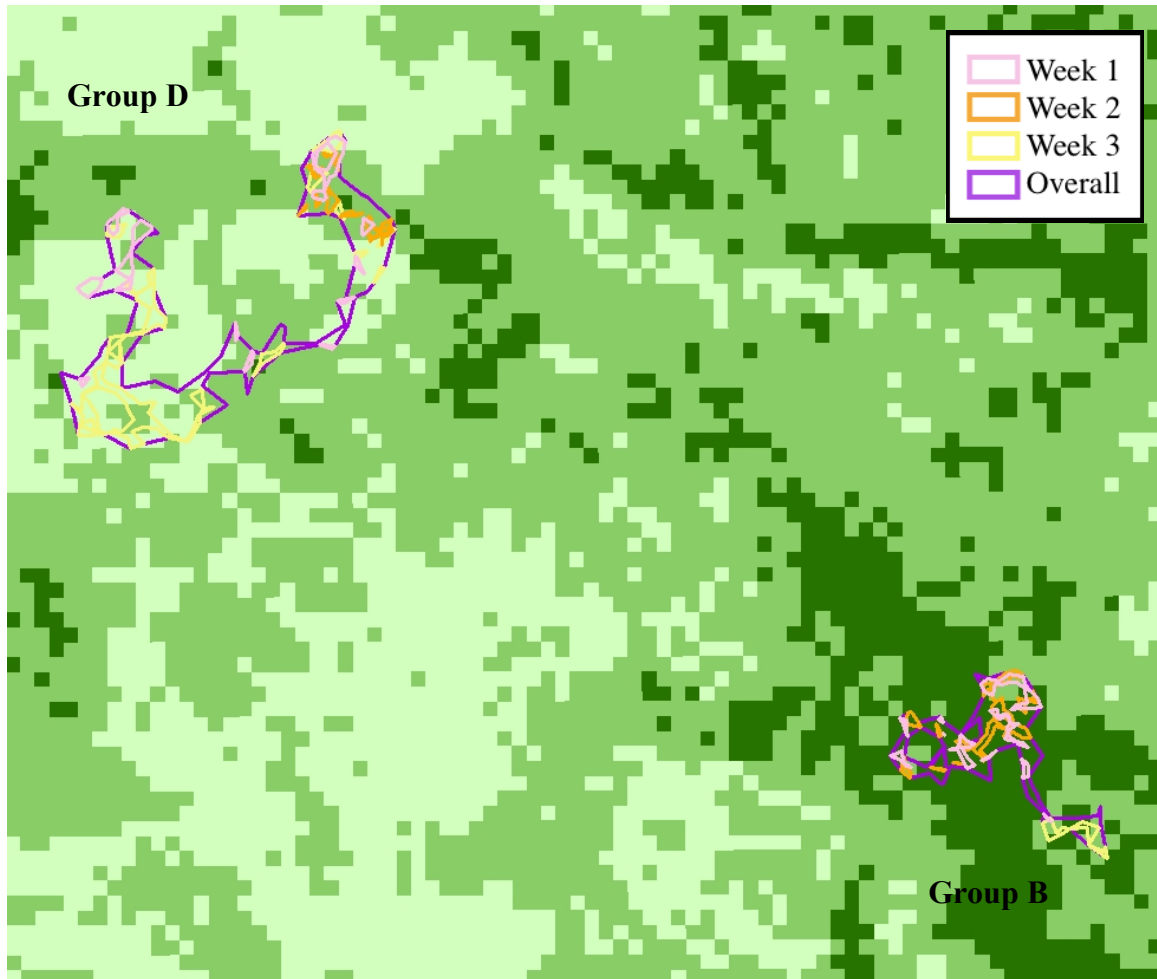


Figure 24. Overall home range with weekly core areas for groups B and D using the FP CHP method.

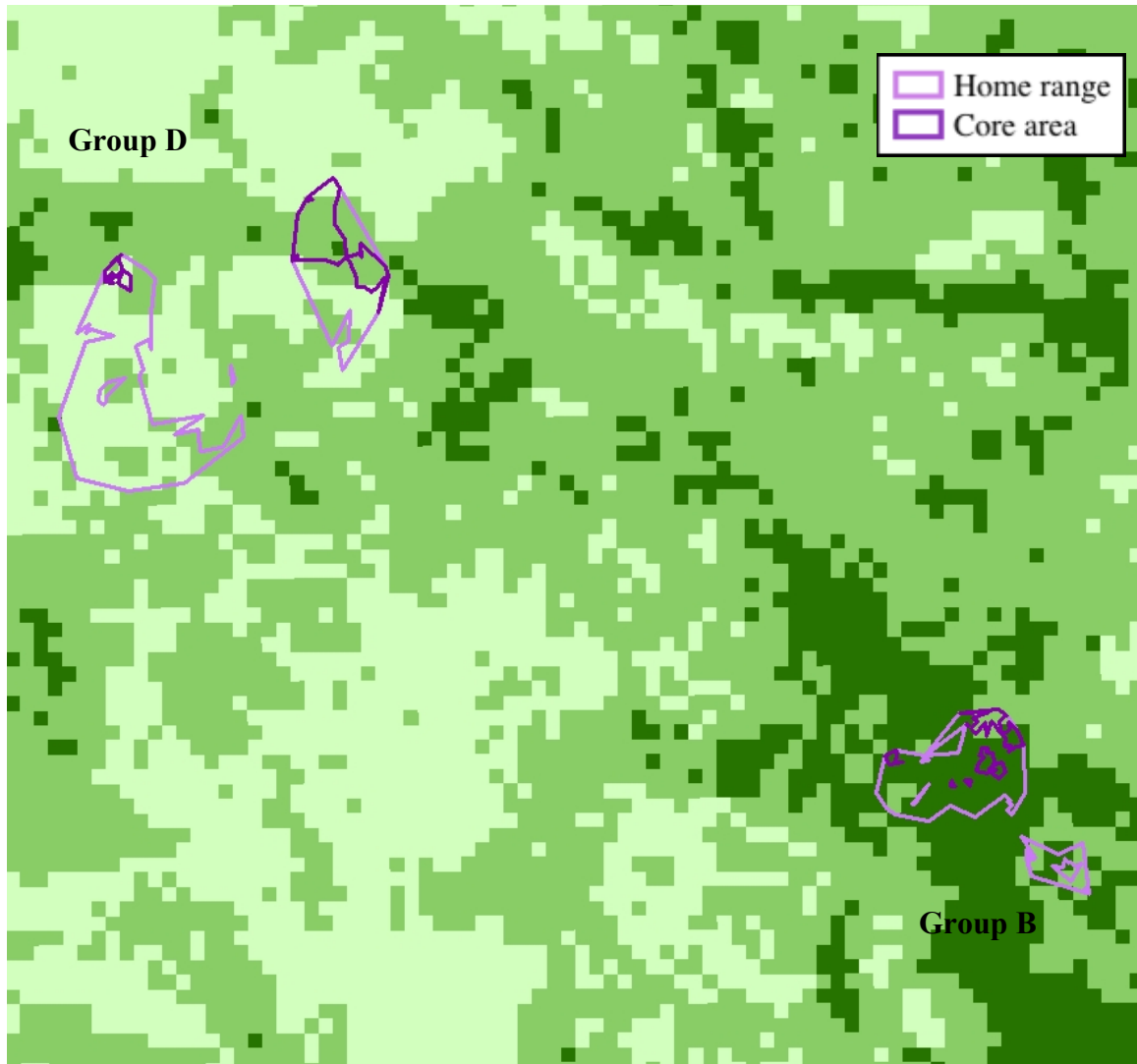


Figure 25. Overall home ranges and overall core areas for groups B and D using the statistical CHP method.

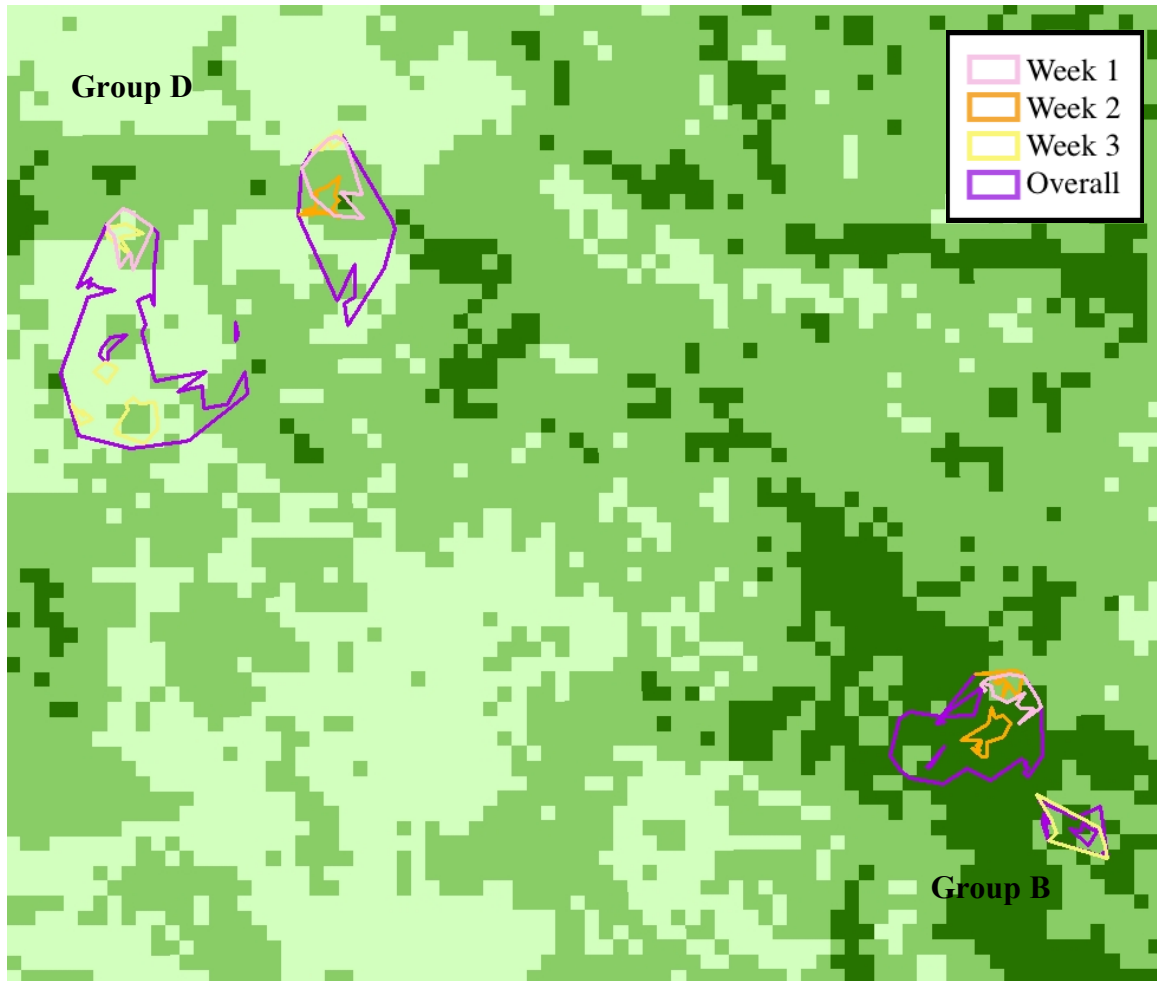


Figure 26. Overall home range with weekly core areas for groups B and D using the statistical CHP method.

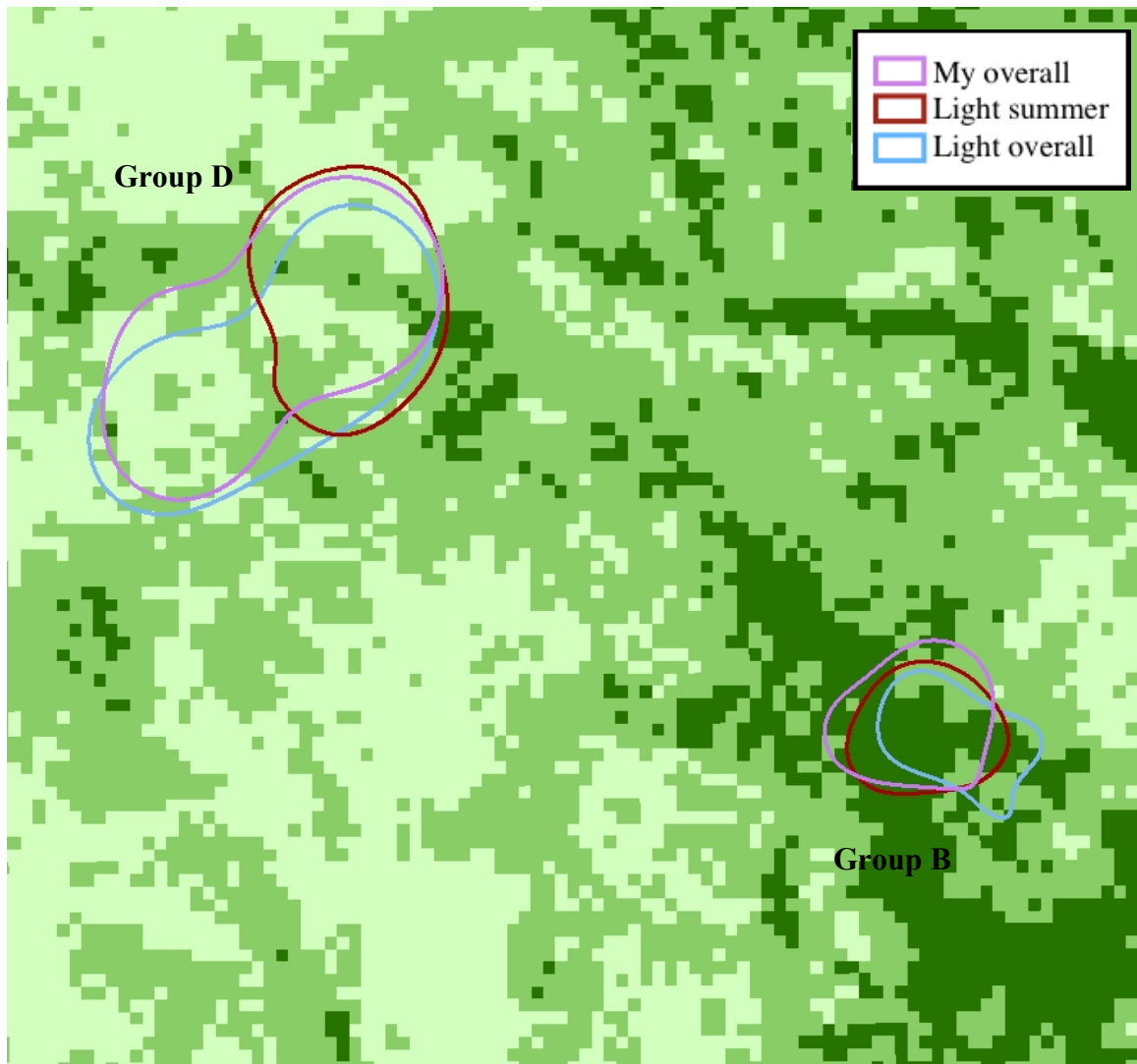


Figure 27. My overall home range, Light's overall home range, and Light's summer range for groups B and D using the REF KDE method.

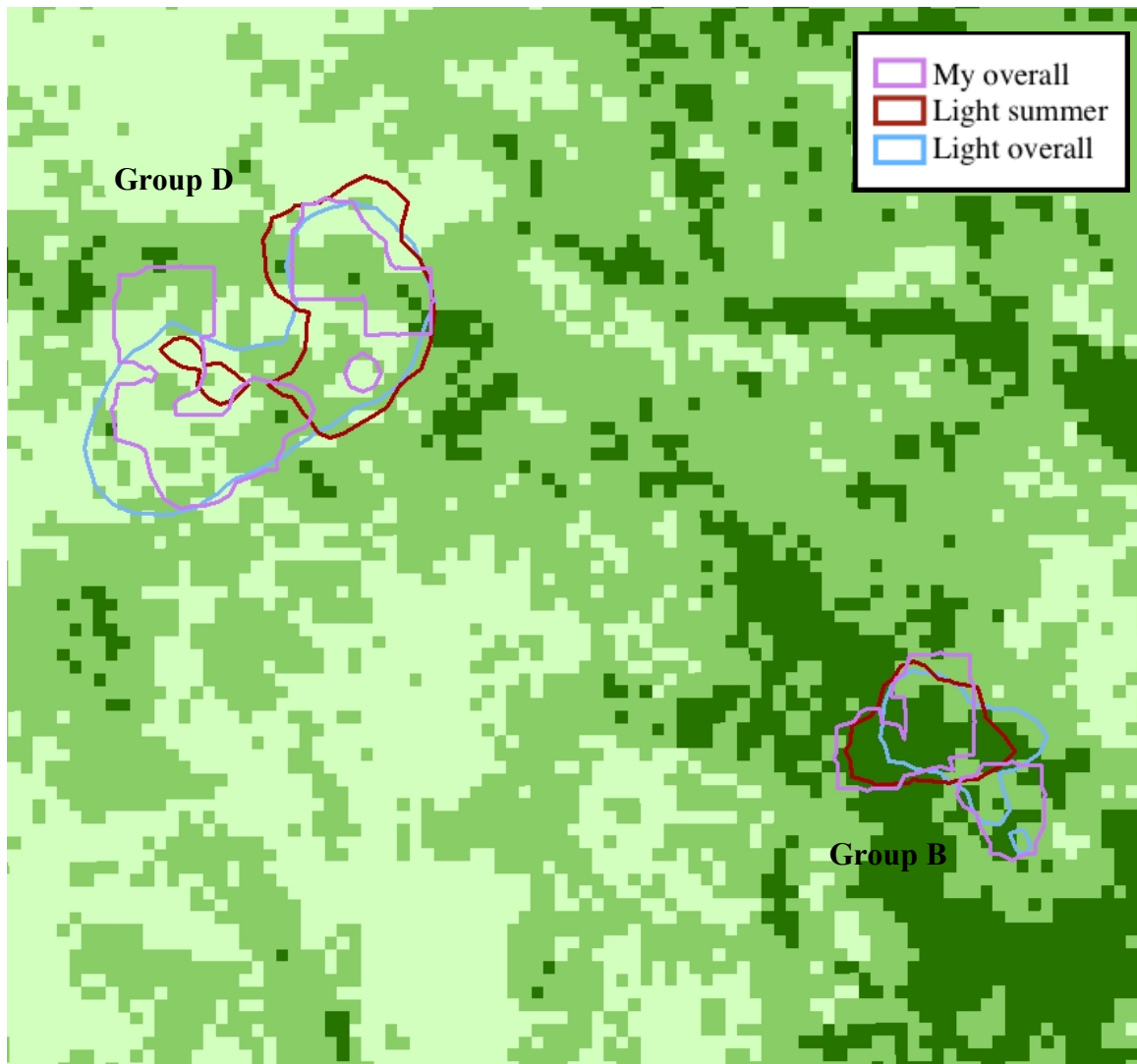


Figure 28. My overall home range, Light's overall home range, and Light's summer range for groups B and D using the LSCV KDE method.

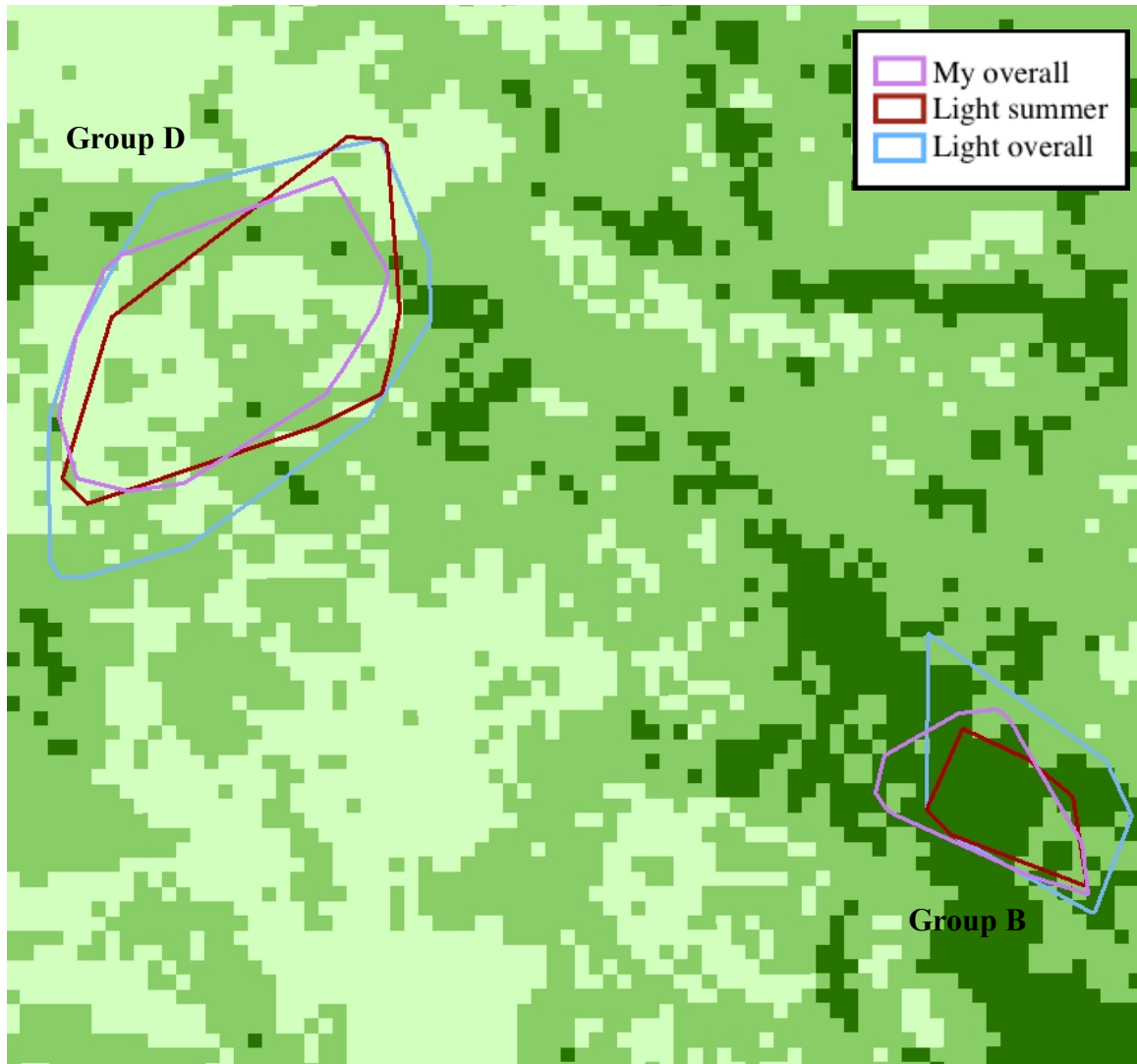


Figure 29. My overall home range, Light's overall home range, and Light's summer range for groups B and D using the 100% MCP method.

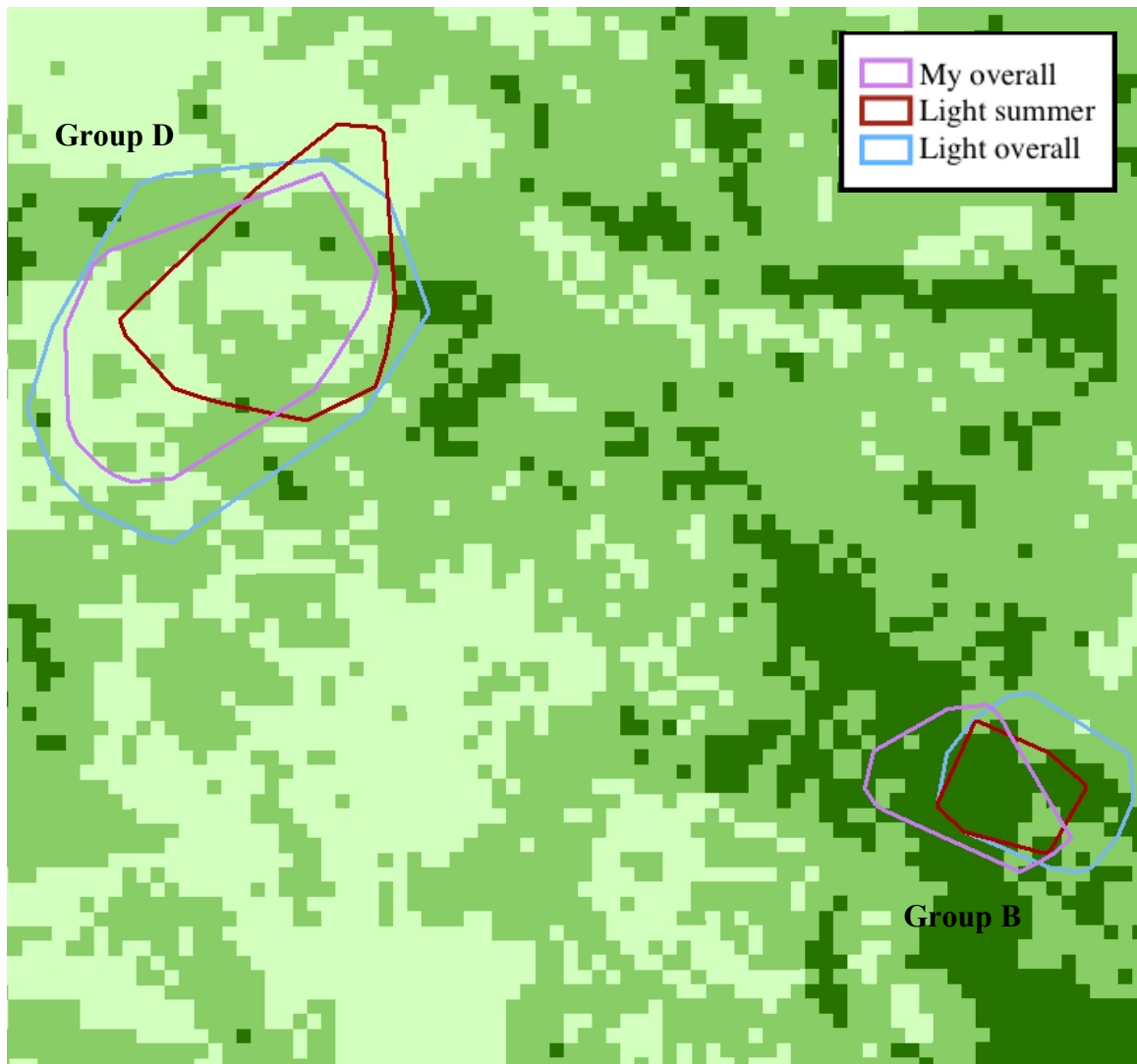


Figure 30. My overall home range, Light's overall home range, and Light's summer range for groups B and D using the 95% MCP method.

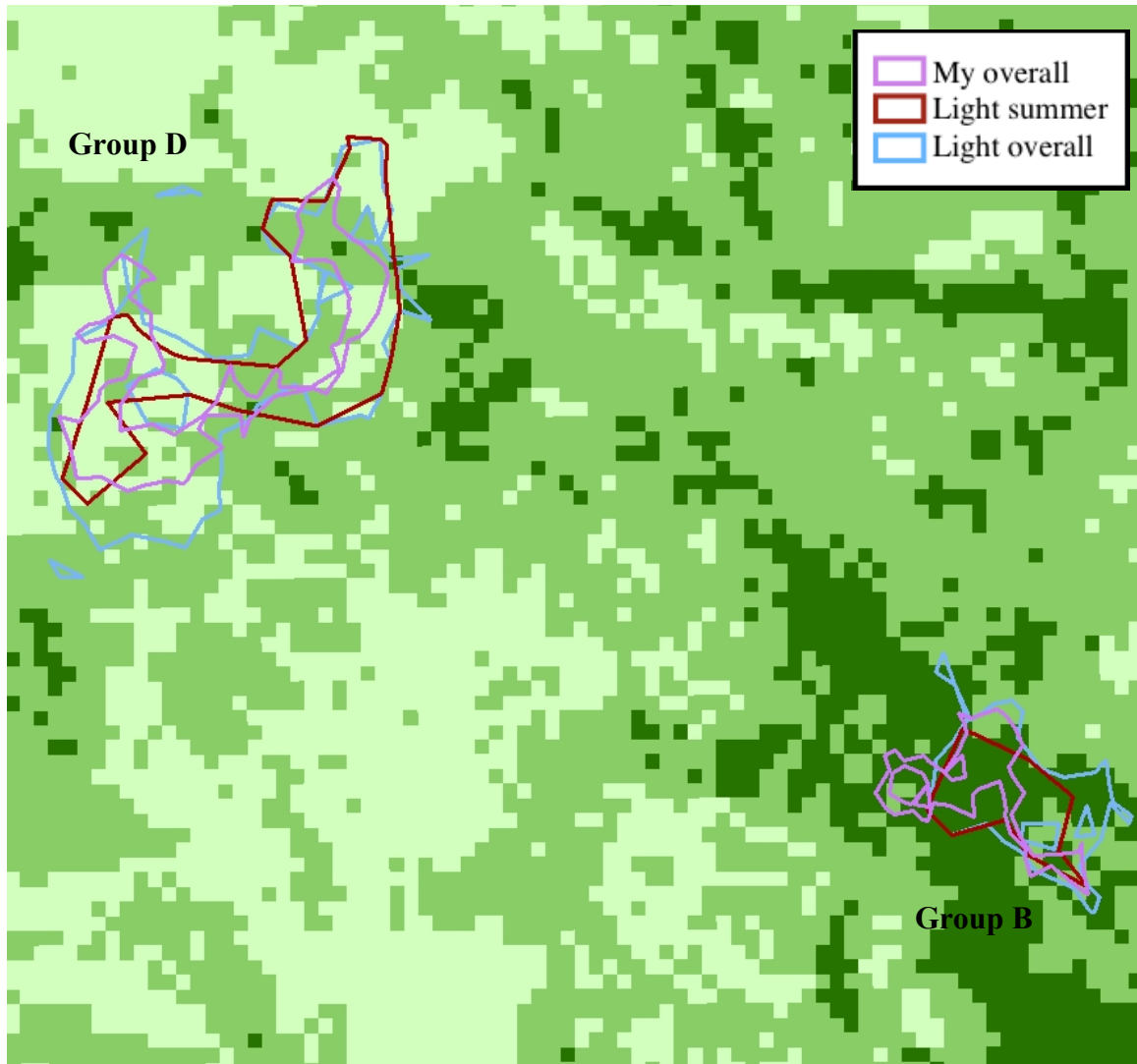


Figure 31. My overall home range, Light's overall home range, and Light's summer range for groups B and D using the FP CHP method.

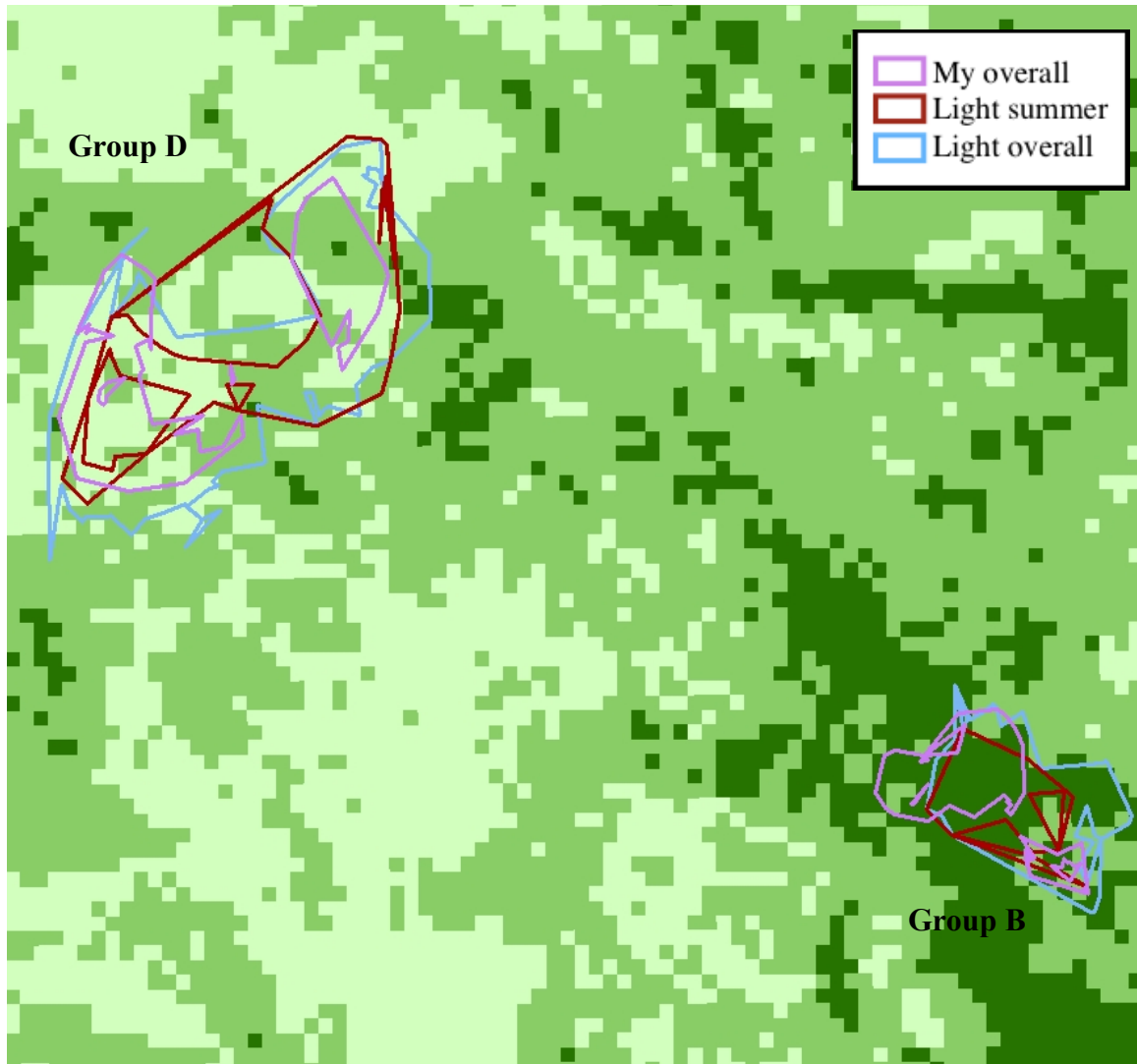


Figure 32. My overall home range, Light's overall home range, and Light's summer range for groups B and D using the statistical CHP method.

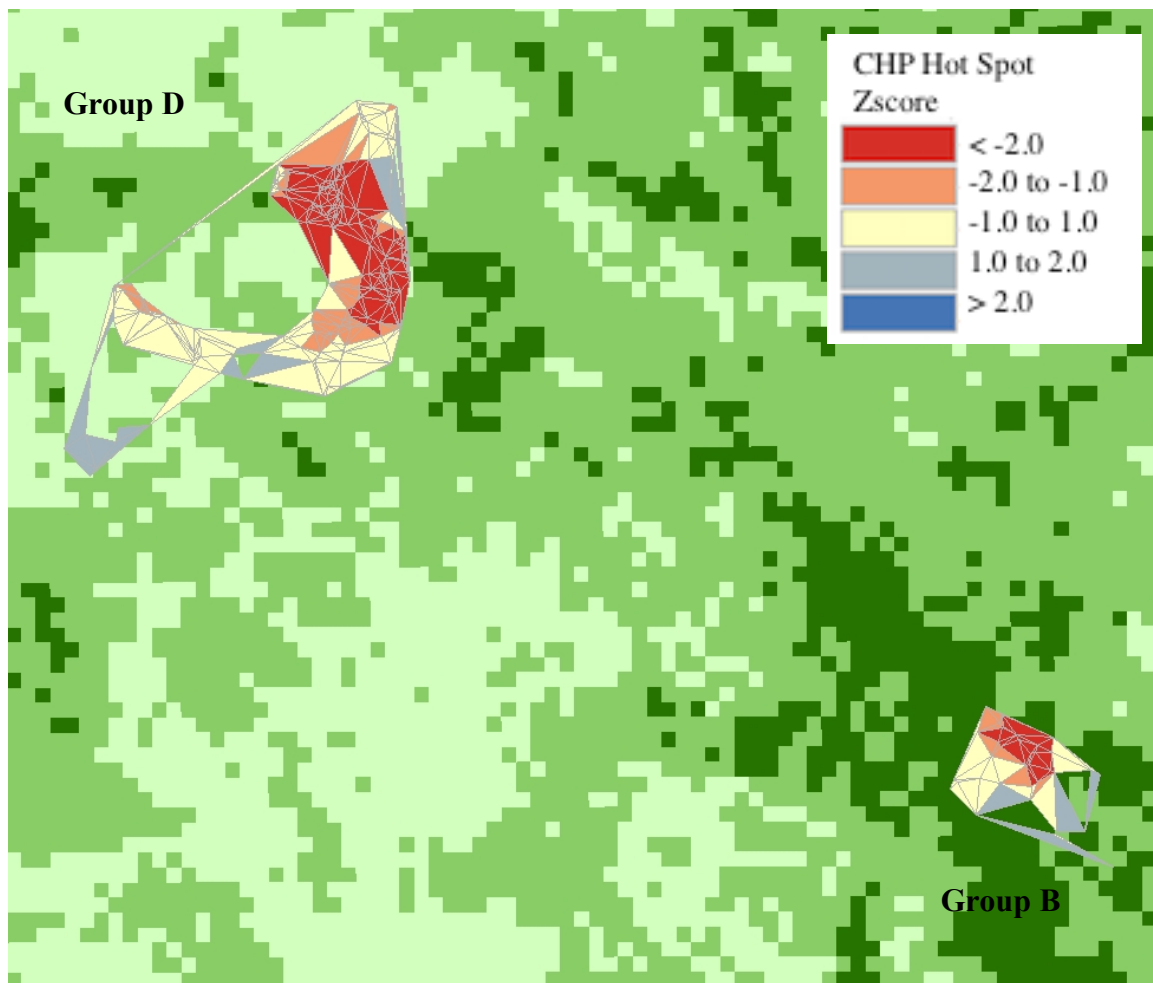


Figure 33. Light's summer ranges for groups B and D using the statistical CHP method with hot spot analysis.

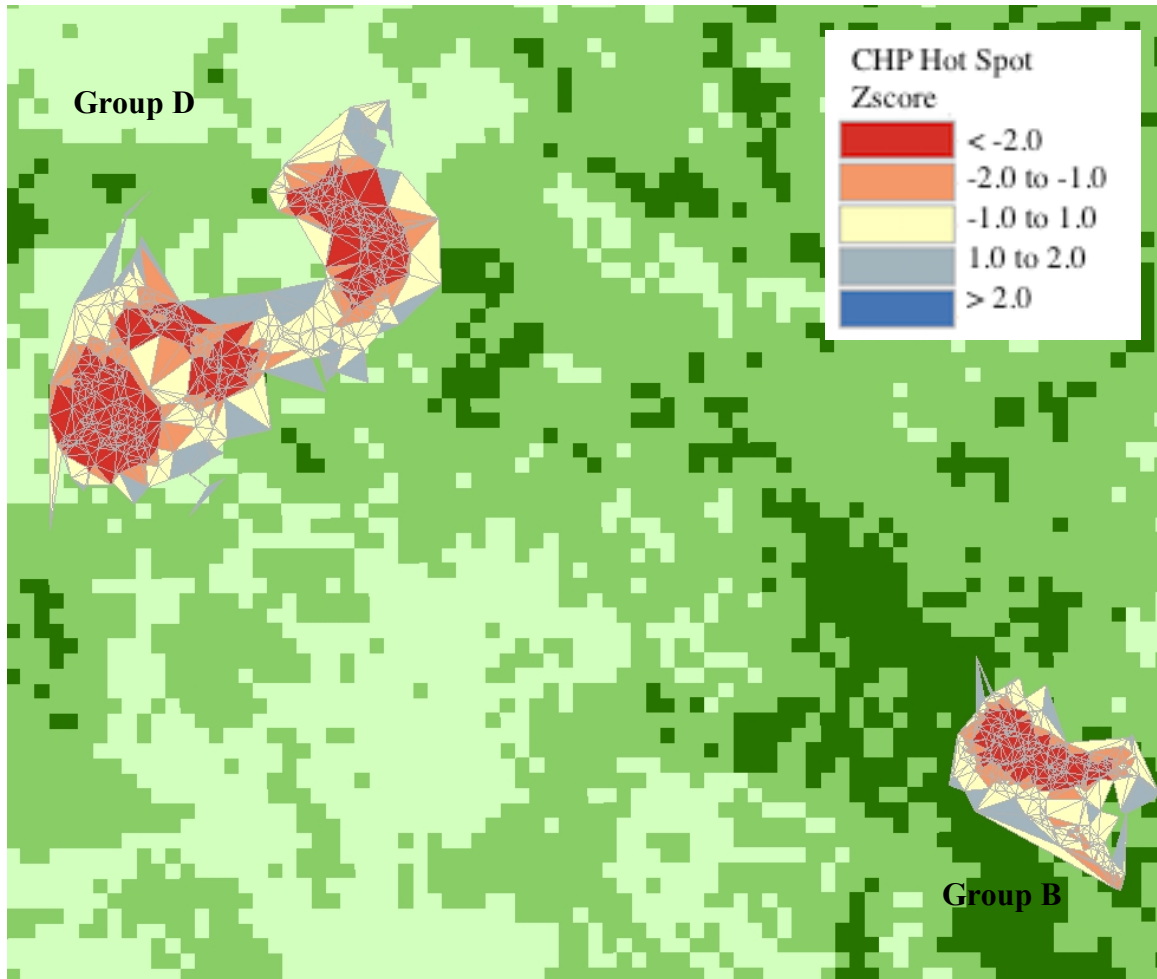


Figure 34. Light's overall ranges for groups B and D using the statistical CHP method with hot spot analysis.