Cheetah of the Serengeti Plains: A home range analysis

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Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University,
in partial fulfillment of the requirements for
the degree of

Master of Science
in
Fisheries and Wildlife Sciences

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November 11, 2005
Blacksburg, Virginia, USA

Keywords: *Acinonyx jubatus*, kernel, asymptote, migration, philopatry, overlap

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(ABSTRACT)

Cheetah (*Acinonyx jubatus*) persist under continued conservation threat in small populations mostly in protected areas in an historically reduced geographic range. Home range, a useful trait for threat assessment, species reintroduction, and population estimation, is plastic in cheetah with sizes ranging from 40 km^2 to over 1000 km^2 depending on location. Previous home range estimates for cheetah used the minimum convex polygon (MCP), assuming asymptotic home ranges and MCP insensitivity to sample size. They reported metrics of home range size and overlap based on only outline methods. I use 6 481 observations of 240 female and 315 male cheetah from > 60 matrilines over 25 years in the Serengeti Plains to investigate lifetime, core, yearly, and seasonal range size with kernel density estimation. I investigate autocorrelation using time to statistical independence of locations. I confront the assumption of asymptotic home ranges by testing the traditional and multiscaled home range predictions and provide a novel method for determining kernel asymptotes. I challenge the notion of Serengeti cheetah as a migratory carnivore with analyses of site fidelity and objectively defined core ranges. I assess year to year and seasonal location shifts, showing that yearly shifting lessens as females age. I provide quantitative evidence for philopatry in female- and juvenile dispersal in male cheetah of the Serengeti Plains. I use simple overlap metrics to show that overlap in lifetime and core ranges is greater in related than unrelated female pairs. I use multi-response permutation procedures (MRPP) to show that overlap in unrelated female pairs varies with season. I use correlation of utilization distributions to show that avoidance is apparent only in unrelated pairs of females. My results call into question previous MCP estimates of cheetah home range size, and provide guidance for future sampling of cheetah locations. My home range results will guide management of this imperiled species and my methodological findings may be general and applicable to a wide range of taxa.

Acknowledgements

I have been fascinated with savannah ecosystems and big cats since I was a boy, and I thank the Lord for the passion and providence that allowed me to do this work. Luke 1:37 has been a comfort and inspiration throughout. I thank Marcella Kelly for her tutelage, mentorship, and unwavering support in giving me unlimited intellectual freedom, financial support and a lot of patience. Most of all, I thank her for the wonderful opportunity to work on this project while experiencing the culture and gracious people of the United States. I thank my committee, Steve Prisley, Dean Stauffer and Jeff Walters, for their support and expertise. Their doors were always open and they kept me steered in the right direction. I thank the Department of Fisheries and Wildlife Sciences, Virginia Tech, and in particular, Don Orth for financial support and teaching opportunities. I thank Roger Powell for many stimulating discussions about home range theory. Roger inspired me to think critically about how and why animals move about a landscape, and has been extremely influential in shaping my understanding and appreciation of this field. I thank Tim Caro, Sarah Durant and the many field technicians and graduate students who collected the data I used, and upon whose shoulders I now ride. I thank Laurie Marker and Sarah Durant for the opportunity of visiting the Cheetah Conservation Fund, Namibia, and the Serengeti National Park, Tanzania, respectively, where I was able to glimpse and be humbled by my study species and study site. I thank the graduate students in our department for all the technical help, and stimulating discussions, especially those over a tall Guinness. In particular I thank Jay McGhee who acted as my sounding board for most of my outrageous ideas. Jay did a lot to both keep me grounded in reality and encourage novel ideas. I thank George Terrell, Bill Carstensen, Art Rodgers, Angus Carr, Mike Sawada, and the numerous other people who helped me develop ABODE and thereby analyze my data. I thank Joe Roggenbuck, Jan and Marleen van Aardt, David and Wendy Chinn, Tom McNamara, Autumn-Lynn Harrison and my many wonderful friends in the United States who made my stay so rewarding. Finally I thank my family and friends in South Africa and abroad for their support and encouragement, and for being there for me when all I wanted was a "lekka ou stuk boerewors".

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Chapter 1

An introduction to home range theory, cheetah (*Acinonyx jubatus*), and the Serengeti Plains

INTRODUCTION

My Oxford Dictionary defines ecology as "the study of organisms in relation to one another and to their surroundings." Similarly, the Ecological Society of America defines ecology as "the scientific discipline that is concerned with the relationships between organisms and their past, present, and future environments." The first definition describes an activity in which almost everybody in the world participates (consciously or sub-consciously). The second definition is more exclusive but still describes an activity that encompasses fields ranging from applied and pure biological sciences to human sciences. Either way, understanding the spatial or geographic context of organisms is a pervasive if not obvious goal of humans. Spatial context varies with scale. A scale with which humans are familiar answers the question "where does it live?" For animals, this scale is either the geographic distribution or the concept of home range. A formal concept of home range has been around for nearly a century (Seton, 1909) though humans have probably had an understanding of this entity for as long as we have hunted animals to feed ourselves. Though home range seems an intuitive concept there is little consensus on what a home range actually is, much less how to measure it (Powell, 2000).

I explore some aspects of the analysis of home range that are poorly defined and rarely performed and I do this with particular reference to a cheetah (*Acinonyx jubatus*) population that has unique movement behavior relative to other populations of the same species. My study will provide an analysis based on 15 years (1980-1994) worth of location data, and 25 years worth of demographic and behavioral data collected between 1969 and 1994 for 240 female and 315 male cheetah from the Central Plains of the Serengeti National Park, Tanzania. My study is unique in having long-term location data on known individuals with known matrilineal lineages (of up to 8

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generations of females). In this chapter, I will begin with a description of home range theory, methodology, and its historical evolution. I will summarize the advances made in cheetah home range research, before providing a brief description of methods of data collection, and my study site.

BACKGROUND INFORMATION

The concept of home range

Burt (1943:351) formalized the concept of home range with a definition to which I will return several times: "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside of the area, perhaps exploratory in nature, should not be considered as in part of the home range." Although Burt (1943) defined home range as spatial extent, the concept inferred the ability of a place to support members of the species. Hawes (1977) continued this thread by linking home range and niche, yet we have traditionally described home ranges in terms of only the boundary around and the area encompassed within that niche. Home range is rarely described quantitatively as a niche (but see Whitaker, 2003).

Even as early as Burt (1943), it was understood that Minimum Convex Polygons (MCP) or "minimum home ranges" (Mohr, 1947) might give a "false impression" of area use, and over-estimate spatial extent. The MCP method is one of the oldest methods for deriving home range size, and is used in most home range studies (White and Garrott, 1990). Continued use of this estimator encourages inappropriate comparison and the notion of home range as a 2-dimensional entity with even space use within a defined boundary (Powell, 2000). This is contrary to the cognitive map proposed by Peters (1978) describing the variable value of both resources and the landscape and strength and type of relationships between the individual and conspecifics and other species. Peters' (1978) map is manifested as a 3-dimensional entity of variable and

potentially clumped use with a "diffuse and general" boundary (Stickel, 1954; Gautestad and Mysterud, 1993; Gautestad and Mysterud, 1995; Powell, 2000). Most researchers cite comparability across studies as a reason for the use of MCPs, yet this method has been shown to be highly sensitive to sample size (n_{obs}) (Seaman *et al.*, 1999; Bekoff and Mech, 1984; Laundré and Keller, 1984; Harris *et al.*, 1990; White and Garrott, 1990; Kernohan *et al.*, 2001), outliers (and the ability to objectively treat them) (Seaman *et al.*, 1999), spatial resolution (Hansteen *et al.*, 1997), and sampling duration (Swihart and Slade, 1985a; Powell, 2000). Henceforth I denote the number of observations as "n_{obs}" and the sample size of independent units in an analysis as "n." MCPs have value in only the most meticulously matched comparative studies. There are also definitional and analytical flaws associated with the MCP technique (Powell *et al.*, 1997; Seaman, 1993; White and Garrott, 1990; van Winkle, 1975; Worton, 1987). I investigate the relationship between MCP home range size and sample size in my study within the context of the multiscaled home range (Gautestad and Mysterud, 1993, 1995) which I describe below. Our ability to define home range is compromised by our poor understanding of an animal's familiarity with area traversed (and resources and conspecifics / other species encountered) and its awareness of conditions and factors extraneous to the home range (Powell, 2000). How important are "sallies," and should they be included in the home range concept? The fundamental concept upon which home range theory rests – that home range is an area (Seton, 1909; Burt, 1943), has even been called into question (Gautestad and Mysterud, 1993).

Variable use within a home range – advances in the home range concept

Home range analysis has become increasingly more complex since its foundation in simple boundary methods (e.g. MCP). Boundary methods have suffered criticism as they are a 2-dimensional delineation of 3-dimensional activity by an animal (Linsdale, 1946). Improvements were made regarding this 3-dimensional aspect of animal activity such as Hayne's (1949) model of intensity of use (Scott, 1943) with a 1-dimensional statistical center of activity. Currently the utilization distribution (UD) is heralded as the best method for describing animal area use (Powell,

2000, Fieberg and Kochanny, in press). A utilization distribution illustrates a 2-dimensional relative frequency distribution (van Winkle, 1975; Worton, 1987), and was used as a basis for home range estimation by Dixon and Chapman (1980). Samuel and Garton (1987) explicitly incorporated time in the utilization distribution (which was previously implied from location frequency), providing the only 3-dimensional description of home range to date. Worton (1989) proposed kernel estimation as a flexible non-parametric estimator for depicting the utilization distribution. Importance of areas (resources) under this model is still inferred from the density of locations.

Lair (1987) advocated a biologically grounded concept of use, using a time-weighted frequency distribution distinguishing between "active" and "total" time. Lair (1987) required areas of high frequency of use to be associated with a biologically hypothesized attraction point (based on behavioral observation) - thus a resource oriented focal center. This would allow modeling of dependence upon resources. Unfortunately, Lair's (1987) methodology is rarely followed, in part because location estimates can be obtained without any direct behavioral observation of an animal (e.g. with radio telemetry). Typically, one delineates areas of high use in a utilization distribution at an arbitrary limit (i.e. 50% of the volume of the UD), labels this the "core" and infers biological importance of that area (or resources in that area) because of the higher use there by the animal. However, cores may be observed for individuals that randomly use space within a home range (Powell, 2000). Core areas should be representative of non-random use of space and should be unique for each individual and home range (Horner and Powell, 1990; Powell, 2000). Delineations based on probability density are usually arbitrary and unable to distinguish between clumped and random use (Powell, 2000).

In my study I attempt a critical analysis of home range for cheetah of the Serengeti Plains. I first question whether home range is the appropriate model for cheetah movement behavior (chapter 2), and then attempt to model movement (chapter 2) and social interaction within the population (chapter 3) using 'intensity of use' (instead of boundary methods). Home

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range analysis has been done before for cheetah, and I describe key findings from the literature next. A brief look at what has been done already will shed light on what remains to be done and on how novel techniques applied to this species may improve our understanding of its ecology.

Cheetah home ranges and territories

I summarize the following findings from previous cheetah home range studies in chapter 2 (Tables 2 and 3; Figures 22 and 23). Frame (1984) estimated areal extent of female home ranges as 800 km^2 using observational locations and Minimum Convex Polygon (MCP) methods. His sample sizes (n_{obs}) were not reported. Caro and Collins' (1987a) discussed the constancy of territorial boundaries for males and the importance of environmental features rather than female or prey presence for territory placement. They estimated male territory size (for those males that hold territories) in the Serengeti as "about 150 km^2," using a polygon estimator, though again, no sample sizes (n or n_{obs}) were reported. Caro (1994) reported home range size estimates for females and males using MCPs, noting the problem of sample size by showing that estimates with n_{obs} < 20 were smaller than those with $n_{obs} \geq$ 20 locations. Telemetered individuals with $n_{obs} \geq$ 20 had larger home ranges than those using solely ground (observational) sightings with a mean (SE) for 19 individuals with $n_{obs} \geq$ 20 of 833.0 (85.1) km^2 (Caro, 1994). Twenty two male territories with $n_{obs} \geq$ 5 were on average 37.4 (5.2) km^2, and 48.3 km^2 using only telemetered individuals (maximum = 74.8 km^2) (Caro, 1994). Floater males home ranges were a mean (SE) of 777.2 (153.0) km^2, based n = 9 individuals with n_{obs} > 10 (maximum = 1892.6 km^2) (Caro, 1994). The early home range studies for cheetah in the Serengeti focused almost exclusively on the home range size estimate.

Durant *et al.* (1988) also found that the stationary male territories were located spatially independent of prey movements and suggested dependence of female and non-territorial male ranging patterns on the prey migration (based upon a visually estimated correlation between population densities of cheetah and Thomson's gazelle (*Gazella thomsoni*) during different

seasons). The relationship between movement behavior and an hypothesized limiting resource formed the beginnings of a more biologically meaningful home range model. Gros *et al.* (1996) studied cheetah home ranges from a utilitarian perspective, trying to predict cheetah density based on area used and overlap between individuals. Using MCPs, sample size (n individuals) and number of locations (n_{obs}) were reported (though only a minimum n_{obs} was reported, which was smaller than that recommended by Bekoff and Mech (100-200) (1984), and was applied indiscriminately to the whole sample (N) as opposed to individual home ranges (Harris *et al.*, 1990; Doncaster and Macdonald, 1991)). Gros *et al.* (1996) did however report "periodic ranges" (Mohr, 1947), with a yearly mean of 414 km^2 and noted that home range size is "park-specific." They analyzed social organization, using overlap as a metric of static conspecific interaction and they also used a prey biomass model as a means of predicting population size. They did not link home range size (and overlap) and dependence upon prey biomass, which may vary spatially across such a large study area. A combination of their methods holds promise for describing cheetah home ranges in a manner that is site general.

Various home range analyses have been performed in other ecosystems. Zank (1995) and Purchase and du Toit (2000) reported MCP home range extent in different years for the same two males (114 km^2 n_{obs} = 40, 157.0 km^2 n_{obs} = 44 (Zank; 1995); and 11.3 km^2 n = 21, 53.8 km^2 n_{obs} = 32 (Purchase and du Toit; 2000)) and one female (236.0 km^2 n_{obs} = 64 (Zank; 1995); and 23.6 km^2 n_{obs} = 25 (Purchase and du Toit; 2000)) in the Matusadona National Park, Zimbabwe. Purchase and du Toit's (2000) habitat selection analysis assumed within patch homogeneity, discrete boundaries, and a relationship between fitness and habitat type (Mitchell and Powell, 2003). Their analysis also assumed availability of a resource based on areal extent (Garshelis, 2000). Purchase and du Toit (2000) used a prey biomass model to predict cheetah "carrying capacity" of the study site and considered home range overlap. Their methodology holds promise for combining variable home range use, a limiting resource, overlap, and home range size in a predictive model for area and resource requirements of cheetah.

Durant (1998) found that cheetah presence was positively correlated with medium to low concentrations of Thomson's gazelle, and negatively correlated with high concentrations (>500 individuals) and areas devoid of gazelle. Durant (1998) also suggested that locations of lactating females (with restricted ranges) were positively correlated with lion presence and with areas devoid of Thomson's gazelle. Though Durant (1998) did not discuss this finding, I hypothesize that lactating females may have restricted mobility and are thus less able to avoid lion and to find suitable concentrations of prey. This was a great stride forward as it focused on the simultaneous presence of cheetah and a resource (or threat) and allowed hypothesis building based upon the biologically meaningful resources (or encounters) that constitute a cheetah home range. Caro and Collins (1987b) discussed the potential link between fitness and home range use by showing correlation between male survival and territoriality. This was the first discussion of cheetah ranging behavior under an evolutionary paradigm.

Durant (2000a) showed experimentally, direct behavioral responses (movement and vigilance) to interspecific interaction (simulated through playback experiments), hypothesizing a process to explain the pattern observed by Durant (1998). Cheetah actively avoid lion, and show increasing avoidance behavior with increasing reproductive success (Durant, 2000a). Importantly, a fitness correlate was used to assess a movement response. Durant (2000b) showed similarly that both male and female cheetah were less likely to hunt and less likely to chase and kill prey after lion and hyena playback experiments and that there was no difference between the responses of females with no cubs versus those of females with cubs or between mothers with cubs of different ages. Durant (2000a, 2000b) was thus able to combine observed pattern with experimental manipulation to improve understanding of the movement behavior of cheetah, with specific reference to the effect of predators and competitors.

Cheetah home ranges have been assessed almost exclusively in terms of simple areal extent (in the form of boundary methods), with a few important attempts to link home range to single resources such as prey migration, prey biomass, habitat type, Thomson's gazelle

densities, and lion presence (all detailed above), and to reproductive performance (male territoriality, see above). These assessments have been made using simple and unreplicable home range estimators. In my study, I attempt to model home range dynamics in terms of intensity of use within the home range. To model home range using intensity of use (e.g. using a UD) adequate sample sizes are required, typically in excess of 30 and preferably 50 locations (Seaman *et al.*, 1999). In addition, certain smoothing methods such as Least Squares Cross Validation (LSCV) (in kernel density estimation) preclude the use of data with exaggerated rounding error (Seaman and Powell, 1996). I briefly review data collection methods to investigate the applicability of kernel estimators for my data.

Data collection

Caro (1994) provided a thorough review of data collection methods which I briefly summarize. Data were collected between 1969 and 1994. Data were collected by Brian Bertram (August 1969 - December 1973), George Frame (March 1973 –March 1978), Tim Caro (March 1980 – December 1983), Anthony Collins (November 1983 – October 1984), Clare FitzGibbon (January 1985 – March 1987), Karen Laurenson (September 1987 – September 1990), and Sarah Durant (March 1991 – December 1994). Reliable location data were available only from 1980 to 1994 but certain individuals and their offspring recognized early in the study later allowed us to reconstruct lineages in the form of matrilines (Kelly, 2001a).

Individual identification of animals was made possible by unique coat patterns which were identified in the field or later through photograph matching (Kelly, 2001b). Locations were collected randomly and opportunistically from field observation (scanning the landscape for cheetahs from vantage points); from ground telemetry, and at discrete intervals using aerial telemetry. A total of 25 cheetah were radio collared (including 2 males), resulting in 285 telemetry observations. The maximum period an individual was collared was 3.3 years, yielding 38 telemetry observations for that individual. Both ground and aerial telemetry (Laurenson, 1995)

were used for homing (White and Garrot, 1990) or radio-assisted surveillance (Harris *et al.*, 1990). Location estimates collected visually in this manner contain marginal error (Springer, 1979; White and Garrot, 1990) while topographic mapping from aerial telemetry also provides estimates with error comparable to GPS methods (Carrel *et al.*, 1997). Data points were rounded to the centers of 0.25 km^2 grid cells. This level of discretization (rounding) affected LSCV estimates for kernel analysis. We circumvented this problem using a feature in program ABODE (Laver, 2005) the software that was used to estimate home ranges.

I had spatial data for cheetah representing each developmental class (dependent - with mother, independent or dispersing with siblings), social dominance class for males (territorial, floater, or transient), level of sociality for males (solitary or coalition member), and breeding status for females (pregnant, with cubs or without cubs). Males were described as singletons (one male) or coalitions (for a group of two or more males). Ancillary data were included from data collection during collaring, and as sighting-specific estimates of an individual's hunger and habituation level and habitat characteristics (prey and predator abundance). Habituation levels of each individual at each observation provided a means of assessing behavioral bias introduced by observer presence (Whitey *et al.*, 2001), specifically the homing technique used (Cochran and Lord, 1963). Methods for ancillary data collection were also reviewed by Caro (1994).

Fifteen years of data collection resulted in large sample sizes (n_{obs}) for females and for the few territorial males with long tenure. Many individuals were observed in the population over multiple years and many were even observed from birth until their senescence (though death was rarely confirmed) (Kelly *et al.*, 1998). A long-term dataset such as this is possible because of the ecological aspects of this ecosystem that have spurred academic interest, and have also allowed for behavioral observation. Savannah ecosystems provide good opportunities for ecological study. They support a large faunal biomass and have floristic structure inherently suited to observation of mega fauna. The Serengeti Ecosystem has been studied rigorously since Grzimek and Grzimek (1960). I now briefly review the ecology of the Serengeti Plains.

Study Site: The Serengeti Plains

My study site forms a portion (2 200 km^2) of the Serengeti plains (5 200 km^2) in the Serengeti National Park, Tanzania (Figure 1), which is part of the Serengeti-Mara Ecosystem (25 000 km^2; 1˚15' to 3˚30' south, 33˚52' to 35˚42' east; altitude: 1 200 – 1 800 m) (Caro, 1994) (Figure 2). The plains are dotted with kopjes (granite and gneiss outcrops) (Figure 3), and the vegetation gradient of short grass in the south and east, to tall grass in the north and west is driven by a topo-edaphic gradient of shallow to deep and decreasingly alkaline soils (Sinclair, 1995). Spatial and temporal heterogeneity of resources is the defining characteristic of this ecosystem (Sinclair, 1995). A wet season from November to May (with 'short' rains in November and December and 'long' rains in March and April) and a dry season from June to October (Caro, 1994) are pivotal in the migration of ungulate herds in this ecosystem (note that I classified June and November as 'transition months'). Two migrations occur. The larger migration of Burchell's zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) takes animals to the northern part of the Serengeti National Park and into the Mara Reserve by the end of the dry season, bringing herds back to the short grass plains in the south and east as they follow the ephemeral pattern of grass regrowth when the rains resume in the wet season (Sinclair, 1995). The timing of the migration is triggered by water quality on the plains at the start of the dry season (Gereta and Wolanski, 1998; Wolanski and Gereta, 2001; Wolanski *et al.*, 1999). In the smaller migration, Thomson's gazelle and some Grant's gazelle (*Gazella granti*) migrate from the short grass plains to the plains-woodland border (and into the woodlands under extremely dry conditions)(Caro, 1994). Many Grant's gazelle remain on the plains throughout the dry season (Caro, 1994).

Sinclair (1995) noted that major perturbations have occurred in the Serengeti in the last 50 years. The elimination of Rinderpest as a wildlife disease in the 1960s led to a five- and sixfold increase in African buffalo (*Syncerus caffer*) and wildebeest numbers (respectively) (Sinclair, 1995). The border between the Mara Reserve, Kenya, and the Serengeti National Park

was also closed and resulted in a huge drop in tourist numbers, leading to a reduction in park funds and subsequent reduction in funding of anti-poaching patrols (Sinclair, 1995). This, with marked increases in the human population to the west of the park led to high poaching pressure and the local extirpation of the white rhinoceros (*Ceratotherium simum*) and dramatic reductions in the African elephant (*Loxodonta africana*) and buffalo populations (Sinclair, 1995).

Though migration is a dominant process in the Serengeti, and though cheetah prey predominantly upon Thomson's gazelle, a migratory ungulate (Caro, 1994), the cheetah's status as a migratory carnivore has not been explored. I briefly review some of the contentious definitions of migration.

A final note on migration

Much like home range, migration is another topic for which there is little definitional consensus. Again we can turn to Seton (1909:26) for an early description: "Some animals have two home-regions, and make a regular seasonal change from one to the other; such animals are said to be migratory." Thomson (1926) defined migration as "changes of habitat periodically recurring and alternating in direction, which tend to secure optimal environmental conditions at all times." Sinclair (1983) defined migration simply as "a regular round trip within a life-span of an individual." Dingle (1996) contended that round-trip movements are insufficient as a definition of migration since foraging and commuting may also include such movements. Dingle (1996) also distinguished nomadism (a long movement without return) from these movement behaviors. Some or all of the five attributes of migration that distinguish it as a specialized behavior must be evident for a movement to be termed migration (Dingle, 1996). They are (Dingle, 1996):

1. a persistent movement of greater duration than normal movement,
2. "straightened-out" movement,
3. initial inhibition and later enhancement of responses to stimuli that bring an individual to a stop or keep it stationary at a resource,

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4. activity patterns unique to arriving or departing,

5. and energy allocation specific to movement processes.

Though cheetah of the Serengeti have been described as migratory (Caro, 1994, Marker *et al.*, under review) and "somewhat nomadic" (Packer, 1986), no investigation has been made into any of the aforementioned factors that would indicate migratory behavior. The perception of cheetah as a migratory carnivore in the Serengeti is thus based on the widely held understanding of migration akin to the descriptions of Seton (1909), Thomson (1926) and Sinclair (1983)(above). Dingle (1996) defined several movement behaviors that contribute to the "lifetime tracks" of organisms. Most of these were divided broadly into movements that were either resource (or home range) directed or non-resource directed (Dingle, 1996). Under the former category, station-keeping and ranging movements result in site fidelity or exploration, respectively (Dingle, 1996). Migration was an example of non-resource directed movement (Dingle, 1996). Station-keeping was further divided into kineses (changes in rate of movement), foraging, commuting and territorial behavior (Dingle, 1996). If cheetah of the Serengeti are not migratory, which behavior best describes their movement? This is a question I investigate in chapter 2.

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FIGURES AND TABLES

Figure 1. The geographic location of the Serengeti-Mara Ecosystem (black) in Tanzania (dark shading), Africa.
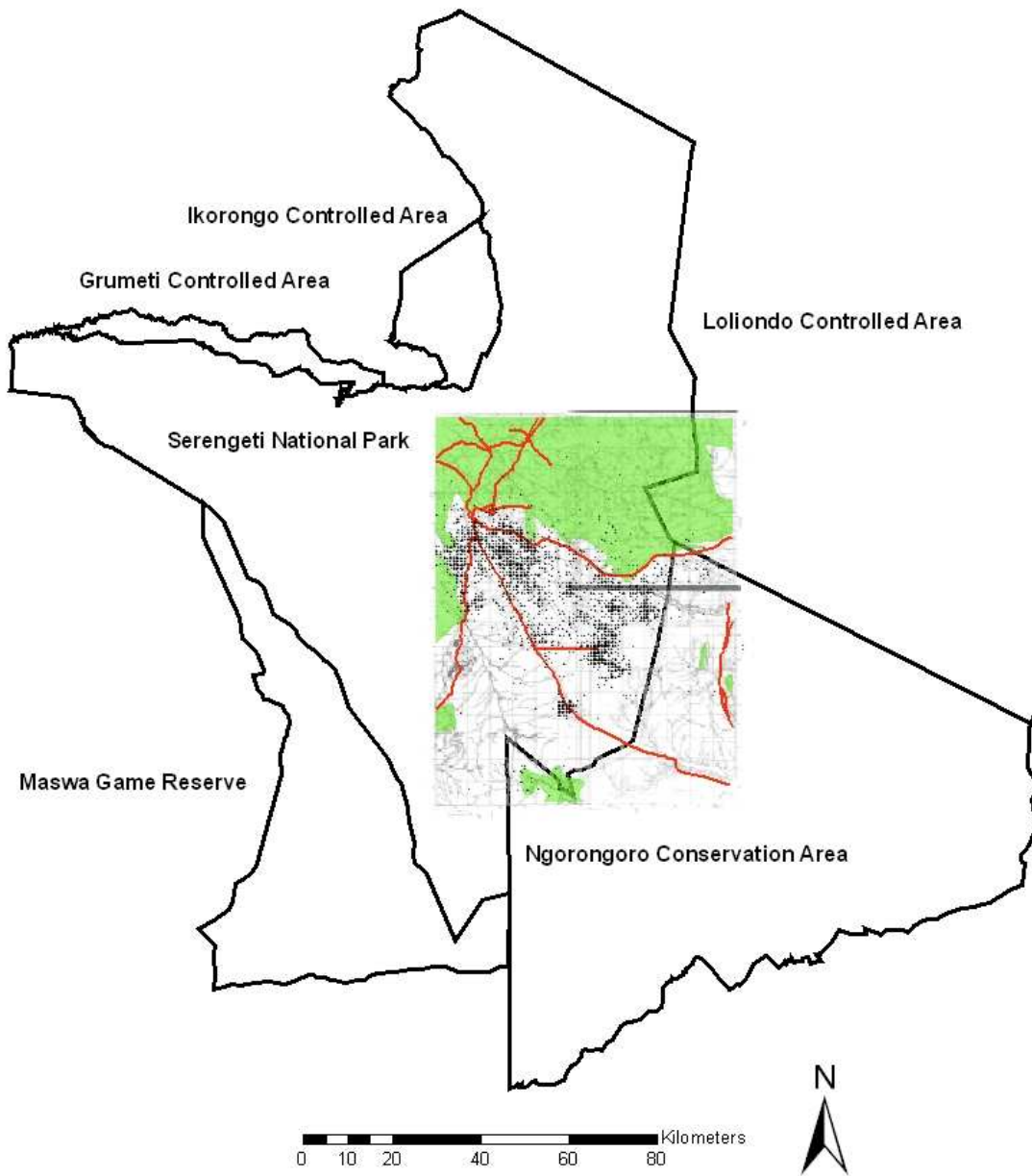
Figure 2. The Serengeti-Mara Ecosystem (in Tanzania) with 6 protected areas shown. My study site (overlaid) was located in 2 200 km^2 of the southeastern part of the Serengeti National Park.
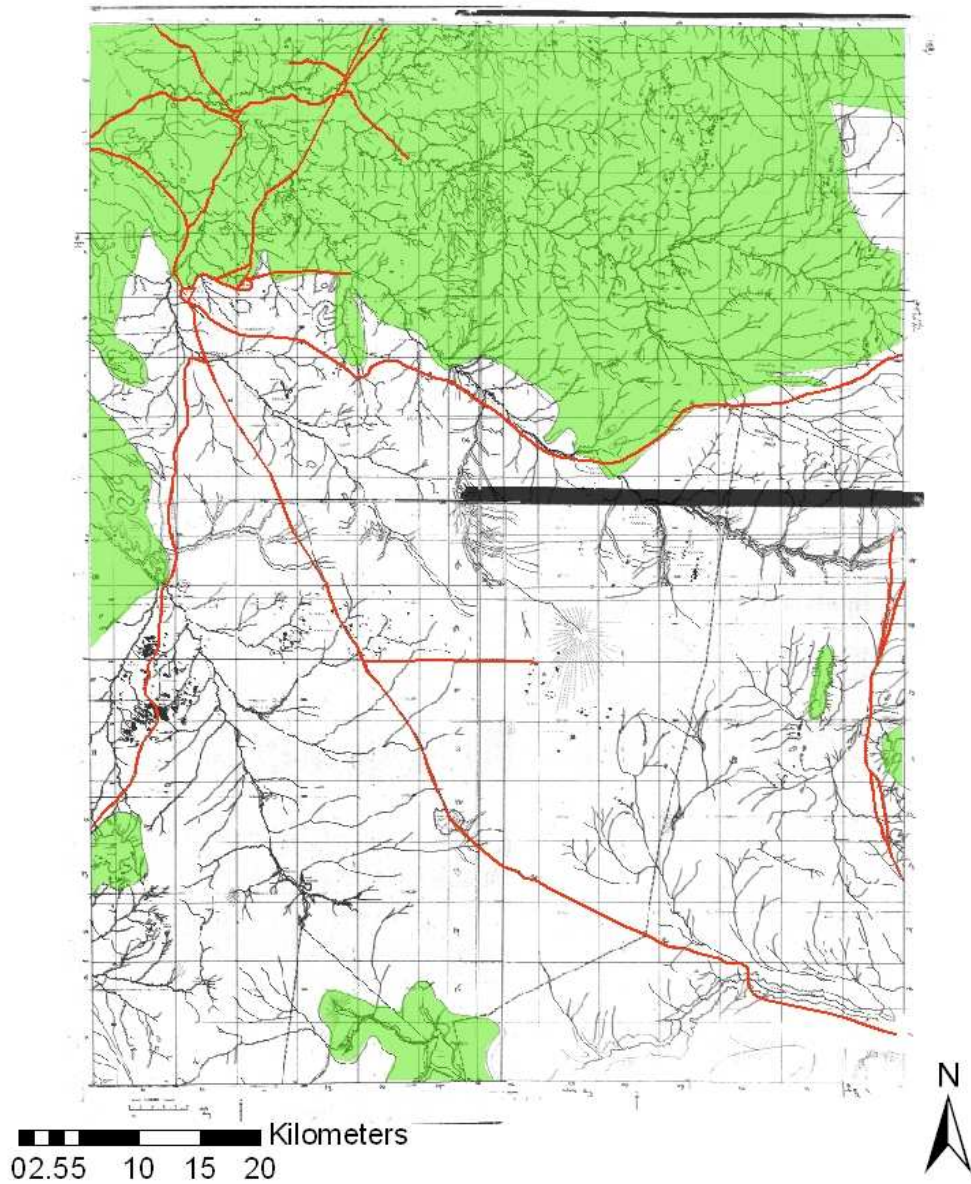
Figure 3. The Serengeti plains, Serengeti National Park, Tanzania. My study was conducted on the short and tall grass plains (white) between the woodlands (green) and the southeastern boundary of the park. Kopjes (black) and roads (red) are indicated. Drainages (black) are mostly ephemeral.

Chapter 2

Moss or a rolling stone? The case for home range in a "migratory" carnivore, lessons from cheetah (*Acinonyx jubatus*) of the Serengeti Plains

INTRODUCTION

The concept of the home range has its basis in the hypothesis that animals choose to restrict their movements to specific parts of a landscape. "No wild animal roams at random over the country, each has a home-region" (Seton, 1909, p26). Thus, Seton introduced two hypotheses, first, that animals make behavioral decisions about where to go, resulting in non-random use of space, and secondly, that this is true for all wild animals. Burt (1943) provided a definition for this and added the caveat that the area be restricted to only regular use, not to include "occasional sallies." Further, Burt (1943) suggested that species-specific limits to home range size exist. Though these concepts are widely applied, Gautestad and Mysterud (1993, 1995) have challenged both the hypothesis about non-random use and the hypothesis about limits to home range size with their multiscaled home range model (which I describe below). Burt (1943) reasoned that one's ability to manage a species is dependent upon one's knowledge of its "fundamental behavior pattern," as is suggested by its movement behavior and gave an example of the significance of this knowledge in practices such as the release of animals into an area (e.g. reintroductions). Woodroffe and Ginsberg (1998) followed similar reasoning in evaluating the importance of home range estimates for species of conservation concern. Though Burt (1943) implied that the resources needed by an individual for survival and reproduction are inherently part of the concept of "home range," he made the clear distinction between "living space" and "other essentials of life." Thus began the quest for a definable areal extent described by Hawes (1977): "the home range provides the physical boundaries within which its niche is realized."

Do Serengeti cheetah establish home ranges?

Home range analysis allows us to make inferences about the behavior and ecology of animals (Powell, 2000). Burt (1943) excluded the area used during "adolescent wandering" and "occasional sallies outside the area, perhaps exploratory in nature" and defined the home range as "after they establish themselves … that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." Site fidelity is the measure of the level of "establishment" by an individual (Danielson and Swihart, 1987) and results from nonrandom movement (Munger, 1984). It is a concept widely used, but rarely defined. I propose a formal definition for site fidelity as "the act of repeatedly choosing a set of resources in a place, given other alternatives." This definition reflects Greenwood's (1980) description of "faithfulness to a site" and Munger's (1984) "affinity for a site." Site fidelity is a prerequisite for making the aforementioned behavioral and ecological inferences (Spencer *et al.*, 1990), and introduces biologically significant delineation as opposed to non-statistical methods (such as MCP) and arbitrary statistical delineations (such as the use of a 95% kernel). My definition closely resembles the definition of a core home range (Horner and Powell, 1990).

While much of the home range literature has focused on species that are relatively small, short ranging and highly visible, less has been done on large or wide-ranging species that are difficult to study. Cheetah provide an interesting model for home range studies. They generally exist in open habitats (Caro, 1994; but see Broomhall *et al.*, 2003), are mainly diurnal (Caro, 1994), and relatively visible from afar (2.5 km: Caro, 1994). Cheetah range extensively (Frame, 1984; Caro, 1994) and hence provide opportunities for building and testing hypotheses about site fidelity for animals with large home ranges. These hypotheses might deal with mechanisms that allow such animals to remain 'familiar' with their home range (Stamps, 1995) or balance the energy budget related to maintaining a home range (Powell, 2000). No study to date has examined whether or not cheetah establish a home range.

Cheetah home range and movement behavior have been studied in several ecosystems including those of the Serengeti National Park, Tanzania (Frame, 1984; Caro and Collins, 1986; Caro and Collins, 1987a,b; Caro, 1994; and Gros *et al.*, 1996; Durant *et al.*, 1988; Durant, 1998; Durant, 2000a; and Durant, 2000b), the Matusadona National Park, Zimbabwe (Zank, 1995; and Purchase and du Toit, 2000), the Kruger National Park, South Africa (Broomhall *et al.*, 2003), and Namibian farmlands (Marker *et al.*, under review). That cheetah exhibit a true home range is implicit but untested in these studies even though female cheetah were described as "somewhat nomadic" by Packer (1986:431) and Namibian cheetah have been hypothesized to be non-migratory (in contrast to Serengeti cheetah) (Marker *et al.*, under review). Site fidelity as a metric for home range should be tested explicitly before drawing ecological and behavioral conclusions from movement behavior (Spencer *et al.*, 1990). My first objective is thus to determine if cheetah of the Serengeti are migratory, nomadic, or station keeping in their movement. I present results for tests of site fidelity in male and female cheetah of the Serengeti Plains, using data collected between 1980 and 1994 (see chapter 1 for data collection methods).

Seasonal range shifts

Though seasonal ranges have been studied for Namibian cheetah (Marker *et al.*, under review), no spatial analysis has been performed on shifting between seasons for any cheetah population. I investigate this in a population of cheetah with a migratory prey base, for which one would expect spatially distinct seasonal ranges.

Year to year site fidelity

Burt (1943) noted that adolescent animals often "wander" from their natal range until they establish what may be either a stationary or a shifting home range ("natal dispersal", Greenwood, 1980). In most mammal species, males show more natal dispersal and hence less philopatry than females (Greenwood, 1980). Shifts in the home range (whether natal dispersals or yearly

shifts) confound tests of independence (below) for lifetime home ranges (McNay *et al.*, 1994; Swihart and Slade, 1997). For example, shifts in center of activity or expansion or contraction of a home range affect the variance-covariance structure of the data and this affects tests of independence (Swihart and Slade, 1997). This phenomenon affects not only one's interpretation of appropriate sampling protocol and of lifetime home range size, but also affects tests for asymptotic trends in home range size (Gautestad and Mysterud, 1995; Kernohan *et al.*, 2001). Caro (1994) suggested that philopatry was exhibited in cheetah of the Serengeti Plains by adolescent and adult females and adolescent males. These findings were based on visual comparisons of minimum convex polygon (MCP) home range boundaries, and static interactions as estimated by range overlap. MCPs are insensitive to the internal pattern of space use and may indicate overlap even when the density of use of an area by two animals (or the same animal in two time periods) is low relative to the use of non-overlapping areas. Yearly home range shifts have not been examined in cheetah. I test explicitly for home range shifting between years in male and female cheetah of the Serengeti Plains. I examine philopatry and natal dispersal in chapter 3.

Time to statistical independence and appropriate sampling interval

Location data are by definition spatio-temporally autocorrelated (Dunn and Gipson, 1977; Rossi *et al.*, 1992; Otis and White 1999). Critique of autocorrelation in animal studies has shown that autocorrelated datasets contain less information than similar sized datasets of independent data (Swihart and Slade, 1985b), that statistical analyses of habitat use require independent data (Swihart and Slade, 1987) and that underestimation of home range size may result from using autocorrelated data (Swihart and Slade, 1985b). Kernel density estimation appears to be robust towards this bias given the appropriate sampling period (Swihart and Slade, 1997; De Solla *et al.*, 1999). The appropriate sampling period exceeds the time needed for an individual to describe each temporal range (Swihart and Slade, 1985b; Lair, 1987; Otis and White, 1999), that is, if inferences are to be made about a yearly range, location data need to be sampled for at least a

year, giving the individual opportunity to visit all the areas it would typically visit in that time period. Biological independence of location estimates is different from statistical independence and considers the physiological constraints of movement and requires a sampling interval long enough to allow the individual to travel anywhere in the range (Lair, 1987). Estimating the time to statistical independence of location data can lead to maximized sampling efficiency and can provide insight into aspects of behavioral ecology such as the rate of home range use, shifting behavior, and temporally predictable and cyclical movements in animals (Swihart and Slade, 1985a; McNay et al., 1994). Shifts in the home range (whether natal dispersals or yearly shifts) confound tests of independence for lifetime home ranges (McNay et al., 1994; Swihart and Slade, 1997). In a review of 36 animal activity publications, Salvatori et al. (1999) found that almost all studies analyzed data with only implicit assumptions of independence of location data, either ignoring or subjectively treating the issue. Swihart et al. (1988) assessed the time to independence for 23 mammal species, of which most were small mammals and species with home ranges smaller than 1 km^2. Salvatore et al. (1999) and Rooney et al. (1998) each added two more mammalian species to this list. Currently, no data are published concerning time to independence for cheetah. I present an assessment of autocorrelation in location data for a population of cheetah from the Serengeti Plains.

Do cheetah home ranges tend towards an asymptote?

Home range size is an important metric for behavioral and ecological studies. As early as Seton (1909), a home range was described as a non-random use of space, posited to scale with animal size. This relationship has subsequently been quantified (Carbone and Gittleman, 2002; Jetz et al., 2004; and Carbone et al., 2005). To have confidence in one's interpretation and application of home range and scaling studies, one must begin with reliable estimates of home range size. The reliability of one's estimates is determined by the quality of the location data (Withey et al., 2001), the home range estimator used (Kernohan et al., 2001; Powell, 2000; Hansteen et al., 1997; Harris et al., 1990; White and Garrott, 1990; Worton, 1987; Swihart and

Slade, 1985; Bekoff and Mech, 1984; van Winkle, 1975), and an appropriate sample size (n_{obs}) as a function of appropriate sampling interval and sampling period (Seaman *et al.*, 1999; Swihart and Slade, 1997; Otis and White, 1999). Sample size can determine the bias of estimators used, and determine whether the location data are an adequate sample of the animal's movements. This issue has traditionally been assessed using home range asymptotes. Home ranges are assumed to reach a functional maximum as indicated by an asymptote of home range size with increasing sample size (Stickel, 1954; Hawes, 1977). Gautestad and Mysterud (1993, 1995) challenged this hypothesis, suggesting that home range size does not reach a limit, but increases as a function of the sample size (n_{obs})(the multiscaled home range). The multiscaled home range (MHR) has fractal properties, not a demarcatable area (Gautestad and Mysterud, 1995), and increases in size proportional to the square root of the number of locations (n_{obs})(Gautestad and Mysterud, 1993). The movement behavior that results in a multiscaled home range is modeled as a "random walk on a random walk" (RW/RW) (Gautestad and Mysterud, 1993). Central to this theory is the concept of a 'grain size' or "step length" which is unique to each taxon, unique to each individual within a taxon, which can change to reflect ecological conditions. This grain size is the scale at which an animal perceives its surroundings (Gautestad and Mysterud, 1993).

Home range size is an expensive and difficult estimate to obtain. Asymptote analyses are thus used to determine a) if one has adequately sampled the movement of the animal, and b) the minimum number of location estimates needed to have a specified confidence in one's sample. Harris *et al.* (1990) showed that the majority of publications that they reviewed had not considered home range asymptotes and had not provided the number of location estimates for the asymptote or home range analysis. Though home range size has been estimated for cheetah of the Serengeti National Park, Tanzania (Frame, 1984; Caro and Collins, 1986; Caro and Collins, 1987a; Caro and Collins, 1987b; Caro, 1994; and Gros *et al.*, 1996), Matusadona National Park, Zimbabwe (Zank, 1995; and Purchase and du Toit, 2000), the Kruger National Park (KNP), South Africa (Broomhall *et al.*, 2003), and Namibian farmlands (Marker *et al.*, under review) the only asymptote analysis to date has been performed for seven individuals of the

Kruger National Park population (Broomhall *et al.*, 2003). Broomhall *et al.* (2003) did not report suggested sample sizes for home range estimation from asymptotes, but did exclude individuals from their home range analyses where an asymptote was not reached. I provide an asymptote analysis for cheetah of the Serengeti Plains and test the contrasting views of the traditional asymptotic home range versus the multiscaled home range (Gautestad and Mysterud, 1993).

Areal extent of space use by cheetah

MCP has been used in all previous cheetah home range studies, though Broomhall *et al.* (2003) and Marker *et al.* (under review) dealt with the problem of outliers by using a 95% peeled polygon (MCP). Broomhall *et al.*'s (2003) was also the only study to investigate home range asymptotes and exclude individuals from the analysis that did not show asymptotes. Broomhall *et al.* (2003) reported the 50% MCP as the core range. Marker *et al.* (under review) reported the 50% fixed kernel contour as the core range. My study provides the first kernel analysis for cheetah based on asymptotic home ranges. I apply Horner and Powell's (1990) statistical clumping core analysis to these data to provide an objective delineation of core areas. I also investigate periodic ranges for wet and dry seasons and yearly ranges, similar to Marker *et al.* (under review). I evaluate 8 kernel estimation techniques for their ability to delineate lifetime home ranges relative to an accepted standard.

In this study, I investigate cheetah home range, in the aim of providing baseline information for future research and management of the species. I first determine whether cheetah exhibit site fidelity and thus have a home range. To guide future location data collection I determine the time to statistical independence of location estimates and determine the number of location estimates required for home range size to reach an asymptote. I test the validity of the multiscaled home range for cheetah home ranges. I investigate shifting in area use from year to year and from season to season. I conclude with estimates of lifetime home range and core range size, as well as yearly and seasonal range sizes.

METHODS AND MATERIALS

Do cheetah establish home ranges?

I tested whether cheetah of the Serengeti Plains use home ranges or roam randomly across the plains within a year. I used site fidelity as a metric for home range establishment, following Spencer *et al.* (1990). I used mean squared distance from the center of activity (MSD) (Calhoun and Casby, 1958) and Linearity Index (LI) (Bell and Kramer, 1979) to investigate site fidelity for 19 male and 44 female cheetah with at least 10 location estimates in a year (Figure 1). Some individuals had more than one year with 10 location estimates, resulting in a total of 110 individual*year combinations. Location estimates were collected between 1980 and 1994 and collection methods are detailed by Caro (1994). MSD is the mean squared distance of every location from the center of activity (calculated as the arithmetic mean of UTM easting and northing). LI is the ratio of 'start to end distance' to the total distance traveled. LI = 1 denotes linear travel. I generated 100 random walks for each individual for each year (individual*year) using the actual distances traveled between consecutive locations, but with randomly generated azimuths (0° to 360°). I assessed the adequacy of a sample size of 100 random walks by evaluating the stability of the mean and standard deviation of MSD and LI for each individual*year combination. If the number of simulations (random walks) is adequate, the mean and standard deviations of the estimated variables (MSD and LI) should reach an asymptote. I compared actual MSD and LI to the mean and 95% confidence interval for each set of 100 random walks. Actual values of MSD and LI that were significantly lower than generated means indicated more concentrated and less linear movement (respectively) than would be expected at random and were measures of site fidelity (Spencer *et al.*, 1990). I analyzed each individual in each year, pooled the yearly results for each individual, and also analyzed separately only those individual*year combinations with at least 30 locations per year. I compared qualitatively the sample of individuals with $n_{obs} \geq 10$ to the sample with $n_{obs} \geq 30$. I assumed that if the two groups

produced qualitatively similar results, 10 location estimates in a year would represent the location of an individual in enough months to capture their yearly movement pattern.

Seasonal range shifts

I assessed adult seasonal range shifts for 48 female and 10 male cheetah for which I had at least 3 location estimates for both the wet and dry season. I used Multi-Response Permutation Procedures (MRPP) (Zimmerman *et al.*, 1985) in Blossom (Cade and Richards, 2001) to investigate shifts in seasonal range use. MRPP test for concentration within groups and are similar to *t* and *F* tests, but can be applied to multivariate data (such as location estimates) and are non-parametric (Zimmerman *et al.*, 1985). In MRPP, significant *P*-values suggest that samples do not come from the same distribution, which I used to define a site shift ($\alpha = 0.05$). I hypothesized that females would shift between seasons since they follow a migratory prey base. I hypothesized that floater males would also shift between seasons, and that territorial males would remain stationary because their territories are centered upon physical features of the landscape.

Year to year site fidelity

I analyzed yearly shifts in area use with Multi-Response Permutation Procedures (MRPP) (Zimmerman *et al.*, 1985) in Blossom (Cade and Richards, 2001). I used individuals with $n_{obs} \geq$ 20 locations spanning consecutive years (n = 32 females; n = 5 males from 3 territorial coalitions, 1 territorial singleton and 1 singleton of unknown social status). I used only 1 male from each coalition since the movements of coalition members are not independent of one another, and I pooled the comparisons between years for each individual (for which multiple comparisons were possible) to prevent pseudoreplication (Hurlbert, 1984). I classified shifting behavior in individuals based on the proportion of yearly comparisons in which they shifted (had significantly different or clumped distributions in consecutive years). This classification is a simplification and obscures

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variation in shifting throughout an individual's lifetime. I arbitrarily set the delineation for the proportion of years in which shifts occurred as: shifters > 0.5; non-shifters < 0.5; and tied = 0.5. For most comparisons I did not have equal sample sizes (n_{obs}) in both years of the comparison. I used PROC LOGISTIC (SAS Institute, 2002) to analyze trends in shifting (0 = did not shift; 1 = shift) as a function of these sample size discrepancies, and to analyze shifting as a function of age.

Time to statistical independence and appropriate sampling interval

For a descriptive assessment of the displacement distances between observations, I plotted displacement as a function of sampling interval for n = 30 female cheetah for which I had $n_{obs} \geq 30$ (maximum sample size n_{obs} = 128) locations throughout their lifetime. For most individuals I had multiple displacement data for each weekly interval. I pooled these by individual, and report the mean displacement for the sample of 30 females. I estimated displacements as the Euclidean distance from every observation to every subsequent observation. I divided the difference between the day of the year for every observation by 7 and rounded to the nearest integer such that weekly interval data represented a range (i.e. a four-week interval represented a 25- to 31-day interval). To estimate the time to statistical independence (Swihart and Slade, 1985a), I calculated Schoener's Index (Schoener, 1981). Schoener's Index is t^2/r^2, the ratio of the mean squared distance between successive observations (t^2) to the mean squared distance from the center of activity (r^2). This index is approximately normally distributed with a mean of 2 (Swihart and Slade, 1997). Simply put, this is the amount of movement between observations relative to the average movement within a home range. I chose as the time to statistical independence of location estimates (TTI), the smallest sampling interval for which the ratio yielded a nonsignificant value (>2) and for which at least two more nonsignificant values followed (Swihart and Slade, 1985a). Thus, movements between observations that are far greater than an average displacement from the center of the home range, are considered independent (autocorrelation is low). I performed this test on the same 30 females (as in the displacement

analysis above) as well as a subset of 7 females that did not exhibit a shifting strategy for yearly ranges (determined from my assessment of year to year site fidelity, above). For each female I searched the dataset for all sets of observations that were 1 through 12 months apart. For each female in each month I used the mean t^2 and r^2 values to calculate Schoener's Index and I report the mean Schoener's Index for all the females. This allowed for an assessment of autocorrelation of location estimates throughout a year and an estimate of the TTI (the minimum sampling interval for which location estimates are independent).

Do cheetah home ranges tend towards an asymptote?

I tested for home range asymptotes in cheetah using 'area-observation plots' (Harris *et al.*, 1990; Otis and White, 1999). My data were irregular (collected at irregular intervals) and discontinuous and required that I randomize (Harris *et al.*, 1990) and resample (Hansteen *et al.*, 1997) location estimates. Adding location estimates randomly in the simulations allowed me to test the independent effect of sample size on home range asymptotes (Hansteen *et al.*, 1997). I estimated home range size for MCP and kernel estimators using Abode (Laver and Kelly, under review), and ran 20 simulations for each of 18 female cheetah with $n_{obs} \geq 50$ and 8 male cheetah with $n_{obs} \geq 20$. I determined whether 20 simulations were enough to provide an accurate and precise mean asymptote by assessing the stabilization of the cumulative mean and standard deviation of the home range estimates with increasing number of simulations.

I defined the home range asymptote for each individual as the point at which the mean home range (obtained from the simulations) was first and thereafter consistently within a specified limit of that individual's final kernel home range size (as calculated using all location estimates for an animal). These limits were arbitrarily chosen as within 5%, 10% and 15% of the final home range size. The mean home range size was defined both in terms of its accuracy and its precision such that the entire confidence interval (CI for $\alpha = 0.05$) for the mean had to fall within the accuracy limit. I assumed that the final home range was the asymptote. This is appropriate

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for many of the individuals in the study: their final home range was a functional maximum because they were observed from birth or early adulthood to senescence. Thus an asymptote would indicate the number of observations at which I can be 95% confident that I can estimate home range size to within 5, 10 or 15% of the final home range size.

The asymptote analysis assumes that home ranges do reach an asymptote (traditional home range model), so I tested for multiscaled home ranges (Gautestad and Mysterud, 1993; 1995) using 4 predictive models (adapted from Gautestad and Mysterud , 1993). Model fit was defined as the percentage of observations for which the predicted and observed home range sizes were not significantly different (at $\alpha = 0.05$). Gautestad and Mysterud (1993, p527) proposed a basic model,

$$HR(area) = C''n^{0.5} \qquad \text{eqn 1}$$

and a final model (eqn 5a, p528),

$$HR(area) = CQn^{H} \qquad \text{eqn 2}$$

n is the number of location estimates (n_{obs}), and H is described below. C'' is the 'grain size'

$$C'' = HR/(n^{0.5}) \qquad \text{eqn 3}$$

while C is the grain size corrected for low sample size (n_{obs}) (eqn 3, p527) for which

$$C(n) = C''\exp(6/(n^{0.7})) \qquad \text{eqn 4}$$

Q is the correction for low sample size relative to others in a set such that each is compared to the largest sample (N) (eqn 4, p528):

$$Q = C(n)/C(N) \qquad \text{eqn 5}$$

N is equal to the maximum sample size (n_{obs}) in a sample. I assessed the basic model (equations 1 and 3), the basic model with C (or small-n) correction (equations 1 and 4), the final model without small-n correction (equations 2, 3 and 5), and the final model which had both small-n and set (Q) correction (equations 2, 4 and 5). Using the best model (greatest model fit), I further tested for the traditional home range (H$_0$: $H = 0$) and for multiscaled home ranges (H$_A$: $H = 0.5$) using a log-linear regression of home range size on n_{obs} (Gautestad and Mysterud 1993,

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1995). *H* represents the slope of the regression. To simplify my analyses, I regressed only data for $n_{obs} \geq 50$, for which n-dependency of the relationship no longer holds (the correction term becomes negligible) (Gautestad and Mysterud, 1993). This occurs because the relationship between n_{obs} and home range size is hypothesized by Gautestad and Mysterud (1993) to be linear above $n_{obs} = 50$ and nonlinear below $n_{obs} = 50$ (unless a correction factor is applied). I also performed a log-linear regression on final home range size using MCP and kernel methods and sample size (n_{obs}). Unlike Gautestad and Mysterud (1993), but consistent with my best model (greatest model fit, see results below), I did not normalize for the largest sample size (N) (Q or set correction).

Areal extent of space use by cheetah

Having tested for the use of a 'home range' (site fidelity, above), for yearly shifts in area use (above), and for the traditional home range with a demarcatable area (above), I further estimated cheetah home range at three temporal scales. These periodic ranges correspond with lifetime home ranges, seasonal ranges, and yearly ranges. For lifetime ranges, I used all males and females for which kernel asymptotes were reached (n = 7 males; n = 18 females). Minimum sample sizes that I report from my asymptote analysis should not be used as cut-offs in *post hoc* analyses of home range where asymptote analyses have not been performed. Ultimately they should guide future data collection. Where possible, home range analysis should rely on individual assessment of asymptotic behavior at varying sample sizes. For periodic ranges at temporal scales less than a year (i.e. seasonal ranges), for which no asymptote analyses were available, I used Seaman *et al.*'s (1999) recommendation of a 30 location minimum. I assumed that 30 would be sufficient to encompass a representative sample of the movement behavior exhibited in that time period.

I estimated lifetime home range for females using 9 kernel estimators. I used least-squares cross validation (LSCV) with 3 standardization techniques: none (LSCVnone), unit

variance (LSCVunit), and x-variance (LSCVxvar). I also used the reference smoothing method (Href) and user defined smoothing (user) with the smoothing factor equal to the population mean daily displacement (Laver and Kelly, under review). I also used ABODE's 4 displacement smoothing methods, where the smoothing factor was calculated for each individual as the mean distance for the displacements at the mean, median and mode sampling intervals, or the mean daily displacement for each individual. For all other analyses I used the LSCVunit method. All analyses used a fixed biweight kernel (Seaman and Powell, 1996), with volume contouring and delineation at 95% of the volume of the utilization distribution. LSCV smoothing methods may be sensitive to discretization (rounding) of data (Seaman and Powell, 1996). My location estimates were recorded as grid intersections on a 500 m grid. I used ABODE's discretization correction in which identical coordinates were displaced by a random distance (from a uniform distribution), between 1 and 250m (a proxy for the maximum rounding error from using 500m grid cells). I estimated core range size following Horner and Powell (1990) and Powell (2000) in ABODE (Figure 2(a & b)). I separated analyses for territorial and floater males. Designation of male social status was by behavioral observation of scent marking (Caro, 1994). I report range analyses for cheetah from the Serengeti and other ecosystems from published literature. I make only qualitative comparisons of home range estimators because true home range size is not usually known for empirical studies (Seaman and Powell, 1996). I also make only qualitative comparisons with previous home range studies for cheetah because all prior analyses (excluding Marker *et al.*, under review) have used minimum convex polygon (MCP) techniques that are sensitive to sample size and are thus not strictly comparable with other MCP analyses or kernel methods. I estimate total area used by male and female cheetah of the Serengeti Plains using MCP and report the maximum area used – these estimates are given only for interest value, and should not be used for comparison because of the shortcomings of MCP techniques (above).

RESULTS

Do cheetah establish home ranges?

For the test of site fidelity within years, comparing MSD and LI of actual movements to the mean of 100 simulations of random walks, the mean and standard deviation for both MSD and LI were stable well below 100 iterations (e.g. Figure 3). A high proportion of yearly movements were more concentrated (Figure 4) and less linear (Figure 5) than expected from random movement (Table 1). Most males (89.5%) and females (72.9%) showed more concentrated yearly movements than random (Table 1). Similarly, a majority of males (57.9%) and females (72.9%) showed less linear yearly movement than random (Table 1). The results were qualitatively similar when only large samples sizes for each year ($n_{obs} \geq 30$) were used (Table 1).

Seasonal range shifts

Most females (40 of 48, 85%) and males (8 of 10, 80%) shifted range between the wet and dry seasons according to MRPP analyses (e.g. Figures 6 and 7). All territorial males (or male groups) (e.g. Figure 8) and both floater males showed statistically significant shifts (e.g. Figure 9). The two males that did not shift were of unknown social status.

Year to year site fidelity

For adult cheetah (>20 months in age), 17 of 32 females (53%) shifted between years, 10 (31%) showed site fidelity, and 5 (16%) were tied. Those females classified as shifters, shifted in most years (93% of years), while those that were classified as non-shifters shifted only infrequently (13% of years) (Figure 10). Of the males, only one territorial singleton shifted home

range between years. Yearly shifting behavior decreased as females aged (Likelihood Ratio $\chi^2_{0.05,1}$ = 5.0733; P = 0.0243) (Figure 11).

Time to statistical independence and appropriate sampling interval

Female cheetah are maximally displaced (from any given starting point) at 6 month intervals, at a mean (SE) distance of 24 (2) km, while at a 12 month interval, mean (SE) displacement is similar to that exhibited at three-week intervals (10 (1) km) (Figure 12). At intervals > 1 year, I observed the same pattern of maximum half-year displacement and yearly return (Figure 13). Location data for 30 females were independent at 3 month sampling intervals (Schoener's Index > 2), showing high autocorrelation again at 9 month intervals (Figure 14(a)). The pattern for all females, including those with shifting strategies was the same as the pattern for only those females without a shifting strategy (Figure 14(b)). Relative to other terrestrial mammalian species for which time to independence has been reported, cheetah require long intervals before observations become statistically independent (Figure 15).

Do cheetah home ranges tend towards an asymptote?

With n_{obs} = 50 location estimates, the mean and standard deviation of home range size stabilized within 20 simulations for 18 female cheetah (Figure 16) (each simulation was one home range estimate for a particular female, using randomly added location estimates from the set of her location estimates over her lifetime). The same stabilization occurred for n_{obs} = 10, 20, 30, and 40 location estimates (not shown). Similarly, using n_{obs} = 10 and 20, the mean and standard deviation for kernel and MCP estimates stabilized within 20 simulations for 4 territorial and 3 non-resident male cheetah (not shown).

Home range size as estimated using MCP did not tend toward an asymptote for any of 18 females or 9 males in the analysis (e.g. Figures 17, 18, 19). MCP home range size increased as

a function of increasing sample size (n_{obs}), and the function that best described this relationship was HR(area) = $Cn^{0.5}$ (C = HR(area)/($n^{0.5}$)) (e.g. Figures 17, 18, 19). As an overall assessment of the fit of the 4 models tested, the initial model (equations 1 and 3) was best, with a fit of 48 (7)% and 43 (7)% of the data for females and males respectively i.e. the predicted value from the model did not differ significantly from the mean for MCP simulations (at α = 0.05) at nearly half of all n_{obs}. For half of the females (assessed individually) this model performed best, with a mean (SE) fit of 74 (6)% (n = 9). A log-linear regression of female home range size (MCP, n = 18) and number of locations ($n_{obs} ≥ 50$) revealed a mean slope (*H*) of 0.41 (95% CI: 0.36 - 0.46).

The relationship for female cheetah home range size (MCP) and number of locations differed significantly (at α = 0.05) from the null hypothesis of no effect of sample size (n_{obs}), H_0: *H* = 0 and Gautestad and Mysterud's (1993) hypothesis of a multiscaled home range, H_A: *H* = 0.5. The observed relationship was close to that proposed by Gautestad and Mysterud (1993) however, and was similarly borne out by the log-linear regression of female home range size and number of locations for only the final home range area for 18 individuals (Figure 20). Sample sizes (n_{obs}) were too small to repeat this analysis for males.

Home range size as estimated using kernel density estimation did tend towards an asymptote for all females at the three accuracy levels (within 5%, 10%, and 15% of the asymptote) I used as my arbitrary asymptote limits (Figures 17, 18, 19). The number of locations required for females to reach these accuracy levels was normally distributed with a mean (SE) of 70(5), 55(4), and 39(3) locations for 5%, 10%, and 15% respectively. Male home ranges were considered asymptotic only for low levels of accuracy (within 10 and 15%). Male home range size was consistently within 10% and 15% of the asymptote with 24(1) and 22(2) locations respectively. Only three males showed accuracy within 5% of the asymptote, at 20, 22 and 30 locations. The log-linear relationship of home range size ($n_{obs} ≥ 50$) to number of locations for kernel estimation was significant (at α = 0.05) for 15 of the 18 females with a mean of *H* = 0.02 and a 95% confidence interval between –0.05 and 0.10. This does not differ significantly from the

null hypothesis, $H = 0$. The relationship using the final kernel female home range size as the regressor was not significant (Figure 20).

Areal extent of space use by cheetah

There was considerable variation in home range size using different estimators (Figure 21). Results from the four groups of smoothing operations differed greatly. Relative to the commonly used least squares cross validation method (LSCV), reference methods (Href) overestimated home range size, the user-defined method (user) underestimated home range size, and the displacement method was highly variable. The displacement method produced qualitatively similar results to LSCV smoothing when the mean displacement of the median interval was used as a smoothing factor (median). The minimum interval methods, in which the population mean daily displacement ("user") and the individual-specific mean daily displacement ("one day") were used, also produced qualitatively similar results. Using a biweight kernel, LSCV with unit variance standardization, volume contouring at 95%, and correction for discretization overlap, female lifetime home range size was 730 (64) km^2 (n = 18, $n_{obs} \geq 55$) with a core area of 225 (22) km^2 (n = 18, $n_{obs} \geq 55$). Core areas were delineated at between 40 and 81% of the volume of the probability density function (that is 40 to 81% volume contours), with a mean of 61 (3)%. Female yearly range size was 596 (88) km^2 (n = 10, $n_{obs} \geq 30$). Female wet season range was 497 (66) km^2 (n = 12, $n_{obs} \geq 30$) and dry season range was 358 (65) km^2 (n = 12, $n_{obs} \geq 30$). For the 6 females with at least 30 location estimates in both seasons, seasonal range did differ significantly (paired t-test, $t_{0.05,5} = 2.72$, $P = 0.0419$). One female ranged over 839 km^2 as a dependent juvenile ($n_{obs} \geq 30$). Four territorial or resident males had lifetime home ranges of 12 km^2 ($n_{obs} \geq 30$), 24 km^2 ($n_{obs} \geq 21$), 141 km^2 ($n_{obs} \geq 21$), and 155 km^2 ($n_{obs} \geq 21$), with cores of 3 km^2 (52% volume contour; $n_{obs} \geq 30$), 14 km^2 (81% volume contour; $n_{obs} \geq 21$), 36 km^2 (60% volume contour; $n_{obs} \geq 21$), and 70 km^2 (75% volume contour; $n_{obs} \geq 21$) respectively. Three non resident or floater males ranged over 168 km^2 ($n_{obs} \geq 30$), 30 km^2 ($n_{obs} \geq 24$), and 190 km^2 ($n_{obs} \geq 24$), with cores of 68 km^2 (71% probability contour; $n_{obs} \geq 30$), 10 km^2 (57% probability contour;

$n_{obs} \geq 24$), 53 km^2 (55% probability contour; $n_{obs} \geq 24$) respectively. I report these results with previous results from the Serengeti and results from Namibia, the Matusadona National Park, Zimbabwe, and the Kruger National Park, South Africa in Tables 2 and 3 and Figures 22 and 23. The maximum MCP lifetime areas for male and female cheetah were 904 km^2 ($n_{obs} = 20$) and 1 813 km^2 ($n_{obs} = 108$) respectively.

DISCUSSION

Do cheetah establish home ranges?

100 simulations is an adequate sample size for generating random walks for this study as evidenced by an asymptote of the mean and standard deviation for both MSD and LI. A high proportion of individuals showed concentrated and non-linear movement within years, which constitute two measures of site fidelity and hence of home range establishment. I conclude that cheetah of the Serengeti Plains do establish yearly home ranges. This is a previously untested theory for cheetah. The conclusion that male cheetah show site fidelity is consistent with the territorial defense strategy adopted by some males in the Serengeti (Caro, 1994). That females show site fidelity is interesting considering that their yearly home ranges have been estimated at 414 km^2 (Gros, *et al.*, 1996). Given their migratory prey base (Thomson's gazelle) and that they use extremely large home ranges (Durant *et al.*, 1988; Caro, 1994), two of the possible mechanisms for the apparent site fidelity shown within a year are: (1) that cheetah are either able to use long lasting site recognition cues over vast areas, or (2) that their site fidelity is an artifact of site fidelity shown by their prey base. Further work is required to test this concept for cheetah found in the Serengeti, as well as other ecosystems. Cheetah from Namibia are found predominantly on commercial livestock farms with a thornbush savanna subject to bush encroachment (Marker *et al.*, 2003) and in the Kruger National Park, South Africa they use woodland savanna. In neither ecosystem do they follow migratory prey, and would thus provide

an opportunity for comparison and for investigating the relationship between habitat quality and the establishment of home ranges in cheetah.

Seasonal range shifts

The high proportion of females that shift between the wet and dry season gives empirical support to the observations of Caro (1994) and Durant *et al.* (1988) that suggested that female cheetah move their range in relation to the migration of their main prey species, Thomson's gazelle. Though I found a statistically significant seasonal shift for territorial males, these movements are probably not biologically significant (only one male shifted between seasons, but still had a dry season location in close proximity to the wet season locations. The movements of territorial males between the seasons were small relative to the movements of females and floater males (compare Figures 7 – 9) and the placement of male territories is based on physical features of the landscape such as vegetation (providing cover while hunting) that are independent of seasonal effects (Caro, 1994).

These results do suggest that the movement behavior of cheetah of the Serengeti Plains is unique when compared to cheetah studied in other ecosystems, and suggest that seasonal resource distribution may be a major factor determining movement dynamics in this population. The Serengeti Plains is the only ecosystem where cheetah with a migratory prey base have been studied. Movement dynamics as inferred from home range size are even vastly different in the Kgalagadi Transfrontier Park (female HR = 320 km^2, male HR = 125 km^2) where cheetah prey upon nomadic springbok (*Antidorcas marsupialis*)(Broomhall *et al.*, under review). The findings of Durant *et al.* (1988) for prey movement, and my findings for cyclical movement behavior in females of this population are consistent with the conclusion that seasonal shifts are in fact displacements rather than simple expansions of area use. Further work is required for determining the prevalence and extent of seasonal shifts for cheetah in systems with migratory

and non-migratory prey species (e.g. Kgalagadi Transfrontier Park, and Kruger National Park or Namibian farmlands respectively).

Year to year site fidelity

Half of adult females shifted their yearly ranges in most of the years they were observed. Though my data suggest a dual strategy in yearly shifting behavior, it should be noted that my classification of individuals as shifters or non-shifters is coarse. Shifts may be the result of breeding dispersal (Greenwood, 1980) or may reflect the spatio-temporal heterogeneity of resources inherent in this ecosystem (Sinclair, 1979). Shifts in home range may reflect avoidance based on social hierarchy among females in the population. My finding that females shift less as they age, suggests that they become more 'established' in their ranges over time, and that shifting is a strategy used more by younger and inexperienced females. This pattern may be explained if females shift their home range after losing a litter – as females age they may become better at concealing cubs or avoiding lion and hyena, with attendant increases in litter success. One should condition one's interpretation of lifetime ranges of cheetah of the Serengeti Plains based on the apparent prevalence of yearly shifts by females. Lifetime ranges for individuals that shift between years will be larger than if those individuals had not shifted. Interpolation to yearly range size from such lifetime ranges would be subject to positive bias (overestimates of yearly range) if the shifts were not accounted for. Conversely, shifting is a strategy that is used in this population, and conservation and management activities requiring knowledge of area use should be cognizant of increased area requirements because of shifting behavior.

Yearly range shifts should be distinguished from dispersal. I investigate philopatry and dispersal in chapter 3. Dispersal relates to a shift in location between two life stages, typically between juvenile and adult ranging areas. Yearly shifts occur at a finer temporal scale, between two years, and in my analyses I only used years for which the individual was an adult. I used field

observation of family groups to determine stage class rather than age in months – that is, individuals with their mothers were juveniles, those in mixed sex sib groups were adolescents, and those that were solitary (females) or in single sex (males) groups were adults.

Time to statistical independence and appropriate sampling interval

It is well established from empirical studies that cheetah of the Serengeti Plains rely heavily on the migratory herds of Thomson gazelle (Caro, 1994; Fitzgibbon, 1990), and it has been hypothesized from correlational studies that female cheetah are associated spatially with these gazelle (Durant, 1998; Durant *et al.*, 1988). However, the migratory nature of their movement behavior has yet to be explicitly tested. The pattern of displacement I observed suggests a cyclical or migratory strategy (as defined by Seton, 1909, Thomson, 1926 and Sinclair, 1983, but see Dingle, 1996). The maximum displacement occurs at 6 months, an interval that is coincident with seasonal variation in resources in this ecosystem (wet season to dry season). The yearly return to within 10 km suggests that these movements are temporally predictable. These patterns are perpetuated for up to ten years, even though the oscillations increase in both amplitude and the size of the associated confidence interval. To be able to predict a female cheetah's location to within 10 km, even 9 years into the future suggests that there is a strong dependence on locally distributed resources throughout the year. The increase in amplitude of the displacements may be explained by shifts between years that cumulatively result in greater displacements from an individual's starting location at t_0. The increase in the confidence interval is probably due to both the increase in the displacement and the reduction in the sample size in later years of the analysis – that is, fewer individuals are contributing to the mean displacement at 9 years than at t_0, because most individuals do not survive that long.

These qualitative results are also reflected in the test for statistical independence. A female cheetah's current location is dependent upon its location 9 months to a year prior. While this exercise provided evidence for cyclical movement behavior, its utilitarian function was to

guide sampling protocol. When given the choice between few or many location estimates, more estimates will always provide more information, but independent data points given the same sample size will provide the most information. My findings suggest that where research resources are limited, the sampling interval should be set to 3 months to maximize the amount of information obtained from location estimates. This is especially true for the aerial radio telemetry data in this study, which were collected at monthly intervals. Cheetah are extreme both in the extent of area they use, and in the rate at which they use this space, as reflected by their lengthy time to statistical independence between location estimates (this study). Future research should focus on understanding the relationship between habitat quality, size dependency of TTI and home range size (Swihart and Slade, 1988). It should also be noted that this analysis focused on lifetime home range, and different values for the time to independence may be obtained depending on the temporal scale of the analysis.

Do cheetah home ranges tend towards an asymptote?

Though Harris *et al.* (1990) suggested the use of randomly added location estimates for irregular and discontinuous data, they did not mention resampling (Hansteen *et al.,* 1997) as a means for dealing with the stochasticity inherent in the method. Given that these estimates are stochastic, my estimates of the mean home range size for each individual from 20 randomly sampled asymptote analyses were reliable, as indicated by the stabilization of the mean and standard deviation as number of simulations increased. This was true for various sample sizes (n_{obs}) for females and both territorial and floater males. This pattern may not be true for other cheetah populations or for other taxa and 20 simulations should not be used indiscriminately in similar analyses. Hansteen *et al.* (1997) used 60 simulations and looked for stabilization in datasets with n_{obs} = 10, 30, 50, 70, and 100, but did not suggest a minimum for the number of simulations required.

Though it is widely held that home ranges tend toward an asymptote given a sufficient sampling period (n_{obs}) (Harris *et al.,* 1990; Hansteen *et al.*, 1997; and Otis and White, 1999) and provided that the individuals are not transient or dispersing (Harris *et al.*, 1990), Gautestad and Mysterud (1995) found that most reported asymptotes were in fact parabolic in nature and tended to increase as a function of the square root of n_{obs} (Gautestad and Mysterud, 1993). My results, both in the form of model fit and log-linear regression of $n_{obs} \geq 50$ home range size, provide corroborative evidence for the multiscaled home range hypothesis proposed by Gautestad and Mysterud (1993), with one stipulation – that home range be calculated using MCP. In cheetah of the Serengeti Plains, MCP home range size does increase with increasing n_{obs} and at a rate roughly resembling the power law. However, this was not true for kernel density estimation which showed clear asymptotes for females and males, though my sample sizes (n and n_{obs}) for the males were admittedly low. For reliable estimation of female lifetime home ranges it is thus important to collect more than the 30 locations suggested by Seaman *et al.* (1999). It should be stressed that Seaman *et al.*'s (1999) value of 30 to 50 provides only the minimum for reduced bias and variance of the kernel estimator, and suggests nothing about the behavior of the study species which may affect when home range size stabilizes. In addition, asymptote analyses are only valid for the sampling period in question – lifetime home range in my case. Analyses for periodic ranges such as yearly or seasonal asymptotes may yield different results. I recommend that in the absence of such analyses, 30 locations be used as a minimum, as proposed by Seaman *et al.* (1999). Further, where asymptote analyses suggest a lower sample size requirement than that recommended for the estimator, the larger of the two requirements should be used – that is for the male cheetah in our study, at least 30 locations should be used for kernel estimation even though asymptotes were reached using a lower number of observations. My definition of the asymptote was arbitrary, but I feel that it provides a more objective approach than common 'eyeballing' techniques, and introduces the use of confidence levels to moderate the interpretation of minimum sample size requirements. Thus, a researcher interested in fine-scaled habitat analyses may need to estimate home range to within 5% of the final size, while basic monitoring of a population may only require accuracy to within 10 or 15%.

Female cheetah of the Serengeti Plains are cyclical in their movement and are thus subject to Gautestad and Mysterud's (1993) second constraint, the 'string stretching threshold.' This hypothesis suggests that an asymptote might be evident because a migratory individual is bound to a resource and is functionally limited by its periodic return to that resource. I did not see this expected asymptote in MCP home range size for females. I hypothesize that the lack of asymptote in home range size will often be an artifact of the home range estimation tool. MCP is by its very nature sensitive to outliers (Seaman *et al.*, 1999). As n_{obs} increases, the number of outliers will increase and thus the MCP will increase. MCP does not model home range according to Burt's (1943) definition. Unlike kernel density estimation, which objectively treats outliers (or 'occasional sallies') and thus models a home range, MCP defines the total area visited. The multiscaled home range may be true for total area visited by an animal as manifested in MCP estimates, but it needs to be tested rigorously across taxa using kernel density estimation. I think that this has not been done because asymptote analyses are time consuming, especially for kernel estimation for which software was until recently not available for this type of automated analysis (Laver and Kelly, under review). The kernel asymptotes observed in this population could be a result of cyclical movement behavior, but because both territorial males, and females exhibited these asymptotes, I conclude that cheetah of the Serengeti Plains do not have multiscaled home ranges. I propose that MCP methods are not suitable for traditional home range asymptote analyses, and that kernel methods be employed instead.

Areal extent of space use by cheetah

Home range estimates produced using LSCV with different standardization techniques were similar as was found by Laver and Kelly (under review). Using LSCV as a standard for comparison (Seaman and Powell, 1996) (absolute truth for home range is unknown) I found that the reference smoothing method greatly overestimated home range size. This result is similar to the findings of others (Worton, 1995; Seaman and Powell, 1996; Seaman *et al.*, 1999), where

Href was used for data that were not from a bivariate normal distribution. Where possible, a user-defined and subjectively chosen smoothing factor (Worton, 1989) may be a better alternative to automated methods for smoothing. My attempt at defining a biologically relevant smoothing factor based on the daily displacement (either as a population mean or individually calculated value) provided gross underestimation relative to LSCV methods. If a biologically significant unit of measurement is available, I feel that it should be used. My results indicate that the population mean for the daily displacement of female cheetah was not a suitable metric to use for smoothing. This suggests that a population parameter of daily displacement is either a poor metric for describing lifetime area use, or simply that a daily interval is not representative of the intervals used for collecting these data. Estimating daily displacement for each female individually produced qualitatively similar results to those for the population estimate and suggests that for purposes of simplification population estimates for smoothing factors may produce results equivalent to those estimated for each individual in turn. More work is needed to test this estimator on cheetah with different types of datasets and on different species. I suspect that the daily displacement will perform better with datasets that have a regular sampling interval (i.e. if the location estimates were collected on a daily basis). The estimates from the daily displacement method were similar to the estimates for core ranges. For these data, the daily displacement may be a useful metric for determining areas of concentrated use. The other displacement methods provided mixed results. Both the mean and mode interval displacements resulted in overestimation of home range size. I think that this was a function of the irregularity of sampling intervals for the dataset. Intervals were not normally distributed, and the mean interval would thus be a poor representative of the sampling. Likewise, with irregular data, the mode estimates may have been based on only a very small sample of identical or similar displacements. I am not confident that these estimates could be used with other datasets that consist of largely opportunistic data but I do think that these methods may be suitable for data that were collected on a regular sampling interval.

With non-normal data the median is often a better measure of central tendency (Zar, 1999). As would be expected from the distribution of sampling intervals in my data, the median interval displacement method produced results that were most similar to LSCV methods. This method holds potential for developing biologically- and data-driven smoothing factors for kernel estimation. This would be especially useful in situations where LSCV methods would be inappropriate such as may be the case for discretized data from location estimates on a trapping grid (e.g. small mammal grid or camera grid) (Silverman, 1986; Chiu, 1991; Seaman and Powell, 1996; and Kernohan *et al.*, 2001).

My estimates of female lifetime home range size were similar to those of Frame (1984) and Caro (1994) for the Serengeti Plains. The vast difference between Serengeti females and those from other ecosystems was highlighted by Caro (1994) who cited resource (prey) patchiness as the cause, and by Broomhall *et al.* (2003) who cited the migratory movements of the main prey species in the Serengeti as the cause. Yet, cheetah on Namibian farmlands, where prey are not migratory, have home ranges even larger than those exhibited in the Serengeti (Marker *et al*, under review). I hypothesize that cheetah of the desert population in Iran may have the largest home range sizes because of the low biomass of prey and thus the need to range extensively to meet energy requirements. A multiple ecosystem comparison is needed to determine the factors that affect home range size in this species.

Female core ranges from my study (235(24) km^2) were similar in size to the lifetime home ranges reported from the Matusadona National Park (236 and 23.6 km^2) and the Kruger National Park (150 km^2). Though the percent probability contours for these core areas were normally distributed, I do not recommend using a population mean delineation indiscriminately. A single value does not reflect the variation among individuals in a population. In my study, core delineation ranged between 40 and 81% (of the volume of the utilization distribution). The probability level at which the concept of a core ends and the concept of a home range begins has not been investigated. For example, can 81% of a utilization distribution be a core? At what point

(contour interval) does the interpretation of core become confounded with traditional 95% delineation for overall home range? I suggest that core areas delineated at high probability levels be considered actual home ranges - they have statistical (if not biological) justification, rather than an arbitrary limit. In fact the statistical definition of a core range as proposed by Horner and Powell (1990) closely matches Seton's (1909) description of a home range. Defining the cline between core and total range needs more investigation, as does determining what effect this type of classification will have on home range comparisons. Ultimately, statistical designation of core areas will always fall short of a biologically grounded concept of clumped use based on behavioral observation and hypotheses about biological attraction or focal points (Lair, 1987).

The mean (SE) yearly range size estimated from this study (596 (88) km^2) was considerably larger than that estimated by Gros *et al.* (1996) (414 km^2). The large yearly ranges suggest that female cheetah cover much of their lifetime home range in any given year. Seasonal ranges were smaller than both the yearly ranges and the lifetime ranges. At a minimum I would recommend a sampling period of one year of a cheetah's adult life for generating estimates of home range size. This time period would allow an individual to describe (or complete) its yearly movement pattern, thus incorporating both the wet and dry season ranges, but it would probably underestimate lifetime home range because any yearly shifts or juvenile dispersal events would not be sampled.

The comparison of seasonal ranges yields more insight into factors that drive home range size. Caro (1994) suggested that expanded female home range size in the Serengeti was a function of the patchiness of prey resources. One would expect that during the wet season, range size should be smaller because of improved resource availability, a result found to be true for Namibian cheetah (Marker *et al*, under review). Instead I found this not to be true. Dry season ranges are located in the north-west of the Serengeti Plains where Thomson's gazelle congregate around the semi-permanent water sources of the Seronera and Mbalageti Rivers (Durant *et al.*, 1988). During the wet season however, prey herds follow the spatially- and

temporally-heterogeneous rainfall pattern (Durant *et al.*, 1988) i.e., they have a patchy distribution and thus following Caro's (1994) interpretation, have a larger seasonal range (wet season range). Resource distribution in this system follows a counter-intuitive pattern, whereby resource paucity may result in aggregation and resource abundance may result in increased spacing and patchiness.

Estimates for male home range and core size were similar among the studies from the three ecosystems. Meaningful comparison is not possible with such low sample sizes, but the discrepancy between male and female home range size in the Serengeti is clear – the anomaly that this represents relative to most other mammalian taxa is discussed by Caro (1994). My results for the home range size of floater males (range: 12 to 155 km^2) do not match those of Caro (mean (SE): 777.2 (153) km^2,1994). For the three floater males for which I had a reasonable sample size ($n_{obs} \geq 20$) and for which kernel asymptotes were evident, outliers in the three datasets greatly exaggerated MCP home ranges relative to the kernel estimates. I feel that Caro's (1994) estimate more adequately depicts the total area used by non-resident or floater individuals but that these areas are not analogous to home ranges. As with the females from this population, core areas for males were delineated across a wide range of probability contours, from 52 to 81% of the volume of the utilization distribution.

CONCLUSION

Though female cheetah of the Serengeti Plains have a cyclical pattern of displacement with autocorrelation in location estimates at < 3 and > 9 month intervals, they exhibit site fidelity and have home ranges and do not exhibit specialized behavior specific to migration. They have more concentrated and less linear movements within a year than would be expected from random. All males and females also exhibit core ranges. Cheetah of the Serengeti Plains are thus not migratory even though they have circannual movements and seasonal range shifts. Depending on the required level of precision, researchers may need more location estimates than

the minimum of 30 suggested for kernel density estimation. Cheetah do not exhibit multiscaled home ranges with kernel density estimation and evidence for multiscaled home ranges may be an artifact of methods used for estimating home range size (i.e. MCP). Biologically- and data-driven smoothing methods for kernel analysis may produce qualitatively similar results to LSCV techniques. Female cheetah of the Serengeti Plains have extremely large lifetime home ranges relative both to males (territorial and floater) of the same ecosystem and males and females of other ecosystems (except in Namibia). Differences in seasonal range size support the hypothesis that range size at a local scale is determined by patchiness of resources. Though home range analyses provide useful information for guiding the management and conservation of a population, cheetah home range size is site specific and further research is required for developing species specific metrics that adequately describe their use of space and resources.

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FIGURE AND TABLES

Table 1. Percentage of individuals exhibiting site fidelity within years for male (floater and territorial males combined) and female cheetah of the Serengeti Plains 1980 - 1994.

Actual movement relative to random	overall		n/year>30		males		females	
	%	n	%	n	%	n	%	n
More Concentrated	77.8	63	76.9	13	89.5	19	72.9	44
Less Linear	68.3	63	69.2	13	57.9	19	72.9	44

Table 2. Female lifetime and periodic (seasonal, yearly) ranges (km^2) as reported in the literature. I present a novel approach to reporting home range size:

% VOLUME CONTOUR MEAN(SE) # OF INDIVIDUALS, MINIMUM # OF OBSERVATIONS

(% Volume contour may be blank, designating MCP methods, or a range, designating an objectively derived contour; (.) indicates SE not reported or not applicable)

Reference	Place	Lifetime	Core	Yearly	Wet	Dry
		Adult Female				
Laver, this study	Serengeti NP	[95]730(64)[18,55]	[40-81]225(22)[18,55]	[95]596(88)[10,30]	[95]497(66)[12,30]	[95]358(65)[12,30]
Caro, 1994	Serengeti NP	833.0(85.1)[19,20]	-	-	-	-
Caro, 1994	Serengeti NP	394.5(.)[1,20]-1269.5(.)[1,20]				
Frame, 1984	Serengeti NP	800(.)[?,?]	-	-	-	-
Gros *et al*., 1996	Serengeti NP	-	-	414(.)[11,10]	-	-
Marker *et al*., under review	Namibia	[95]2160.7(802.4)[8,30]	[50]397.8(204.4)[8,30]	[95]1226.5(145.8)[18,?]	[95]1405.1(326.5)[10,10]	[95]2158.5(893.5)[7,15]
Zank, 1995	Matusadona NP	236(.)[1,64]	-	-	-	-
Purchase & du Toit, 2000	Matusadona NP	23.6(.)[1,25]	-	-	-	-
Broomhall *et al*., 2003	Kruger NP	192(.)[1,70]	36(.)[1,70]	-	-	-
Broomhall *et al*., 2003	Kruger NP	179(.)[1,25]	35.7(.)[1,25]			
Mills, 1998 KTP *	Kgalagadi TP	320(.)[?,?]	-	-	-	-
		Juvenile Female				
Laver, this study	Serengeti NP	[95]839(.)[1,30]	-	-	-	-

* Mills (1998) as cited in Marker *et al*., (under review)

Table 3. Male lifetime and periodic (seasonal, yearly) ranges (km^2) as reported in the literature. I present a novel approach to reporting home range size:

$$\text{\% VOLUME CONTOUR } \textbf{MEAN(SE)} \text{ \# OF INDIVIDUALS, MINIMUM \# OF OBSERVATIONS}$$

(% Volume contour may be blank, designating MCP methods, or a range, designating an objectively derived contour; (.) indicates SE not reported or not applicable)

Reference	Place	Lifetime	Core	Yearly	Wet	Dry
Territorial Males						
Laver, this study	**Serengeti NP**	$_{95}12(.)_{1,30}$	$_{52}3(.)_{1,30}$	-	-	-
Laver, this study	**Serengeti NP**	$_{95}24(.)_{1,21}$	$_{81}14(.)_{1,21}$	-	-	-
Laver, this study	**Serengeti NP**	$_{95}141(.)_{1,21}$	$_{60}36(.)_{1,21}$	-	-	-
Laver, this study	**Serengeti NP**	$_{95}155(.)_{1,21}$	$_{75}70(.)_{1,21}$	-	-	-
Caro, 1994	**Serengeti NP**	$37.4(5.2)_{22,5}$	-	-	-	-
Floater Males						
Laver, this study	**Serengeti NP**	$_{95}168(.)_{1,30}$	$_{71}68(.)_{1,30}$	-	-	-
Laver, this study	**Serengeti NP**	$_{95}30(.)_{1,24}$	$_{57}10(.)_{1,24}$	-	-	-
Laver, this study	**Serengeti NP**	$_{95}190(.)_{1,24}$	$_{55}53(.)_{1,24}$	-	-	-
Caro, 1994	**Serengeti NP**	$777.2(153)_{9,10}$				
Caro, 1994	**Serengeti NP**	$? - 1892.6(.)_{1,10}$				
Coalition Males						
Marker *et al*., under review	Namibia	$_{95}1463.8(529.4)_{7,30}$	$_{50}231.4(111.7)_{7,30}$	$_{95}630.1(134.0)_{8,?}$	$_{95}1013.2(322.3)_{7,10}$	$_{95}1154.2(211.3)_{5,15}$
Mills, 1998 KTP *	**Kgalagadi TP**	$125(.)_{?,?}$	-	-	-	-
Singleton Males						
Marker *et al*., under review	Namibia	$_{95}1390.5(334.6)_{13,30}$	$_{50}205.1(65.2)_{13,30}$	$_{95}1083(302.8)_{13,?}$	$_{95}1136.5(254.3)_{13,10}$	$_{95}1901.4(471.8)_{13,15}$
Zank, 1995	**Matusadona NP**	$114(.)_{1,40}$	-	-	-	-
Zank, 1995	**Matusadona NP**	$157(.)_{1,44}$				
Purchase & du Toit, 2000	**Matusadona NP**	$53.8(.)_{1,32}$	-	-	-	-
Purchase & du Toit, 2000	**Matusadona NP**	$11.3(.)_{1,21}$				
Broomhall *et al*., 2003	**Kruger NP**	$170(.)_{1,177}$	$14.1(.)_{1,177}$	-	-	-
Broomhall *et al*., 2003	**Kruger NP**	$261(.)_{1,27}$	$21.5(.)_{1,27}$			

* Mills (1998) as cited in Marker *et al*., (under review)

$$MSD = \frac{\Sigma\ (\rightarrow)^2}{n_{obs}}$$

$$LI = \frac{\text{--} \rightarrow}{\Sigma\ \longrightarrow}$$
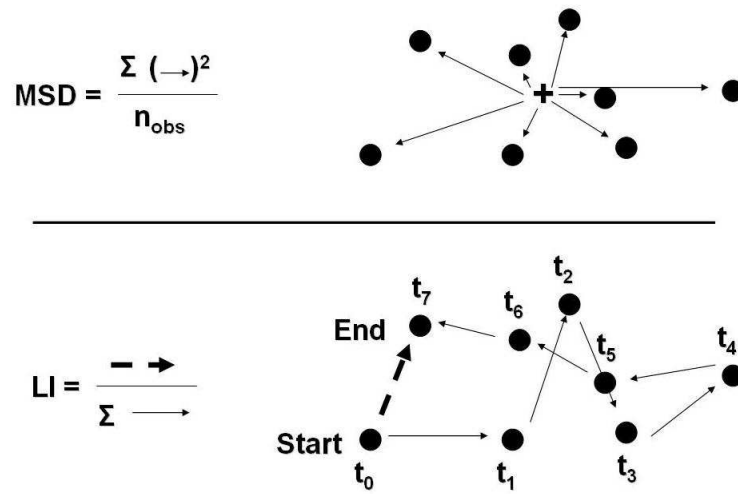
Figure 1. Mean squared distance (MSD) and linearity index (LI) are two measures of site fidelity. MSD is the mean squared distance to the arithmetic center of a distribution (denoted by "+"). LI is the ratio of the start to end distance to the sum of the consecutive distances between locations taken in order from the start (e.g. t_0) to the end (e.g. t_7) of a movement path.
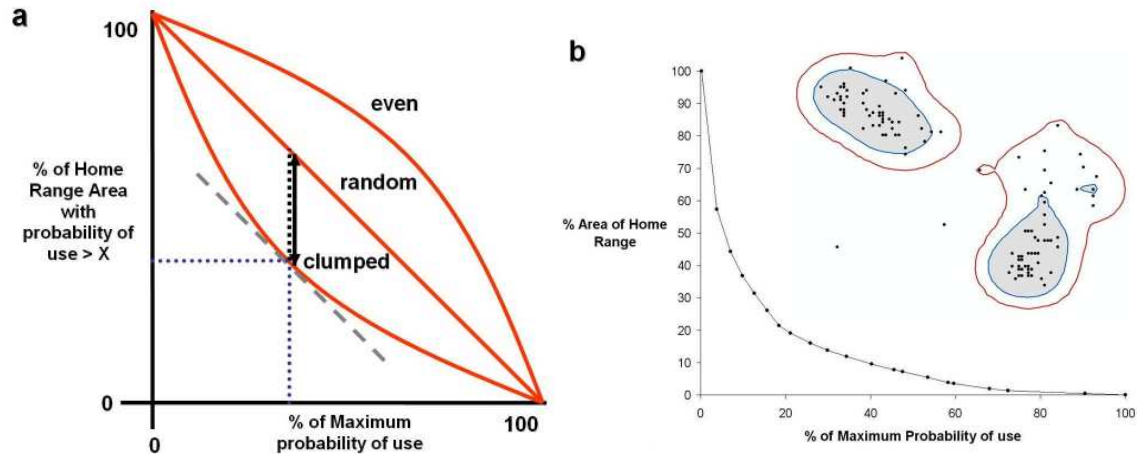
Figure 2. a) Methodology for delineating core ranges following Horner and Powell (1990) (figure adapted from Powell, 2000 and Laver, 2005). Core areas (concave line) are delineated where the probability density is greater than expected from random (straight line) or even (convex line) distributions. b) An example of the delineation of a core for a female cheetah of the Serengeti Plains. The home range outline is the 95% volume contour. The core area (shaded) is delineated at 70% of the volume contour for this individual.
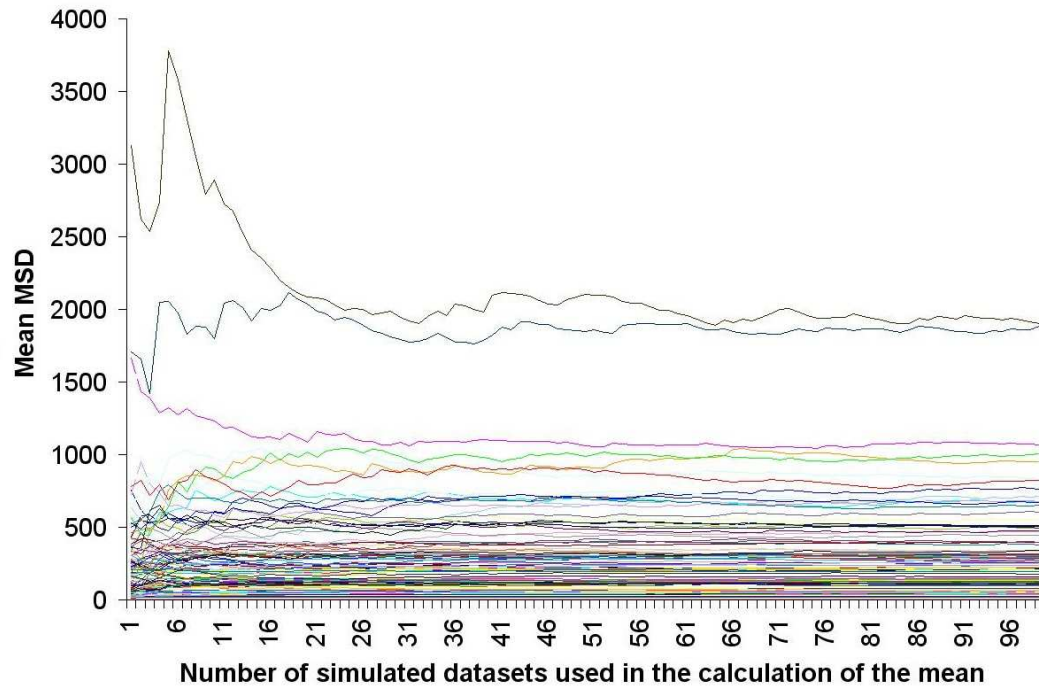
Figure 3. Mean of the mean squared distance (MSD) of simulated datasets calculated iteratively for 2 to 100 datasets, for each combination of individual*year (represented by one line). The mean reaches an asymptote well before the 100th simulated dataset.
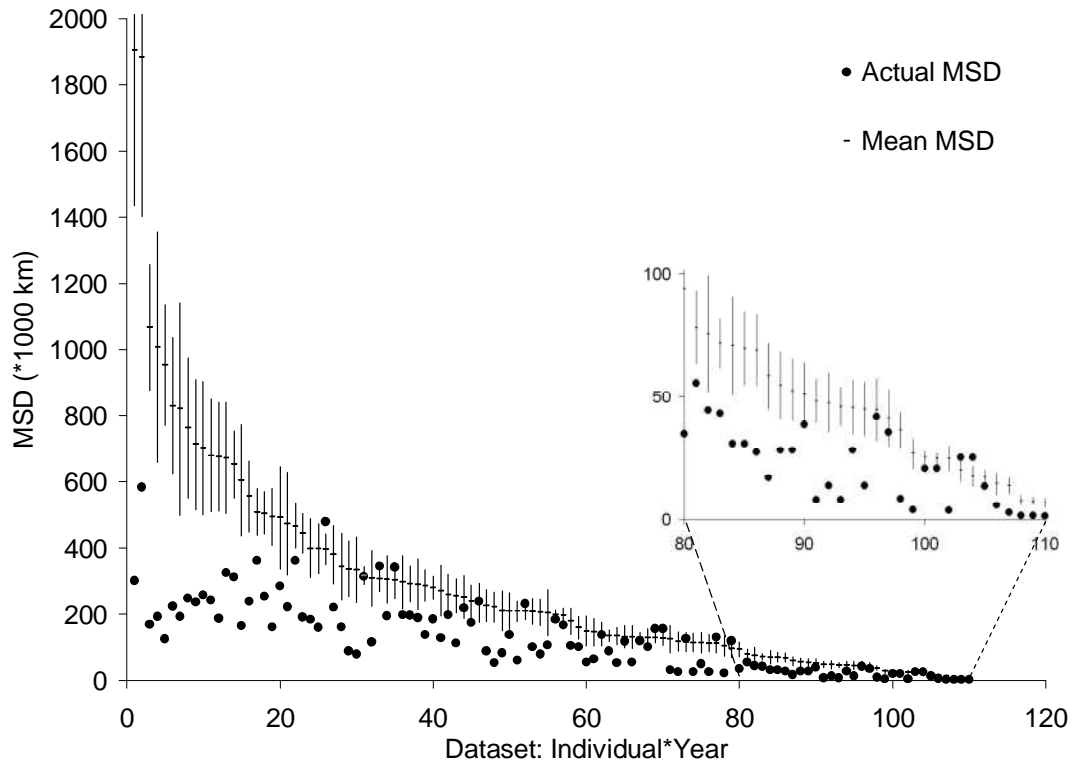
Figure 4. Comparison of actual mean squared distances from center of activity (MSD) to the mean and 95% confidence interval of 100 simulated random walks per combination of individual*year (63 individuals with some individuals analyzed in more than one year – 110 analyses in total). Each dataset has at least 10 locations per year. Data are in decreasing order of the mean MSD. Where actual MSD values fall below and outside the mean and 95% confidence interval for the 100 simulations, individuals show more concentrated area use than would be expected from random movement within a year.
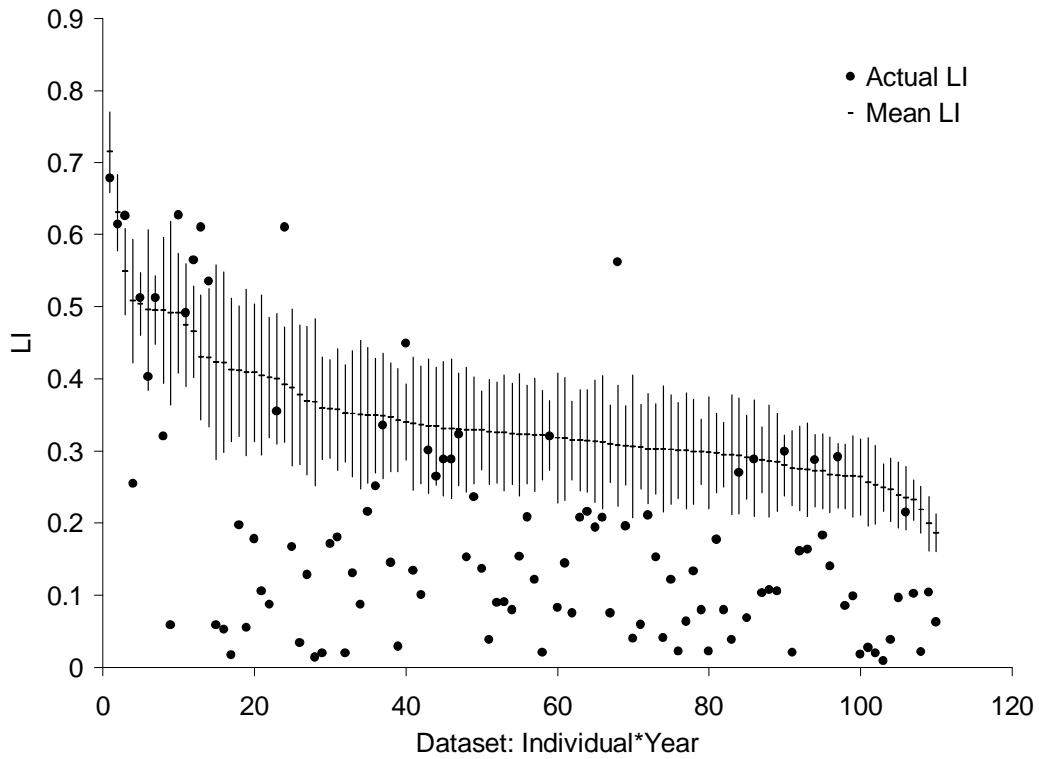
Figure 5. Comparison of actual linearity index (LI) to the mean and 95% confidence interval of 100 simulated random walks per combination of individual*year (63 individuals with some individuals analyzed in more than one year – 110 analyses in total). Each dataset has at least 10 locations per year. Data are in decreasing order of the mean LI. Where actual LI values fall below and outside the mean and 95% confidence interval for the 100 simulations, individuals show less linear movement than would be expected from random movement within a year.
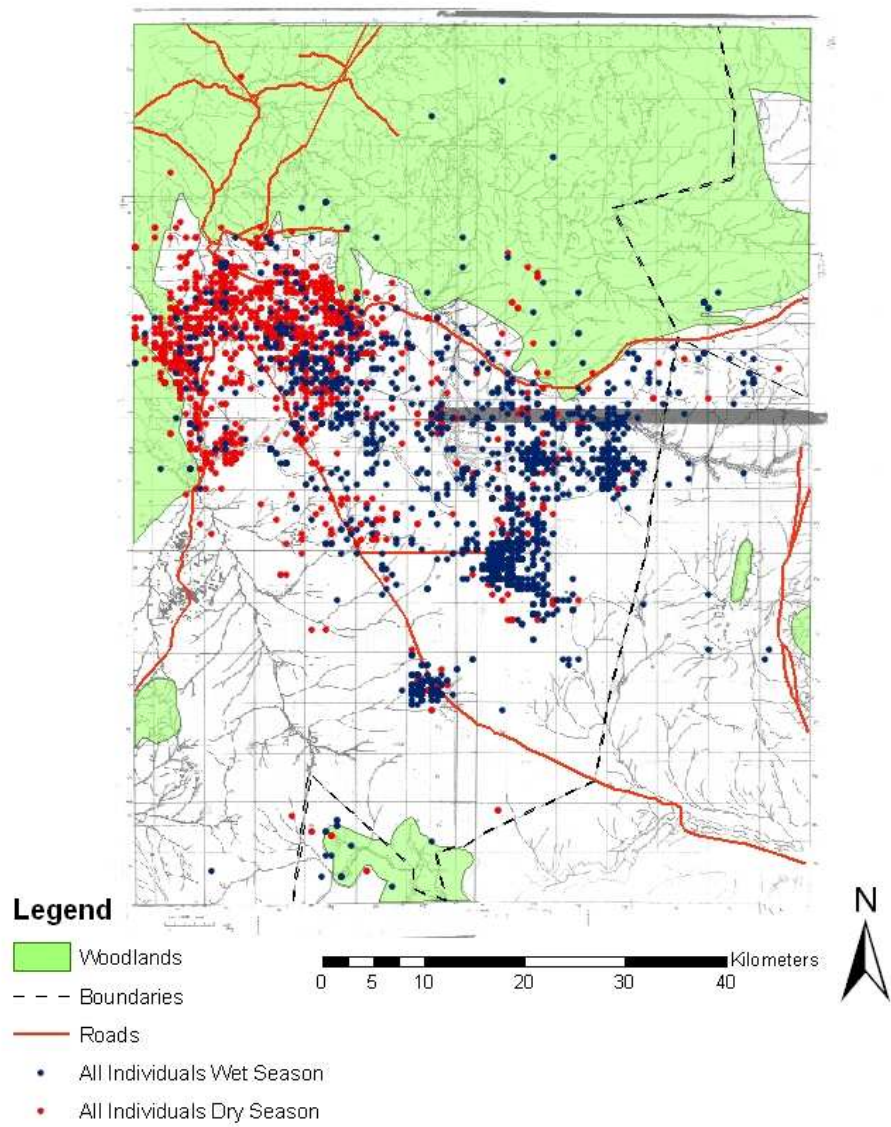
Figure 6. Wet (blue) and dry (red) season location estimates for all individuals in the Serengeti Plains cheetah population (1980 – 1994).
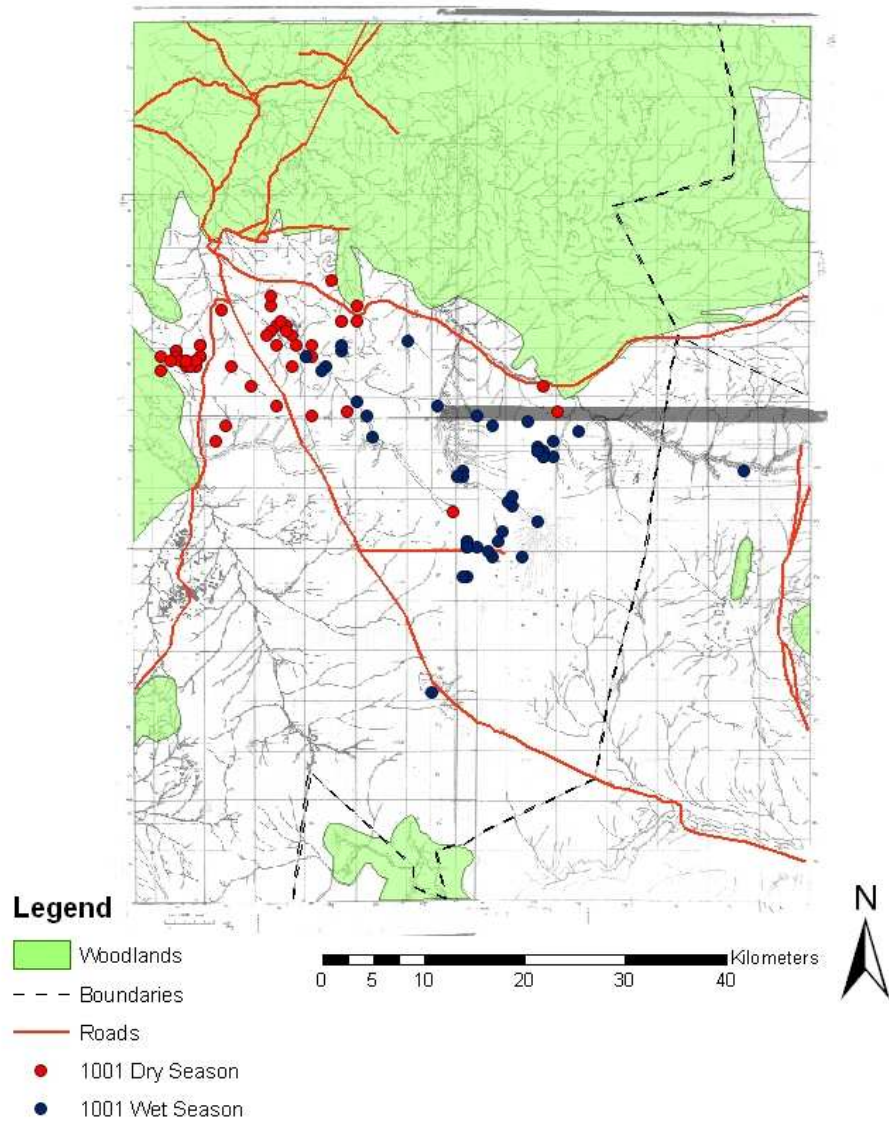
Figure 7.   Representative example of seasonal shift of location distribution in female cheetah.
Female 1001 is shown with 43 wet season (blue) and 50 dry season (red) location estimates.
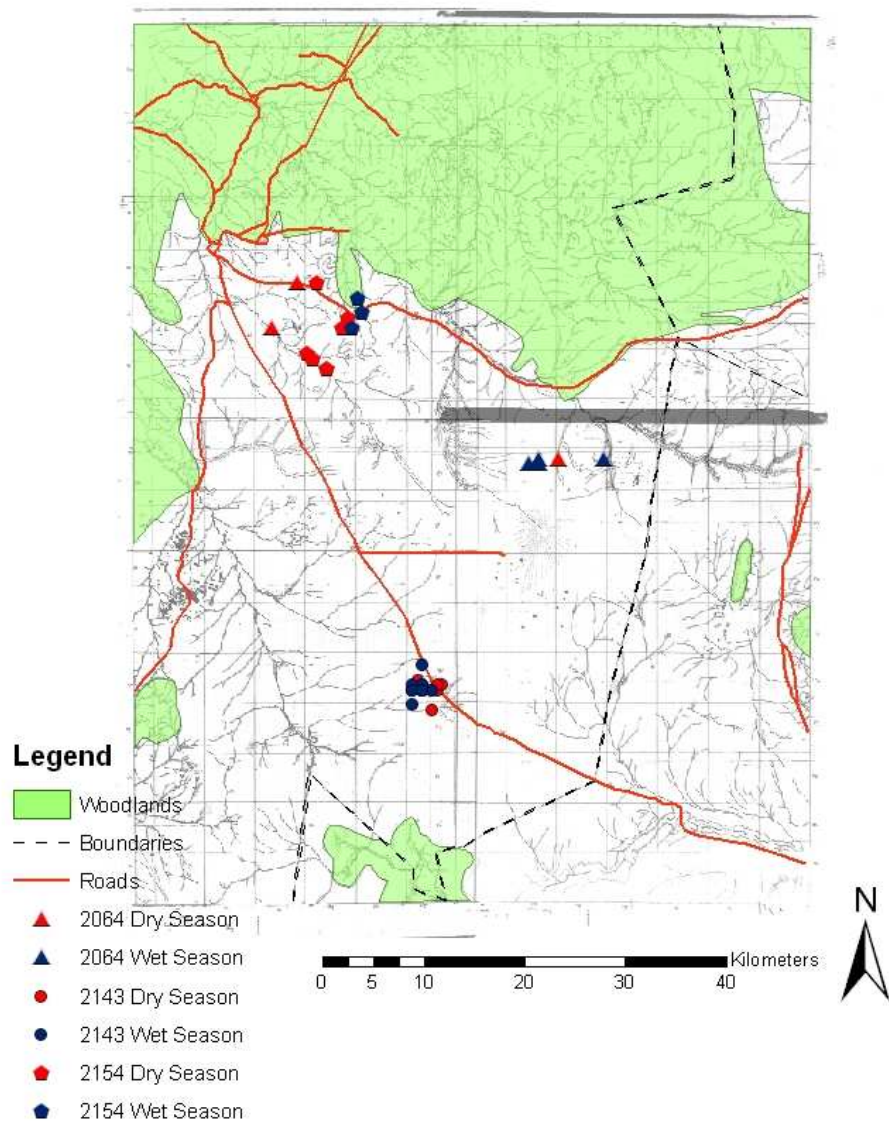
Figure 8. Seasonal shift of territorial male cheetah. 2064 is shown with 5 wet and 3 dry season locations. 2143 represents a two-male coalition, shown with 12 wet and 8 dry season locations. 2154 represents a two-male coalition, shown with 3 wet and 8 dry season locations.
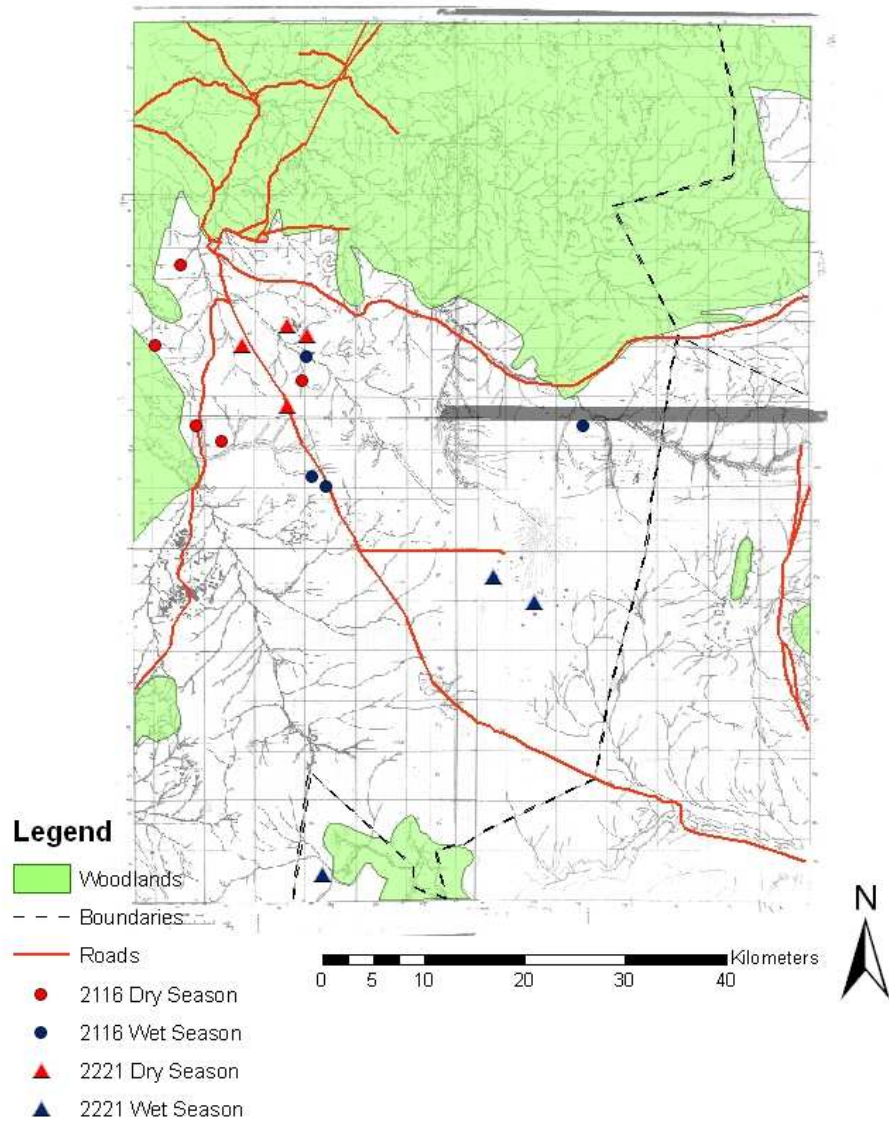
Figure 9. Representative example of seasonal shift of location distribution in non-territorial or floater male cheetah. 2116 is shown with 4 wet season (blue) and 5 dry season (red) location estimates. 2221 is shown with 3 wet season (blue) and 4 dry season (red) location estimates.
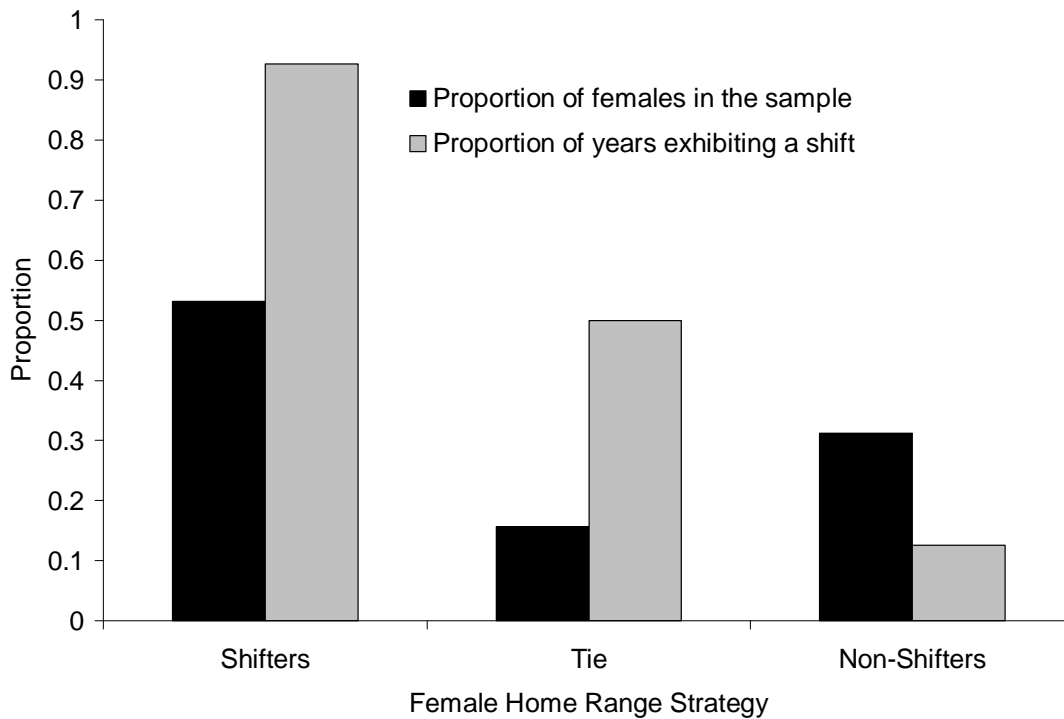
Figure 10. Home range site fidelity strategies for female cheetah of the Serengeti Plains 1980-1994. Dark bars show the proportion of the population that shift yearly ranges at least 50% of the time ("Shifters"), that shift less than half the time ("Non-Shifters") and that show no clear trend ("Tie"). Gray bars show for each strategy, the proportion of years in which shifts occur. These data are for adult females only and for yearly comparisons with at least 20 locations spanning 2 consecutive years.
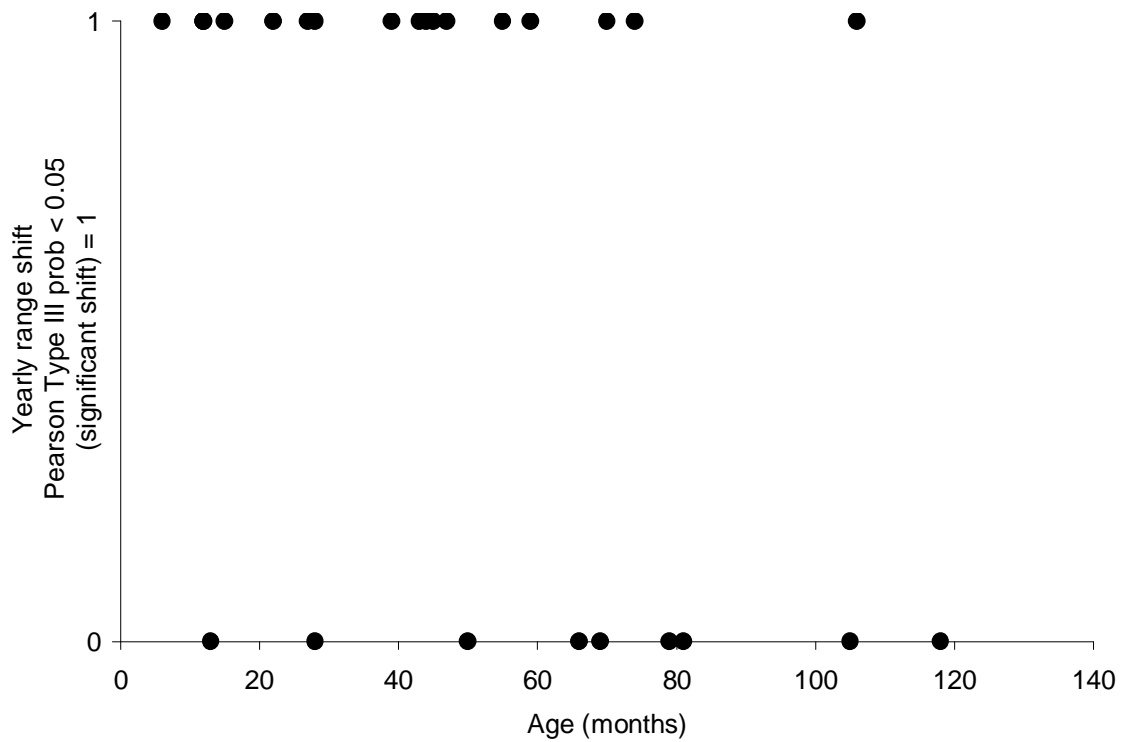
Figure 11. Yearly home range shifts at various ages for female cheetah of the Serengeti Plains (no shift = 0; shift = 1). Females shift home range less from year to year, as they age. 27 yearly comparisons were made from data for 14 females where all comparisons consisted of at least 20 locations. Likelihood ratio χ^2_1= 5.0733, p=0.0243.
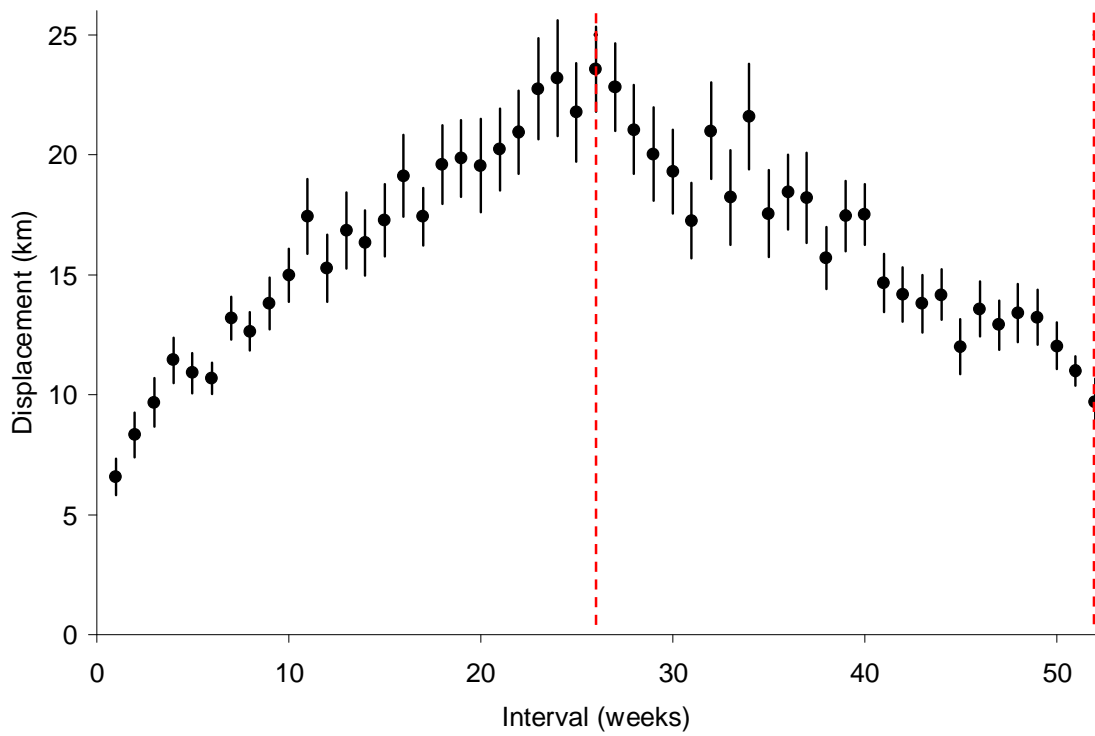
Figure 12. Displacement (mean and SE) of 30 female cheetah from their original location for sampling intervals between 1 and 52 weeks, pooled by individual and pooled by week. Vertical dashed lines indicate 6 months and 12 months.
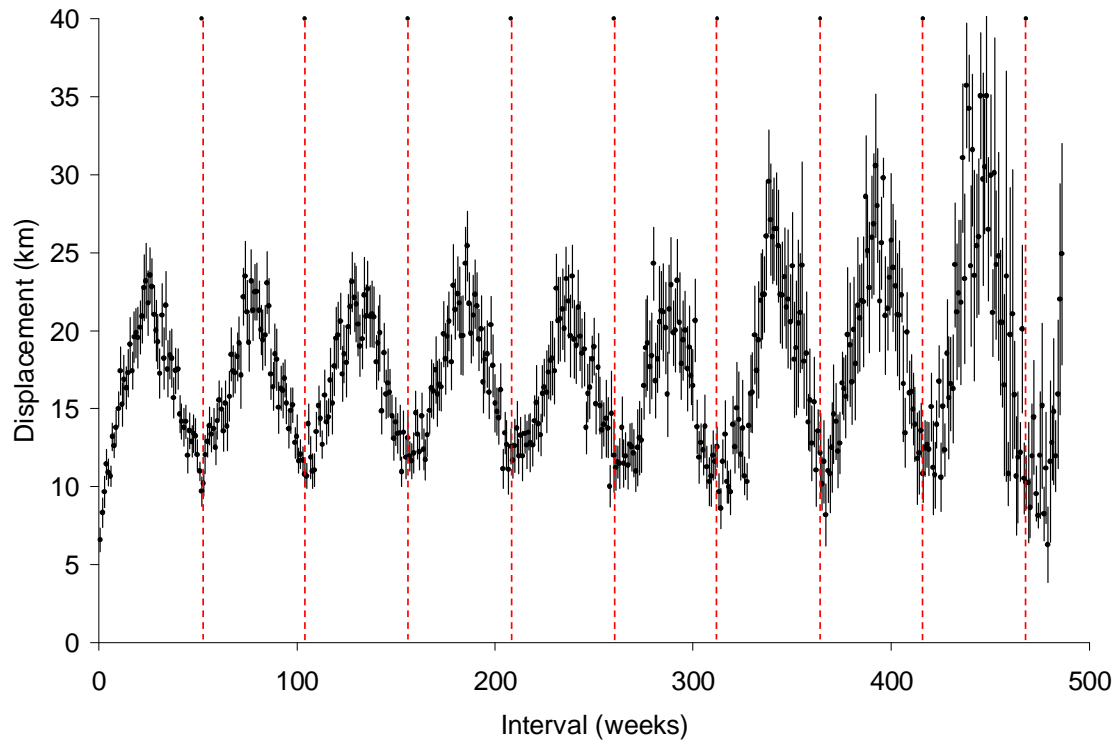
Figure 13. Displacement (mean and SE) of 30 female cheetah from their original location for weekly sampling intervals spanning 10 years, pooled by individual and pooled by week. Vertical dotted lines indicate years. t_0 is an arbitrary starting point for each individual and the interval (weeks) is simply time since t_0 and is not the calendar year.
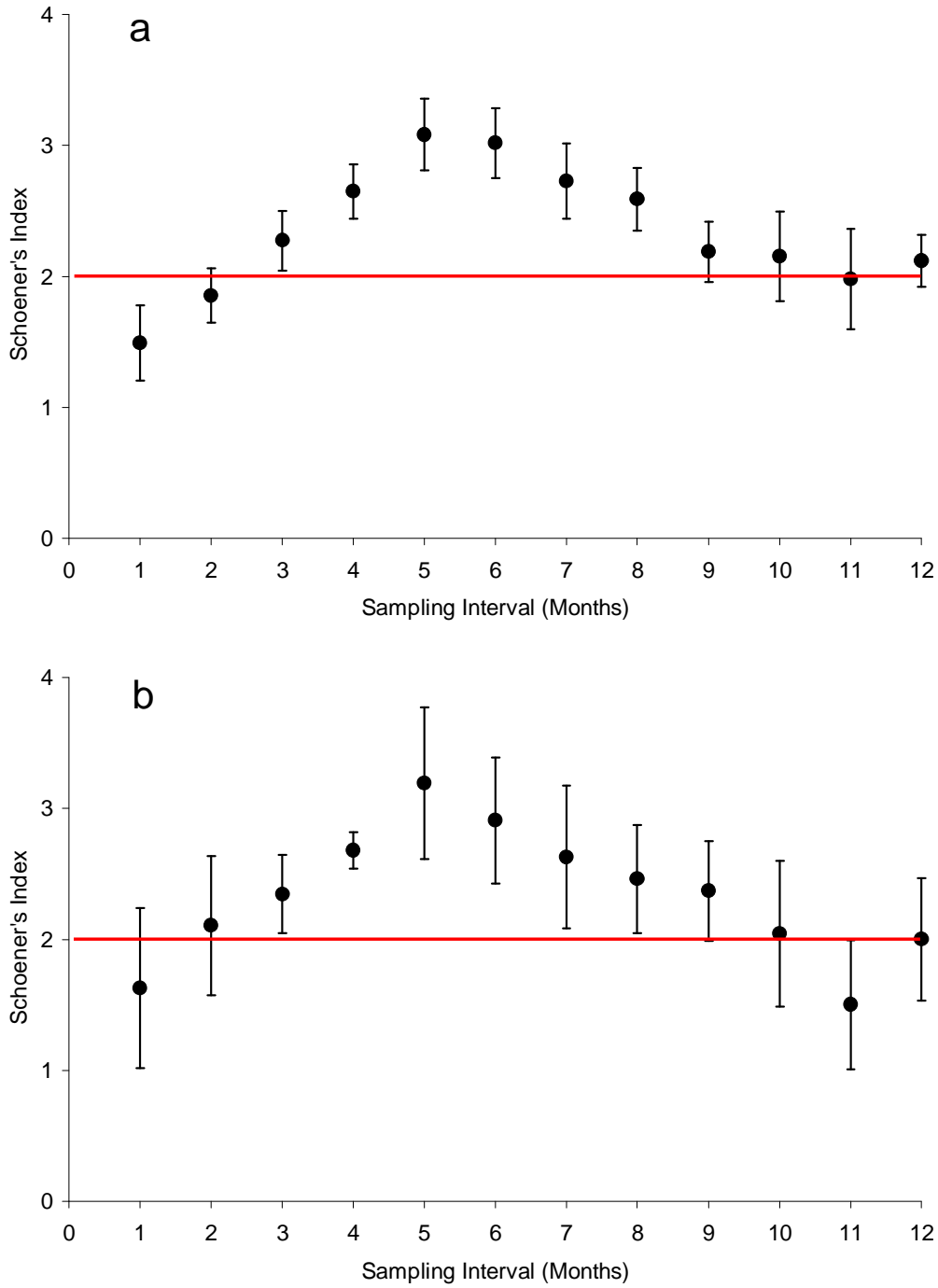
Figure 14. Schoener's index (t^2/r^2) as a function of sampling interval for (a) female cheetah of the Serengeti Plains and (b) only 7 females that did not shift ranges between years. Bars indicate confidence intervals ($\alpha = 0.05$). At a value > 2, spatio-temporal autocorrelation between locations is considered minimal (i.e. locations are independent).
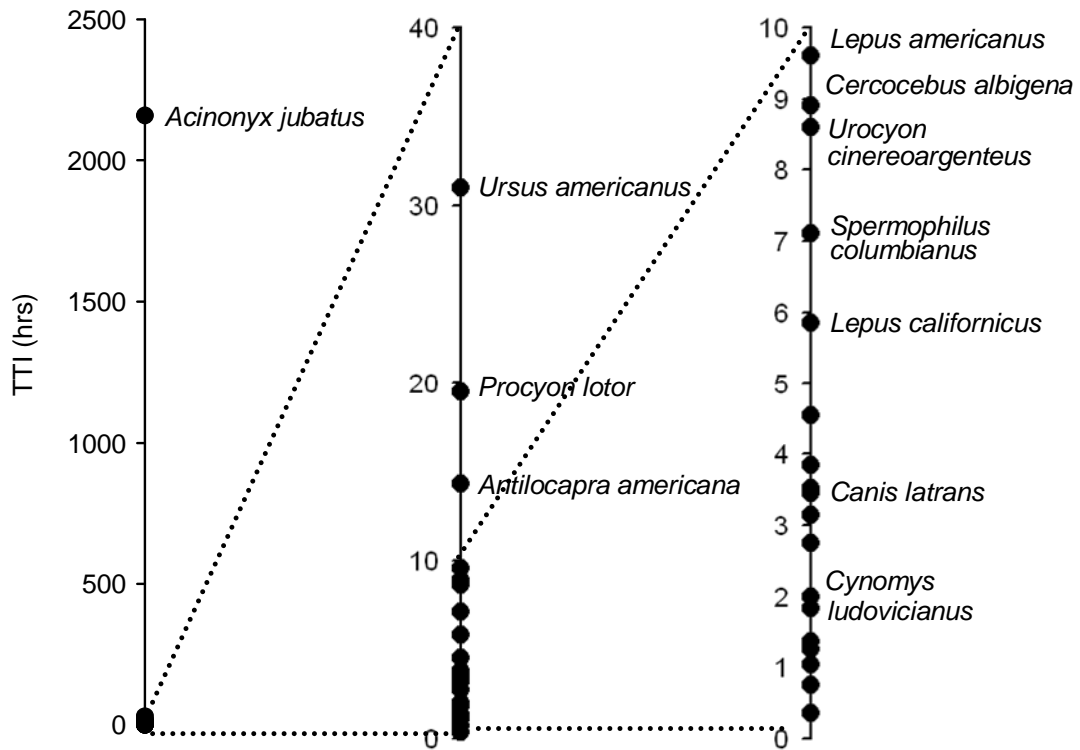
Figure 15. Time to statistical independence (TTI) of mammalian species as estimated by Swihart *et al.* (1988) and this study.
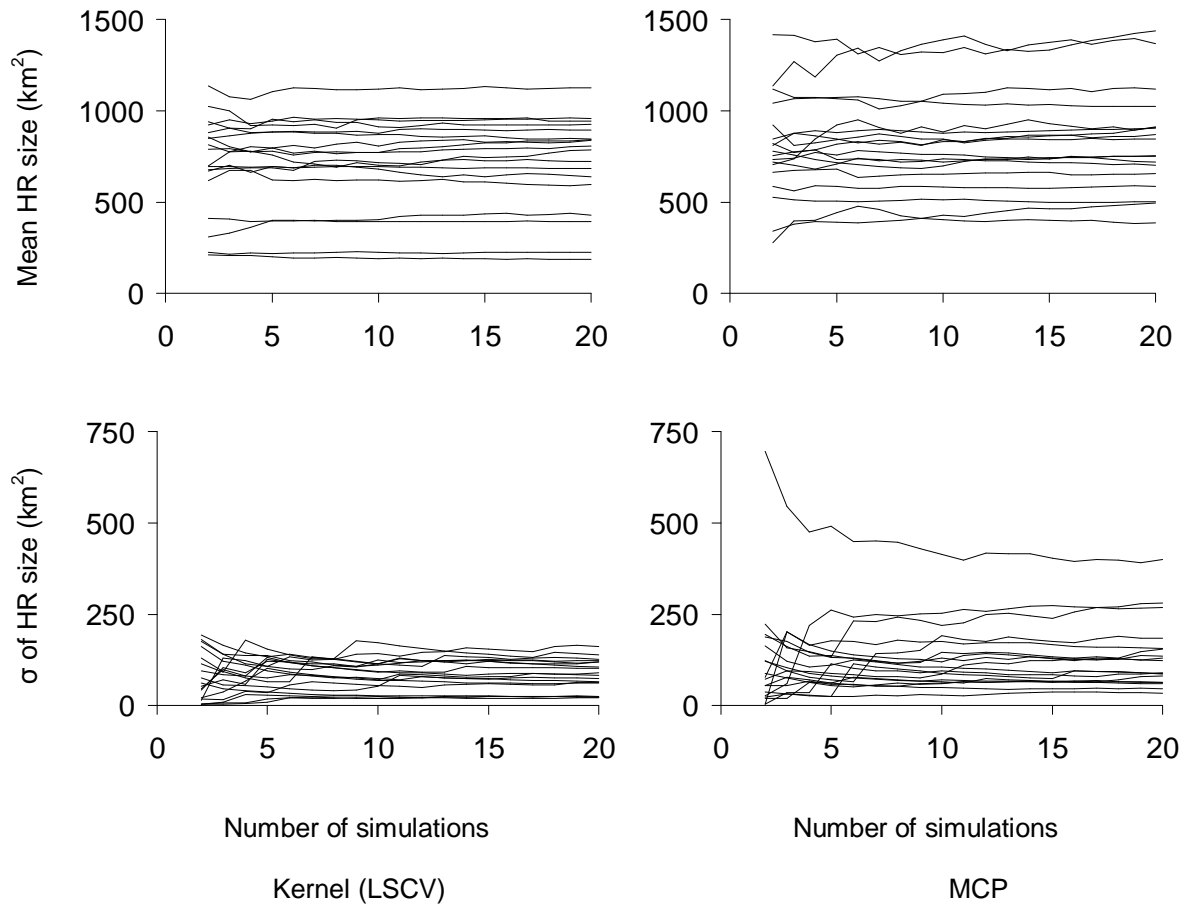
Figure 16. The mean and standard deviation of home range size (using 50 location estimates) for each of 18 individuals, as a function of increasing number of simulations. All estimates tend to stabilize at fewer than 20 simulations, where each simulation was one home range estimate for a particular female, using randomly added location estimates from the set of her location estimates over her lifetime
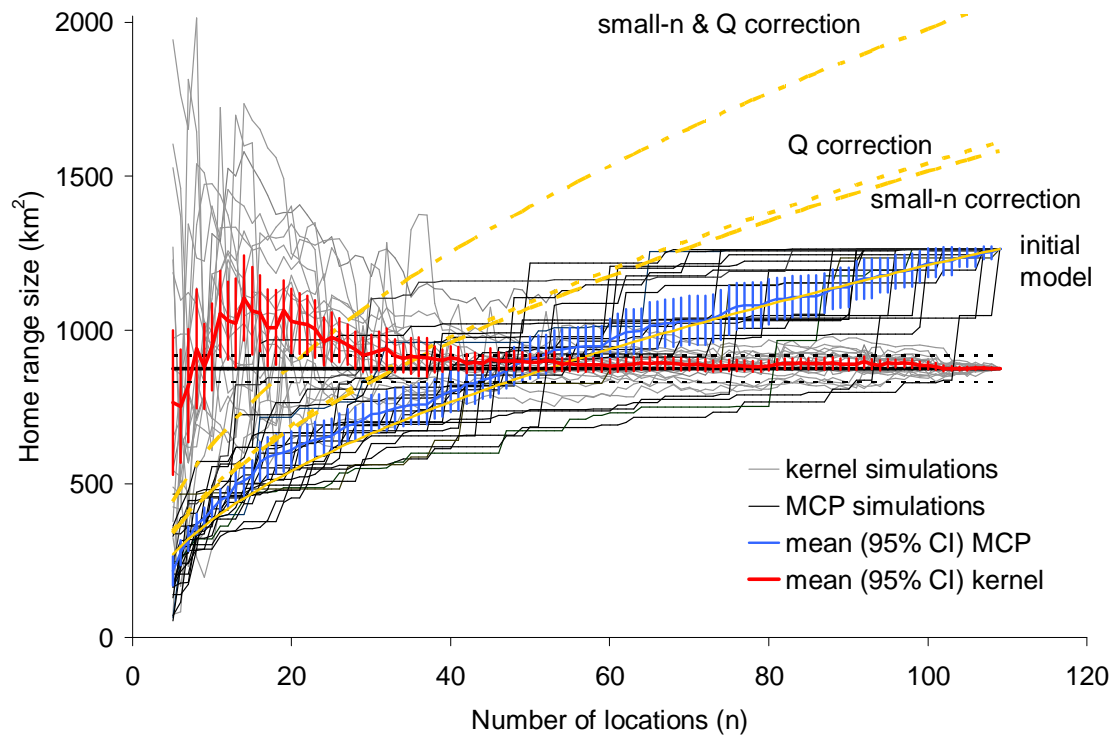
Figure 17. Home range asymptote analysis for female cheetah '1001'. Twenty simulations (thin black and gray lines) of asymptote analyses using randomly added points for MCP (black) and kernel (gray) and their mean (95% CI) function (blue and red respectively). Kernel home range (red) did reach an asymptote, with a mean value consistently within 5% (dashed black line) of the final home range size (thick black line) at 54 locations. The MCP method (blue) did not reach an asymptote, but was best described by HR = C"$n^{0.5}$ (solid yellow line) as opposed to using a small-n correction factor or a Q correction (dashed yellow lines).
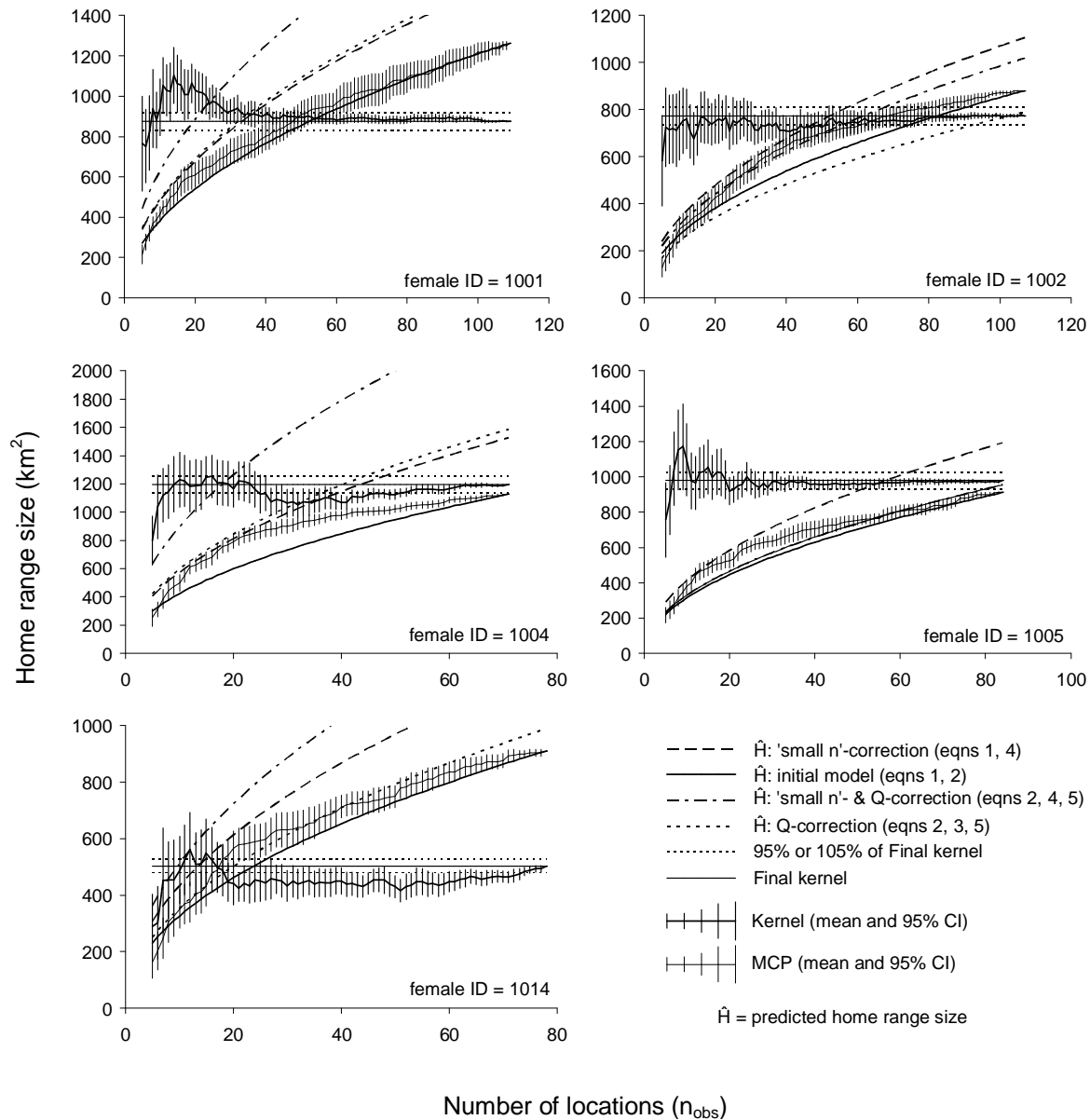
Figure 18. MCP and kernel home range asymptote analyses for 5 female cheetah. Kernel methods generally reached an asymptote (means with 95% CI in bold), while the MCP method did not (means with 95% CI in thin black lines). The model that best predicted MCP home range size was HR = $C''n^{0.5}$ (initial model – solid projection) as opposed to using a small-n correction factor or a Q correction factor (dashed projections).
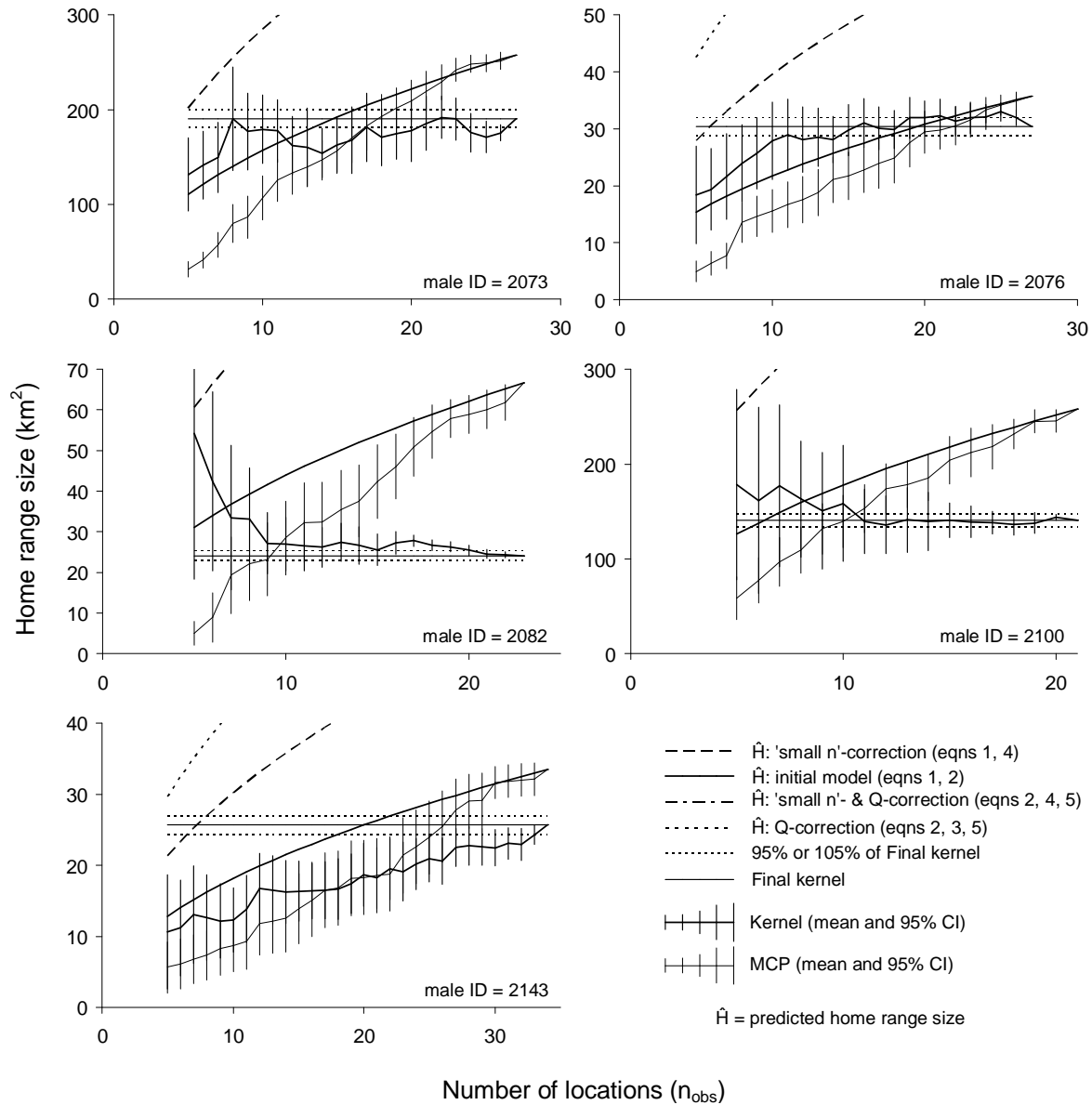
Figure 19. MCP and kernel home range asymptote analyses for 5 male cheetah. Kernel methods generally reached an asymptote (means with 95% CI in bold), while the MCP method did not (means with 95% CI in thin black lines). The model that best predicted MCP home range size was HR = $C''n^{0.5}$ (initial model – solid projection) as opposed to using a small-n correction factor or a Q correction factor (dashed projections).
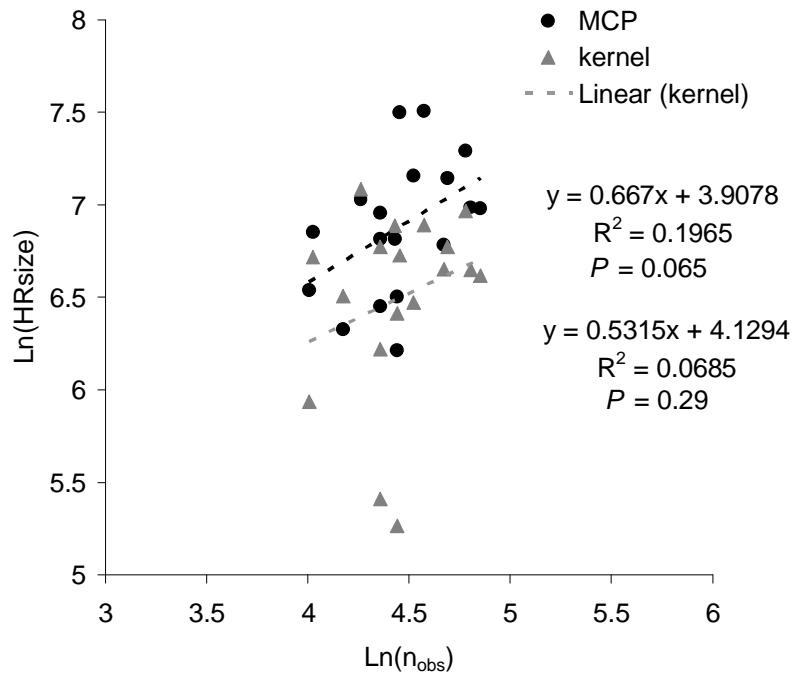
Figure 20. Log-linear relationship between home range size and number of location estimates (n_{obs}) for both MCP and kernel methods. The relationship was nearly significant for MCP methods (y = 0.667x + 3.9078, R^2 = 0.19, P = 0.065) though not for kernel methods (y = 0.5315x + 4.1294, R^2 = 0.07, P = 0.29).
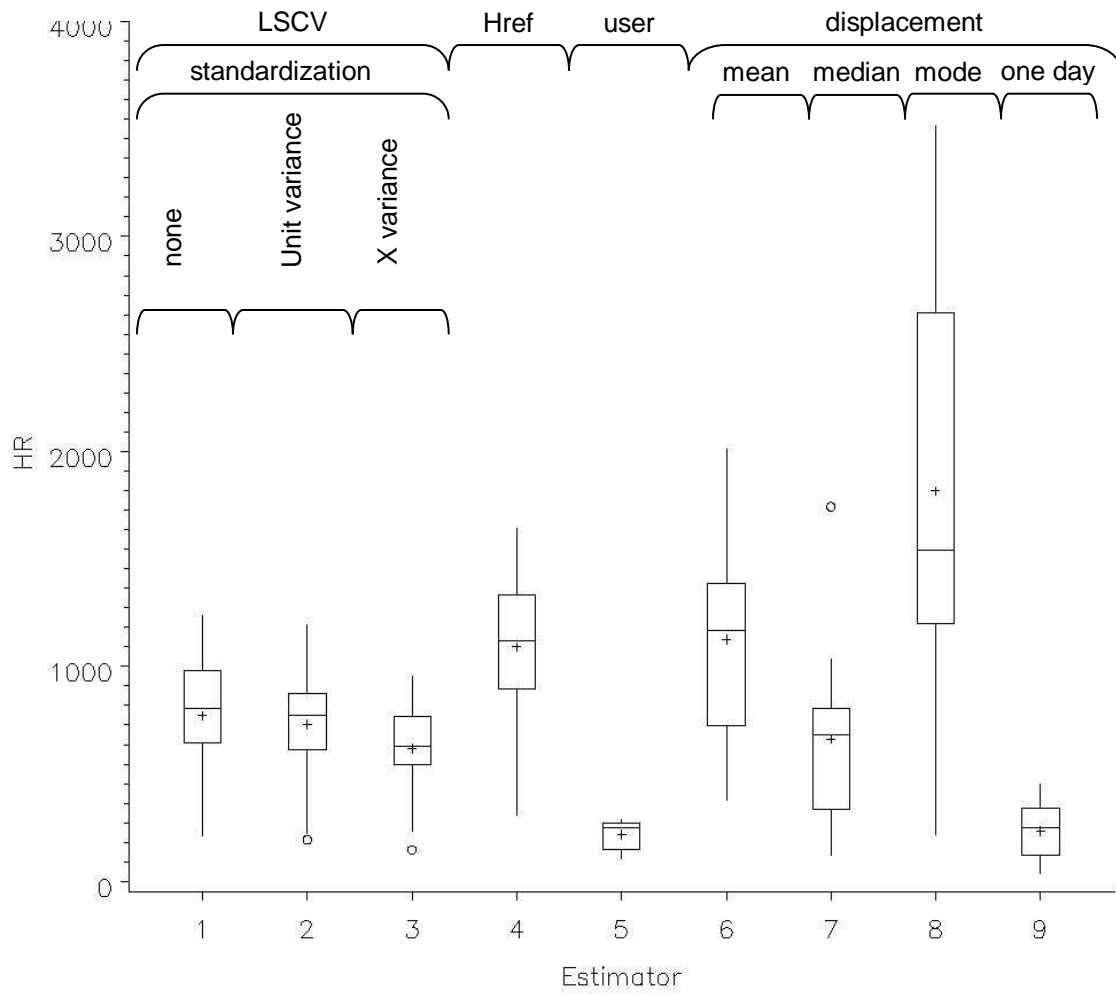
Figure 21. Lifetime home range size (km^2) for 18 female cheetah of the Serengeti Plains (1980-1994), as estimated using kernel density estimation (all 18 home ranges reached a kernel asymptote). Estimators used least-squares cross validation (LSCV), reference smoothing (H$_{ref}$), user-defined smoothing (user), and displacement smoothing (displacement).
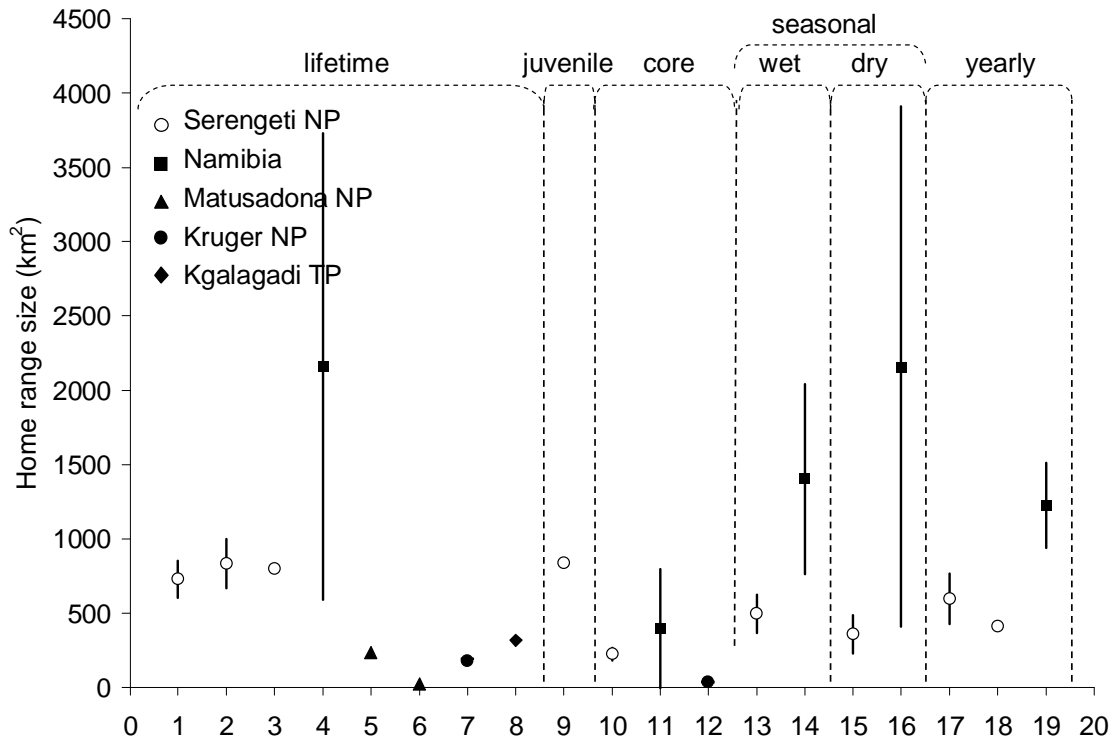
Figure 22. Lifetime and periodic (seasonal, yearly) ranges for female cheetah from the Serengeti National Park (SNP), Tanzania (○), Namibia (■), the Matusadona National Park (MNP), Zimbabwe (▲), the Kruger National Park (KNP), South Africa (●), and the Kgalagadi Transfrontier Park (KTP), Botswana and South Africa (♦), from this study (1; 9; 10; 13; 15; 17), and studies by Caro (1994)(2), Frame (1984)(3), Marker *et al.* (under review)(4; 11; 14; 16; 19), Zank (1995)(5), Purchase and du Toit (2000)(6), Broomhall *et al.* (2003)(7; 12), Mills (1998, cited in Marker *et al.*, under review)(8), and Gros *et al.* (1996)(18). Bars indicate 95% confidence intervals. Where bars are absent, a measure of variance was not reported in the study, or few individuals were sampled and their point estimates are given.
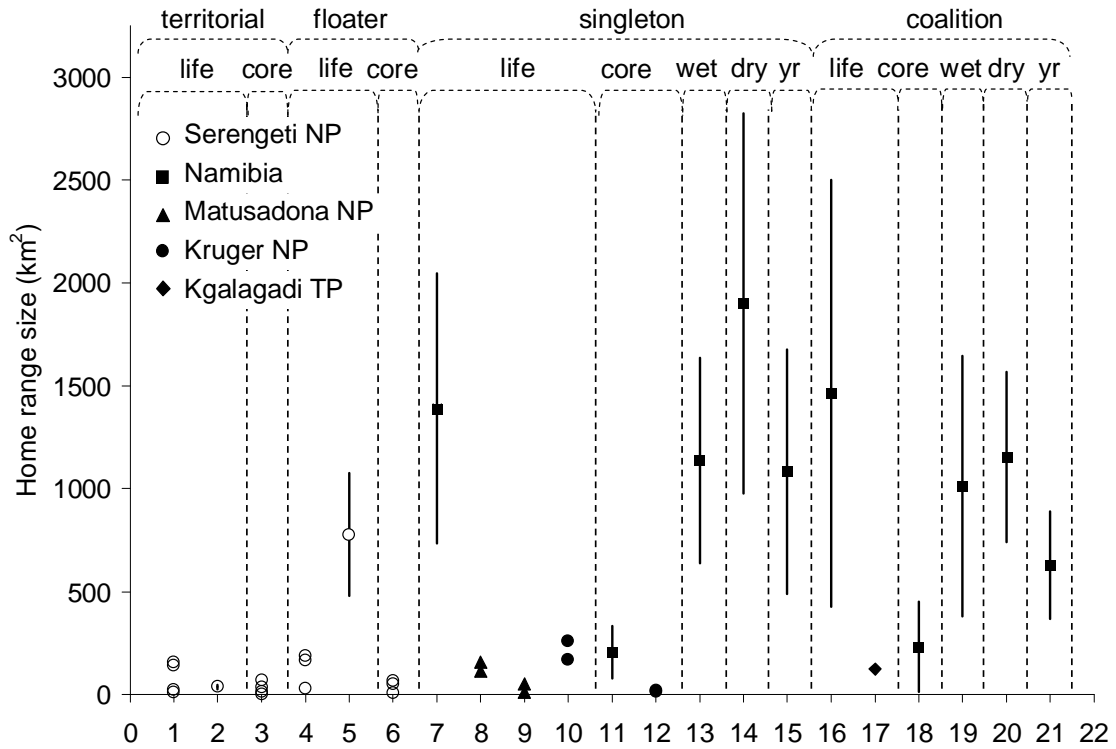
Figure 23. Lifetime and periodic (seasonal, yearly) ranges for male cheetah from the Serengeti National Park (SNP), Tanzania (○), Namibia (■), the Matusadona National Park (MNP), Zimbabwe (▲), the Kruger National Park (KNP), South Africa (●), and the Kgalagadi Transfrontier Park (KTP), Botswana and South Africa (♦), from this study (1; 3; 4; 6), and studies by Caro (1994)(2; 5), Marker *et al.* (under review)(7; 11; 13; 14; 15; 16; 18; 19; 20; 21), Zank (1995)(8), Purchase and du Toit (2000)(9), Broomhall *et al.* (2003)(10; 12), Mills (1998, cited in Marker *et al.*, under review)(17), and Gros *et al.* (1996)(18). Bars indicate 95% confidence intervals. Where bars are absent, a measure of variance was not reported in the study, or few individuals were sampled and their point estimates are given.

Chapter 3

Moving in social circles: A spatial perspective on philopatry and interaction in Serengeti cheetah

INTRODUCTION

Animal interactions form a central part of behavioral ecology and evolutionary biology. The study of area use for a species is inextricably linked to its sociality (Jetz *et al.*, 2004). Similarly, theories regarding mating systems are often grounded in discussions of dispersal and philopatry (Greenwood, 1980). A species' mating system may be reflected in social interactions in the form of territoriality, attraction, avoidance and tolerance. Some interactions are best studied through behavioral observation, but spatial data may also help elucidate behavioral patterns. Reviews of several techniques for assessing interaction from spatial data are provided by Powell (2000) and Kernohan *et al.* (2001), and comparisons between estimators used in assessing interaction have recently been provided by Millspaugh *et al.* (2004) and Fieberg and Kochanny (in press).

Excluding lions (*Panthera leo*), females of all species of the Felidae are solitary (in relation to other adults) and intolerant of conspecifics (with a few exceptions), and their spatial interaction ranges from exclusive and defended home ranges (territories) (e.g. tigers, bobcats, lynx, European wildcat, servals, leopards) to large undefended and overlapping home ranges (cougars, cheetah) (Packer, 1986). Felids make an interesting taxon for the study of resource dispersion and home range dynamics with their diversity of home range size, varying degree of home range defense and varying degree of interaction with conspecifics.

Juvenile dispersal

The pattern of dispersal in a species is often linked to its mating system, and for mammals generally follows a pattern of increased likelihood for male natal dispersal than for females in mate-defense mating systems, whereby the males seek access to and defend the philopatric females (Greenwood, 1980). Cheetah of the Serengeti Plains may adopt a mixed strategy, with some males displaying facultative sociality (Caro, 1994) and forming stationary territories that are not linked to prey concentrations (Durant *et al.*, 1988), while other males, floaters, roam across large undefended home ranges as singletons or in coalitions (Caro, 1994). It appears that the choice of strategy may depend on resource availability, with some individuals adopting either strategy at different times (Caro, 1994). Caro and Collins (1987a) showed that male territories did not have high prey abundance, but were vacated when the number of Thomson's gazelle or female cheetah seen, were low. Caro and Collins (1987b) also found that territorial males were no more likely than floater (non-territorial) males to encounter females though Caro (1994) saw more females while observing territorial males than non-territorial males.

Cheetah natal dispersal has not been systematically analyzed to date. However, from overlap indices between mothers and daughters and from qualitative comparisons of the natal and adult ranges of females, Caro (1994) concluded that females remain philopatric. Caro (1994) similarly concluded that almost all males show natal dispersal, using as lines of evidence a qualitative comparison of the ranges of one family group, anecdotal evidence for dispersal of two males from Frame and Frame (unpublished data cited by Caro, 1994), and the perceived increased shyness in males relative to females. Caro (1994) showed qualitatively that daughters generally remained on their natal ranges after sib group dissolution, and showed about 62% overlap with their mothers and 73% overlap with each other. A sib group is a group of siblings. One consequence of this dispersal pattern is inbreeding avoidance (Greenwood, 1980). Whether this reduced inbreeding is an effect or cause of dispersal in this species is not clear, and for the cheetah, more proximate factors may initially be a mother's long-term reproductive considerations

(family dissolution), and then avoidance of occupied territories and associated harassment by residents (after sib group dissolution), and finally, competition for mates (Caro, 1994).

The benefits of female philopatry cited by Caro (1994) revolve mainly around familiarity with the resources (prey, lair sites, water supplies) found within the home range. While the mothers may initiate family dissolution, female siblings generally initiate sib group dissolution (around the time of first estrus); their obligate asociality conferring higher risk from predation and kleptoparasitism, but their movement away from the males in a sib group precluding mating with brothers (Caro, 1994).

Home range overlap and static interaction

Spatial interaction between individuals can be assessed using static and dynamic interaction methods (Doncaster, 1990). Static interaction assesses spatial overlap while dynamic interaction assesses interdependent movements of individuals (Doncaster, 1990). Home range overlap has been assessed to varying degrees for cheetah. In addition to the overlap for female family members (above)(Caro, 1994), Gros *et al.* (1996) found an average of 4.82 females overlapping throughout the Serengeti Plains. In the Matusadona National Park, two males and a female overlapped (visual comparison of MCP ranges, Purchase and du Toit, 2000). Broomhall *et al.* (2003), using visual comparison of MCP ranges, reported a large amount of overlap in home range and mixed results for core overlap for adult cheetah in the Kruger National Park. Using MCPs, Marker *et al.* (under review) found that Namibian cheetah overlapped 15.8% with greater overlap between males than between females. Though reported spatial overlap is considerable, temporal overlap is avoided through visual and olfactory cues, first described by Eaton (1974) and corroborated by Caro's (1994) behavioral observations of scent marking. Caro (1994) also cited rarity of approaches between females and rarity of sharing kills as evidence of female avoidance. From qualitative comparisons of ranges, Caro (1994) hypothesized that within matriline overlap does not differ from overlap between unrelated females, a similar finding to that

for pride relatedness and overlap in lions (Spong, 2002), but contrary to findings of Marker *et al.* (under review) for Namibian cheetah where there was greater overlap between related females than between unrelated females.

There is a need to further examine the qualitative findings of Frame (1984) and Caro (1994). In this study I provide quantitative analyses of juvenile dispersal and social interaction in cheetah of the Serengeti Plains. I repeat some of the overlap analyses of Caro (1994), using kernel home ranges rather than minimum convex polygon (MCP) methods, and add a core range overlap comparison as well as two other measures of overlap and interaction using multi-response permutation procedures (MRPP) and the Spearman rank correlation coefficient. I explore relatedness and hence fitness considerations in each analysis in an attempt to explain the variability in overlap and interaction in this population.

METHODS AND MATERIALS

Juvenile dispersal

I compared the location distributions of individuals as dependent juveniles and as independent adults for an assessment of juvenile dispersal. I used only those datasets where the juvenile and adult datasets were represented by equivalent months. If equivalent months in the dry and wet seasons were not represented by location estimates, then I eliminated that individual from the analysis – that is location estimates at the beginning or end of the season may result in a shift because of seasonal movement and not dispersal. One male had no data for the wet season and another had no data for the dry season, as either a juvenile or as an adult. For these individuals, juvenile and adult data represented the same seasons however and were considered adequate for the analysis. I assessed juvenile dispersal for 12 females and 3 males (or male groups where male siblings remained together as a coalition and were not considered to be statistically independent samples) for which I had comparable juvenile and adult location

estimates. I use the term 'dispersal' with caution since I have no data for paternity in this population and am thus unsure if emigrating males actually sire offspring in their new location (Howard, 1960, but see Dingle, 1996). I assessed the juvenile and adult data for similar representation of seasons. I used Multi-Response Permutation Procedures (MRPP) (Zimmerman *et al.*, 1985) to assess shifts in area use, using program Blossom (Cade and Richards, 2001). Where juvenile and adult ranges were significantly different or statistically clumped (at α = 0.05), I concluded that a shift had occurred between the two time periods and I then estimated the dispersal distance as the Euclidean distance between the arithmetic mean or center of seasonal ranges. I visually compared the location distributions of the males (or male groups) and their mothers, post dispersal to determine if males moved away from their mothers as a mechanism for avoiding inbreeding. Investigating post dispersal location distributions of both the male and his mother simultaneously contributes more to understanding the mating system than does the male pre- and post-dispersal analysis alone. I hypothesized that females should show philopatry while males should disperse from their natal range.

Home range overlap

I defined home range overlap as the proportion of the area used by two individuals that was shared by those individuals, following Millspaugh *et al.* (2004):

$$Overlap = \frac{A_{1,2}}{(A_1 + A_2) - A_{1,2}}; \qquad \text{eqn 1}$$

A_1, A_2, and $A_{1,2}$ are the areas of home ranges for animals 1 and 2 and the area shared by the pair, respectively (note that A_2 is mislabeled in Millsapaugh *et al.*, 2004). I determined overlap indices for lifetime ranges and for lifetime core ranges. Both lifetime and core ranges were estimated using kernel density estimation in program Abode (Laver and Kelly, under review). These ranges were estimated with fixed biweight kernels (Seaman and Powell, 1996) using Least Squares Cross Validation (LSCV) with unit variance standardization, and volume contouring. Lifetime ranges were contoured at 95% of the volume of the utilization distribution.

Core ranges were estimated following Horner and Powell (1990) and Powell (2000) in program Abode (Laver, 2005). I compared 15 mother-daughter pairs, 6 pairs of sisters, one grandmother with two granddaughters, 3 aunt-niece pairs, and 68 pairs of females unrelated along the female lineage. I hypothesized that degree of overlap for core and lifetime ranges would differ with varying degrees of relatedness, and that degree of overlap of core ranges would be different from the degree of overlap of lifetime ranges. For tests comparing overlap between unrelated and closely related pairs of individuals, I used a two-sample t test (Zar, 1999:123) using PROC TTEST (SAS Institute, 2002) and the Mann-Whitney test (Zar, 1999:147) using PROC NPAR1WAY (SAS Institute, 2002). I tested the latter hypothesis separately for related and unrelated individuals with a paired-sample t test (Zar, 1999:162), using PROC TTEST (SAS Institute, 2002) and the Wilcoxon paired-sample test (Zar, 1999:165) using PROC UNIVARIATE (SAS Institute, 2002). I estimated degree of lifetime range overlap separately for 6 mother-daughter pairs similar to Caro's (1994) MCP overlap analysis.

I also assessed the similarity of location distributions for pairs of related and unrelated females at 3 temporal scales – adult ranges, yearly ranges and monthly ranges using MRPP in program Blossom. For adult range, I compared the same individuals as in the home range and core range overlap analysis (above). For each temporal scale, I used only those location estimates from each individual that overlapped temporally. I used a minimum of 10 location estimates for each individual in the analyses for adult (11 – 118 locations) and yearly (10 – 54 locations) range comparisons, and a minimum of three location estimates for monthly range comparisons (range: 3 - 13). I assumed for yearly comparisons that at least 10 locations would be an adequate representation of the year. I classified ranges as non-overlapping where distributions differed significantly from one another ($P < 0.05$). Where pairs of individuals were represented in > 1 year in the yearly comparisons, I used only the comparison for that pair with the smallest disparity in sample size (n_{obs}) between the two years of that comparison. Similarly for pairs of individuals that were represented in the same month in > 1 year for monthly comparisons, only the comparison with the smallest disparity in sample size (n_{obs}) was used. I

pooled comparisons by month to determine the proportion of overlap in pairs of unrelated individuals throughout the year. I pooled wet and dry season monthly comparisons to compare proportion of overlap in pairs of unrelated individuals by season. For yearly range I compared 4 mother-daughter*year combinations, and 51 pair*year combinations of unrelated individuals. For monthly range I compared 7 mother-daughter*month combinations, 6 sib-pair*month combinations, and 240 pair*month combinations of unrelated individuals. For unrelated individuals I used 5, 13, 22, 16, 51, 17, 9, 23, 30, 29, 17, and 8 pair*combinations for months January through December, respectively (in some cases, pairs of individuals were analyzed in the same month in different years).

Static interaction

Doncaster (1990) defined static interaction as "the spatial overlap of two home ranges and congruence in at least part of their utilization distributions." Dynamic interaction is the "dependency in the simultaneous movements of a pair of individuals." (Doncaster, 1990) I assessed static interaction for pairs of related and unrelated females using the Spearman rank correlation coefficient (r_s) (Zar, 1999; 395), following Doncaster (1990) in PROC CORR (SAS Institute, 2002). I obtained a utilization distribution (UD) for the location estimates of individuals using program Abode. A utilization distribution is "the two-dimensional relative frequency distribution for the points of location of an animal over a period of time" (van Winkle, 1975: 118). Utilization distributions were estimated using a fixed biweight kernel (Seaman and Powell, 1996) with no standardization and a fixed grid cell size of 5 km. The results of Spearman rank correlation coefficient method are sensitive to choice of grid size, which is a drawback of this estimator relative to other metrics for static interaction analyses (Fieberg and Kochanny, in press). My choice of 5 km for grid size represented the tradeoff between the number of cells in the comparison and the potential density of location estimates in any given cell. Grid cells must be large enough that a relatively smooth utilization distribution is obtained rather than having cells with low probability values centered over location estimates, with large interstitial areas of empty

grid cells. Ideally, a power analysis should be performed to determine the number of grid cells required for an analysis and hence to determine what the grid size should be. Grids representing UDs were perfectly overlapping and of equal extent for pairs being compared. Each grid cell in a comparison was multiplied by a constant dummy variable such that density values were represented by whole numbers. I removed from the analysis all cells with zero values for both individuals (unused cells) in the comparison.

Statistically significant r_s values (at $\alpha = 0.05$) suggest association (where H_0: $r_s=0$), from which I inferred interaction between individuals (Doncaster, 1990). Positive r_s values suggest attraction, while negative r_s values suggest avoidance (Doncaster, 1990) but see Fieberg and Kochanny (in press) for a commentary on the interpretation of r_s. I followed Martin and Bateson (1993:144) for my interpretation of the size of r_s values such that $0.4 > r_s > 0.7$ indicates moderate correlation and a substantial relationship. I compared the same individuals as I did for the home range and core range overlap and for adult range MRPP analyses (above), using only temporally overlapping location estimates for the adult stage class. I hypothesized that the utilization distributions of female cheetah would be associated with each other and that related individuals would show attraction, and that unrelated individuals would show avoidance of each other. This hypothesis follows from Caro's (1994) preliminary findings, from typical behavior in solitary felids (Packer, 1986) and from postulation about the fitness benefits and costs of sharing (competing for) resources between individuals of varying relatedness.

For all analyses, I estimated confidence intervals for proportions or percentages. I pooled comparisons of pairs of individuals according to relatedness using the proportion of genetic material shared by descent from a common ancestor. Thus, mothers and daughters were related by 0.5 (closely related), siblings were related by 0.5 (closely related), aunts and nieces by 0.25 (moderately related), and grandmothers and granddaughters by 0.25 (moderately related). I made two simplifying assumptions, firstly, that related individuals avoid matings (i.e. the daughter of a pair of related individuals shares more genetic material with her mother than does the

daughter of an unrelated pair), and secondly that the females first seen as adults at the beginning of the study were not related. Under these assumptions, relatedness by common descent through a matriline is a robust measure of relatedness. It is possible that these assumptions were violated and that pairs presumed to be unrelated would actually encompass the full range of levels of relatedness. Since females were known in the population for ten years prior to the use of their location data in these analyses it is likely that the females of unknown relatedness had already been lost from the population by the time of these comparisons.

RESULTS

Juvenile dispersal

Based on MRPP, only 2 of 12 (17%) females significantly shifted their ranges from their juvenile to adult stage (the sample was too small to be able to reliably estimate a confidence interval). These females shifted 13 km and 15 km from their wet season natal ranges and 5 km each from their dry season natal ranges respectively (Table 1, Figures 1 and 2). Both females reproduced in their new ranges, with 1053 raising 2 male and 2 female cubs to independence, and 1081 losing 2 litters. For the three males (or male groups) for which I had enough data, all three (100%) showed shifts from their juvenile to adult ranges (Table 1). The coalition of males 2038 and 2039 and their mother (female 1073) did not overlap in lifetime range after the dispersal, even though outliers in their mother's location data post dissolution may have resulted in contact between these individuals (Figure 3). The coalition of males 2081 and 2085 moved out of their mother's (1133) lifetime range, with only two locations overlapping an area that had been used by their mother while they were dependent juveniles (Figure 4). Post dispersal, she was observed only one more time in the population. Singleton male 2073 overlapped only marginally on his mother's (1117) lifetime range (Figure 5). Post family dissolution, 2073 was not observed in the population for two years, during which time 1117 was observed. Upon returning, 2073 was seen outside the lifetime range of 1117 though she was no longer observed. The low sample

size (n) for males in this population with location data both before and after family dissolution may in itself provide an indication of dispersal (Figure 6) (see discussion).

Home range overlap

Kernel lifetime home ranges and core ranges of all of 26 pairs of related individuals overlapped (e.g. Figures 7(a) and 7(b)). Lifetime home ranges overlapped in 66 of 68 (97%) pairs of unrelated individuals (e.g. Figure 8(a)), and core ranges overlapped in 60 of 68 (88%) pairs of unrelated individuals (e.g. Figure 8(b)). Using Millspaugh *et al.*'s (2004) simple overlap metric, mothers and daughters, and sisters overlapped over a mean (SE) of 47 (4)% of their combined lifetime ranges, and over a mean (SE) of 34 (3)% of their combined core ranges (Figure 9). Separately, mother-daughter pairs overlapped over a mean (SE) of 50 (4)% of their combined lifetime ranges and sisters overlapped 38 (9)%. A grandmother and two granddaughters, and aunts and nieces overlapped over 35 (7)% of their combined lifetime ranges and over 23 (5)% of their combined core ranges. Unrelated pairs of females had a mean (SE) of 25 (2)% and 16 (2)% overlap of their combined lifetime and core ranges respectively. Pairs of unrelated individuals differed significantly from pairs of highly related individuals in the degree of core and lifetime range overlap (Figure 9) (core overlap: $U_{0.05(2),68,21}$ = 1382, P < 0.0001; lifetime overlap: $t_{.05(2),87}$ = -5.70, P < 0.0001). Overlap results were normally distributed for all categories, excluding core overlap between unrelated individuals. Core overlap between unrelated individuals was bimodal with a relatively high frequency of low overlap values. A pairwise comparison of lifetime and core overlap indices for related individuals, and similarly for unrelated individuals, revealed that the percent core overlap was significantly different from percent lifetime range overlap (related individuals: $t_{0.05(2),20}$ = 3.47, P = 0.0024; unrelated individuals: $S_{0.05(2),68}$ =, P < 0.0001). Only 6 of 21 (29%) mother-daughter and sister pairs had greater core overlap than lifetime range overlap, and only 8 of 68 (12%) of unrelated pairs showed this trend.

The proportion of pairs of related individuals that had similar area use remained constant at three temporal scales – monthly, yearly, and lifetime ranges (Figure 10). The proportion of unrelated pairs of individuals with similar location distributions increased as the sampling period decreased such that a higher proportion of pair*month combinations had similar location distributions than did pair*lifetime combinations. At the monthly sampling period, unrelated and related individuals did not differ in the proportion of pair*month combinations that have similar location distributions, however, a higher proportion of pair*period combinations were similar in adult range location distributions for related than for unrelated individuals (Figure 10).

At the monthly sampling period, the proportion of pairs of unrelated individuals with similar location distributions was lower in May (the end of the wet season) than in October (the end of the dry season) (Figure 11). When I pooled monthly results for unrelated individuals by season, the dry season months had a higher proportion of pairs with similar location distributions than did wet season months (Figure 12). I could not repeat these analyses for related individuals for which I had only 16 monthly comparisons.

Static interaction

Most closely related pairs (14 of 20, 70%) and moderately related pairs (4 of 5, 80%) and only 18 of 67 (27%) unrelated pairs showed a significant positive association between their utilization distributions (Figure 13). Some pairs of unrelated females (11 of 67, 16%) showed a significant negative association while none of the related pairs showed this association (Figure 13). Groups were not compared since correlation values were not independent of one another. Examples of interaction for a related pair and an unrelated pair are given in Figures 14 and 15 respectively.

DISCUSSION

Juvenile dispersal

My data provide the first quantitative evidence of a pattern of dispersal in juvenile males and philopatry in juvenile females of cheetah of the Serengeti Plains (but small sample sizes should be noted, especially for males). These results do provide corroborative evidence for Frame's (1984) description of males establishing territories about 20 km from their natal ranges, for Caro's (1994) conclusion about dispersal in this population, and do follow the general trend for male-biased natal dispersal in mate-defense mating systems. It appears that male cheetah disperse regardless of the mating strategy (floater or territorial) that they adopt. It is not clear whether related matings are prevented by this sex-biased dispersal, and thus, inbreeding cannot be excluded as a possibility for this population.

Though sample sizes were small, it appears that dispersal distances are greater in the wet than in the dry season. During the dry season, Thomson's gazelle may be concentrated near the plains-woodland border where water sources may be more reliable (Durant *et al.*, 1988; Caro, 1994) and may preclude the wide spacing of females possible during the wet season. Females may thus be displaced further from their natal range during the wet season because resource distribution allows greater spacing of individuals. For the two females that shifted, their shift between natal and adult ranges can appropriately be called "dispersal," as both individuals produced offspring in their new ranges, thus following Howard's (1960) classic and commonly used definition (but see discussion of "dispersal" continued below). For one two-male coalition (2081 and 2085), the apparent wet season dispersal is probably an artifact of ranging over a much larger area while with their mother and then establishing a territory of contracted size that happened to be closer to their dry season juvenile range than their wet season juvenile range.

These findings are based on small sample sizes and further work should focus on obtaining larger samples both from this population and from populations in other ecosystems throughout the cheetah's geographic range. The low sample size of males for which I had data is in itself an indication of dispersal. I had only 7 males (or male groups) with at least 3 locations in both their juvenile and adult age classes. If I assume that researchers showed no preference for finding females, then the number of observations of males reflects their presence and tenure in the population. A bias would be possible if males used only specific parts of the Serengeti Plains that researchers avoided. Caro and Collins (1987a) found that territories were associated with vegetation cover and further that 8 areas were consistently occupied by males, most of which were located near kopjes (Caro, 1994). These kopjes were used by researchers as vantage points for scanning for cheetah and researchers made extra effort in looking for male territories in areas with more cover (Caro, 1994). Thus, it is likely that the sample sizes (n_{obs}) are a result of males leaving the study area shortly after leaving their mother or siblings, and others moving in. Dispersal data alone are insufficient evidence for inbreeding avoidance, but a genetic analysis to determine paternity in this population would allow for an investigation of inbreeding, and might help to clear up the contention about sources and threats of genetic paucity in the species (Caro and Laurenson, 1994; Caughley, 1994, O'Brien, 1994). An analysis of male-female static interaction may provide better spatial evidence for or against inbreeding, in the absence of genetic information.

According to Dingle (1996), the term "dispersal" has been widely misused in home range literature. The movements made by two juvenile females and three males (or male groups) in this population would appropriately be described as "ranging" according to Dingle's (1996) definition. Though these movements do not result in the dispersion of individuals in the population, they do result in the dispersion of family members - a process that may be important for inbreeding avoidance and thus fitness consequences. I feel that Dingle's (1996) treatment of "dispersal" is too stringent and that this term may be appropriately applied to family group processes and not just population processes, especially in taxa that are not colonial, or

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communal, and where individual movement behavior plays out at a scale smaller than the population level.

Home range overlap

Determining the extent of philopatry in cheetah of the Serengeti Plains is difficult due to the unique spatial structure of this population. With exception of territorial males, individuals in this population appear to follow their migratory prey – a process that may increase aggregation and hence overlap of individuals even though females may have extensive home ranges (chapter 2). In fact, only 2 of 94 pairs of females did not overlap in lifetime home range. From this it might be hypothesized that females are familiar with many other adult females concurrently in the population. That unrelated individuals show less overlap than related individuals in both lifetime and core ranges is evidence of female philopatry and/or tolerance of related individuals. Conversely, less overlap may indicate avoidance of unrelated females which may serve to decrease competition for resources and mating opportunities. Eaton (1974) provided a mechanism for temporal intraspecific avoidance, with female cheetah spacing themselves temporally through scent marking. Similarly, Caro (1994) observed avoidance and scent marking among females.

One would expect increased overlap with increasing relatedness since competition for resources or mating opportunities would be less consequential for an individual's fitness when between related individuals than between unrelated individuals. If degree of overlap were simply a consequence of matriline spacing and female philopatry, and if females were tolerant of each other in all parts of their home range, then core and lifetime overlap should be similar between individuals. I did not find this. Rather, pairwise comparisons of core and lifetime range in both related and unrelated individuals showed that core overlap was significantly less than lifetime range overlap. This suggests that although females overlap to a large degree over their entire

lifetime ranges, they may be spacing themselves within the home range so as to avoid each other in key areas.

My study is the first to report home range overlap for cheetah using kernel home ranges. My results indicate a level of overlap for mothers and daughters (50 (4)%) and for sisters (38 (9)%) similar to the 62 (9)% for mothers and daughters but considerably lower than the 73% overlap for sisters reported by Caro (1994). The sororal overlap that I report is within the range for overlap of sisters (30 – 90%) from Frame and Frame (unpublished data) cited by Caro (1994). The difference between the results from these studies is likely due to differences in home range estimation methods (kernel density estimation, this study; MCP, previous studies). Minimum convex polygon techniques, as used by Caro (1994) tend to overestimate home range area by including outliers and areas rarely or never used (Seaman *et al.*, 1999). Inflated home ranges would likely lead to inflated estimates of overlap and increased variance. Outline home range techniques such as MCP may provide spurious overlap results in that overlap areas may be observed in the tails of the distribution of location data, which may have lower biological relevance to an animal.

My results using kernel estimation suggest greater overlap between female cheetah of the Serengeti Plains than between females on Namibian farmlands. Marker *et al.* (under review) showed that males overlapped more than females. Female overlap is thus less than the 15.8% they report for males and females combined. This value is considerably lower than even the unrelated females in my study (25%). Further, Marker *et al.*'s (under review) estimates of overlap were probably inflated from using MCPs, and thus the equivalent kernel overlap would probably be even lower still. Such extreme differences in ranging behavior and social interaction between individuals of the same species in two ecosystems warrant further investigation. My results could not be compared to studies in the Matusadona National Park and Kruger National Park for lack of quantitative results in those ecosystems.

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I provide the first core range overlap analysis for cheetah, as well as the first overlap analysis to use statistically determined cores areas. Core areas, whether arbitrarily set at 50% of the volume of the utilization distribution or objectively defined, indicate areas of a home range that are used with relatively high frequency. From this, one typically infers that core areas and the resources they contain are more important to the animal than peripheral areas. Analyzing overlap in core areas should thus allow for a better understanding of social dynamics than traditional methods that look only at total home range. Creel and Creel (2002) used this method effectively to show that overlap of African wild dog (*Lycaon pictus*) packs in the Selous Game Reserve increases as probability of use decreases (i.e. packs overlap regularly in peripheral areas, but rarely in core areas - which they delineated at the 50% probability contour). I found that the percent probability contours of objectively defined core ranges in this population deviated from the typically used 50% value (female range: 40 – 81%; chapter 2). I suspect that studies using the 50% rule of thumb may be subject to error in estimating the degree of overlap in core areas.

A comparison of the location distributions provides a further line of evidence that females are philopatric and show greater tolerance to related than unrelated individuals. A relatively high proportion of related pairs (43%) had similar location distributions as compared to only 6% for unrelated individuals for adult range comparisons. Not only did a higher proportion of related individuals overlap, and overlapped to higher degrees, but a higher proportion also used the same areas with similar location distributions (patterns of area use). For related females, similarities in patterns of area use were observed for various temporal scales, while similarity in area use increased at decreasing temporal scales for unrelated individuals. This result is counter-intuitive. Similar area use over a lifetime for two individuals does not necessarily result in competition, as the individuals may be using different areas and resources concurrently. Similar area use over a short time period, such as a month, suggests increased likelihood that the individuals will be competing for the same resources. This may be the situation during the dry

season but probably not in the wet season (below). Cheetah should space themselves so as to avoid competition but still gain access to the best resource patches.

Monthly overlap for unrelated individuals appears to be a seasonally driven phenomenon, with higher overlap during the dry months than the wet months. It appears that within seasons, overlap may decrease as the wet season progresses, before increasing to a peak at the end of the dry season. Females may be forced to overlap with unrelated individuals in resource limited periods when Thomson's gazelle are aggregated around a few reliable water sources near the plains woodland border. But, Thomson's gazelle also tend to form ephemeral aggregations in the wet season, lasting a few weeks to 5 months, which are centered on 'green flushes' that follow the heterogeneous rainfall pattern on the plains (Caro, 1994). Thus, when prey are more widely and patchily distributed, females may be able to space themselves further away from each other to decrease competition.

Static interaction

Simple overlap indices may mask subtle variability in use within discrete polygons (even those of core ranges). Using correlation allows for a finer-scale measure of interaction than does inference from core and lifetime range overlap indices and comparisons of utilization distributions (above). Related females showed moderate attraction to each other in their temporally overlapping adult ranges, a result that reflects at a fine spatial scale (relative to cheetah home range size) (5 km grid cells) the lifetime overlap of related females – one would expect higher r_s values if the overlap of core areas was consistent with the overlap of lifetime ranges. Contrary to my expectations, roughly half of the pairs of unrelated females showing a significant association, showed a similar direction of interaction, the other half showed avoidance. Unrelated pairs appeared to exhibit strong avoidance (r_s = -0.86) to moderate attraction (r_s = 0.64) and I suspect that this wide range of interaction is partly due to my coarse definition of relatedness. The fact

that no related pairs of individuals showed statistically significant avoidance is remarkable when compared to the level in unrelated pairs.

Simple metrics of extent of overlap might simply reflect spacing of matrilines. For this reason, a correlation analysis may be beneficial in elucidating behavioral interactions in spite of its inherent shortcomings (see Kernohan et al., 2001 and Fieberg and Kochanny, in press). Fieberg and Kochanny (in press) contend that r_s values, and in particular, negative r_s values are difficult to interpret. Correlation may not provide the most sensitive statistic for estimating the extent of overlap, but I see the directional quality of r_s as an intuitive and helpful property rather than a hindrance.

Future work is required to assess interaction in this species in different ecosystems, at a finer resolution than the simple boundary comparisons that have been done to date. I hypothesize that the direction and extent of static interaction will vary predictably with resource quality, availability and distribution. I also believe that the overall tolerance exhibited in my findings may mask the interactions that take place at a finer temporal and spatial scale. I hypothesize that less attraction or greater avoidance would be exhibited where females are forced to aggregate around patchily distributed herds of Thomson's gazelle. To fully understand the spatial dynamics of cheetah in relation to conspecifics I recommend analyses of dynamic interaction – interdependcy of simultaneous movements of two individuals (Doncaster, 1990).

As a final note, all of my analyses depend on the assumption that sociality in cheetah is determined by resource-driven factors and intraspecific interaction. I ignored the fitness consequences of foraging in areas where competition may be low with conspecifics but high with lion and hyena, and where intraguild predation may play out. There is both correlative (Durant, 1998) and manipulative evidence (Durant, 2000) of the effect of lion and hyena on cheetah movement. Future efforts should be directed towards understanding cheetah sociality and movement dynamics in the context of community-level interactions. Comparisons with the

Namibian population may be especially useful for this, where the large predators that are sympatric with cheetah elsewhere, are absent (Marker et al., 2003). The presence of lion and hyena in the Serengeti may alone account for the higher levels of association with conspecifics than found in Namibia.

CONCLUSION

My data suggest that cheetah of the Serengeti Plains do follow the male-biased natal dispersal pattern common to mammals with mate-defense mating strategies even though male behavior reflects a dual mating strategy. It also appears that, for females that do disperse, dispersal distance is reduced in the dry season - possibly due to resource limitation and aggregation. Related females show more overlap in both lifetime and core ranges than unrelated females. In addition, a higher proportion of related females have similar adult range use patterns than do unrelated females. This pattern of attraction and avoidance was also borne out in static interaction analyses where roughly one third of unrelated pairs that showed a significant interaction, showed moderate to strong avoidance at a fine spatial scale, while related individuals showed moderate attraction and no avoidance. Finally, unrelated individuals showed variable tolerance of each other at different times of the year, showing more similar area use patterns during dry months than during wet months. The level and direction of interaction among female cheetah in this population could be determined by a trade-off between the fitness consequences of competition for matings and resources and the benefits of foraging in the most productive areas that are temporally and spatially unpredictable in this ecosystem.

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FIGURES AND TABLES

Table 1. Juvenile dispersal distances for male and female cheetah that had significantly different natal and adolescent or adult location distributions. Most females did not shift between ranges, but for two that did, shifts were greatest in the wet season. All three males (or male groups) with enough pre- and post-dispersal data shifted significantly.

Sex	Social status	ID	Natal Dispersal Distance (km)	
			Wet season	Dry season
Female		1053	13	5
		1081	15	5
Male	2-sib territorial coalition	2038; 2039	-	17
	2-sib territorial coalition	2081; 2085	30	10
	singleton of unknown status	2073	9	-
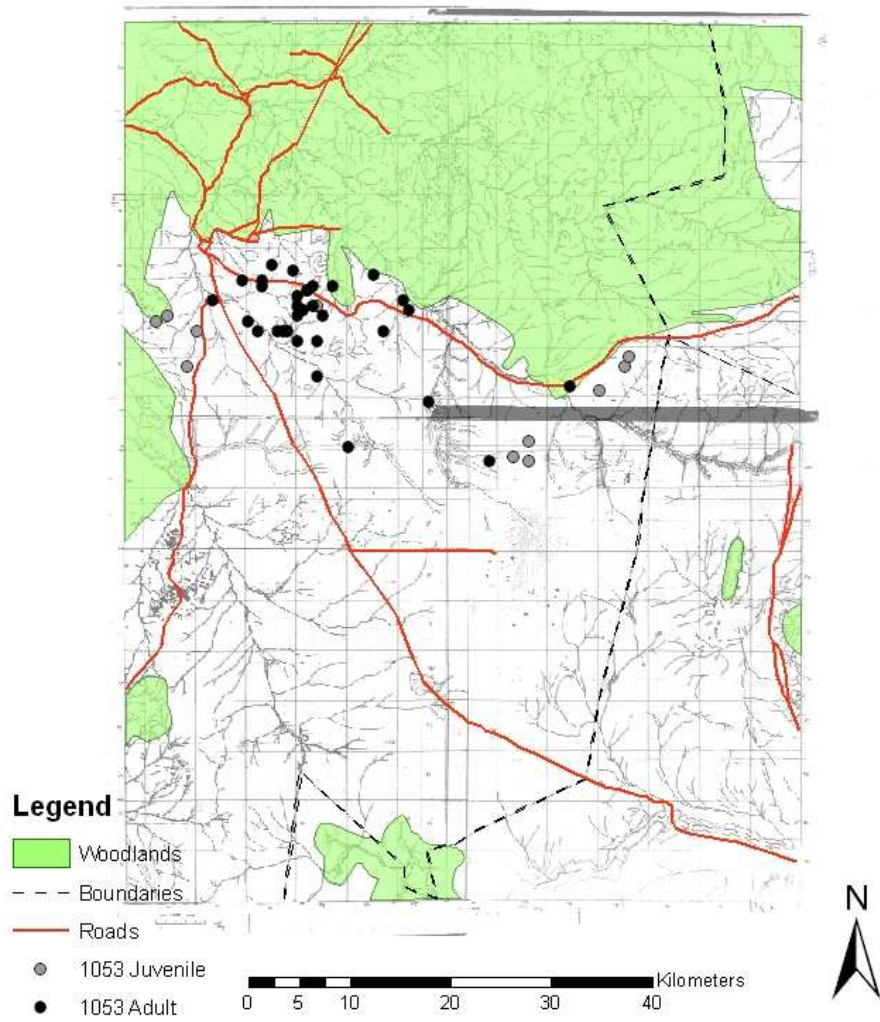
Figure 1. Location estimates for female 1053 as a dependent juvenile (gray) and as an adult (black).
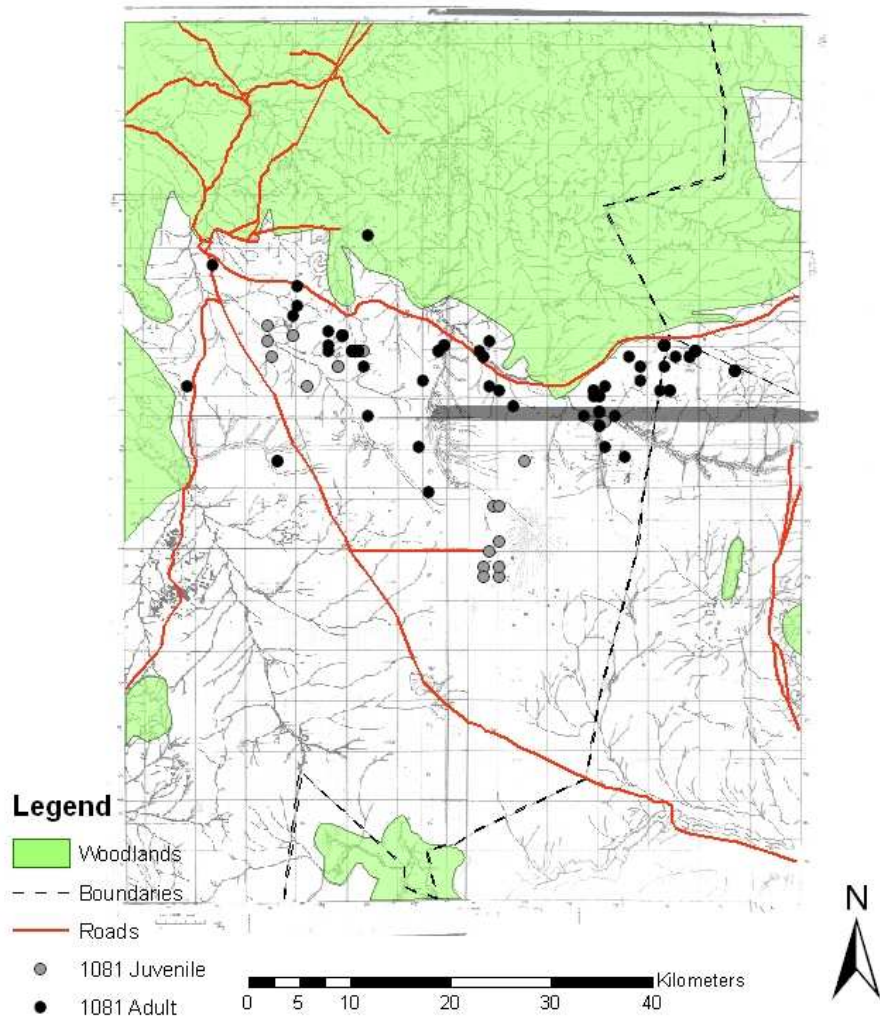
Figure 2. Location estimates for female 1081 as a dependent juvenile (gray) and as an adult (black).
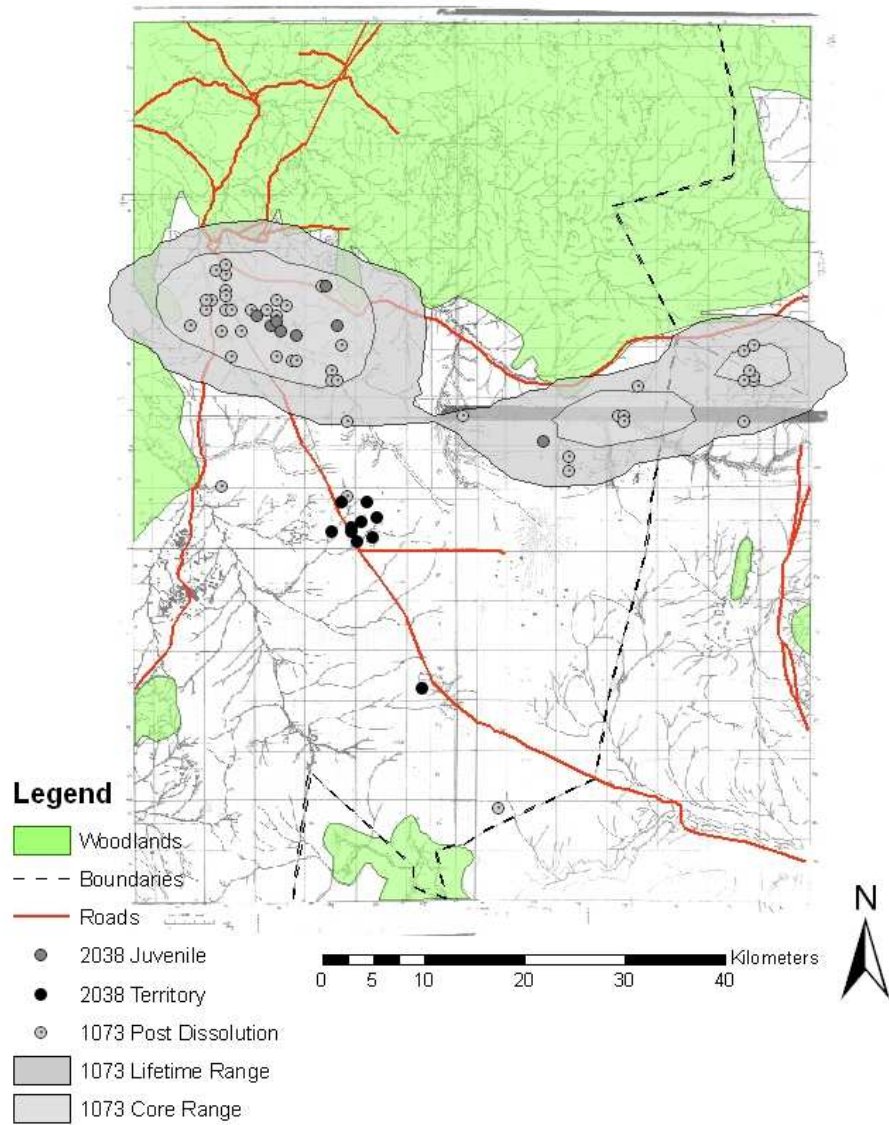
Figure 3. Dispersal of a two-male coalition (males 2038 and 2039) relative to their mother's (1073) post family dissolution location estimates and her lifetime and core ranges (for her entire lifetime - not post dissolution).
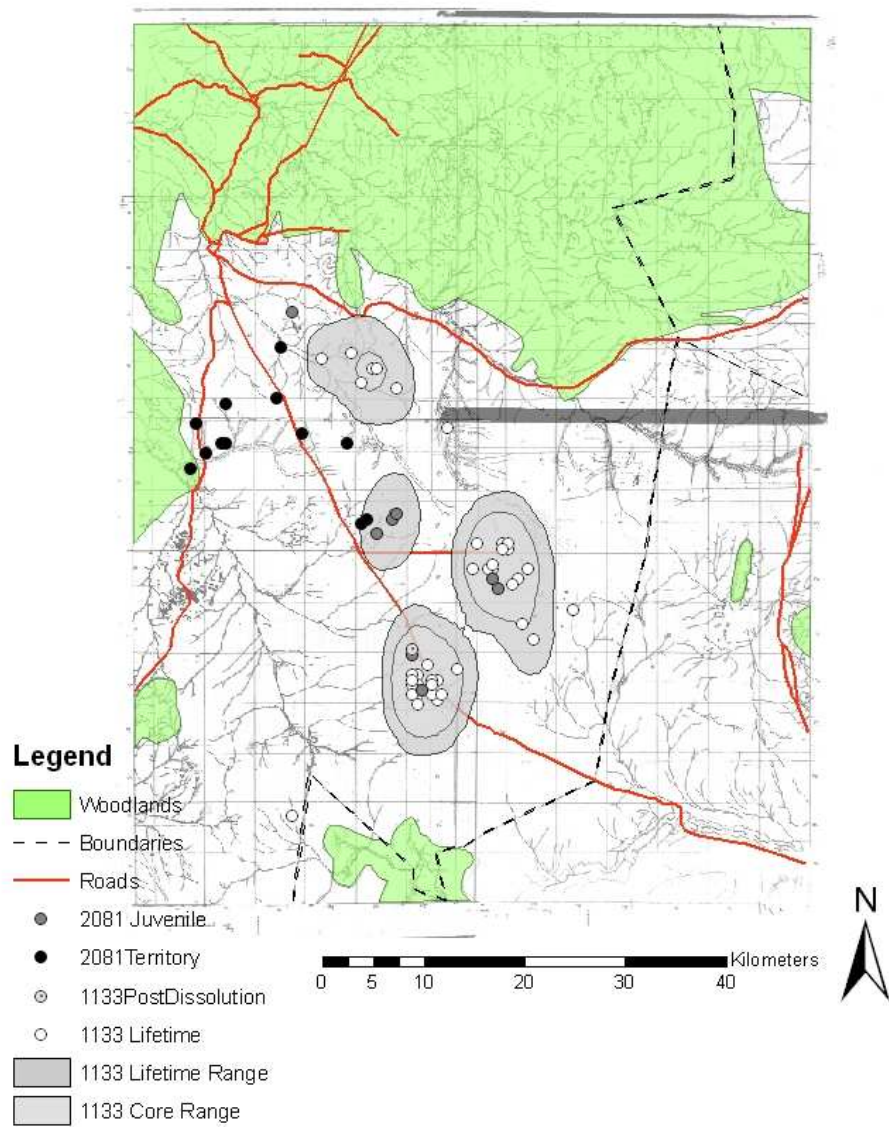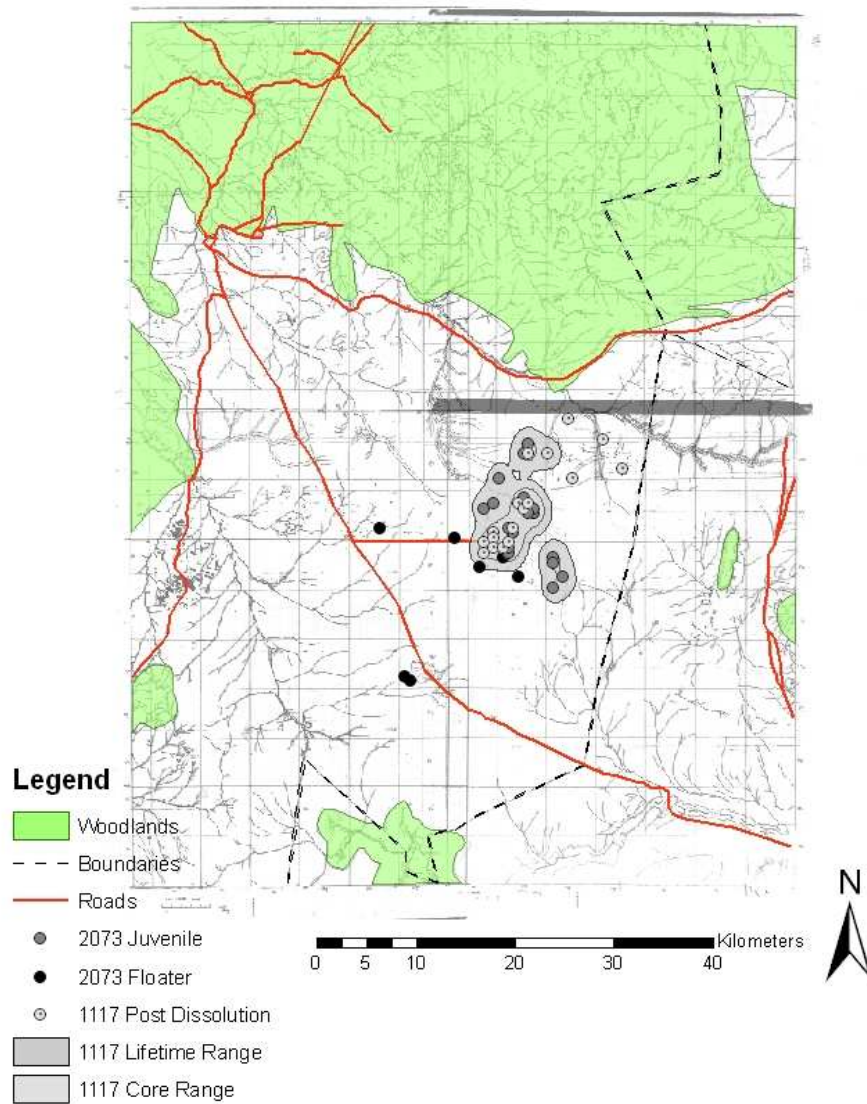
Figure 4. Dispersal of a two-male coalition (males 2081 and 2085) relative to their mother's (1133) post family dissolution (1 location) and lifetime location estimates, and her lifetime and core ranges.

Figure 5. Dispersal of a male of unknown social status (2073) relative to his mother's (1117) post family dissolution location estimates and her lifetime and core ranges (for her entire lifetime - not post dissolution). 2073 was not observed in the population for two years after family dissolution, and 1117 was never observed after the return of her son.
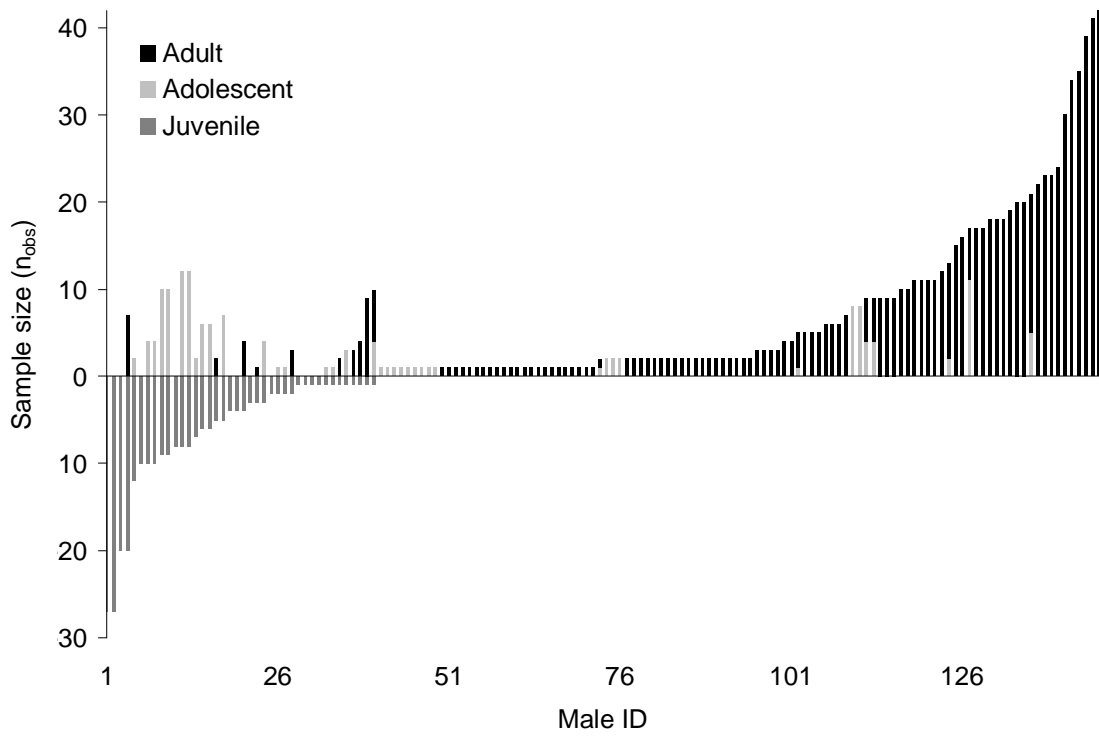
Figure 6. Sample sizes (n_{obs}) for male cheetah of the Serengeti Plains 1980 – 1994. Very few males were observed as juveniles and post family dissolution. The majority of males were observed as adults only.
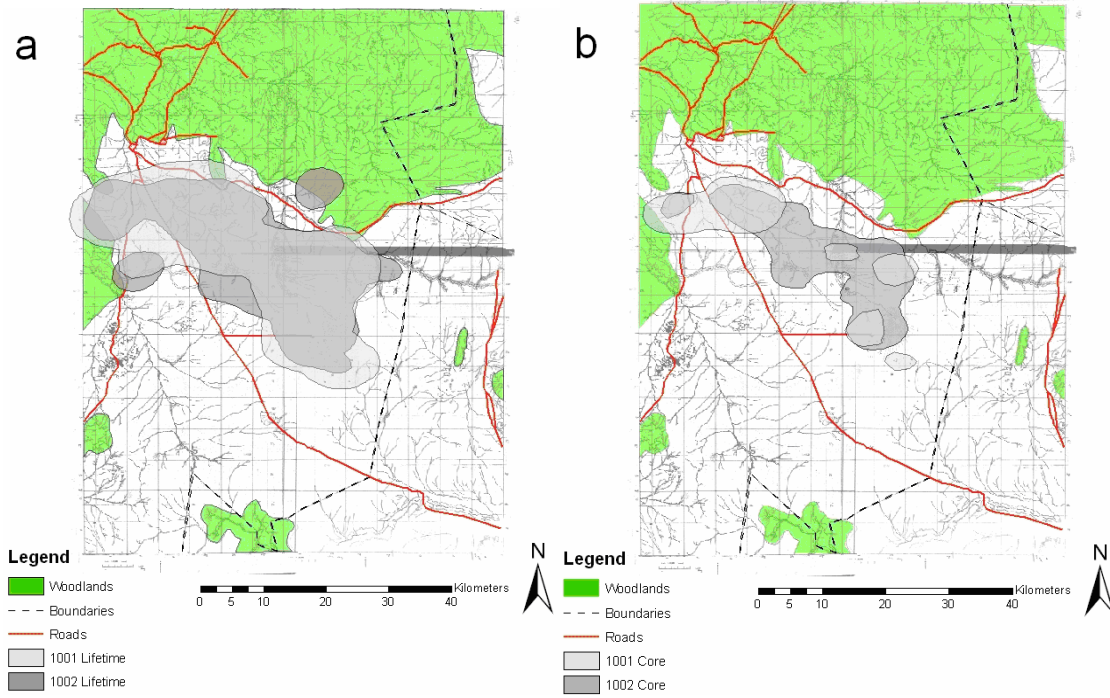
Figure 7. Lifetime (a) and core (b) kernel home range overlap for a mother-daughter pair of cheetah of the Serengeti Plains. Percent overlap for this pair was 66% and 31% respectively.
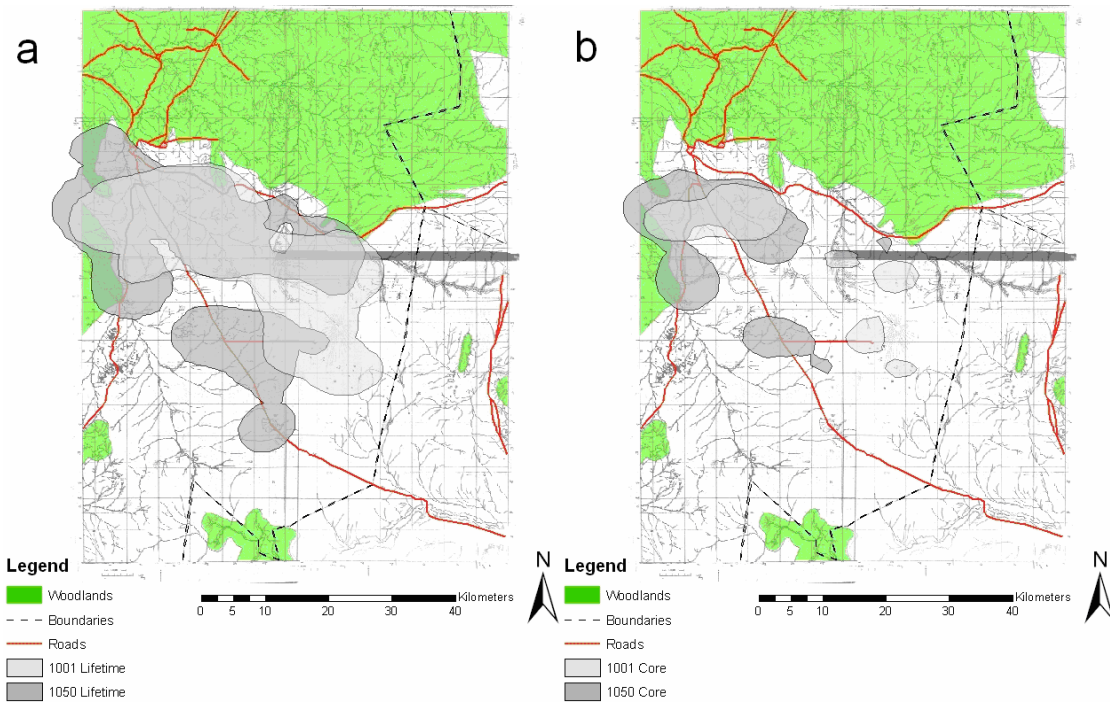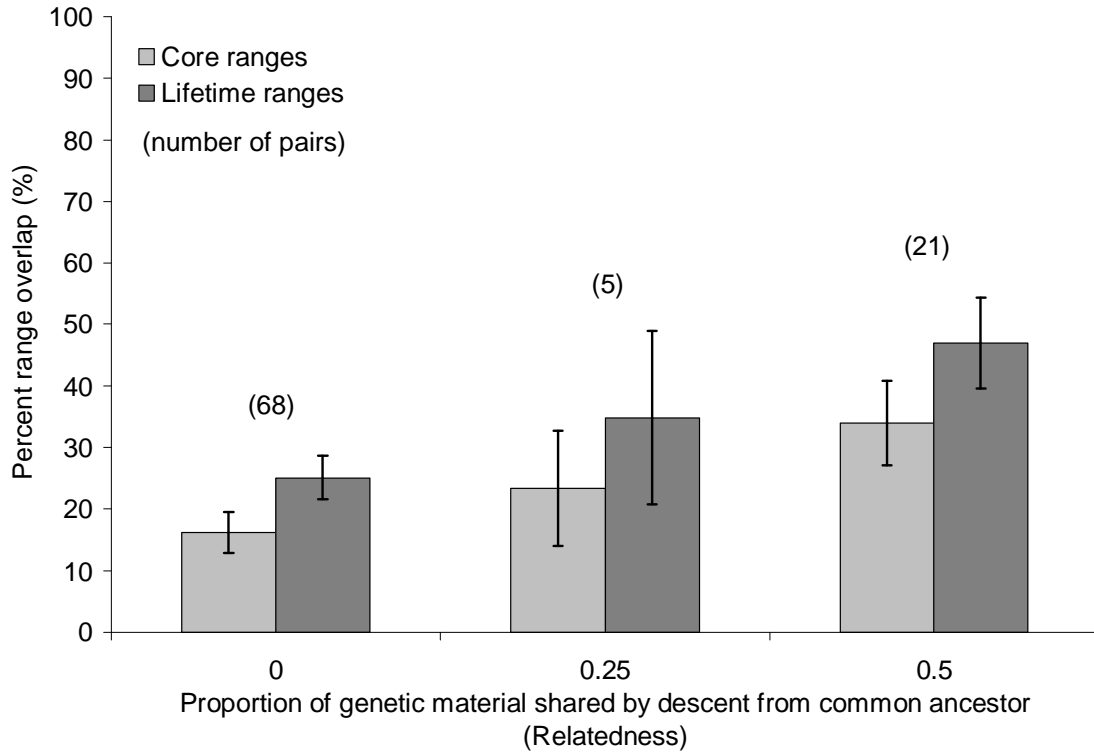
Figure 8. Lifetime (a) and core (b) kernel home range overlap for a pair of unrelated female cheetah of the Serengeti Plains. Percent overlap for this pair was 45% and 27% respectively.

Figure 9. Mean (bars represent the 95% CI) core and lifetime kernel range overlap for pairs of female cheetah of the Serengeti Plains (1980-1994). Comparisons were summarized by relatedness such that mother-daughter and sister pairs share half of their genetic material, aunt-niece and grandmother-granddaughter pairs share a quarter and unrelated individuals share none.
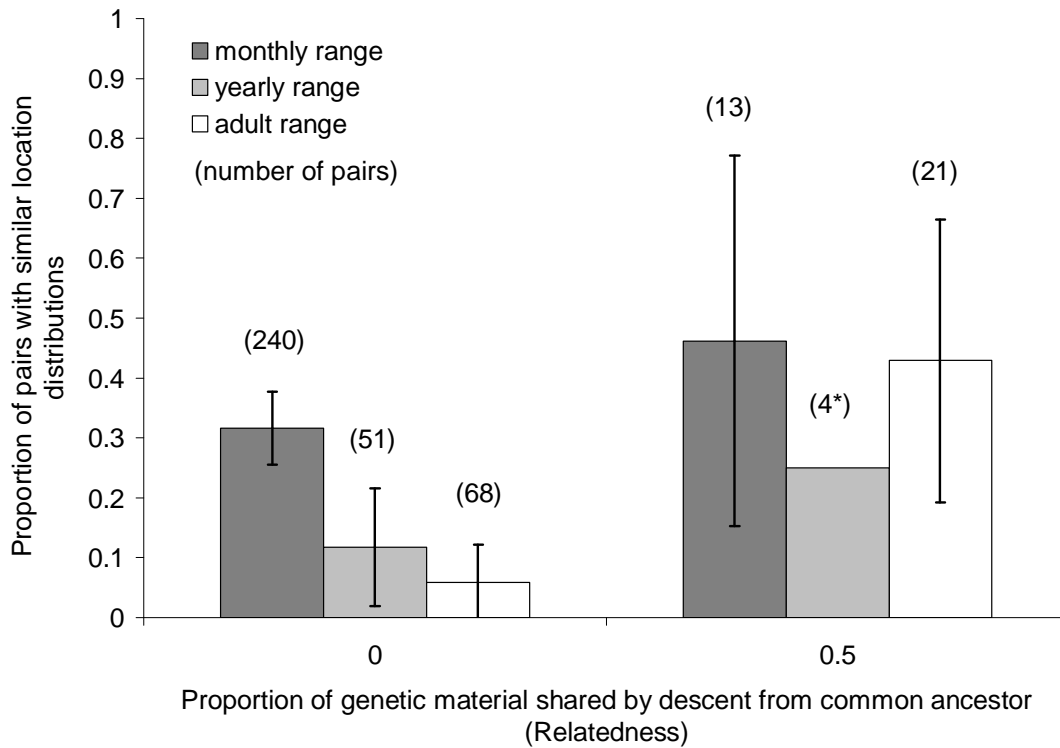
Figure 10. Proportion (bars represent the 95% CI) of pairs of individuals with similar location distributions at three temporal scales. Similarity in location distributions was determined using multi-response permutation procedures (MRPP). Comparisons were summarized by relatedness such that mother-daughter and sister pairs share half of their genetic material, and unrelated individuals share none. *The proportion (*p*) is too close to 0 with a low sample size (n = 4) to reliably estimate a confidence interval about the mean (Zar, 1999:529).
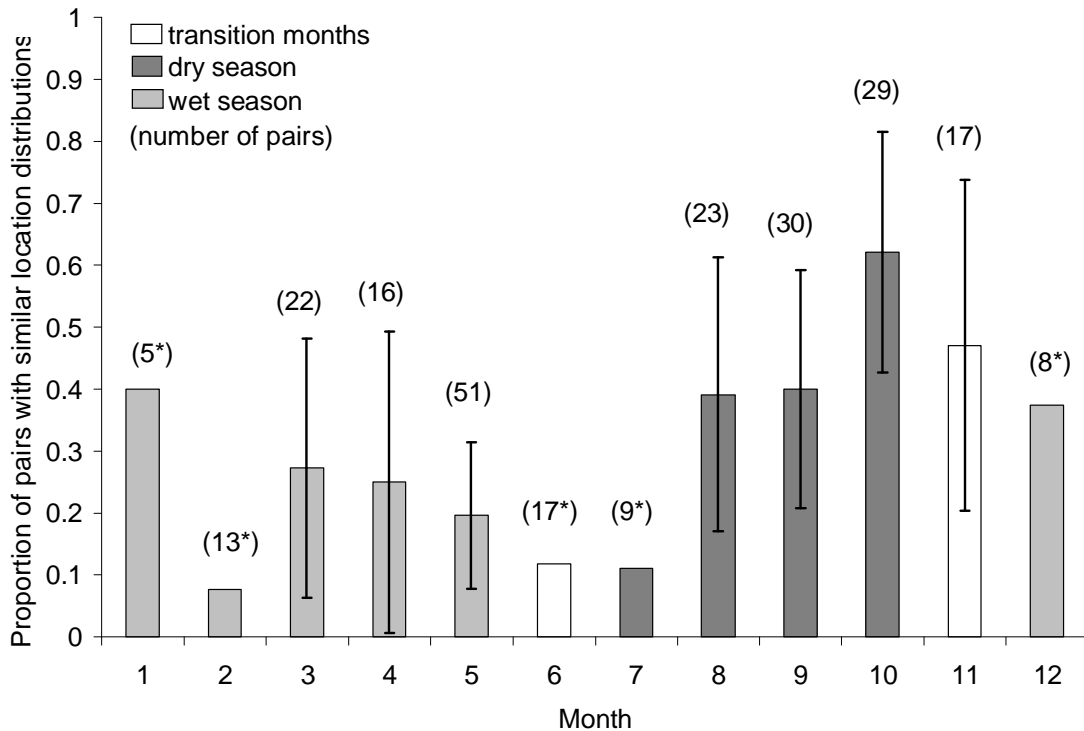
Figure 11. Proportion (bars represent the 95% CI) of unrelated pairs of females with similar location distributions throughout the year. Similarity in location distributions was determined using multi-response permutation procedures (MRPP). The wet season is indicated by light gray bars. The dry season is indicated by dark gray bars, and transition months are white. I had too few monthly comparisons (n = 16) to repeat the analysis for related pairs of individuals. *Sample sizes, for months 1, 2, 6, 7 and 12, were too small for reliable estimates of a confidence interval about the mean. The proportion (*p*) is too close to 0 with a low sample size to reliably estimate a confidence interval about the mean (Zar, 1999:529).
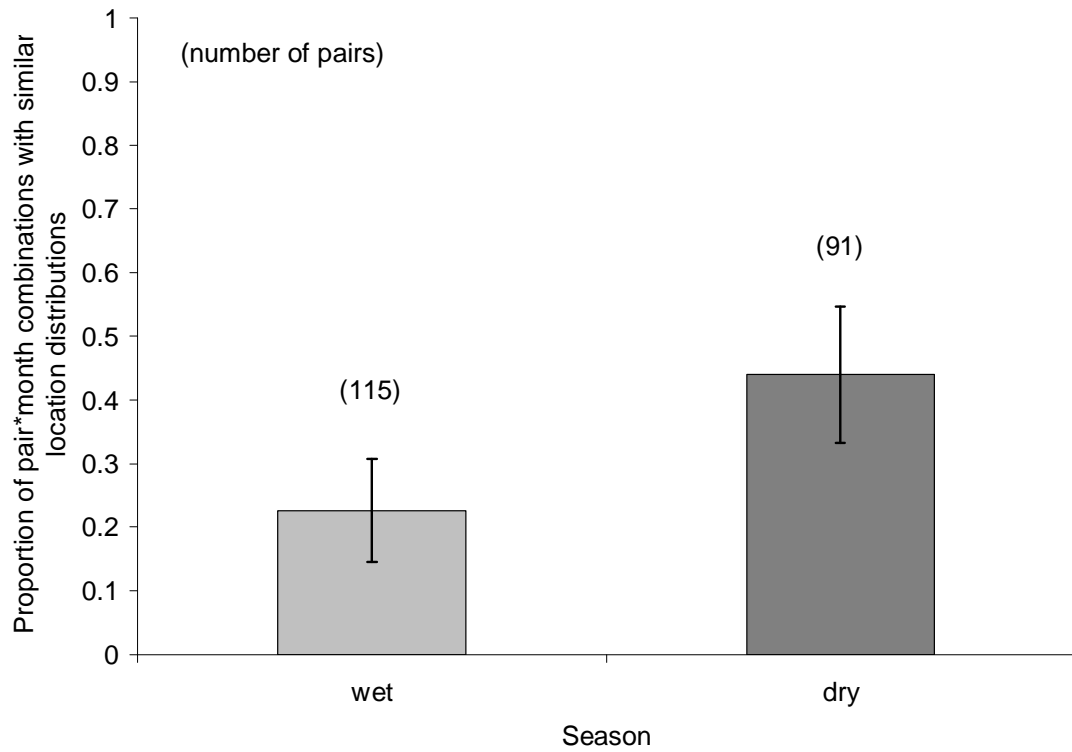
Figure 12. Proportion (bars represent the 95% CI) of pairs of unrelated individuals with similar monthly ranges pooled by season. Similarity in location distributions was determined using multi-response permutation procedures (MRPP). I had too few monthly comparisons (n = 16) to repeat the analysis for related pairs of individuals.
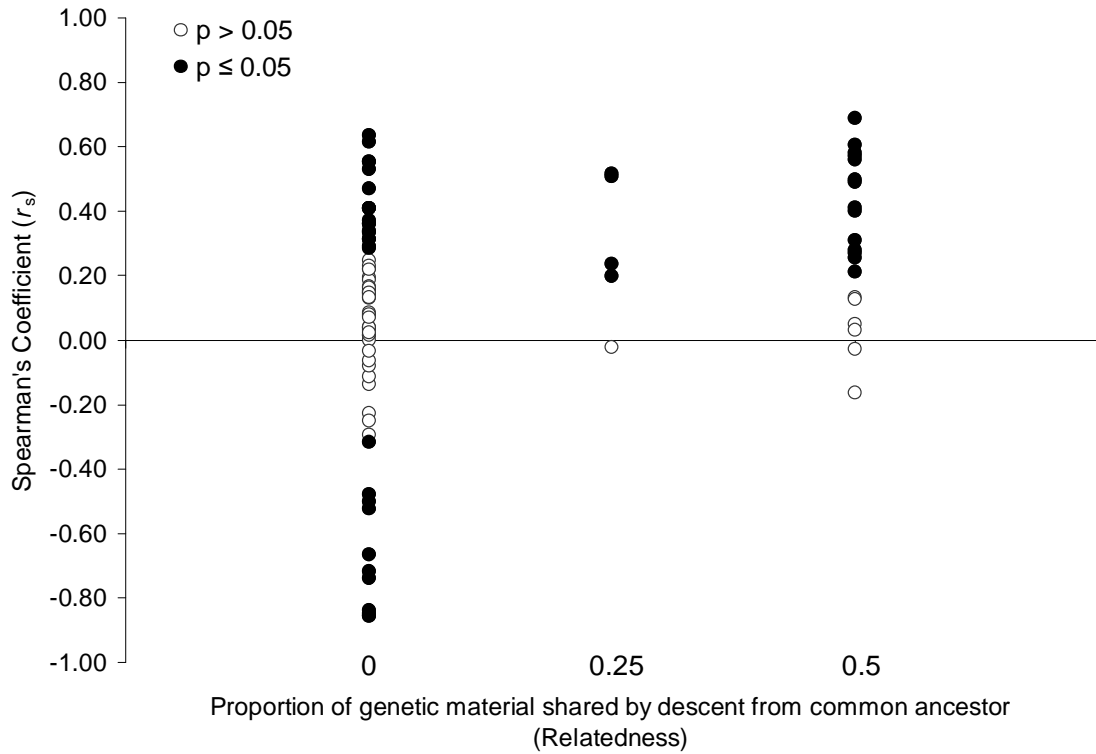
Figure 13. Spearman's Rank Order Correlation Coefficient (r_s) as a measure of static interaction in temporally overlapping adult ranges for pairs of female cheetah. Comparisons were summarized by relatedness such that mother-daughter and sister pairs share half of their genetic material, aunt-niece and grandmother-granddaughter pairs share a quarter and unrelated individuals share none. Positive r_s shows attraction while negative r_s shows avoidance (Doncaster, 1990).
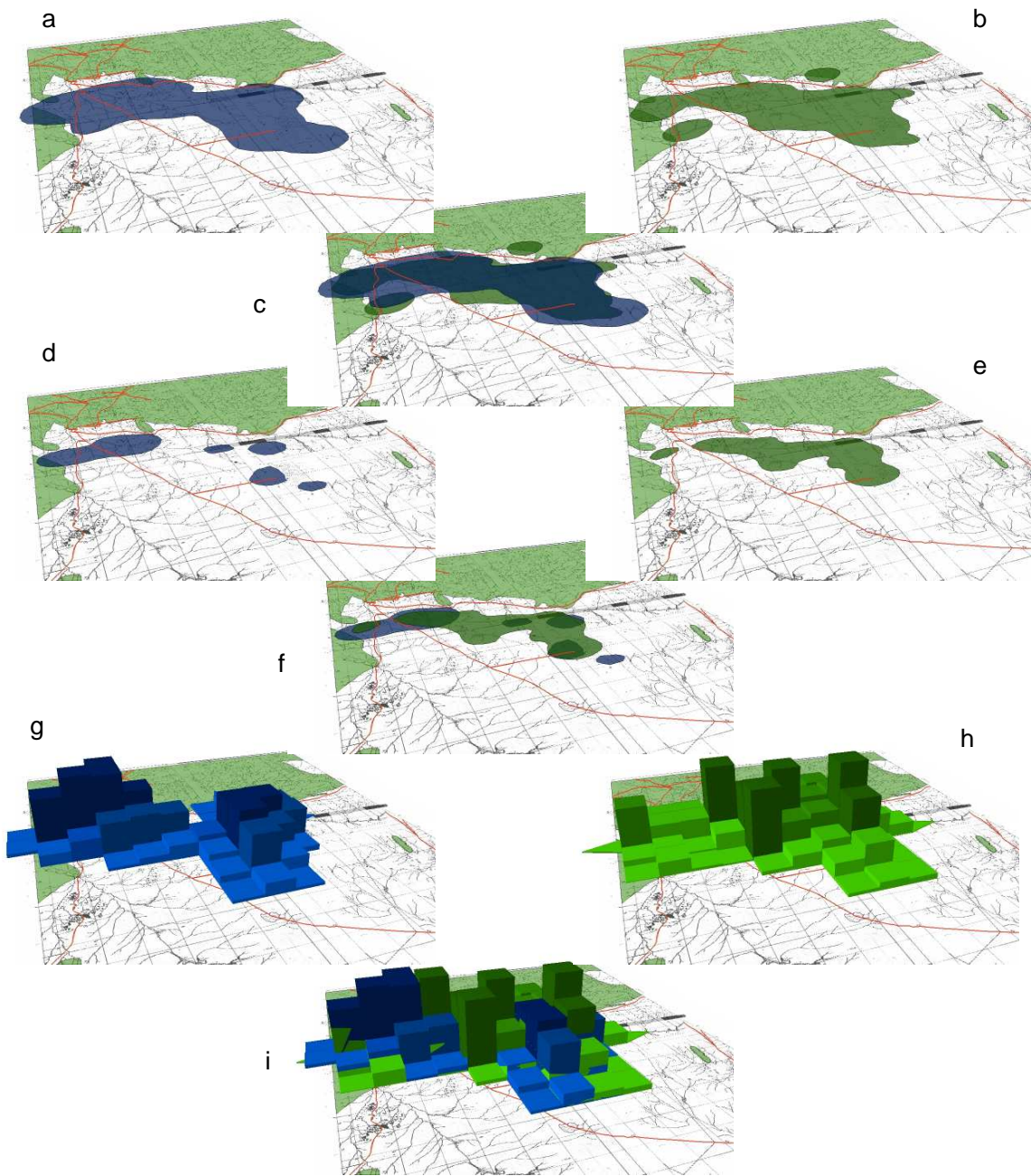
Figure 14. Static interaction between a pair of related female cheetah: a mother-daughter pair (1001:blue and 1002:green). These females overlapped by 66% for their lifetime home ranges (a – c), by 31% for their core ranges (d – f), and showed moderate attraction (r_s = 0.56, p < 0.0001). g – i are the raw utilization distributions, and were converted to ranks to determine the Spearman rank order correlation coefficient.
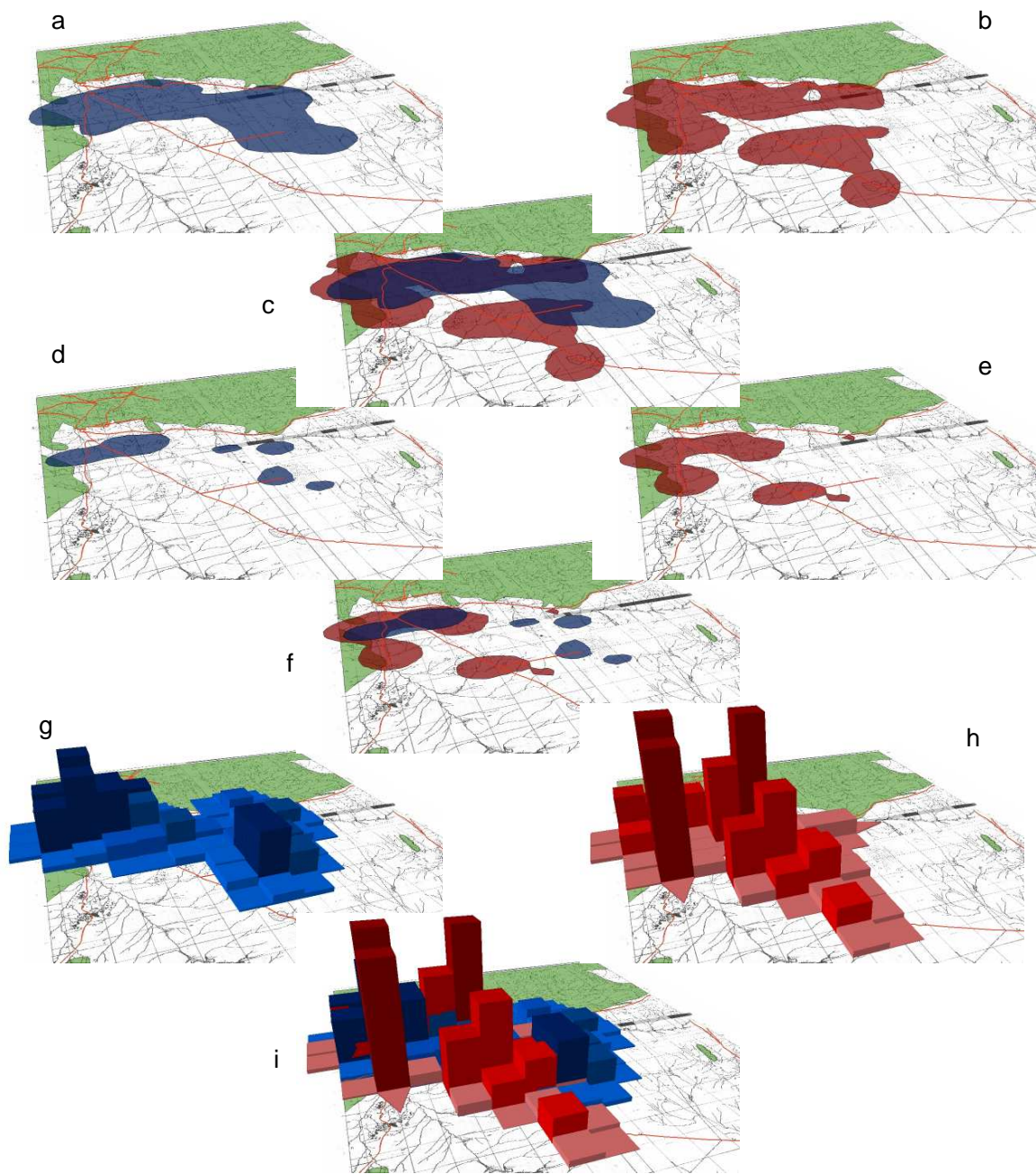
Figure 15. Static interaction between a pair of unrelated female cheetah (1001:blue and 1050:red). These females overlapped by 45% for their lifetime home ranges (a – c), by 27% for their core ranges (d – f), and showed a weak and non-significant interaction ($r_s = 0.22$, p = 0.057). g – i are the raw utilization distributions, and were converted to ranks to determine the Spearman rank order correlation coefficient.