Spatial ecology of free-ranging cheetah (*Acinonyx jubatus*) and its applications to mitigate the farmer-cheetah conflict in Namibia

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Table of Content

1. ACKNOWLEDGEMENTS 5

2. ZUSAMMENFASSUNG.. 8

3. SUMMARY 12

4. GENERAL INTRODUCTION 15

   4.1 Global distribution of cheetahs 15

   4.2 Threats and conservation status of cheetahs 16

   4.3 The Cheetah Research Project (CRP) of the Leibniz-IZW 18

   4.4 Social and spatial organization of cheetahs 21

   4.5 Estimating population abundance and density in cheetahs 23

   4.6 Human-cheetah conflict and its mitigation.. 26

   4.7 Objectives of this thesis.. 31

   4.8 References.. 35

5. Queuing, take-overs, and becoming a fat cat: Long-term data reveal two distinct male spatial tactics at different life-history stages in Namibian cheetahs.. 46

6. Coping with intrasexual behavioural differences: Capture-recapture abundance estimation of male cheetah.. 65

7. Shifting cattle herds away from communication hubs of cheetahs solves the cheetah-farmer conflict 79
7.1 Abstract 80
7.2 Introduction 80
7.3 Results 85
7.4 Discussion 88
7.5 Methods 97
7.6 References 101
7.7 Figure legends and figures 108
8. GENERAL DISCUSSION 121
8.1 Spatial tactics of cheetah males represent life-history stages 121
8.2 Best capture-recapture models for cheetah allowing for heterogeneity in detection 124
8.3 Novel and successful mitigation strategy for human-cheetah conflicts 128
8.4 Conclusion and perspectives 133
8.5 References 136
9. CURRICULUM VITAE 141
10. PUBLICATION LIST 142
10.1 Journal Publications 142
10.2 Book Chapters 147
11. INNOVATIONS/PATENTS 148
12. SELBSTÄNDIGKEITSERKLÄRUNG 154

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2. ZUSAMMENFASSUNG

Die Bestände und die Verbreitung des Geparden (*Acinonyx jubatus*) sind in den letzten Jahrzehnten weltweit dramatisch zurückgegangen. Der Gepard kommt heute nur noch auf 9% seines ursprünglichen Verbreitungsgebietes vor. Ungefähr 77% dieser Fläche liegen außerhalb von Schutzgebieten. Hier geraten Gepard und Mensch häufig in Konflikt. Das südliche Afrika beherbergt mit ca. 4.000 Individuen den größten Teil der weltweiten Bestandes von ca. 7.100 Individuen. Davon leben in Namibia etwa 1.500 Individuen, die zusammen mit den Geparden Botswanas die größte zusammenhängende Population weltweit bilden.

Allerdings ist diese Population bedroht, da die meisten Tiere auf Rinderfarmen vorkommen, wo sie zum Teil ernsthafte ökonomische Auswirkungen haben und deshalb regelmäßig von den Farmern bejagt werden. Aus Sicht des Naturschutzes ist es von hoher Bedeutung, dass diese Gepardenpopulation erhalten bleibt und überlebt. Dafür müssen Maßnahmen und Handlungsempfehlungen entwickelt werden, die den Farmer-Geparden Konflikt entschärfen.

Diese Dissertation entstand im Rahmen des „Cheetah Research Projects“ (CRP) im Leibniz-Instituts für Zoo- und Wildtierforschung (IZW) in Berlin. Ich habe selbst über elf Jahre Langzeitdaten zum Bewegungsverhalten der Geparde erhoben mit dem oben genannten Ziel, Maßnahmen und Handlungsempfehlungen ableiten und testen zu können.

In einem ersten Schritt habe ich in **Kapitel 5 (Publikation 1)** die soziale und räumliche Organisation frei lebender Geparde auf kommerziellem Farmland in Namibia untersucht. Obwohl Geparde seit Jahrzehnten in mehreren Gebieten weltweit erforscht wurden, war ihre soziale und räumliche Organisation bis dato noch nicht abschließend geklärt. Die umfangreichste Studie wurde in den 1990iger Jahren im Serengeti Nationalpark (NP) in Tansania durchgeführt. Sie beschrieb eine einzigartige soziale Organisation unter Säugetieren: Erwachsene Männchen sind entweder territorial oder aber ziehen als „Floater“ in großen Streifgebieten umher. Die Territorien sind verglichen mit den Streifgebieten der Floater klein und werden von den Besitzern an auffälligen Landmarken, wie großen Bäumen, Termitenhügeln oder Felsen markiert. Territorien schließen nicht direkt aneinander an sondern liegen voneinander getrennt in einer Matrix aus Niemandsland. Die Streifgebiete der Floater beinhalten jeweils mehrere Territorien, deren Markierungsstellen regelmäßig von den Floatern aufgesucht werden. Auch die adulten Weibchen bewegen sich in großen Streifgebieten über mehrere Territorien hinweg. Sie halten sich aber vorwiegend in der Matrix zwischen den Territorien auf. Sowohl die territorialen Männchen als auch die Floater kommen einzeln oder in Gruppen von zwei bis drei Männchen vor.

Nachfolgende Studien erkannten dieses System allerdings nicht, hauptsächlich weil sie die Männchen in einzel- oder gruppenlebende Männchen einteilten und somit in ihren Analysen die zwei räumlichen Taktiken unbewusst kaschierten. In diesem Kapitel 5 zeige ich, basierend auf Bewegungsdaten von 133 Männchen und 31 Weibchen, dass die soziale und räumliche Organisation der Geparde aus dem Serengeti NP auch in Namibia existiert. Dazu wurden mehrere Vorhersagen getestet, die aus dem Gepardensystem in Tansania abgeleitet wurden. Die daraufhin aus publizierten Studien neu analysierten Daten bestätigten das gleiche System auch für diese Studien. Aus den Tatsachen, dass territoriale Männchen bevorzugten Zugang zu Weibchen haben, die Floater heftig um die Territorien kämpfen und das System jetzt für alle vorliegenden Studien bestätigt werden konnte, schließe ich, dass es sich hierbei um einen evolutionären „trait“ der Geparden handelt und erwarte ihn auch in anderen Populationen zu finden.

Kapitel 6 (Publikation 2) untersucht die Auswirkung von diesem Gepardensystem auf Kamerafallen-Studien und Fang-Wiederfang-Modelle, die die Abundanzen und Dichten von Tierpopulationen abschätzen. Solche Modelle verlangen üblicherweise hohe Fang- und Wiederfangraten und eine für alle Individuen homogene Detektionswahrscheinlichkeit an den Kamerafallenstationen. Fang- und Wiederfangraten waren an den Markierungsbäumen am höchsten. Hierher kommen die markierenden territorialen Männchen beinahe täglich, die Floater häufig und regelmäßig und die Weibchen selten vorbei. Dies bedeutet in der Konsequenz, dass die Detektionswahrscheinlichkeit von territorialen Männchen, Floatern und Weibchen sehr unterschiedlich ist. Somit wurden in früheren Studien die statistischen Annahmen der Fang-Wiederfang Modelle verletzt mit mutmaßlich negativen Auswirkungen auf deren Ergebnisse. In Kapitel 3 haben wir vier Arten von Fang-Wiederfang Modellen getestet, die für heterogene Detektionswahrscheinlichkeiten von Individuen entwickelt wurden. Die daraus resultierenden Abundanzschätzungen wurden mit den wahren Abundanzen in den Untersuchungsgebieten verglichen. Daraus konnten wir die beiden besten Modelle ableiten, von denen ein Modell den Vorteil hat, dass die räumliche Taktik der Männchen nicht a priori bekannt sein muss. Die Schätzwerte dieser beiden Modelle entsprachen der bekannten Abundanz.

Mit den gewonnenen Erkenntnissen habe ich in **Kapitel 7 (Manuskript)** die lokale Dichte und Aktivität der Geparde auf Farmland und in Bezug auf Mensch-Tier Konflikte und das Farmmanagement analysiert. Einige Farmen überlappten mit einem Territorium, andere nicht. Die Zentren der Territorien mit den jeweiligen Markierungsstellen wiesen eine hohe

Gepardenaktivität im Vergleich zu anderen Gebieten auf. Für diese Zentren schlagen wir den Begriff „cheetah communication hub“ vor, da sie eine wichtige Rolle im Sozialsystem der Geparde spielen. Aus Sicht der Farmer sind sie lokale „Hotspots“ mit hohem Prädationsrisiko für ihre Nutztiere. Mithilfe eines experimentellen Ansatzes konnte gezeigt werden, dass Farmer, die ihre Mutterkuhherden in einem solchen Hotspot weiden ließen, wesentlich höhere Kälberverluste verzeichneten als Farmer, die ihre Mutterkuhherden weit entfernt von einem Hotspot hielten. Diese Entdeckung wurde genutzt, um einen Nutztier-Managementplan für Farmer zu entwickeln, deren Farmen mit einem Hotspot überlappen. Wenn sie ihre Mutterkuhherden aus dem Hotspot nahmen, reduzierten sich ihre Verluste drastisch. Die Hotspots verschoben sich nicht und die Geparde folgten nicht den Mutterkuhherden. Stattdessen erbeuteten sie die lokal natürlich vorkommenden Wildtierarten auf der Farm. Die hier vorgestellte und getestete Maßnahme stellt somit eine hoch effektive und insbesondere nachhaltige Lösung zur Minderung des Farmer-Geparden Konfliktes in Namibia dar und ist sehr wahrscheinlich auch auf andere Gebiete übertragbar.

3. SUMMARY

The global distribution of the cheetah (*Acinonyx jubatus*) has decreased dramatically during the past decades. Cheetahs are currently confined to only 9% of their former range. Approximately 77% of the cheetah range lies outside protected areas, frequently exposing cheetahs to conflict with people. Southern Africa represents with approximately 4,000 individuals the stronghold of the global cheetah population which comprises approximately 7,100 individuals. Namibia hosts approximately 1,500 individuals, which together with the cheetahs in Botswana form the largest connected population worldwide. This population is threatened because most of these cheetahs roam on livestock farms and are persecuted by farmers. From a conservation point of view it is therefore of utmost importance to develop non-lethal mitigation strategies to reduce this long-lasting farmer-cheetah conflict.

This dissertation thesis was conducted to use long-term data of the Cheetah Research Project (CRP) of the Leibniz Institute for Zoo and Wildlife Research (IZW) in Berlin, Germany, to develop and test such a mitigation strategy in Namibia. In **chapter 5 (publication one)**, I investigated the socio-spatial organization of free-ranging cheetahs on commercial farmland in central Namibia. Although cheetahs have been studied in several areas in the world for decades, their socio-spatial organization had not yet been clarified. The most comprehensive study was conducted in the 1990s in the Serengeti National Park (NP) in Tanzania and described a unique social organisation in mammals. Adult males either defended small territories separated from each other by some distance or roamed in large home ranges that encompassed several territories. The latter males are termed “floaters” and regularly visited the territories within their home ranges. Females also roamed in large home ranges which

encompassed several territories but stayed mainly in the area between territories. Both territory holders and floaters can be solitary or occur in coalitions of two to three males.

Subsequent studies elsewhere did not recognise such socio-spatial organization because of the method by which they categorized the individuals for data analysis. In this chapter I analysed the movement data of 133 males and 31 females to demonstrate that the socio-spatial organization of cheetahs described in the Serengeti NP also exists in Namibia. Several predictions were derived from the social organisation described for the Tanzanian cheetahs and tested with the data of the CRP. Consecutively I re-analysed published data of previous studies and could confirm the two tactics also in these datasets. Territory holder have preferred access to females, floaters heavily fight for territories, and the pattern can be found in all studies populations. Therefore I conclude, that this behavior may be a general trait of the species.

In **chapter 6 (publication two)** we investigated the consequences of this spatial system for camera trap studies and capture-recapture models that estimate abundance and density of animal populations. Such models require high capture and recapture rates and a homogeneous detection probability of all individuals at camera trap stations. Capture and recapture rates were highest at the marking trees of territories, where territory holders frequently marked and which were regularly visited by floaters and irregularly visited by females. This meant that the detection probability at marking trees differed strongly between territory holders, floaters and females. Thus, the assumptions of most capture-recaptures models were violated in previous studies that provided abundance and density results of cheetahs by applying such techniques and are therefore likely to be biased. Chapter 6 tested the performance of four types of capture-recapture models whose assumptions permitted heterogeneity in the detection probability and compared the estimated abundance with the true abundance of cheetahs in the study area. This revealed two best suited models for the socio-spatial organization of cheetahs with one being favorable if spatial tactic is not known a priori. The results matched with the known abundances.

On the basis of this information, I looked in **chapter 7 (manuscript)** at the local density and activity of cheetahs within the landscape and in relation to human-wildlife conflict and farm management. Some farms overlapped with a cheetah territory, others did not. The marking trees in the core area of cheetah territories had a substantially higher cheetah activity than other areas. We termed these core areas of the territories "cheetah communication hubs", because they play an important role in the social system of cheetahs. From the perspective of the farmers, these hubs are local hotspots of predation risk for the cattle. We used an experimental approach to demonstrate that farmers who stationed their suckler cows and calves in such a hub suffered substantially higher losses of calves than farmers who had stationed their breeding herds far away from such a hub. This discovery was used to develop a livestock management plan for farmers overlapping with a cheetah hub. When their breeding herds were shifted away from the hub, their losses decreased substantially. This is because the hub did not shift, nor did the cheetahs conduct excursions to pursue and hunt the calves. Instead, they preyed on the local, naturally occurring wildlife prey. The mitigation strategy presented and tested here is therefore a highly effective and sustainable solution to reduce the farmer-cheetah conflict in Namibia and potentially also elsewhere.

4. GENERAL INTRODUCTION

4.1 Global distribution of cheetahs

Historically, the cheetah (*Acinonyx jubatus*) was widely distributed throughout Africa and Asia (Durant et al. 2017). During the last decades, its distribution has shrunk dramatically (Figure 1) and is currently confined to only 9% of its previous range, with an estimated 7,100 adult and juvenile individuals (Durant et al. 2017). The current global cheetah population consists of 31 populations distributed in 20 countries of Africa and the Middle East (Durant et al. 2017, 2018). The largest populations occur in southern and eastern Africa with approximately 4,000 and 2,300 adult and juvenile cheetahs, respectively (Durant et al. 2017), whereas in Asia there is only one population known with as few as 50 cheetahs (Farhadinia et al. 2016). In most countries, the status of the species is unknown and little data are available on population distribution or size (Durant et al. 2015). Namibia and Botswana are the global strongholds of the cheetah in terms of abundance and area. Namibia hosts approximately 1,500 adults and juveniles (Melzheimer et al. in review) that are part of a trans-boundary population with Botswana (Figure 1). Population trends are largely unknown. When they were assessed, most of them were judged to be declining (Durant et al. 2017).

Most of the current cheetah range, i.e. 77%, lies outside of protected areas (Figure 1), where cheetahs potentially come into contact with people (Durant et al. 2017, Weise et al. 2017). In such areas, cheetahs are not protected from prosecution and sometimes are even allowed to be legally killed when people have some evidence that a particular cheetah has preyed upon a livestock animal (Marker et al. 2003). As this is often difficult to demonstrate beyond reasonable doubt, many cheetahs are killed indiscriminately (Marker et al. 2003, Weise et al. 2017).

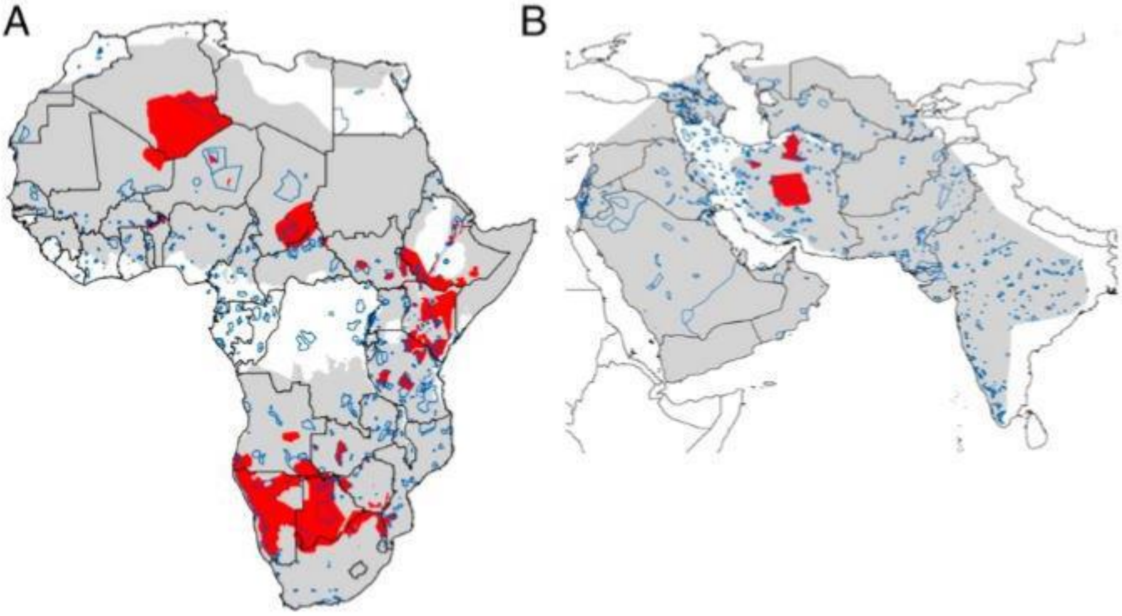

Figure 1: Currently known cheetah distribution (red) and historical range (grey) in A) Africa and B) Asia. Boundaries of protected areas are marked in blue. This map was originally published in Durant et al. 2017, of which the author of this thesis is a co-author and therefore holding "the right to reuse the original figures and tables in future works" as per PNAS license terms.

4.2 Threats and conservation status of cheetahs

The main reasons for the global decline of cheetahs are human-wildlife conflicts, human-induced habitat loss and fragmentation, illegal trade and competition with other large carnivores (Laurenson 1994, Ripple et al. 2014, Maxwell et al. 2016, Joe et al. 2018). Good information on illegal trade is scarce. There is evidence that cheetahs are captured in the wild in southern Africa and are regularly exported through the Horn of Africa into other countries, mainly to the Arabian peninsula, as pets for private owners (Tricorache et al. 2018). For cheetahs inhabiting areas where other large carnivore species such as lions (*Pathera leo*) and spotted hyenas (*Crocuta crocuta*) are present, their main threat is competition with and predation by these carnivores (Caro 1994, Laurenson 1994). Competition occurs when the physically superior lions or spotted hyenas steal (kleptoparasite) prey animals killed by cheetahs. Predation of cheetahs occurs when mostly lions kill cheetahs cubs in the lair or when encountered in the field with their mothers (Caro 1994, Laurenson 1994). In the Serengeti National Park (NP) in Tanzania, East Africa, the latter has a major effect on the cheetah population, because only 23% of the cubs survive to adulthood (Laurenson 1994). In areas without lions and spotted hyenas, such as the commercial farmland in Namibia, cub survival is 79% and thus substantially higher (Wachter et al. 2011).

Climate change might become an additional threat in the future, if the semi-arid environments where the majority of free-ranging cheetahs roam become drier and as a consequence prey availability for cheetahs may decrease (Midgley et al. 2005, Muntifering et al. 2006). Legal trophy hunting is allowed in Namibia and Zimbabwe with a quota of 150 and 50 animals per year, respectively (CITES 1992), but is not considered a threat to these populations (Cristescu et al. 2018). It is presently unclear whether such quotas may have a detrimental effect if they coincide with other detrimental factors. In particular when adult females are removed it is unclear whether the populations are large enough to remain viable (Crooks et al. 1998, Cristescu et al. 2018).

The unusually low genetic diversity has also been suggested to be a threat to the populations, because it was assumed that it hampers successful reproduction and prevents adequate immune responses towards pathogens (O’Brien et al. 1983, 1985, Wildt et al. 1993). It has now been recognised that free-ranging cheetahs successfully reproduce and have a strong innate immune system to fight pathogens (Laurenson 1994, Wachter et al. 2011, Heinrich et al. 2016, 2017). Nevertheless, low levels of genetic diversity might affect the ability of the cheetah to adapt to rapid environmental changes or to newly emerging diseases (Castro-Prieto et al. 2011, Schmidt-Küntzel et al. 2018).

Because of the substantial decline of its range and numbers and the numerous threats, the cheetah is considered to be the most threatened large felid species in Africa (Durant et al. 2015). It is categorised as “vulnerable” by the Red List of the International Union for Conservation of Nature (IUCN) and recently was suggested to be upgraded to the category “endangered” (Durant et al. 2015, 2017). Although most cheetah populations are undoubtedly decreasing, precise assessments of population sizes are often not available (Durant et al. 2017). This is because cheetahs, similar to many other carnivores, are notoriously difficult to count – because of their elusive behaviour, large home ranges, their unique socio-spatial organization the wide variety of habitats which they use and their variable low densities (Caro 1994, Sunquist and Sunquist 2002, Dalerum et al. 2008, Portas et al. 2018). It is crucial for any management or protection plan to work with reliable population assessments and to understand the movement ecology of the cheetahs to develop non-lethal mitigation strategies for the wide spread farmer-cheetah conflict.

4.3 The Cheetah Research Project (CRP) of the Leibniz-IZW

In 2002, the Leibniz Institute for Zoo and Wildlife Research (IZW) initiated the Cheetah Research Project (CRP) in central Namibia together with a local cooperation partner (Okatumba Wildlife Research). The CRP hired two houses on farmland as research stations and collaborated from the very beginning with the commercial farmers on whose land the cheetahs roam. The farmers were involved in the development of the research questions and regularly informed on progress and results of the research activities. This close interaction grew over the years into a relationship based on mutual trust and understanding from which both sides profit until today (Frigerio et al. 2018).

I joined the CRP in 2005 and was responsible, among other tasks, for maintaining existing farmer contacts and initiating new contacts with farmers and other stakeholders such as hunting operators, government officials, wildlife rangers and media people. I also collated much information on livestock losses of farmers and their perception towards carnivores and cheetahs in particular. This close contact resulted in mutual trust and farmers helping the CRP to capture cheetahs with box traps at marking trees (Figure 2). Captured cheetahs are immobilized and fitted with GPS collars, weighted and measured, and biological samples such as blood, feces, ectoparasites and hair are collected for various studies on health, endocrinology, genetics, immunology and reproduction (e.g. Thalwitzer et al. 2010, Castro-Prieto et al. 2011, Wachter et al. 2011, Ludwig et al. 2013, Krengel et al. 2013, Voigt et al. 2013, Heinrich et al. 2016, Costantini et al. 2017).

The mutual trust between farmers and project members was the foundation for this dissertation, particularly for Chapter 7, which presents a novel and sustainable non-lethal mitigation strategy for the long existing cheetah-farmer conflict in Namibia. To develop this strategy, it was necessary to first understand the movement ecology and socio-spatial organization of cheetahs and their abundance and density in the study area.

Figure 2: Cheetah capture and handling. A) drone photo of a box trap at a marking tree with a thorny kraal around the tree. In this setting, the only possibility for a cheetah to approach the marking tree is the way through the trap. B) handling of the cheetah with farmers as guest. Cheetahs are immobilized, fitted with a GPS collar and samples collected.

4.4 Social and spatial organization of cheetahs

Mammalian species exhibit a variety of social and spatial organizations. The main driving factors are the ranging behavior of the females, the capability of males to defend the females and/or their ranges against other males, and on the female sociality (Clutton-Brock 2016). If female ranges can easily be defended by males, males do so (e.g. Columbian ground squirrel *Spermophilus columbianus*, Festa-Bianchet and Boag 1982, or lions *Panthera leo*, Schaller 1972). If ranges of females cannot easily be defended and females live in stable groups, males temporarily occupy the range of one or several female groups (e.g. red deer *Cervus elaphus*, Clutton-Brock et al. 1982, or Cape buffalo *Syncerus caffer*, Sinclair 1977). If females live in groups which are unstable, males defend territories comprising only a portion of the range of a female group (e.g. white rhinoceros *Ceratotherium simum*, Owen-Smith 1972) or leks (e.g. fallow deer *Dama dama*, Clutton-Brock et al. 1988). And if females are solitary, live at low density and range widely, males also roam widely in search of females (e.g. polar bear *Ursus maritimus*, Ramsay and Stirling 1986).

The social and spatial organization of cheetahs does not fit into this classification scheme of mammals. This was recognized in the 1980s, when Clutton-Brock (1989) suggested that cheetahs represent a unique variant of the system that white rhinoceros exhibit. In the 1990s this was confirmed and elaborated by Caro (1994), who conducted extensive observational studies and some radio-tracking in the Serengeti NP. Caro (1994) described the social system as consisting of adult males that are either solitary or in groups (coalitions) of two to four brothers, and sometimes also of non-related males, and solitary adult females with or without offspring. Males (solitary or in coalitions) either defended small territories (48 km2) separated from each other by several kilometers or they roam as “floaters” in large home ranges (mean 777 km^2), visiting frequently the marking trees of territory holders in the small territories. These floaters are not dispersing males in search of a home range away from the natal area, but established adult males with a stable home range. Females also roam in large home ranges (mean 833 km^2), normally avoiding the territories but visiting them at infrequent, irregular intervals (Caro 1994). Competition over territories was high because holding a territory enhanced access to females (Caro and Collins 1987, Caro 1994). Paternity analyses, however, did not clearly reveal whether territory holders or floaters had a higher reproductive success (Gottelli et al. 2007).

Subsequent studies did not describe these features of socio-spatial organisation of the Tanzanian cheetah males in other study populations (Broomhall et al. 2003, Marker et al. 2008a, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). At first sight this seems surprising, because socio-spatial organizations of mammalian species are generally stable traits of a species, with only some variation in terms of adaptations to local environmental conditions (Clutton-Brock 2016), even though such intraspecific variation (Lott 1991) can sometimes be considerable (e.g. in spotted hyenas *Crocuta crocuta*, Hofer and East 1993). Also, holding a territory seemed to be under strong selective pressure as it may increase access to females, thus explaining why floaters might heavily fight for territories (Caro and Collins 1987, Caro 1994). At a closer look, it turned out that subsequent cheetah movement ecology studies reported range sizes for solitary males and males in coalitions, without detecting a difference between their range sizes (Broomhall et al. 2003, Marker et al. 2008a, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). Since both territory holders and floaters can be solitary or occur in coalitions (Caro 1994), studies contrasting solitary males with coalitions will not detect the two spatial tactics described in the Serengeti NP. It was therefore still unclear whether the socio-spatial organization of cheetahs in the Serengeti NP is unique or whether it occurs in other populations but was masked by inappropprisate categories by which ranging data of cheetah males were analysed and interpreted.

Chapter 5 investigates the socio-spatial organization of cheetahs on farmland in Namibia and re-analyses data reported by previous studies in Namibia. For this purpose, I used long-term data from 2002 to 2014 from the CRP of the Leibniz-IZW in Namibia and tested predictions derived from the socio-spatial organization of cheetahs in the Serengeti NP. I demonstrate that the socio-spatial organization of cheetahs in Namibia is similar to the one in the Serengeti NP, i.e. that cheetah males either as solitary individuals or in coalitions are either territory holders or floaters and females use large home ranges.

4.5 Estimating population abundance and density in cheetahs

Knowledge of the socio-spatial organization of cheetahs is crucial to estimate abundance and density of cheetahs and to potentially extrapolate the results to areas not yet studied in detail. The marking trees in the core area of the territories are areas of high cheetah activity. As I show in chapter 5, territory holders mark these marking trees at high rates to advertise their ownership and floaters regularly visit the marking trees of several territories to inspect them; females also visit the territories every now and then (Caro 1994, Chapter 5). The matrix between territories is used by floaters to move from one territory to another (Chapter 7) and by females in a non-predictable manner (CRP, unpublished data). As a consequence, encounter probability varies substantially and depends on the location of the observer or camera trap, the sex and the spatial tactic of the cheetah. This has some profound consequences when estimating cheetah abundance and density, which had been previously ignored.

Camera traps are an established method to estimate abundance and density of rare and elusive animal species, particularly for species which can be individually identified by their spot pattern (e.g. tiger (*Panthera tigris*) Karanth and Nichols 1998, jaguar (*Panthera onca*) Sollman et al. 2011, leopard (*Panthera pardus*) Gray and Prum 2012, Sunda clouded leopard (*Neofelis diardi*) Wilting et al. 2012). Cheetahs can be individually identified by their spot pattern (Caro 1994) and such assessments have been conducted already in the past (e.g. Marnewick et al. 2008, Boast et al. 2015, Brassine and Parker 2015). To estimate abundance and density from camera trap data, a variety of capture-recapture models are commonly used (Sollmann 2018). These models make certain statistical assumptions which need to be accommodated in the study design to generate reliable estimates (Pledger 2000, Sollmann et al. 2011, Sollmann 2018).

One common assumption of such models is that the probability that the camera captures a particular individual is equal for all demographic and social classes (homogeneity of detection, Pledger 2000, Boulanger et al. 2014). Another assumption is the independence of detections based on a full mixture of the population between capture and recapture events. An important factor for robust estimates is a high recapture rate, thus the camera trap location is a crucial element of the study design (Soisalo and Cavalcanti 2006, Brassine and Parker 2015).

Capture probability of individuals is often heterogeneous and may depend on sex, age, social status, breeding status or an individual’s response to the presence of camera traps (Lebreton et al. 1992, Krebs 1999, Perret et al. 2003, Wegge et al. 2004, Sollmann et al. 2011).

If differences of detection probabilities for different segments of a population are known, then they can be incorporated into the capture-recaptures models, and even unmeasured but known factors can be considered (Pledger 2000, Sollmann 2018). Previous studies which applied such models to cheetahs did not consider the two spatial tactics of cheetah males as a source of heterogeneity because these tactics were not considered to exist outside the Serengeti NP (Marker et al. 2008b, Marnewick et al. 2008, Boast et al. 2015, Brassine and Parker 2015, Fabiano et al. 2018) until now (Chapter 5). This also violates the assumption of independence of detections.

Similarly, the spatial organisation of cheetah males strongly influences the probability of capture and recapture at camera trap locations. Camera traps located at marking sites in the core area of territories captured substantially more cheetahs per 100 trapping nights than camera traps located along roads or game trails or distributed evenly within a pre-set grid (Soisalo and Cavalcanti 2006, Brassine and Parker 2015, Portas et al. 2017). Although previous studies have recognised the importance of locating camera traps at cheetah marking sites to increase camera trap success, they did not recognise that males operate two different spatial tactics and thereby violated the above mentioned assumptions (Marker et al. 2008b, Marnewick et al. 2008), resulting in biased abundance and density estimates (Chapter 6, Portas et al. 2017).

Recently, studies estimating the abundance and density of highly mobile species roaming across large ranges started to use the newly developed spatially explicit capture-recapture (SECR) models (Royle et al. 2014) instead of simple capture-recapture models. SECR models overcome the difficulty of conventional models of determining what the realised sampling area is, since individuals of the study population usually use areas beyond the camera trap grid (Royle et al. 2014). These models assume that the detection probability of individuals decreases with increasing distance from the centre of their home range (Royle et al. 2014). This may be the case for some species but clearly not for cheetah floaters, as Chapter 5 demonstrates. Floaters oscillated between territories, with their detection probability being highest at marking trees within the territories of the territory holders, which are not necessarily in the center of their large home range as it usually encompasses several territories (Chapter 7). Therefore, SECR models are not applicable to cheetahs. Previous studies that did not recognize the spatial organization of cheetah males used SECR models to determine density estimates (Boast et al. 2015, Brassine and Parker 2015), resulting in biased estimates (Chapter 6).

Chapter 6 investigates the performance of four types of capture-recapture models for cheetah males in Namibia which accommodate heterogeneity in detection probabilities in different ways. The chapter considers for the first time the two spatial tactics of cheetah males for estimating the abundance of cheetahs in an area. The study area was part of the long-term CRP of the Leibniz-IZW and all territory holders and floaters visiting the monitored territories were known. Thus, it was possible to compare the model performance with true abundance of cheetah males and to identify the best model.

4.6 Human-cheetah conflict and its mitigation

Approximately 77% of the current cheetah range is located outside protected areas (Figure 1). One reason for this is that within protected areas often larger carnivore competitors such as lions, spotted hyenas, brown hyenas (*Hyaena brunnea*) or leopards co-exist with cheetahs, and cheetah abundance and density are low (Caro 1994, Durant 1998, Mills et al. 2014). Areas outside protected areas are often inhabited by people who over at least the last century persecuted large carnivore species to protect their livestock (Marker-Kraus et al. 1996). One method to eliminate large carnivores in southern Africa was to provide them with poisoned prey carcasses (Marker-Kraus et al. 1996). Luckily, for cheetahs, such poisonings had little effect on cheetahs since cheetahs do not scavenge from carcasses and only feed on self-killed prey (Caro 1994). This resulted in entire regions where all large carnivores except cheetahs were wiped out. With its competitors removed, the latter increased in numbers (Marker-Kraus et al. 1996). Today, the freehold farmlands in Namibia and Botswana host the largest cheetah population worldwide (Durant et al. 2017, Weise et al. 2017), and these countries carry a particular responsibility for the survival of the species. It is therefore of utmost importance to find non-lethal mitigation procedures to minimize the cheetah-farmer conflict, preferably by an evidence-based approach (Kareiva et al. 2018), i.e. understand their biology, movement ecology, diet and population dynamics to develop sustainable non-lethal conflict mitigation strategies.

Livestock and game farmers, hunting operators on freehold land as well as subsistence pastoralists in the communal areas are in conflict with cheetahs to this day (Marker-Kraus et al. 1996, Marker et al. 2003, Durant et al. 2017, Weise et al. 2017, Dickman et al. 2018). Farms also contain local, naturally occurring wildlife species such as warthog (*Phacochoerus africanus*), springbok (*Antidorcas marsupialis*), hartebeest (*Alcelaphus buselaphus*), gemsbok (*Oryx gazella*) and greater kudu (*Tragelaphus strepsiceros*) (Mendelsohn et al. 2003). Farmers, hunters and pastoralists often display low tolerance towards predators because carnivores may kill livestock and/or valuable trophy animals, thereby reducing returns of investment which can range from minimal to substantial economic losses (Marker et al. 2003, Weise et al.

2017, Dickman et al. 2018). Verified cheetah kills are only rarely documented and detected on commercial farms, as these farms have an average size of approximately 45 km^2 and the large livestock herds live semi-wild without herders or protecting guard dogs (Mendelsohn et al. 2003). During calving season, the herds are visited more regularly by their owners because calves need to be registered with the studbook, ear tagged and vaccinated. If calves are suddenly missing, these losses are then often attributed to the cheetahs (Marker-Kraus et al. 1996), and alternative explanations such as mortality from injuries, snake bites and disease rarely considered.

Between 1980 and 1991, 6,293 cheetahs were reported to the Ministry of Environment and Tourism (MET) as “removed problem animals”, or on average 572 cheetahs per year (CITES 1992). The actual number is likely to be higher, because not all removed cheetahs might have been reported. Between 1997 and 2004, the MET recorded 1,088 removed cheetahs, or on average 155 cheetahs per year. The lower number is probably a consequence of the declining number of cheetahs on farmland rather than a general reduction in the perceived threat of cheetahs to livestock.

This is also apparent from a recent study. On 185 commercial farms in central Namibia, 50% of the land managers reported that they consider cheetahs to be responsible for conflicts and approximately half of these farmers actively persecuted cheetahs (Weise et al. 2017). The land owners reported to have lethally removed 196 cheetahs. The 10 least tolerant farm managers destroyed 72% of the animals (Weise et al. 2017). This resulted in an annual removal of 0.30 adult cheetahs/100km^2 (Weise et al. 2017). Although the removal rate by the interviewed farmers was not evenly distributed and therefore its effect on the cheetah population in central Namibia cannot easily be assessed, the removal seems high in comparison to an estimated density of 1.1 adult cheetahs/100km^2 in central Namibia (Portas et al. 2017).

During the last decades, several human-cheetah non-lethal conflict mitigation methods have been tested and/or are in place in Africa (Dickman et al. 2018). Most methods focus on better livestock protection and game management, such as using livestock guarding dogs, fitting livestock animals with protective metal collars or using electrified fences (McManus et al. 2014, Potgieter et al. 2016, Dickman et al. 2018). Other methods focus on cheetahs and translocate the animals to other areas or bring them into permanent captivity (Marker et al. 2003, Fontúrbel and Simonetti 2011, Weise et al. 2015). Yet other methods emphasise financial aspects and either introduced a compensation scheme for lost livestock or issued a certificate for beef produced on "carnivore-friendly farms", i.e. farms where carnivores are not eliminated by farmers (Maclennan et al. 2009, Marker et al. 2010, Marker and Boast 2015). Livestock guarding dogs and protective metal collars around the neck of livestock to prevent a bite are suitable for small livestock such as goats and sheep, not for cattle (McManus et al. 2004, Marker et al. 2005, Potgieter et al. 2016). Livestock guarding dogs are cost and time intensive (food, medical care, training) and if not properly trained were reported to kill medium-sized carnivore species such as black-backed jackals (*Canis mesomelas*) or calves of ungulates valuable to sports hunting such as greater kudu. Their usefulness therefore depends on the degree of investment and training (Potgieter et al. 2016). Electrified fences can prevent carnivore species from passing through, but they are also expensive and labour intensive to keep them functional (Dickman et al. 2018).

Translocation of "problem animals" is a method regularly conducted in Namibia (Marker et al. 2003, Marker et al. 2008a). When cheetahs were translocated in this way, they were not routinely fitted with a GPS collar to follow their movements after the release in the new area. One recent study investigated the fate of translocated cheetah into various areas and over various distances and showed that most translocations were not successful in the long run, i.e. cheetahs either successfully returned to or at least moved towards their place of origin (homing behaviour) or were killed in the new area (Weise et al. 2015). Bringing cheetahs into permanent captivity is not a sustainable conservation solution either, because these animals are not allowed to breed, females have to be sterilised (MET 2012) and if this is not the case, then they are likely to develop welfare-relevant reproductive pathologies (Wachter et al. 2011). Compensating livestock losses from predation has been tested with various concepts in eastern and southern Africa (Nyhus et al. 2003, Maclennan et al. 2009, Dickman et al. 2011). They were rarely successful because the prospect of compensation acts as a lure to "over-report" (blaming cheetahs for losses that were a consequence of other processes), difficulty to quickly verify that the livestock animal was killed by a predator, lack of access to the compensation scheme in remote areas or not accounting for the full market value of animals (Dickman et al. 2011). In addition, the success of the concept of certified beef is uncertain, because it is dependent on the willingness of consumers to pay more for such meat (Marker and Boast 2015)

All described mitigation methods did not mitigate the conflict to such an extent that the cheetah population has recuperated and improved its threat status according to the IUCN guidelines, nor did they induce a substantial change in the perception of farmers towards cheetahs. Chapter 7 presents a new approach, which uses the insights from the observed socio-spatial organization of cheetahs to experimentally test and refine a truly sustainable, tailor-made non-lethal mitigation measure.

As described in chapter 5, some cheetah males occupy small territories whereas others roam over larger areas. Chapter 7 looked in detail at the movements of floaters in relation to the location of territories and marking locations. I further investigated the stability of territories across several generations of territory holders and looked at these territories from a perspective of information and communication hubs at a cheetah population level. If territories are highly frequented by a large proportion of the regional cheetah population, this should result in local hotspots of cheetah activity, density and predation risk for livestock animals. If this is the case, then this source of the farmer-cheetah conflict is the key to its solution. Simply stated, farm management needs to be adjusted in such a way that cattle breeding herds are kept away from these hotspots.

This novel non-lethal mitigation strategy has now been used by farmers in central Namibia for several years and resulted in a change of perception of the threat cheetahs pose to their business. As a consequence, the farmers in the study area widely stopped persecuting cheetahs and are now a crucial partner contributing towards the conservation of Namibian cheetahs.

4.7 Objectives of this thesis

The global cheetah population has declined dramatically during the last decades (Durant et al. 2017). Namibia is a stronghold for cheetahs with a large distribution across the country and approximately 1,500 adult cheetahs occurring there (Durant et al. 2017, Weise et al. 2017, Melzheimer et al. in review). Most Namibian cheetahs live outside protected areas where they regularly come into conflict with humans (Durant et al. 2017, Weise et al. 2017). The farmland of Namibia is therefore one of the most important areas in the world to develop and test research-based / evidence-based non-lethal mitigation strategies in order to enhance the viability of this globally valuable cheetah population.

The first objective of this thesis was to investigate whether the socio-spatial organization described in the 1990s in the Serengeti NP (Caro 1994) is unique to the Tanzanian cheetah population or whether other populations also consist of territorial males defending small territories and floater males and females roaming across large home ranges that encompass the small territories which they would regularly visit. Since the long-term observational study of Caro (1994), no other study has described the cheetah system of the Serengeti NP for any other cheetah population (Broomhall et al. 2003, Marker et al. 2008a, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). I demonstrate that the cheetah population in Namibia operates in the same socio-spatial organization as the Serengeti and explore why previous studies did not detect this organization.

The second objective of this thesis was to assess and adapt existing abundance and density estimation techniques for cheetahs and critically examine the validity of all underlying statistical assumptions and requirements based on the uncovered socio-spatial organization of Namibian cheetahs. Chapter 6 investigates the performance of four types of capture-recapture models which allow for heterogeneity in detection and identify the best models applicable to cheetahs.

The third objective of the thesis was to use all the previously gained knowledge to develop research-based non-lethal mitigation strategies for Namibian farmers to reduce their livestock losses from cheetahs. Using an experimental approach, chapter 7 identifies spatial zones with high and low predation risk and provides information to farmers to adjust their farm and livestock management. The success of the mitigation strategies is documented and future extensions discussed.

The results of my studies are presented in two publications and one manuscript in preparation in the Chapter 5, 6 and 7:

Chapter 5 tests whether the socio-spatial organization described in the Serengeti NP is also valid for the cheetah population on farmland in Namibia. For this study, 133 males and 31 females were used for various analyses. The specific aims were to:

- determine home range sizes of male and female cheetahs,
- determine the marking behaviour of territory holders and floaters,
- describe territory take overs and the identity and fate of winners and losers,
- investigate how group size, age and body condition of males is linked to territoriality,
- identify factors with which territory holders and floaters can be easily identified by reliable biological markers at capture sites without any information on movement data.

Chapter 6 investigates the performance of four capture-recapture models which allow for heterogeneity in detection with data from five territories and compares the results with the true abundance of territory holders and visiting floaters in these five territories. The specific aims were to:

- model male abundance with (a) a spatial tactic model, (b) a finite mixture model, (c) a floater-only model and (d) a heterogeneity M_h model,
- determine the true male abundance in the five territories using camera traps,
- compare the results from the four models with the true abundance and determine the best model for cheetahs.

Chapter 7 uses an experimental approach to derive non-lethal mitigation strategies for farmers with livestock losses and assesses their success on the basis of the socio-spatial organization of cheetahs. The specific aims were to:

- identify the location of territories across the study area,
- investigate the temporal stability of territories,
- understand the movement behavior of floaters in relation to the location of territories,
- determine areas of high and low predation risk for each farm,
- identify areas where the breeding herds are likely to be safe until the calves are six months of age, in order to develop a management plan,
- follow the fate of livestock before and after the implementation of the management plan.

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Publication one

5. Queuing, take-overs, and becoming a fat cat: Long-term data reveal two distinct male spatial tactics at different life-history stages in Namibian cheetahs

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Queuing, takeovers, and becoming a fat cat: Long-term data reveal two distinct male spatial tactics at different life-history stages in Namibian cheetahs

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Abstract. In mammals, male spatial tactics and sociality can be predicted from the size, degree of overlap and ease of defense of female individual or group home ranges (HRs). An exception is apparently the cheetah (*Acinonyx jubatus*) for which studies from East Africa describe a socio-spatial organization where resident males defend small territories, which cover a portion of large ranges of solitary females, and non-territorial males (floaters) roam over vast areas whilst queuing for access to territories. Most studies from southern Africa did not report the existence of territorial males and floaters, but a system with both males and females roaming over vast areas with overlapping HRs. Here, we derive and test predictions from previously described spatial tactics in felids by studying the movements, behavior, and/or physical characteristics of 164 radio-collared Namibian cheetahs on commercial farmland from 2002 to 2014. The results demonstrate the existence of male territory holders and floaters and a, by mammalian standards, unique sociality in that commonly groups of males, sometimes solitary males defended small areas partially overlapping with large ranges of solitary females. When a solitary male or a group of males switched between both tactics, floating usually preceded territory holding, suggesting that both spatial phases are equivalent to distinct life-history stages. Switching from roaming as a floater to holding a territory was also associated with an increase in body mass index (BMI) and a change in the observed behavior of animals captured in traps when approached by humans. Both BMI and this behavior are therefore reliable, quick biomarkers of an individual's space use tactic and life-history stage. We elaborate the implications of this socio-spatial organization for models of ecological movements and on conflict mitigation measures such as translocations or the planning of future protected areas. We suggest that such implications also apply to other species where one sex exhibits two space use tactics and two sets of range sizes.

Key words: cheetah; free-ranging; GIS; GPS-collar; life-history stage; movement ecology; Namibia; spatial tactic; territoriality.

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INTRODUCTION

In mammalian species, males operate within a wide variety of social and spatial forms of organizations. Male ranging behavior mainly depends on female ranging behavior and the degree of sociality (Clutton-Brock 2016). If females move within ranges that are easily defended, one male defends the range of one female, as in bobcat (*Lynx rufus*, Bailey 1974), or several females, as in Columbian ground squirrel (*Spermophilus columbianus*, Festa-Bianchet and Boag 1982), or a group of males defends the range of several females, as in lions (*Panthera leo*, Schaller 1972). If females move within ranges that are not easily defended and females live in stable groups, single males or several males temporarily occupy the range of one or several female groups, as in red deer (*Cervus elaphus*, Clutton-Brock et al. 1982) or Cape buffalo (*Syncerus caffer*, Sinclair 1977). If females live in groups which are unstable, males defend territories comprising only a portion of the range of a female group, as in white rhinoceros (*Ceratotherium simum*, Owen-Smith 1972) or very small, clustered territories such as leks as in fallow deer (*Dama dama*, Clutton-Brock et al. 1988). Finally, if females are solitary, live at low density and range widely, males also roam widely in search of females as in polar bear (*Ursus maritimus*, Ramsay and Stirling 1986).

The social and spatial organization of cheetahs (*Acinonyx jubatus*) does not appear to fit into this classification scheme. Characteristics of a unique organization emerged from extensive observational and radio-tracking studies in the Serengeti National Park in Tanzania, East Africa (Caro 1994). Here, males either formed long-lasting coalitions consisting of two to four brothers, sometimes also of non-related males, or remained solitary (Caro and Collins 1986). Caro (1994) suggested that cheetahs therefore represented a unique variant of the socio-spatial organization in which males defend mating territories that comprise only a portion of the range of females (Clutton-Brock 2016) but with the unique characteristic that solitary males or groups of males defend access to parts of large ranges of solitary females. Not all Serengeti adult cheetah males defended small territories (mean 48.3 km^2), which were regularly visited by females whose range sizes were much larger (mean 833.0 km^2; Caro 1994). Adult males that did not hold a territory (floaters) roamed over large ranges with a size (mean 777.2 km^2) similar to that of the solitary females (Caro 1994). Competition over territories was high because holding a territory enhanced access to females (Caro and Collins 1987*a*, Caro 1994). Paternity analyses, however, did not clearly reveal whether territory holders or floaters had a higher reproductive success (Gottelli et al. 2007).

Subsequent studies on radio-collared male cheetahs in Botswana, Namibia, and South Africa, all Southern Africa, mostly reported range sizes for solitary males and males in groups (coalitions) without detecting a difference between them (Broomhall et al. 2003, Marker et al. 2008, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). A recent study with a small sample size of one radio-collared solitary males and three radio-collared coalitions of males distinguished between ranges of territory holders and floaters, with the solitary floater having a larger range than the territory holders (Van der Weyde et al. 2016). Both territory holders and floaters can be solitary or occur in coalitions, with most territory holders consisting of coalitions (Caro 1994). Thus, studies contrasting territory holders with floaters and studies contrasting solitary males with those in coalitions cannot be directly compared. It is therefore still unclear whether the socio-spatial organization of cheetahs varies between populations, perhaps as a consequence of environmental variation, or whether apparent differences in results were a consequence of differences in data collection, classification, and analyses. Cheetahs are a threatened species under high pressure, mainly because of human persecution and habitat fragmentation (Durant et al. 2017, Weise et al. 2017). Thus, understanding the socio-spatial organization and ultimately the mating system is not only of theoretical interest but also a key to their successful conservation when translocations are planned or the size and delineation of future protected areas should be determined.

Here, we present the results of a long-term study (2002–2014) with a large samples size (n = 164 tracked individuals) on the socio-spatial organization of free-ranging cheetahs on commercial Namibian farmland, where one of the largest free-ranging cheetah populations worldwide exists (Durant et al. 2017). We captured cheetahs in central Namibia, fitted them with GPS-collars or VHF-collars, and used an intensive sampling regime to test predictions for Namibian cheetah males derived from the results and arguments of previous studies. In the Serengeti, the chance to take over and defend a territory was higher when male coalition size was big and individuals large (Caro and Collins 1987*b*). When coalition size was reduced, the remaining male(s) eventually lost their territory to larger coalitions (Caro and Collins 1987*b*). Territory holders had a better body condition than floaters as measured by coat quality, extent of sarcoptic mange on ears, and the ease with which the vertebrae could be palpated (Caro et al. 1989). Territory holders marked landmarks such as large trees or rocky outcrops inside their territory with urine or feces, whereas floaters sniffed landmarks and typically did not overmark these (Caro 1994).

If the Namibian cheetah socio-spatial organization is similar to the one in Serengeti, we expect that (1) we will find males which occupy small territories and males which roam over large areas; (2) only territory holders but not floaters mark landmarks; (3) floaters fight for and take over territories, but territory holders do not fight for and do not take over home ranges (HRs) of floaters; (4) takeovers of territories should only be successful when floaters have a larger group size than territory holders; (5) males in coalitions are more likely to hold a territory than solitary males and solitary males are more likely to be floaters; and (6) territory holders have a better body condition than floaters, as measured by a body mass index (BMI; Table 1). In the Serengeti study it remained unclear whether an improved body condition was a requirement for floaters to take over a territory or whether body condition improved after taking over a territory. We therefore repeatedly measured body size and determined body condition in males during different life-history stages.

Methods

Study animals

Between 2002 and 2014, we captured, immobilized, and collared 133 adult males and 31 adult females in box traps at marking trees on farmland in central Namibia as described by Thalwitzer et al. (2010). In addition, we captured (but did not collar) or sighted seven additional adult males which were used in some analyses. At capture, 78 males were classified as young adults (age class 6; 24–42 months of age), that is, after they had separated from their mother, dispersed, and settled down in a new area, 52 males as prime adults (age class 7; >3.5–7.0 yr of age) and three males as old adults (age class 8 > 7.0 yr of age). At capture, 11 females were classified as young adults, 20 as prime adults, and none as an old adult. The age of cheetahs was estimated as described by Caro (1994). When a cheetah was captured, we assessed whether and how many other cheetahs were possibly part of the same group by inspecting the spoors in the vicinities and/or checking pictures from camera traps set up next to the box traps (how camera traps were mounted see

Table 1. Predictions derived from the cheetah socio-spatial organization in the Serengeti National Park, Tanzania, and tested for cheetahs on commercial Namibian farmland.

No.	Prediction	Confirmed?
1	We expect to identify males which occupy small territories and males which roam over large areas	Yes
2	We expect that only males holding territories but not floaters mark landmarks	Yes
3	We expect that floaters fight for and take over territories, but territory holders do not fight for and do not take over home ranges of floaters	Yes
4	We expect that takeovers of territories are only successful when floaters have a larger group size than territory holders	Yes
5	We expect that male in coalitions are more likely to hold a territory than solitary males and solitary males are more likely to be floaters	Yes
6	We expects that territory holders have a better body condition than floaters, as measured by a body mass index	Yes

Fig. 1. Behavior of cheetahs in the box trap. (A) Territory holder showing proactive behavior such as attacking and hissing, (B) floater showing anxious behavior such as retreating, (C) floater showing ambivalent behavior such as aggressively approaching and simultaneously submissing by flattening the ears against the head.

below). If we had indications that there was one or several coalition partners, we set additional box traps at the same location to capture the other cheetah(s). Coalition partners were rapidly captured in all except three cases within at most 24 h. In three cases, the coalition partner approached the second trap, but did not fully enter to set the trigger mechanism. We recorded the behavior of the cheetahs in the traps when we first approached the animals by categorizing their behavior as (1) proactive—approaching aggressively, threatening, attacking, hissing, and/or appearing undisturbed thereby either standing or sitting but not lying down, (2) anxious—retreating, crouching, appearing frightened or depressed, showing submission by flattening ears against the head and regularly lying down on the ground, or (3) ambivalent—aggressively approaching and retreating, often turning in circles and often showing mixed behaviors from both categories described before, for example, approaching aggressively and flattening ears against head (Fig. 1).

We fitted the animals with a GPS-collar (Vectronics Aerospace GmbH, Berlin, Germany; e-obs GmbH, Grünwald, Germany) or a VHF-collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). GPS-collars recorded between 2 and 96 locations (fixes) per day and were equipped with a mortality signal when the animal did not move for more than 12 h. Battery lifetime of GPS-collars varied between 10 and 26 months and depended on battery capacity, producer, firmware, type of data transmission, and on the GPS recording schedule. Battery life for VHF-collars was approximately 36 months. Females, solitary males and one or two male(s) per coalition were fitted with a GPS-collar, whereas other captured coalition partners received a VHF-collar or were not collared. All cheetahs were released at the site where they were captured. If a GPS-collared cheetah was recaptured ($n = 61$), the collar was renewed if more than three months had elapsed since the last collaring ($n = 32$), in order to extend the tracking period. This enabled us to collect GPS data from individual cheetahs for up to five consecutive years.

Radio tracking

We conducted regular aerial tracking flights with a 2-seater Piper Super Cub equipped with a Yagi antenna on each wing to receive VHF signals and a dipole antenna for data communication via a UHF band between GPS-collars and the handheld receiver. Flights covered an area of approximately 12,000 km^2 per flight in a study area of approximately 40,000 km^2 (Fig. 2). Flights were usually conducted twice per month between 08:00 and 14:00 hours at an altitude of approximately 400 m above ground. At this height, we could expect to receive VHF-collar signals at distances of up to 30 km. When a signal was detected, we estimated the bearing to the animal and the pilot would set the flight course accordingly to approach the animal. During approach, we descended to an altitude of 100 m above ground to permit visual contact with the animal. When a GPS-collared animal was located, the pilot circled above the animal (radius 500 m) for up to 20 min to download the data stored onboard of the device. Per flight we usually located between six and 14 cheetahs, depending on weather conditions and the number of animals collared in the area covered by the airplane. When collared individuals belonged to a group, pilot and observer ensured that all group members were located visually to record group size.

Spatial analyses

The average tracking period for solitary males or for coalitions of two or three males was 381.8 ± 414.4 d (mean ± standard deviation [SD], $n_{sol} = 33$, $n_{co2} = 17$, $n_{co3} = 6$; Table 2). This analysis revealed that some solitary males and some coalitions occupied small areas, which they defended and marked, whereas others roamed over large areas (*Results*). We therefore termed the former males territory holders and the latter floaters sensu Caro (1994) and consider the utilization of areas of different sizes as two spatial tactics of cheetah males.

To compare the HR sizes between territory holders and floaters we determined the 95% minimum convex polygons (MCP) of GPS-collared males with ArcGIS Desktop 10.0 (Esri, Kranzberg, Germany) and GME (Beyer 2012) by using two fixes per day during peak activity times, that is, during twilight (Cozzi et al. 2012). If males belonged to a coalition, the sampling unit was the coalition and not the individual. We therefore report both the number of radio-collared animals and the total number of individuals if some are

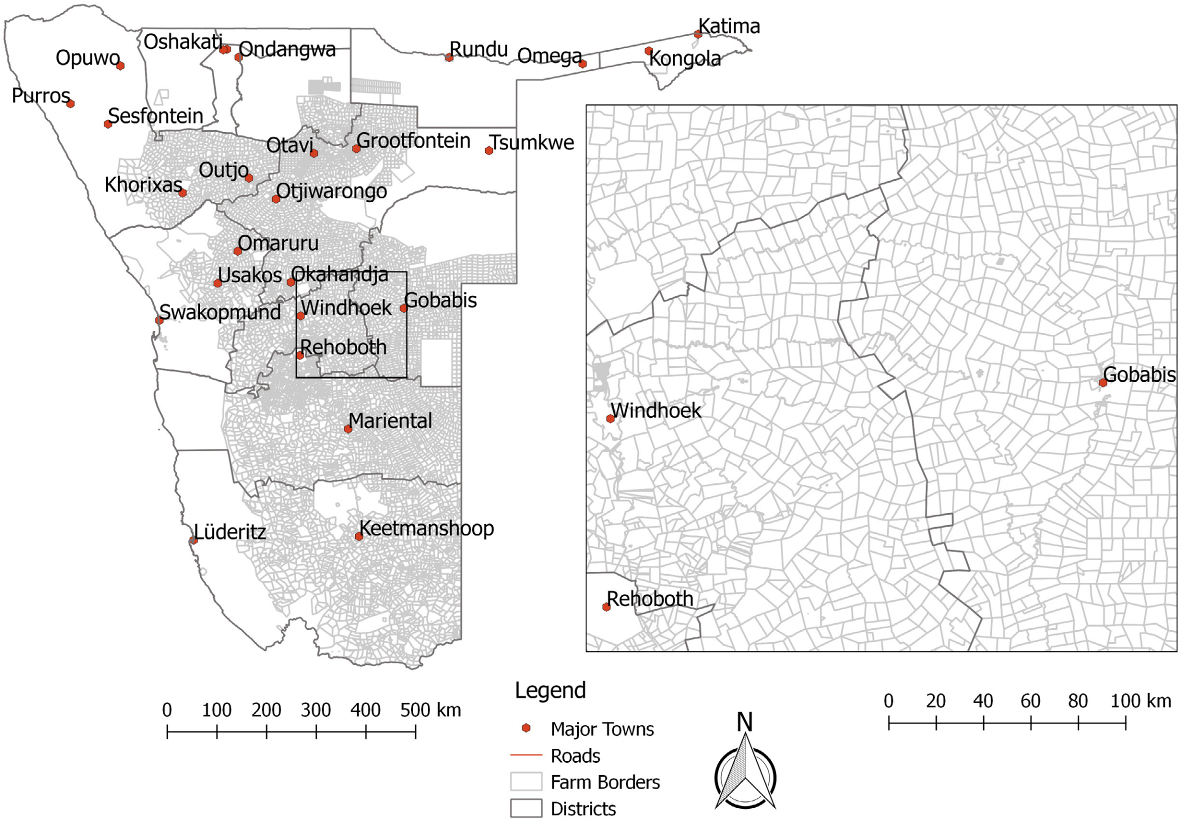

Fig. 2. Location of study area of approximately 40,000 km^2 on farmland in central Namibia.

not collared and are members of coalitions and thus represented by these calculations. Since HR size typically reached an asymptote after 90 consecutive days (Appendix S1: Fig. S1), we restricted the determination of stable HR sizes to data from the 56 units of solitary males or male coalitions (in total 70 collared individuals, representing 74 solitary males and members of coalitions) from which we had more than 90 d of GPS data.

For 36 male units (representing 50 males) with less complete data, we computed approximate HR in order to assign individuals to either of the two spatial tactics (used to test predictions 5 and 6). For 14 males units we had GPS information of fewer than 90 d of data ($n_{\text{sol}} = 9$, $n_{\text{co2}} = 3$, median = 67.5 d, range: 6–85 d) or more than 90 d but with many missing data due to temporary collar failures ($n_{\text{sol}} = 2$). For 18 males units, we had VHF information for at least 6 months ($n_{\text{sol}} = 10$, $n_{\text{co2}} = 4$, $n_{\text{co3}} = 1$, median = 465 d, range: 187–2125 d) or which we located on at least 6 different days ($n_{\text{sol}} = 1$, $n_{\text{co2}} = 2$). Four additional male units ($n_{\text{sol}} = 2$, $n_{\text{co2}} = 1$, $n_{\text{co3}} = 1$) were assigned to a spatial tactic by using sightings during aerial tracking flights.

Fourteen males units provided information for both spatial tactics (Table 2). These included six units that provided data on stable HR sizes for both spatial tactics, four units with stable HR sizes as territory holders and approximate estimates for HR sizes as floaters, 1 unit with an approximate estimate for HR size as territory holder and a stable HR size as floater and three units where HR sizes were approximate for both spatial tactics.

Data of 28 further males could not be used for this study because two GPS-collars failed, four GPS-collars produced non-interpretable data, and 22 VHF-collared males did not meet the VHF-collar criteria of having VHF information of at least 6 months or which were located on at least six different days.

Table 2. Identity of males, coalition size, spatial tactic after collaring, the number of days the GPS-collars provided locations for, the size of the home range (HR) as minimum convex polygon (MCP 95%) in km^2, information on whether the individual switched spatial tactic and its body mass index (BMI).

ID	Coalition size	Spatial tactic	Days GPS-collar	MCP 95% (km^2)	Switch of tactic observed?	BMI
AO†	1	Territory holder	176	481.36	Yes	–
AR†	1	Territory holder	122	556.39	Yes	–
BJ†	1	Territory holder	100	451.83	Yes	–
BQ‡	1	Territory holder	208	663.95	Yes	33.35
BQ‡	1	Territory holder	135	82.6	Yes	–
DA†	1	Territory holder§	§	§	Yes	–
DS†	1	Territory holder	207	447.58	Yes	–
DT†	1	Territory holder§	§	§	Yes	–
DX†	1	Territory holder	159	293.41	Yes	33.48
AF	1	Territory holder§	§	§	No	27.60
AG	1	Territory holder§	§	§	No	26.89
BD	1	Territory holder	438	545.16	No	29.09
BV	1	Territory holder	151	782.71	No	31.12
BX	1	Territory holder	99	307.87	No	24.23
BZ	1	Territory holder	1231	360.77	No	30.38
CA	1	Territory holder	142	205.61	No	27.28
CB	1	Territory holder§	§	§	No	25.98
CR	1	Territory holder	133	424.56	No	–
AL†, AM†	2	Territory holder	110	227.72	Yes	–
AT†, EB†	2	Territory holder§	§	§	Yes	–
CC†, CD†	2	Territory holder§	§	§	Yes	–
DC†, DE†	2	Territory holder	404	400.23	Yes	30.10
AV, AW	2	Territory holder	116	281.36	No	31.11
AZ, BA	2	Territory holder	772	497.76	No	31.38
BH, BI	2	Territory holder	99	622.31	No	29.31
BL, BM	2	Territory holder	890	244.73	No	28.89
CH, CM	2	Territory holder§	§	§	No	31.20
CS, DB	2	Territory holder	1687	259.85	No	33.40
CY, CZ	2	Territory holder	461	387.96	No	28.39
DJ, EG	2	Territory holder	181	364.7	No	29.08
DQ, DR	2	Territory holder§	§	§	No	30.50
DU, DV	2	Territory holder	1591	384.04	No	29.20
DY, DZ	2	Territory holder	230	293.68	No	34.34
CJ†, CK†, CL†	3	Territory holder	837	208.54	Yes	27.82
DG†, DH†, EF†	3	Territory holder	97	147.89	Yes	–
AA, AB, AC	3	Territory holder§	§	§	No	28.98
AH, AJ, AK	3	Territory holder	1814	255.98	No	29.32
CV, CW, CX	3	Territory holder	1291	433.23	No	30.47
AO†	1	Floater§	§	§	Yes	22.78
BJ†	1	Floater	305	5445.61	Yes	21.93
BQ‡	1	Floater§	§	§	Yes	27.39
BQ‡	1	Floater	94	1113.26	Yes	–
DA†	1	Floater	331	3223.17	Yes	25.25
DS†	1	Floater	121	1608.26	Yes	–
DT†	1	Floater§	§	§	Yes	26.01
AD	1	Floater§	§	§	No	28.42
AE	1	Floater§	§	§	No	24.86
AI	1	Floater§	§	§	No	28.40
AN	1	Floater	407	1793.29	No	25.39
AQ	1	Floater§	§	§	No	25.51
AS	1	Floater§	§	§	No	26.04

(Table 2. *Continued*).

ID	Coalition size	Spatial tactic	Days GPS-collar	MCP 95% (km^2)	Switch of tactic observed?	BMI
AU	1	Floater	287	1223.96	No	25.92
AY	1	Floater	344	1477.36	No	26.64
BB	1	Floater	903	1728.84	No	23.64
BC	1	Floater§	§	§	No	25.16
BK	1	Floater	209	1885.29	No	26.91
BN	1	Floater§	§	§	No	28.80
BO	1	Floater§	§	§	No	–
BR	1	Floater	334	1226.32	No	–
BS	1	Floater	168	1180.82	No	24.69
BT	1	Floater	207	4861.79	No	26.79
BU	1	Floater	173	1100.91	No	28.96
BW	1	Floater	141	663.8	No	26.14
BY	1	Floater§	§	§	No	22.44
CE	1	Floater§	§	§	No	24.93
CF	1	Floater§	§	§	No	24.97
CG	1	Floater§	§	§	No	26.71
CI	1	Floater§	§	§	No	23.75
CN	1	Floater	251	988.71	No	24.82
CO	1	Floater§	§	§	No	27.02
DF	1	Floater§	§	§	No	24.33
DI	1	Floater	271	1267.21	No	29.40
DK	1	Floater	162	1097.16	No	24.06
DL	1	Floater§	§	§	No	22.61
DM	1	Floater	139	918.00	No	24.97
DN	1	Floater	139	1353.61	No	28.83
EA	1	Floater	90	639.52	No	26.58
AL†, AM†	2	Floater	162	1249.88	Yes	26.10
AP, AR†	2	Floater§	§	§	Yes	25.53
AT†, EB†	2	Floater§	§	§	Yes	24.64
CC†, CD†	2	Floater§	§	§	Yes	26.92
DW, DX†	2	Floater§	§	§	Yes	26.87
AX, EH	2	Floater§	§	§	No	25.48
BE, BF	2	Floater	462	1879.83	No	24.31
BG, EC	2	Floater	254	1431.34	No	25.24
BP, ED	2	Floater	296	1411.85	No	25.06
CP, CQ	2	Floater	486	1250.79	No	27.79
CT, CU	2	Floater	274	723.74	No	28.30
DO, DP	2	Floater§	§	§	No	28.01
CJ†, CK†, CL†	3	Floater§	§	§	Yes	23.76
DC†, DD, DE†	3	Floater	241	1374.5	Yes	27.23
DG†, DH†, EF†	3	Floater	248	530.51	Yes	25.45

Note: En dash indicates that BMI was not determined because body mass and/or body length was not measured.

† Males appear in both spatial tactic categories. Males in such groups without symbols died before the switch in spatial tactic. To test prediction 5, only the group size of the territory holder was used.

‡ Male BQ switched spatial tactic three times, thus appearing four times in the list.

§ Spatial tactic identified from reduced data, approximate 95% MCP HR sizes; used to test predictions 5 and 6.

Of 31 collared females, 23 were fitted with a global positioning system collar and eight with a VHF collar. Seventeen females with GPS-collars produced stable HR sizes with data for more than 90 d. HR sizes were determined for females as described for the males.

Marking behavior

Cheetahs use urine and feces to mark prominent landmarks (Caro 1994) such as granite intrusions left standing after erosion took the surrounding soil away (kopjes), termite mounts, or conspicuous trees. In southern Africa, the main marking landmarks are trees, often with a low sloping branch or trunk that cheetahs use to climb up (Marker-Kraus et al. 1996).

Marking trees were identified using the spatial data of territorial males which produced clusters of GPS locations, because such trees were visited frequently. Marking trees were then visited in the field to assess the number and freshness of scats. We assumed that the number of scats was positively related to the frequency of cheetah visits and scat freshness to recent cheetah activity. Hence, the marking trees with a combination of both fresh and numerous scat were short-listed. The final 10 trees for camera trap placement were chosen such that camera trap locations were spread across the HR of the territorial animal (S. Edwards, M. Fischer, B. Wachter, and J. Melzheimer, *unpublished manuscript*). We then monitored these marking trees for 28 d with Reconyx PC900 HyperFireTM cameras with a passive LED infrared system (Reconyx, Holmen, Wisconsin, USA). Each tree was equipped with two cameras opposite to each other with a lateral offset to eliminate flash interference. Cameras were placed 3–5 m away from marking trees and mounted on poles 80 cm above ground. As cheetahs can be individually identified from their unique spot patterns (Caro and Durant 1991, Caro 1994), we recorded the individual identities of the cheetahs visiting the marking trees and whether they marked the tree by spraying urine or defecating.

Defining switching between spatial tactics

Males that switched from one spatial tactic to another did so within a transition period of approximately three months. We have evidence from at least three cases of switching that the transition period starts when a solitary floater or a coalition of floaters begins to scent mark at a marking tree inside an existing territory. In terms of movements, this is easily detected by noting that these floaters spend a week or more near such scent-marking trees. After this, the switchers gradually decrease their HR size because they focus their movements on this territory and give up visits to other territories. At some point the challenger(s) and the territory holder(s) meet and fight over the territory, at least sometimes with serious consequences (*Results*). After a successful takeover, the new owners substantially shrink their HR further down to the size of the new territory. In terms of movements, we therefore defined the end of the transition period and thus the start of the territorial phase as soon as this substantial shrink in HR size stabilized (Fig. 3). To determine the date of a switch from a territory phase to a floater phase, we took the date when the male(s) expanded the HR again.

Assessment of body size and body condition

As an assessment of body condition, we used a BMI calculated as body mass/body length^2 (kg/m^2). For the statistical comparisons of BMIs of territory holders and floaters, we averaged the values of coalition members to avoid pseudoreplication. If a solitary male or a male coalition were captured repeatedly whilst using the same spatial tactic, a mean BMI across these measurements was calculated. Recaptured animals that switched tactic between recaptures were used to compare BMI values before and after they became territory holders (Fig. 3). To determine the BMI for the floater phase, we used the most recent measurement before the tactic switch to minimize potential age effects when comparing this BMI with the one from the territorial phase. The measurement closest to the tactic switch was typically the last capture before switching, a capture during the transition period, or the first capture during territory ownership. The BMI for the territory holder phase was then determined from the next capture(s) as described above. This is a conservative estimate in that it was likely to minimize any potential difference between the floater phase and the territorial phase. If there was a difference, then the change could have only taken place during the territorial phase, that is, after the takeover of the territory.

Body mass was determined using a spring scale attached to a stretcher carrying the cheetah or by calculating the difference between the two weights of a person standing on a balance with and without carrying the cheetah. Body masses were recorded to an accuracy of 0.1 kg. Body length was determined by measuring the animal from the tip of the nose to the sacro-coccygeal joint. Measurements were made with a flexible measuring tape to an accuracy of 0.5 cm.

Data analysis

Lilliefors tests revealed that BMI data of territory holders and floaters were normally

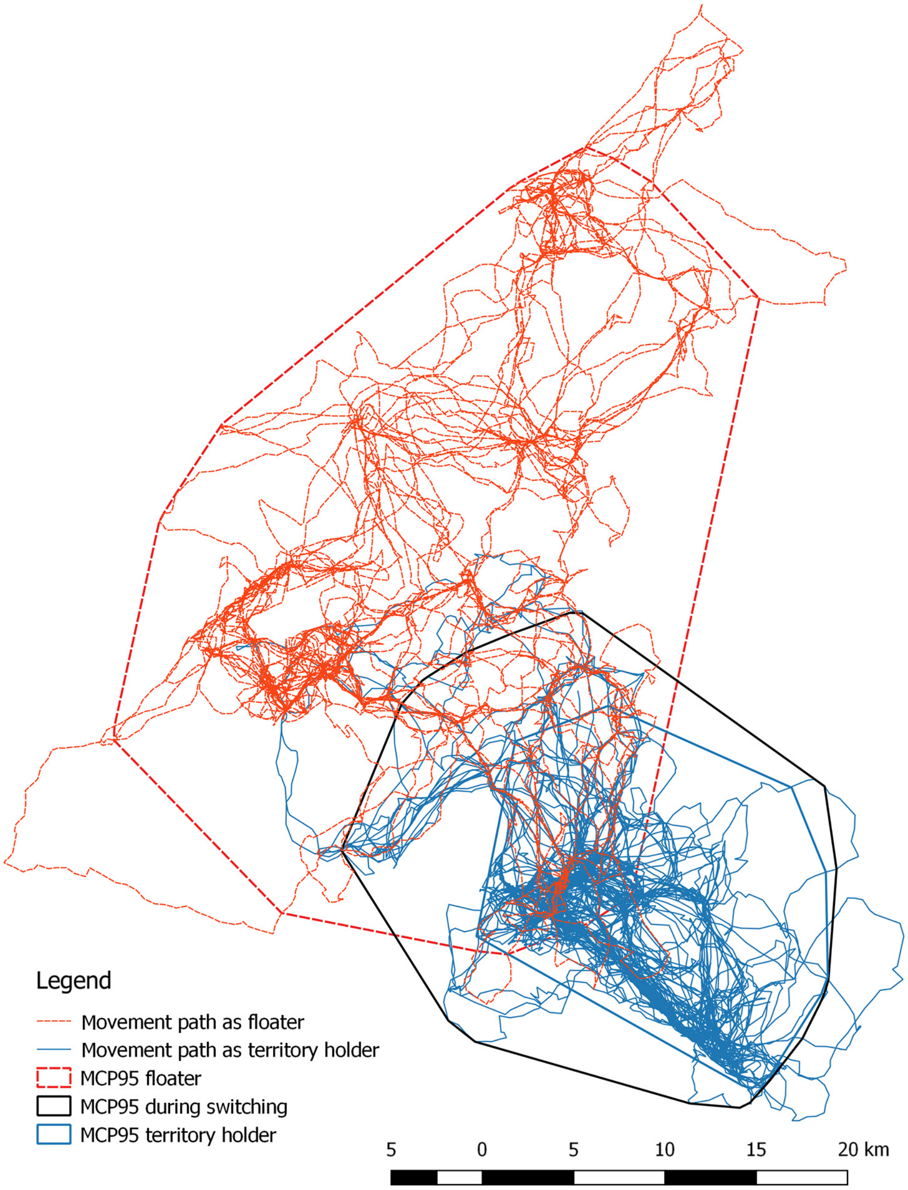

Fig. 3. Example of the home range and movement paths of a male that switched from a floater, covering 1116 km^2 during 357 d, to a territory holder covering 289 km^2 during 443 d.

distributed; thus, a comparison between the two tactics was conducted using a parametric *t* test. Lilliefors tests further revealed that MCP values of territory holders were normally distributed, whereas MCP values of floaters were not normally distributed. Thus, for the comparison of the two spatial tactics a nonparametric Mann–Whitney *U* test was conducted. All other data were not normally distributed; thus, nonparametric statistics such as Mann–Whitney *U* tests, Wilcoxon signed-ranks tests, and chi-square tests of independence were used (Hollander et al. 2014). All test were conducted with SYSTAT 13.0 (Systat Software, Richmond, Virginia, USA), and results are reported as means ± SD, and for HR sizes additionally also with 95% confidence limits.

RESULTS

Cheetah males either occupied stable HRs in the form of small territories of 379 ± 161 km^2 (95% confidence interval [CI]: 313 km^2, 441 km^2, $n_{sol} = 13$, $n_{co2} = 11$, $n_{co3} = 4$) or ranged over large areas of 1595 ± 1131 km^2 (95% CI: 1156 km^2, 2033 km^2, $n_{sol} = 20$, $n_{co2} = 6$, $n_{co3} = 2$, Table 2, Mann–Whitney U test, $U = 10$, $P < 0.0001$). Stable HRs of cheetah females had intermediate sizes of 650 ± 278 km^2 (95% CI: 507 km^2, 793 km^2, $n = 17$), implying that territorial males could only cover a portion of the range of any individual female.

The trees in each of the six areas (territories) monitored for 28 d were frequented by several solitary males or male coalitions (range: 1–5 male units). However, in each of the monitored areas only one male or one male coalition repeatedly marked trees ("residents") whereas the other males visited only briefly, that is, one or two days, did not mark and only sniffed the marking sites. The residents visited in total 47 of the 60 monitored trees (median = 8.5, range = 5–10 trees) and marked with urine or feces 43 (91.5%) of them (median = 8.5, range = 4–9 trees) during this period. Across all territories, residents visited one of the ten monitored trees in their HR on 258 occasions during the 28 monitoring days, per territory on 43.0 ± 86.1 occasions, implying a visiting rate of 1.5 trees per day and territory. Across all territories, residents marked 149 times (57.8%), per territory on 24.8 ± 48.6 occasions, or a marking rate of 0.9 trees per day and territory. In contrast, none of the other males ($n_{sol} = 5$, $n_{co2} = 1$) marked at a monitored tree during the recorded 60 visits, or a visiting rate of 0.4 visits per day and territory. All males that marked the trees occupied small HRs, whereas all males that did not mark ranged over large areas. Thus, we concluded the former males held territories, and consequently, territory holders were significantly more likely to mark than non-territorial males (Chi^2 test, $\chi^2 = 65.20$, $n = 318$, $P < 0.0001$).

On 16 occasions, study animals switched their spatial tactics. In 15 cases, floaters became territory holders (out of 54 floater units; Table 2, Fig. 3), and in one case, a territory holder became a floater (out of 38 territory holder units; Chi^2 test, $\chi^2 = 9.82$, $n = 92$, $P = 0.0017$). This male first switched from being a floater to becoming a territory holder, was then expelled from the territory by a coalition of males, and therefore became a floater again. Three months later, this male successfully obtained a territory 38 km away from his first territory. In both cases, this male took over an empty territory.

Territory owners were expelled and territories taken over by floaters if the group size of floaters was larger or the same size than that of territory holders: Group sizes of territory owners and floaters were in one case one male each, in four cases, one territory owner and two floaters, and in one case, one territory owner and three floaters (Wilcoxon signed-ranks test, $n = 6$, exact $P = 0.031$). In four out of these six cases, the inspection of cheetah carcasses located in these territories and/or GPS data implied that the previous territory holders were killed by the new territory owners. Not all attempts of floaters to take over a territory were successful. In two cases, we had circumstantial evidence from GPS data that a fatal fight occurred and the challengers died. In both cases, the carcasses of the floaters were located inside territories and close to marking locations of territory holders.

Males in coalitions were significantly more likely to hold a territory than solitary males, whereas solitary males were more likely to be floaters ($\chi^2 = 10.81$, coalition males: $n_{ter} = 20$, $n_{flo} = 7$, solitary males: $n_{ter} = 17$, $n_{flo} = 32$, $n = 76$, $P = 0.001$; Table 2).

Several lines of evidence strongly indicate that these male coalitions were tightly knit social units: (1) When one coalition member was captured, in all cases his partner(s) quickly came to the trap and if a second and/or third trap was set up, were rapidly captured his partner(s) in all but three cases and within at most 24 h. In three cases, the coalition partner did not fully enter the trap to release the mechanism. (2) Coalition members were photographed and sighted together during the intensive camera trapping period when visiting marking trees and all members of the observed territory holder coalitions marked at least at some of the trees. (3) During aerial tracking, coalition members were always located together and if sighted at all usually sighted together. Such tightly knit social units indicate a strong and intensive social relationship typical for and well known from strategic alliances or coalitions of males in other species.

These Namibian male groups therefore satisfy the criteria why Caro (1994) called male groups in the Serengeti coalitions.

Territory holders had a significantly higher BMI of 29.7 ± 2.4 (range 24.2–34.3) than floaters with 25.8 ± 1.8 (range 21.9–29.4, *t* test, $t = 7.98$, $n_{\mathrm{ter}} = 26$, $n_{\mathrm{flo}} = 50$, $P < 0.0001$; Fig. 4, Table 2). The BMI of males increased significantly after they became territory holders, from 27.3 ± 1.3 to 30.3 ± 2.6 (Wilcoxon signed-ranks test, exact $n = 7$, $P = 0.016$, Fig. 5). The average time elapsed between both measurements was 27.5 ± 12.5 months. The increase in BMI from floater state to territory holder was not a function of time elapsed between the two measurements ($R^2 = 0.006$, $n = 7$, $P = 0.87$).

Territory holders significantly differed in their behavior to floaters when approached by people when caught inside the box traps, with territory holders significantly more likely to behave in a proactive manner and floaters more likely to behave in an anxious manner ($\chi^2 = 8.73$, territory holders: $n_{\mathrm{pro}} = 34$, $n_{\mathrm{anx}} = 19$, $n_{\mathrm{amb}} = 23$, floaters: $n_{\mathrm{pro}} = 15$, $n_{\mathrm{anx}} = 29$, $n_{\mathrm{amb}} = 18$, $n = 138$, $P < 0.05$), a distinction preserved when animals showing ambivalent behavior were excluded from the comparison ($\chi^2 = 8.69$, $n = 97$, $P < 0.01$).

DISCUSSION

Spatial tactics of Namibian cheetahs

Cheetahs in Namibia exhibited a similar ranging pattern as described for cheetahs in the Serengeti, Tanzania. Males displayed two spatial tactics with territory holders marking and defending a small area and floaters roaming over large areas. All but one individuals observed to switch their spatial tactic were floaters which became territory holders, with the exception of one male which set out as floater, switched repeatedly between tactics and ended by being a territory holder.

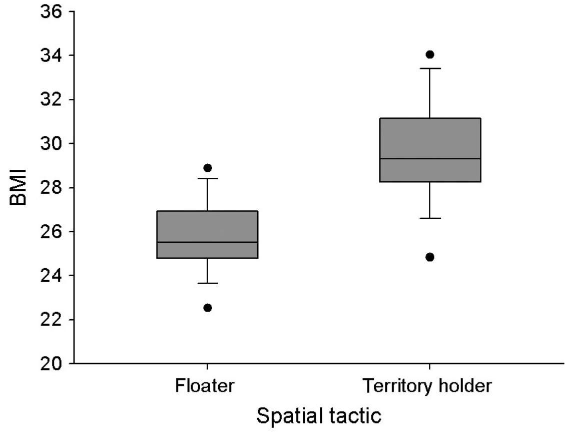

Fig. 4. Body mass index (BMI) of floaters and territory holders.

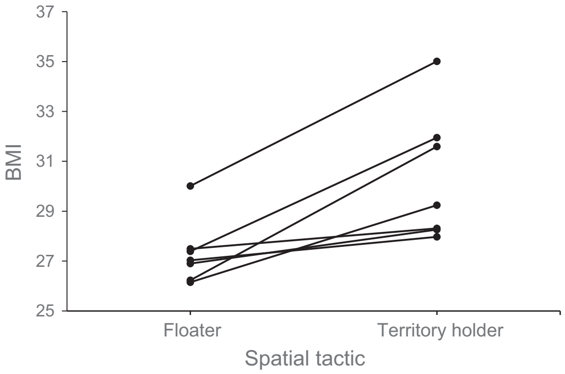

Fig. 5. Comparison of the body mass index of males that switched from floater to territory holder.

In the Serengeti, competition for territories is high and fights between territorial males and floaters can be severe (Caro 1994). We have similar information from GPS data, and all retrieved carcasses from territory holders as well as floaters that most likely were killed by conspecifics during territorial fights were found inside territories. This suggests that fights took place and were about territory ownership. Thus, the Namibian males start out as floaters and aim to become territory holders, suggesting that territories are likely to contain valuable resources. Floaters were successful in taking over a territory when their coalition size was larger than that of territory holders. The BMI of males captured repeatedly during their life history increased significantly after switching from being a floater to becoming a territory holder, suggesting that a high BMI is not a requirement but a consequence of the takeover of a territory, in terms of dietary, physiological, and/or hormonal changes. Perhaps territory holders have improved access to food resources (Caro et al. 1989) or males might apply a different rule of allocation of internal body resources once they have settled as residents, favoring the build-up of muscles. This might improve their chances of retaining the territory, for instance in one-to-one encounters of single territory holders against single floaters. However, body size or a higher BMI as such are no guarantee to maintain a territory if a single territory owner is challenged by a coalition of floaters —group size is more important than individual body size. This is consistent with the outcome of territorial encounters between clans of spotted hyenas (*Crocuta crocuta*) in which the larger group also always won (Hofer and East 1993).

Our findings indicate that the spatial tactics described for Serengeti cheetahs (Caro 1994) is not unique to that population. Not only does our identification of two spatial tactics reflect those found in the Serengeti, the large size of average female HRs found in our study also indicates that the social and sexual relationships between males and females are very similar, if not identical to the set-up in the Serengeti. Namibian females have such large HRs that they will overlap with more than one male territory because of the small size of male territories, preventing males from monopolizing females and ensuring female access to several (coalitions of) males. The mating system of Namibian cheetahs is therefore likely to be similar to the one in the Serengeti, and we suggest it is likely to occur in other populations as well. In addition, the behavioral evidence presented here shows that the observed male coalitions were tightly knit social units on a par with the coalitions as defined by Caro (1994) and therefore deserve to be called by this term. Irrespective of whether only territory holders or also floaters sire offspring, the cheetah clearly has, at least in some populations, a unique social organization amongst mammals in that coalitions of males (rather than solitary individuals) defend access to parts of solitary female ranges (rather than female group ranges).

How do both spatial tactics relate to life-history stages of male cheetahs?

The spatial tactics identified here are those of established adults, not those of subadult males after they separate from their mother (Caro 1994), become independent and then disperse. They therefore do not include dispersers setting out to find a new home after separating from their mother. Our results show that territory ownership usually is the final stage in the life history of a male cheetah, with floating preceding territory ownership. Male life-history stages of cheetahs are therefore best classified as following a trajectory of dependent subadult, independent subadult disperser, floater and then—if successful—territory owner, as a solitary male or as a member of a coalition with other males.

We expect that both spatial tactics (territory holders and floaters) will be found across the entire range of the cheetah, including ecosystems differing from the protected Serengeti National Park and Namibian commercial farmland, for example in the Namib Desert, the Kalahari Desert, the Sahara, the farmlands in Southern Africa and the mountain areas in Iran. Previously, most other studies have categorized cheetah males into males in coalition and solitary males and not into territory holders and floaters, and did not detect a difference in HR sizes between males in coalition and solitary males (Broomhall et al. 2003, Marker et al. 2008, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). Since both territory holders and floaters can occur as solitary males or males in coalitions (Caro 1994), these studies do not provide reliable information on the presence or otherwise of the two spatial tactics. Two recent studies reported as having identified both spatial tactics but did so without investigating or reporting marking and defending behavior, used a limited sample and took the smallness of the observed HR sizes as their sole clue (Van der Weyde et al. 2016, $n = 4$, one solitary male, two coalitions of two, one coalition of four; Marker et al. 2018, $n = 20$, 10 units of territory holders, 10 units of floaters, no information on coalition sizes).

The importance of distinguishing between tactics becomes apparent from another study on Namibian farmland (Marker et al. 2008, 2018). Marker et al. (2008) did not detect differences in mean HR sizes between solitary males (range sizes from 266 to 5658 km^2) and males in coalitions (range 385 to 3403 km^2; Table 1 in Marker et al. 2008), concluding that cheetah males generally use large HRs. A follow-up analysis with data from Marker (2002) revealed a mean range size of 531 km^2 for assumed territory holders, that is, with no behavioral support of territoriality, and 2300 km^2 for floaters, demonstrating a significant difference in range size between the spatial tactics (Marker et al. 2018).

However, similar HR sizes as in our study are obtained when data from Marker et al. (2008) are reanalyzed. Table 1 in Marker et al. (2008) consists of males with small HRs, probably territory holders, and males with large HRs, probably floaters. When we use the largest HR size of a territory holder of our study (782 km^2) as a cut-off value for the two spatial tactics, the dataset then separates into five males or male coalitions holding a territory and six floaters, after excluding data from eight translocated cheetahs. The average 95% MCP size of the assigned territory holders was then 475 km^2 ($n = 5$) and of the assigned floaters 1710 km^2 ($n = 6$). These values are similar to our results. Translocations were conducted because the farmers on whose farms the cheetahs were captured did not agree to have them released on their farm (Marker et al. 2008). Inclusion of translocated cheetahs will overestimate HR sizes because cheetahs might travel back to their original capture site and/or display exploratory movements during an orientation phase after their release and thereby cover ranges of up to 19,743 km^2 (Weise et al. 2015).

Implications for data analyses

The occurrence of several life-history stages in cheetah males associated with separate spatial tactics makes the interpretation of location data difficult, if marking behavior, territorial defense, and the life-history stage of males are not recorded. Treating the data as coming from a homogeneous set of individuals and failing to distinguish life-history stages or spatial tactics might lead to erroneous results in terms of the calculation and interpretation of HRs and their sizes, local cheetah density and for studies on disease susceptibility or immunocompetence, because territory holders and floaters might differ in their exposure and contact probability to pathogens. The effect might be even stronger, when the analyses directly depend on or include spatial information such as spatial mark recapture models (SCR). Many models assume identical capture probabilities across individuals and statistical independence of capture events (Krebs 1999), an assumption which will be violated in cheetahs because of the two distinct spatial tactics. Many models also use the mean maximum distance moved (MMDM) to calculate density from an estimated abundance (O'Connell et al. 2010). An MMDM calculated from a mark recapture survey across several floaters and one territorial male or a coalition of males is unlikely to produce a biologically meaningful value. Such density estimates are therefore likely to be neither statistically nor biologically correct. For SCR, we suggest to calculate densities of territorial males and floaters in separate models and then add them, or use finite mixture models that do not require the spatial tactic of each male to be identified (Pledger 2000, White 2008; S. Edwards, M. Fischer, B. Wachter, and J. Melzheimer, *unpublished manuscript*). Similarly, an explicit acknowledgement of the spatial tactics of cheetah males is likely to be relevant for population viability models (Lacy 2000) and spatially explicit population models (Dunning et al. 1995, Kramer-Schadt et al. 2005), because important population parameters will be affected such as (1) mortality (the population consequences of territorial encounters, the improved body condition of territory holders), (2) reproduction (the number of territory holders and the number and location of territories if territory holders are more likely to reproduce than floaters), and hence (3) effective population size (if territory holders are more likely to reproduce than floaters). Similarly, ecological movement models should take into account the spatial tactics of cheetah males to improve their results.

Although the socio-spatial organization of cheetahs is unique for mammals, males in other carnivore species can also exhibit spatial tactics differing in range sizes. For these species, the above-mentioned implications are also valid. For example, in lions, adult nomads roam alone or in small groups in vast areas whereas males defending a female pride use smaller ranges (Schaller 1972). Ignoring such differences when analyzing spatial data is likely to produce incorrect results.

Implications for conservation

Our results have important implications for the management of free-ranging cheetah populations. For instance, the two spatial tactics and associated life-history stages of males have to be considered when cheetahs are translocated to a new area, a common practice in Namibia to reduce the conflict between a particular farmer and a specific cheetah individual (Marker et al. 2008, Weise et al. 2015). Some translocated males travel back to their original area where they were captured, whereas others stay in the new area (Massei et al. 2010, Weise et al. 2015). The chance of males traveling back to their capture site may well depend on whether the translocated male(s) were territory owners or floaters. Territorial males might travel back to their territory to quickly re-occupy it and defend it against possible intruders, whereas floaters might stay in the new area and start to search for a territory. It is therefore important to immediately and reliably identify territory holders and floaters when captured. We identified two parameters that can be quickly measured and assessed in the field. First, when cheetahs in a trap are approached by the observer, territory holders differ in their behavior from floaters. Whereas territory holders mainly displayed aggression and threatened the observer, floaters mainly retreated to the opposite site of the trap and crouched down. This behavior can be used as first assessment to judge whether a male is more likely to be a territory holder or a floater. Second, the BMI of territory holders is higher than that of floaters. Thus, if body length and weight were measured, the BMI can be used as an additional parameter to predict the life-history stage and spatial tactic of the caught individuals. Implementing this information in decision-making during translocation operations is likely to increase the success of such translocations.

Some farmers with high losses of livestock do not accept non-lethal solutions of conflict mitigation activities such as increased protection of livestock or controlled translocations (Weise et al. 2015). Instead, they try to end the conflict in their favor by capturing and killing the cheetah suspected to have killed the livestock animal(s) using traps at marking trees on their farm (Marker-Kraus et al. 1996). Because such marking trees are located within the territories (Caro 1994), the chance to capture and kill a territory holder is likely to be higher than that of capturing and killing a floater. Such a removal is likely to accelerate the rate of turnover of territory ownership, either by increasing the chance for floaters to take over a territory with a reduced group size of territory holders or by occupying a vacant territory. As a result, cheetah activities on such farms are likely to increase until new territory ownership is established and thus possibly exacerbate also the conflict with farmers, thereby having the opposite result of the intended effect. This has been already shown in the case of lethal control of cougars (*Puma concolor*) where the removal of territorial males led to increased livestock predation because it stimulated the immigration of young cougars (Peebles et al. 2013). Similarly, experimental culling of Eurasian badgers (*Meles meles*) to reduce infection of cattle with bovine tuberculosis typically leads to an increase rather than a decrease of infection prevalence because of the social perturbation and increased movements in badger populations (Woodroffe et al. 2006, Carter et al. 2007). If the establishment of new territory ownership takes place within a short time period, the intended effect of killing territory holders might also be very limited. This has been shown for recreational hunting of Eurasian lynxes (*Lynx lynx*) which resulted in such a small reduction of losses of domestic sheep that it is now considered to be of little practical use (Herfindal et al. 2005).

Eliminating floaters, on the other hand, has an impact on a much larger scale than probably anticipated by the person responsible for it. The mean size of a farm in central Namibia is approximately 50 km^2 (Mendelsohn et al. 2003). With a mean HR size of 1595 km^2, floaters encompass approximately 32 farms. Thus, the elimination of floaters on one farm will affect the number of apparent floaters roaming on other farms as well. However, farmers of these other farms might not become aware of the reduced number of cheetahs on their farms and eliminate additional cheetahs. Such eliminations are likely to affect the resource holding potential (Allen et al. 2018) of the surviving males from the same coalition, which would lower the probability of winning a contest with other coalitions. Whether such eliminations actually decrease livestock predation is currently unclear. A recent review on lethal and non-lethal methods to prevent livestock predation revealed several non-lethal approaches to be effective in the USA and Europe (Treves et al. 2016). It might therefore be wise to identify more non-lethal solutions to mitigate the farmer–cheetah conflict on Namibian farmland.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2308/full

Ecosphere
The fat cat tactic: long-term GPS data reveal two distinct male spatial tactics in Namibian cheetahs
Joerg Melzheimer, Sabrina Streif, Bernd Wasiolka, Manuela Fischer, Susanne Thalwitzer, Sonja Heinrich, Annika Weigold, Heribert Hofer, and Bettina Wachter

Appendix S1

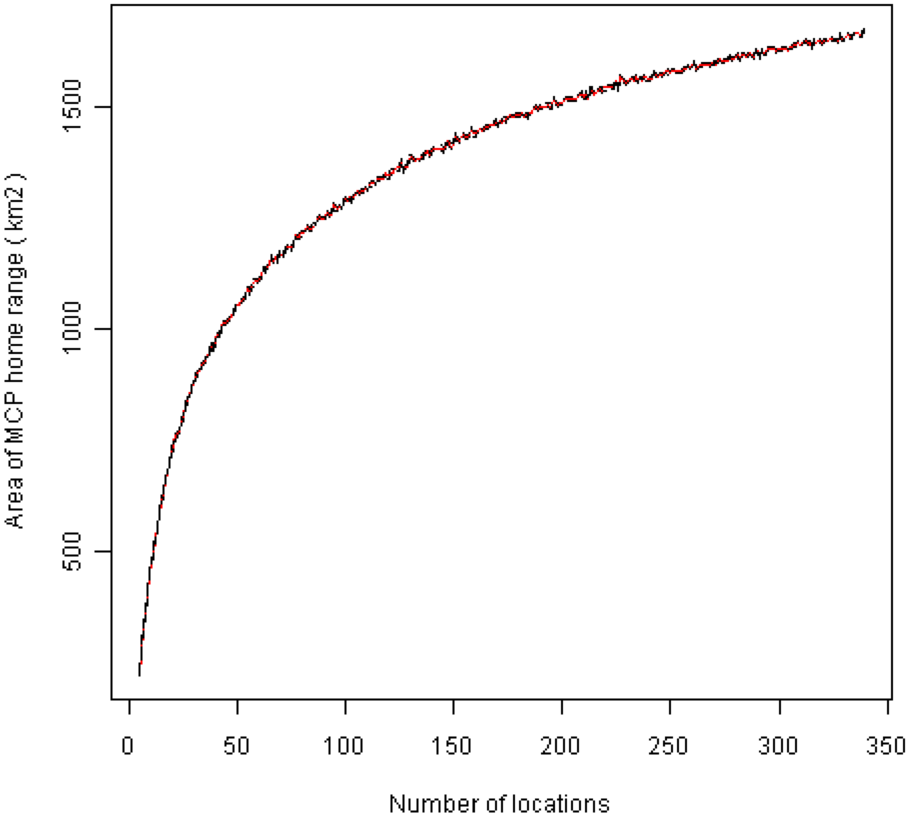

Fig. S1. Function of home range size against number of locations used for calculation of 95% minimum convex polygons (MCP) using a bootstrapping routine. The dataset consisted of two locations per day, therefore 90 days equal 180 locations.

Publication two

6. Coping with intrasexual behavioural differences: Capture-recapture abundance estimation of male cheetah

Edwards S, Fischer M, Wachter B, Melzheimer J

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ORIGINAL RESEARCH

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Coping with intrasexual behavioral differences: Capture–recapture abundance estimation of male cheetah

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Abstract

1. Population estimates are a fundamental requirement of ecology and conservation. While capture–recapture models are an established method for producing such estimates, their assumption of homogeneous capture probabilities is problematic given that heterogeneity in individual capture probability is inherent to most species. Such variation must be accounted for by abundance models; otherwise, biased estimates are risked.
2. Here, we investigate the performance of four types of heterogeneity models for estimating abundance of male cheetah *Acinonyx jubatus*, a species with two distinct spatial tactics of territorial and nonterritorial (floater) males. The differences in spatial movements of territory holders and floaters are expected to result in intrasexual heterogeneous capture probabilities. Four heterogeneity models were used to model male abundance at five territories in central Namibia; (a) a spatial tactic model, (b) a finite mixture model, both run in program MARK, (c) a floater-only model, and (d) a heterogeneity M_h model, both run in the program CAPTURE. Camera trap data of cheetah, taken at frequently visited marking trees, were used to derive true abundance. Model results were compared to the true abundance to assess the accuracy of estimates.
3. Only models (a), (b), and (c) were able to consistently produce accurate results. Mixture models do not require prior knowledge regarding spatial tactic of males, which might not always be available. Therefore, we recommend such models as the preferred model type for cheetahs.
4. Results highlight the potential for mixture models in overcoming the challenges of capture probability heterogeneity and in particular their use with species where intrasexual behavioral differences exist.

KEYWORDS
abundance, capture–recapture model, cheetah, heterogeneity, intrasexual behavioral differences

1 | INTRODUCTION

Estimates of population size are an important and fundamental requirement of ecology and the conservation management of wildlife (Baker, 2004; Otis, Burnham, White, & Anderson, 1978), requiring robust, reliable, and efficient methodology (Harmsen, Foster, & Doncaster, 2010). Unbiased and precise estimates are especially essential for species under threat, as well as for exploited species, for which overestimates of abundance could lead to unsustainable take-off levels (Baker, 2004). Factors such as large geographical ranges

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and low detection probability often mean entire populations cannot be surveyed simultaneously. Thus, surveys usually seek to monitor a proportion of the population, which requires methods accounting for imperfect detection of individuals (Sollmann et al., 2013; Williams, Nichols, & Conroy, 2002). Capture–recapture models are used in many ecological studies (Foster & Harmsen, 2012), including photographic capture–recapture sampling methods, which were originally developed to estimate tiger *Panthera tigris* density (Karanth & Nichols, 1998). They are one method to estimate animal abundances if species can be individually identified. These models are frequently used in combination with camera traps or other noninvasive devices such as hair snares, to repeatedly sample marked individuals at fixed locations (Otis et al., 1978; Royle, Nichols, Karanth, & Gopalaswamy, 2009). Individual encounter histories are then used to calculate capture probability, such that the abundance estimate is regarded as the size parameter of a binomial distribution (Royle, Chandler, Sollmann, & Gardner, 2014).

One of the major challenges facing estimation of population size is the heterogeneity in capture probability among individuals (Boulanger, Stenhouse, & Munro, 2004), because equal capture probability is a general assumption of traditional capture–recapture models (Krebs, 1999). Violation of the assumption usually leads to biased abundance estimates (Burnham & Overton, 1978; Cubaynes et al., 2010). Significant variation in capture probability has been suggested as the reason for negatively biased abundance estimates in Hawaiian monk seal *Monachus schauinslandi* (Baker, 2004) and painted turtles *Chrysemys picta* (Koper & Brooks, 1998), in comparison with true abundance.

Heterogeneity in capture probability has been suggested to be inherent in any animal population (Lebreton, Burnham, Clobert, & Anderson, 1992) and may arise for a multitude of reasons (Harmsen et al., 2010), for example, differences in sex, for example, jaguar *Panthera onca* (Sollmann et al., 2011), age, breeding status, for example, southern right whale *Eubalaena australis* (Carroll, Steel, & Baker, 2013), behavior, and social status of individuals, for example, coyote *Canis latrans* (Larrucea, Brussard, Jaeger, & Barrett, 2007). In addition, heterogeneity may arise when the home range of the species is large in comparison with the surveyed area. Such a factor may result in the study area containing only a partial home range of some individuals, with these individuals experiencing exposure to less camera traps than others (Oliver, Morgan, Durant, & Pettorelli, 2011; Royle et al., 2009).

Intrasexual heterogeneity in capture probability is expected for species in which differences in social status or behavior exist within the sexes, which may result in different use of a study area (Perret, Pradel, Miaud, Grolet, & Joly, 2003). Although capture–recapture methods have been developed for populations in which transience or temporary emigration occurs, these models were primarily designed for survival estimation, rather than abundance estimates (Pradel, Hines, Lebreton, & Nichols, 1997). Otherwise, when abundance is estimated, models only produce resident abundance estimates or permit raw data entries for transients with only one capture during the survey period (Conn, Gorgone, Jugovich, Byrd, & Hansen, 2011). However, for species in which transient or nonterritorial individuals are expected to be captured more than once, these models are not appropriate.

Cheetah *Acinonyx jubatus* is one species which exhibits intrasexual behavioral differences of adult males after they dispersed from their natal home range and established in a new area (Caro, 1994; Melzheimer et al., 2018). Adult males are either territory holders occupying small territories (in Namibia: 379 ± 161 km^2 [mean ± standard deviation]) or floaters ranging over large areas (in Namibia: 1,595 ± 1,131 km^2, Melzheimer et al., 2018). Territorial males mark and defend their small territory, while floaters roam over much larger areas which they do not actively defend (Melzheimer et al., 2018). Territorial male cheetahs mark at prominent landmarks (Caro, 1994), which in southern Africa are typically trees with low, sloping branches (Marker-Kraus, Kraus, Barnett, & Hurlbut, 1996). In Namibia, territorial males marked such trees in approximately 94% of their visits to these trees with urine or feces. In contrast, floaters were never or rarely recorded scent marking at such trees and, rather, visit trees to sniff markings of territorial males (Melzheimer et al., 2018; Wachter et al., 2018). Territory ownership is usually the final stage in the life history of a male cheetah; however, not all individuals will become territorial, some will remain floaters throughout their lives (Melzheimer et al., 2018). Such differences in the spatial ecology of adult males are likely to result in differential use of a survey area, thus creating heterogeneity in capture probability.

Cheetah has been identified as a species in need of accurate and precise population estimates due to its rapid decline (Broekhuis & Gopalaswamy, 2016). The species is currently occupying only 9% of its historical range, and a total global population of approximately 7,100 individuals is estimated with the majority of the animals occurring in southern African (Durant et al., 2017; Weise et al., 2017).

Here, we aim to identify the most reliable model for producing male cheetah abundance estimates within single territories, by comparing the results of a number of models accounting for heterogeneity against known abundance estimates from five territories in central Namibia. Population estimates across larger landscapes can then be calculated on the basis of such smaller units, that is, the territories. Producing accurate abundance estimates at a territory level is therefore crucial for subsequent analyses and provides a first step in the process of producing accurate population estimates.

2 | METHODS

2.1 | Study area

Data for this study were collected from September 2011 to March 2012 at five male cheetah territories, A to E, located within the east-central highlands of Namibia, approximately 150 km east of the capital Windhoek (Figure 1). All territories were located on commercial game and cattle farms, in habitats dominated by shrub savannah (Barnard, 1998), with an average annual rainfall of 370 mm (http://en.climate-data.org/location/904176/). The five territories were

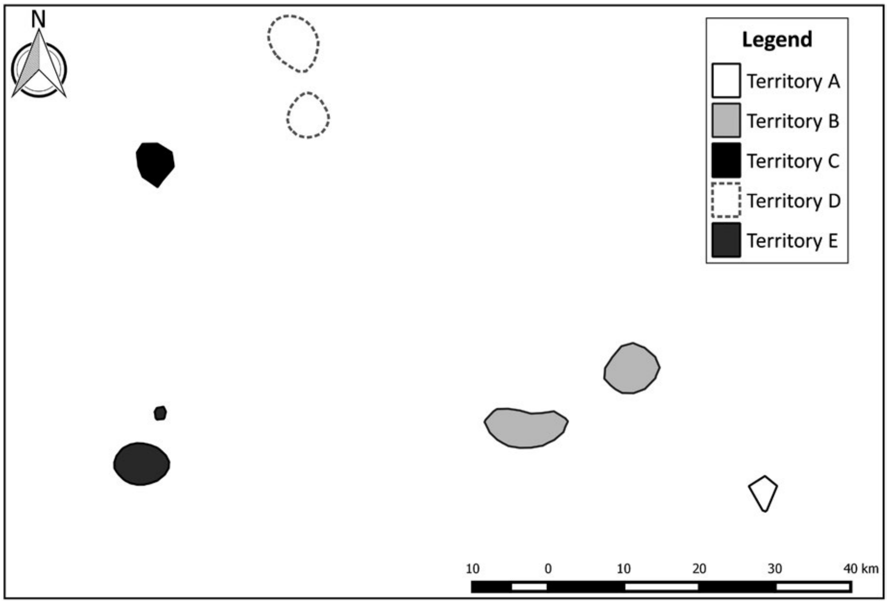

FIGURE 1 Five cheetah territories, represented by 50% kernel density polygons derived from territorial male spatial data, used for estimating male cheetah abundance

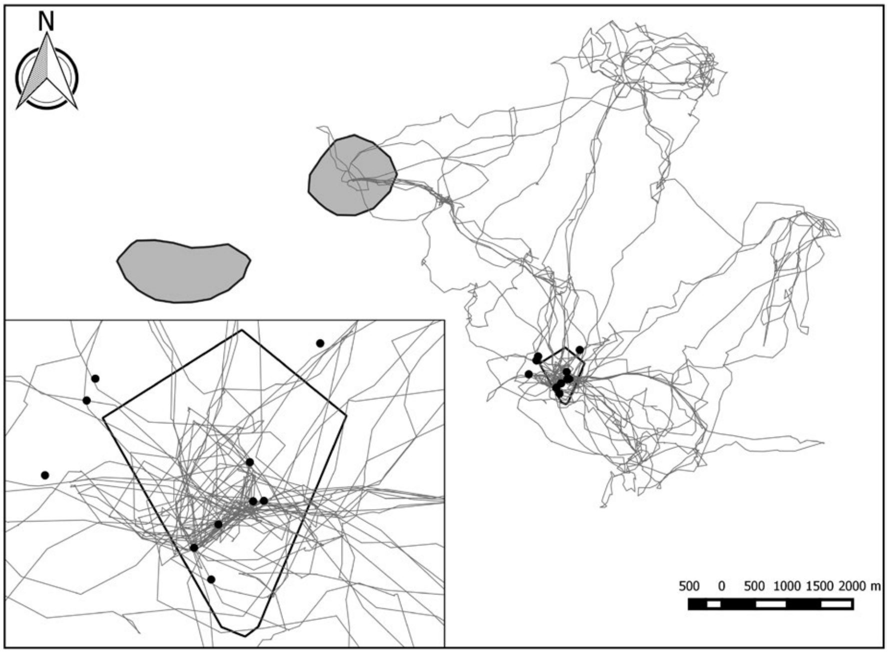

FIGURE 2 Spatial data movement from a single floater male during the survey period (September 2011–March 2012). Insert showing the movement of the same floater male with reference to the 10 camera traps in territory A

chosen as those best known from a long-term study of cheetahs in the area, which included the use of camera traps to detect marking behavior for a previous study (Melzheimer et al., 2018; Wachter et al., 2018). Due to the long-term monitoring of these specific territories, the identities of all territorial and floater males were known.

2.2 | Camera trap methods

To maximize capture probability, camera trap stations were placed at marking trees, which represent predictable locations of cheetah activity (Caro, 1994). Marking trees were identified using the spatial data of territorial males which were shown as clusters of locations when plotted. Male cheetahs were captured in box traps at marking trees and immobilized as described in Thalwitzer et al. (2010). Single males were always collared with a GPS collar (VECTRONIC Aerospace GmbH, Berlin, Germany; e-obs GmbH, Grünwald, Germany), and when coalitions of males were captured, at least one male was fitted with a GPS collar and the other(s) with a VHF collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). Due to the higher frequency of locations obtained from GPS collar (up to one position every 15 min) than VHF collars, only GPS positions were used to identify the clusters representing marking trees. Identified marking trees were visited in the field to assess the number and freshness of scats. We assumed that the number of scats was positively related to the frequency of cheetah visits and scat freshness identified recent cheetah activity. Hence, the marking trees with a combination of both fresh and numerous scat were chosen for camera trap placement. The final ten marking trees used for camera trap placement were spread across the home range of the territorial animal, defined as the 95% kernel density polygon derived from the spatial data of the territorial animal occupying that territory. Most marking trees fell within the core of the home range; the 50% kernel density polygon (Figure 2; territory A shown as an example). For each territory, a 28-day survey length was used, which falls within the recommended closed period for large felidae (Karanth & Nichols, 1998). Some territories were survey simultaneously, others consecutively, which was due to the number of camera traps available. This resulted in a total survey period of 95 days. The program CloseTest (Stanley & Burnham, 1999) was used to test for demographic closure. Each camera trap station consisted of two Reconyx PC900 HyperFire camera traps (Reconyx Inc, Holeman, Wisconsin, USA), positioned opposite each other, with enough offset to eliminate flash interference. Camera traps were positioned within 3–5 m from a marking tree facing the tree and mounted on poles approximately 70–90 cm above ground. Traps were programmed to be active 24 hr a day, taking three photographs per trigger, with no delay between triggers. Camera stations were revisited every 7–10 days, to change SD cards and batteries and check for camera functioning.

2.3 | Comparison of model type and performance

Detection histories for all adult male cheetah at each territory were constructed, using their unique pelage pattern for individual identification (Caro, 1994), and the presence of testes for identification of sex. Male cheetahs roam solitarily or in coalitions of two or three, rarely four males (Caro, 1994). Coalition members were treated as one unit, resulting in one detection history per unit, as male coalitions are stable, and the close proximity of coalition members results in identical movement patterns (Caro, 1994). Detection histories consisted of seven sampling occasions each of 4 days in length (Supporting Information Figure S1). A 4-day sampling occasion was chosen because existing movement data of collared cheetah individuals indicated that floater males were present in a territory every 7–10 days (Fischer, 2012). Therefore, seven 4-day sampling occasions should ensure each floater male is recaptured at least once during the survey period of 28 days. A closed population, that is, a population which remains constant in size and composition throughout the period of investigation is a crucial assumption for the model types compared here (White et al., 1982). It was considered that the assumption of a demographically closed population was met as a trapping period of 28 sampling days was short enough that mortality, birth, and migration in and out of the population was not expected. The movements of the floater males in and out of a sampled territory could be interpreted as the population not being geographically closed. However, floaters do have stable home ranges and include the small territories as part of their large home range (Figure 2). Therefore, we consider the population as closed.

Male cheetah abundance at each territory was estimated using four heterogeneity model types: (a) a Huggins type covariate model, that is, a spatial tactic model, run in program MARK; (b) a Pledger model (Pledger, 2000), that is, a finite mixture model, henceforth referred to as mixture model, ran in program MARK; (c) a “floater-only” model, in which only floater males were included in the detection histories run in program CAPTURE; and (d) a heterogeneity M_h model with the jackknife and Chao estimators, run in program CAPTURE. The spatial tactic model was run with spatial tactic coded as an attribute group affecting both capture and recapture probabilities, rather than a traditional Huggins model, because the former calculates abundance in the likelihood (Cooch & White, 1999), thus allowing direct comparisons with mixture models to be made (Williams et al., 2002). Mixture models were run using two mixtures of capture and recapture probabilities; one for territory holders and one for floaters (White, 2008). Mixture models do not require the spatial tactic of each male to be identified. In addition to an abundance estimate, these models produce an estimate of π, the probability of any individual in the population being, in this case, a floater. Four predefined models were ran for the spatial tactic and mixture models: (a) M_o (null model in which all capture and recapture probabilities are equal); (b) M_h (heterogeneity model with two mixtures, each of equal capture and recapture probabilities for territory holders and floaters, respectively); (c) M_b (behavioral model with one mix of different capture and recapture probabilities, but territory holders and floaters having the same capture and recapture probability); and (d) M_{bh} (behavior and heterogeneity model with two mixtures of capture and recapture probabilities, plus a behavioral response, which considers a differential response if the individual has been previously captured, that is, trap-happy or trap-shy (Anile, Amico, & Ragni, 2012). In addition, for spatial tactic models, combinations of M_o and M_b for territorial and floater males were run. Model fit was ranked using Akaike information criterion (AIC) values (Akaike, 1973), adjusted for small sample size (AICc) to indicate the level of support given to each model (Burnham & Anderson, 2002).

The program CAPTURE, accessed via MARK, was used to estimate male cheetah abundance using the floater-only model and the heterogeneity M_h model with the jackknife and Chao estimators for both models, respectively, with Chao models being theoretically more robust to small sample sizes (Boulanger et al., 2004). For these two models, the M_o, M_b, and M_h predefined models were run. When running floater-only models, CAPTURE's model selection test was used to select the most appropriate model from the candidate set of M_o, M_b, and M_h (both jackknife and Chao) by ranking model fit (Burnham & Anderson, 2002).

Spatial tactic models require that each cheetah unit is identified as having either a territorial or floater spatial status. Spatial tactic was determined by examination of spatial data, with spatial tactic coded as a dummy variable. During the survey period, the identity of the territorial individuals at territory D was uncertain, because two different male coalitions were scent marking; therefore, for this territory only, the mixture model and the CAPTURE's heterogeneity M_h model were used, given that these models do not require identification of spatial tactic.

2.4 | True male cheetah abundance at each territory

GPS data from all collared floaters ($n = 8$) within the study area were used to validate that each floater entering a territory core of territory males was captured on camera trap, and thus, true abundance was known for each individual territory. GPS data of collared floaters that entered a territory core were compared with sampling events to check that all floaters were captured on camera trap each day and every respective sampling occasion they were present within a territory. As this was verified (see Section 3), we assumed that also all VHF-collared and noncollared floater males were captured each time they entered a territory. Some marking trees were located outside of the 50% kernel density polygon (Figure 2), due to the fact that monitored marking trees were selected based on the number and freshness of cheetah scats present. However, this did not influence analysis, as peripheral trees were also included in comparison of sampling events and GPS data (Figure 2).

3 | RESULTS

3.1 | Camera trap statistics

Cheetah photographs were classified into independent events, using a criterion of a minimum of 30 min between consecutive photographs of the same individual (O'Brien, Kinnaird, & Wibisono, 2003), giving a total of 603 cheetah events for the study. Females accounted for 24 (3.98%) events, and 27 (4.48%) events were unidentifiable to the individual level. Thus, these events were excluded from analysis and the remaining 552 events used. A total of 36 floater males were recorded, four of which were recorded at two territories (Figure 2; one floater shown as an example), and one was recorded at three territories. Cheetah was detected at eight to ten marking trees per territory. Camera trap success within a territory ranged from 13.21 to 35.71 events/100 trap nights for territory holders, from 7.86 to 20.07 events/100 trap nights for floater males within territories, and from 24.63 to 56.82 for all males combined within territories. Capture probability using a 4-day sampling occasion ranged from 0.85 to 1.00 for territory holders males and from 0.29 to 0.36 for floater males. Performance of the CloseTest supported the assumption of population closure for all territories, with the exception of territory A ($\chi^2 = 12.59$, $df = 5$, $p = 0.03$).

3.2 | True male cheetah abundance at each territory

During the study, spatial GPS data showed that all collared floaters were present within territory cores on a total of 95 days. Camera traps detected individuals within the cores on 91 of the 95 days, when using a temporal resolution of 24 hr, giving a detection probability of 95.79%. When using a 4-day sampling occasion, as used in the capture–recapture models, every time a collared floater entered a territory it was captured on camera trap during the respective sampling occasion, resulting in a 100% detection probability. The 100% detection probability, for detecting floaters entering a territory core, therefore justifies the critical assumption that the true abundance of individuals visiting a territory is known and thus allows meaningful comparisons of true abundance and capture–recapture model estimated abundance to be made in order to assess their performance.

3.3 | Comparison of model type and performance

The spatial tactic model M_o (Territorial), M_b (Floater) was the best fitting model for each territory (Table 1). This model suggests equal capture and recapture probabilities for territorial males and different capture and recapture probabilities for floater males. The top fitting mixture model varied between territories, with the behavior and heterogeneity model (M_{bh}) being the best fit for two territories (A and B), while the heterogeneity model (M_h) was the best fitting model for two other territories (C and E, Table 1). When using program CAPTURE to select the most appropriate model for the floater-only approach, the null model (M_o), was always ranked as the best fitting. For a full comparison of all predefined spatial tactic and mixture model abundance estimates, see Supporting Information Table S1.

The spatial tactic, mixture, and floater-only models always correctly estimated male cheetah abundance, while the heterogeneity M_h (jackknife) and M_h (Chao) models showed less consistent results

TABLE 1 Comparison of best fitting spatial tactic and mixture models for each territory

Territory	Top spatial tactic model	AIC_c spatial status	Parameters	Top mixture model	AIC_c mixture	Parameters	Delta AIC_c
A	M_o (Territorial) M_b (Floater)	60.10	4	M_{bh}	60.60	6	0.50
B	M_o (Territorial) M_b (Floater)	42.39	4	M_{bh}	44.08	6	1.69
C	M_o (Territorial) M_b (Floater)	42.39	4	M_h	48.68	4	6.29
D	NA[a]	NA[a]	NA[a]	M_o	38.66	1	NA[a]
E	M_o (Territorial) M_b (Floater)	29.26	4	M_h	35.71	4	6.45

[a] Identification of territory holders is unclear, because two different male coalitions were scent marking.

(Supporting Information Table S1). The heterogeneity M_h (jackknife) models correctly estimated abundance for two of the territories (B and E), while the heterogeneity M_h (Chao) models correctly estimated abundance for two other territories (A and C). Neither model correctly estimated abundance for territory D. Incorrect abundance estimates were always overestimates by 3.00 ± 5.61 (mean ± standard error [*SE*]) male cheetahs for the jackknife and 1.20 ± 2.17 (mean ± *SE*) male cheetahs for the Chao estimators, respectively. The spatial tactic and mixture models showed similar performance regarding precision, with each top model showing a *SE* of less than 0.001, and a range matching the abundance estimate. The estimation of π by the mixture models showed variation in its accuracy across territories, correctly estimating π for two out of four measurable territories (C and E, Supporting Information Table S1). The three models ran with program CAPTURE showed less accuracy in comparison with the two models run with MARK. Of the three models ran in program CAPTURE, the floater-only models showed the greatest degree of precision in abundance estimates, followed by the M_h (Chao) models, while the M_h (jackknife) models showed the lowest degree of precision and performed approximately equally for the different territories (Supporting Information Table S1).

4 | DISCUSSION

In this study, we compared the results of four closed capture–recapture heterogeneity models to true abundances of male cheetah from five territories. We demonstrated that three out of the four model types were able to accurately and precisely estimate male cheetah abundance, when camera traps were placed at predictable locations of cheetah activity. The three models were a spatial tactic model, a mixture model, and a model estimating only floater abundance. Due to the mixture model not requiring information regarding the spatial status of individuals, we recommend this model for accurately estimating the abundance of male cheetahs. The calculation of abundance at territories is the first vital step in producing population estimates across landscapes and to monitor trends in the population. The movement of floater males between multiple territories (see Section 3) need to be considered for the next steps when conducting population estimation. In this study, floaters visited two or three different territories, thus models calculating population estimates need to incorporate the average number of territories visited per floater and the available space for territories per region.

Spatial tactic and mixture models both gave consistently accurate and highly precise abundance estimates, with every associated *SE* being <0.001, and all ranges containing the abundance estimate itself. Such precision has not yet been recorded in closed capture–recapture studies with cheetahs. For example, two studies using the heterogeneity M_h model in CAPTURE recorded an abundance estimate of seven males with a *SE* of 1.93 and a range of 6–14 males in South Africa (Marnewick, Funston, & Karanth, 2008) or an abundance estimate of five males with a *SE* of 1.36 and a range of 5–11 males in Algeria (Belbachir, Pettorelli, Wacher, Belbachir-bazi, & Durant, 2015). The precision of abundance estimates as in our study, coupled with the accuracy of abundance estimates, is an obvious and important advantage of spatial tactic and mixture models in MARK, over the traditionally used heterogeneity M_h model in CAPTURE.

Precision of abundance estimates in comparison with those produced by heterogeneity models used for other large felids, further highlight the favorable results of this study. Gray and Prum (2012) compared mixture models and a Huggins type gender model (comparable to the spatial tactic model used here) for leopard *Panthera pardus* and detected differences in abundance estimates between the model types. However, true abundance of leopard was unknown, thus inferences regarding the accuracy of estimates could not be made. Leopard abundance estimates had relatively large standard errors, for example, an abundance of 22.4 animals had a *SE* of 10.7 for the best fitting mixture model, and an abundance of 19.8 animals had a *SE* of 8.6 for the best fitting gender model. It was suggested that the low precision of abundance estimates were due to a low sample size of 12, combined with low detection probability. However, our study produced precise abundance estimates with lower sample sizes, and Selvan, Lyngdoh, Habib, and Gopi (2014) found mixture models to be robust even to small sample sizes when estimating tiger *Panthera tigris* abundance. A relatively high detection probability may therefore provide a better explanation for the high precision of cheetah abundance estimates, which may in turn be due to the placement of camera trap stations at marking trees.

Placement of camera trap stations at marking trees has previously been recommended as a method of increasing detection probability of cheetahs, albeit biased toward males (Boast, Reeves, & Klein, 2015; Brassine & Parker, 2015; Marker, Fabiani, & Nghikembua, 2008; Marnewick, Bothma, & Verdoorn, 2006). Camera trap success from our study was relatively high in comparison with others, ranging between 24.63 and 56.82 events/100 trap nights within a territory. In addition, it resulted in a 100% detection probability for those collared floaters entering a territory core, using a 4-day sampling occasion. When placing camera traps at marking trees in north-central Namibia, Marker et al. (2008) recorded 21.36 events/100 trap nights, while Marnewick et al. (2006) recorded 14.95 events/100 trap nights at a single marking tree in South Africa. Such comparisons may suggest that the use of spatial GPS data from male cheetahs to find marking trees to be key in selecting the most optimal marking trees. Other studies using combinations of roads, trails, and marking trees for camera trap placement have produced lower success rates with 0.98 events/100 trap nights in Botswana (Boast et al., 2015) and 10 events/100 trap nights in South Africa (Marnewick et al., 2008). The resulting high capture probability of male cheetahs in our study may have led to the distinct differences in capture probability between territorial and floater males. Such heterogeneity may have been masked if a different survey design was used which resulted in lower capture probabilities. Further research into the utility of such models for other species in which heterogeneity is expected, but which suffer from low capture probabilities, would be of use in gaining a better understanding of the applicability of such models across species.

We recommend mixture models as the most appropriate model for estimating male cheetah abundance, despite spatial tactic models giving the best model fit at each territory. Mixture models have the strong advantage of requiring no prior information regarding the spatial tactic of each male present in a territory, that is, it is not needed to know whether a male is a territory holder or a floater. Mixture models also produced accurate and precise abundance estimates, with no differences seen between spatial tactic top model results. In addition, mixture models were robust even when the identity of the territorial male was unclear, such as for territory D, where two different male coalitions were scent marking, maybe being in the process of sorting out territory ownership. However, the ability of mixture models to correctly estimate π, the probability of being a floater, was inconsistent. Thus, comparison of all individual encounter histories with each other to identify those individuals with a high frequency of detection and those with a lower frequency of detection, that is, territory holders and floater, respectively, rather than reliance on this estimate, is recommended in determining the number of floaters.

CAPTURE heterogeneity M_h models (jackknife and Chao estimators) were unable to consistently estimate true abundance, and when incorrect, overestimated abundance, although the correct abundance was contained within the estimate ranges in four of the five territories. Positive bias in abundance estimates from M_h estimators has been previously described when nearly all individuals in a survey population were captured (Chao & Huggins, 2005), as in our study. Such a situation is rare, given the typically low capture probability of target species, especially large felids, reported in published studies (Foster & Harmsen, 2012). The positive bias reported here for CAPTURE models is therefore likely due to the fact that the territorial animals, and all visiting floaters, were captured on camera traps, a result again attributed to the placement of camera trap stations at marking trees.

Due to the poor performance of the CAPTURE heterogeneity M_h model for large carnivore species, this model has recently been deemed inappropriate for the use with these species (Gray & Prum, 2012). Our study confirms this, and thus previous studies having used this model for estimating cheetah abundance, might be inaccurate and represent overestimates of abundance (e.g., Marker et al., 2008; Marnewick et al., 2008). Although true abundance was unknown in these studies and therefore inferences regarding bias cannot be made, the lack of precision in estimates clearly hampers the effective use of model results in wildlife management. In contrast to CAPTURE heterogeneity M_h models, the CAPTURE models for estimating the floater-only abundance performed well, always estimating abundance correctly with high precision. However, like the spatial tactic models, these models require a prior knowledge of the spatial tactic of all males detected, which may not always be available.

The recently developed spatial explicit capture–recapture models (secr) were not considered appropriate for male cheetahs as these models presume the probability of detection decreases with movement away from the center of a home range (Royle et al., 2014). Such models are useful when the spatial extent of the study area needs to be defined to convert abundance into density. They produce density estimates from the onset and as a result are gaining popularity within the literature (Royle et al., 2014). However, for floater males, the probability of capture is not so much related to distance away from the center but rather from the position of territories within their home range (Figure 2, unpublished data).

The heterogeneity in capture probability for male cheetahs within a territory is largely due to floater males moving in and out of the territory, each of which is defined as a survey area, whereas territorial males spend the majority of their time within a territory (Caro, 1994). Thus, all individuals were potentially available for detection at marking trees throughout the survey period. This differs from other studies with heterogeneity in capture probability. For sex-specific heterogeneity, for example, it was suggested that the difference between the sexes to be detected was based on the location where the camera traps were deployed, which was along roads that might have been used differently by the sexes (e.g., Gray & Prum, 2012). In such cases, the individuals of one group (sex) moved off and on the survey area and thus for certain periods were not available for detection. The distinction between the two scenarios and its ramifications for abundance modeling are unclear; however, we suggest that a scenario in which all individuals are potentially available for detection throughout the survey period are reasonably reliable.

Our study adds to the growing body of literature examining models accounting for heterogeneity in sex, social status, etc., which have been found to be a better fit than models not accounting for these differences. Both Cubaynes et al. (2010) and Cubaynes (2011), used mixture models for estimating wolf *Canis lupus* abundance using a noninvasive genetic sampling approach. These studies used two-class mixture models, representing highly detectable (resident adults) and lowly detectable (pups, juveniles, and migrants) individuals, which may have moved out of the study area during the survey. In both studies, the heterogeneity mixture models showed better model fit than those with homogenous detection probabilities. Multievent models are another potential option for species for which capture probability or other parameters such as survival, may be influenced by the individual state. Originating from multisite models (Arnason, 1972), which were designed when individuals may be recorded successively at different sites, multievent models can be used to study repeated transitions among states, for example, breeding and nonbreeding states (Pradel, 2005). However, such models would not be considered appropriate when the studied states in a species are not reversible states, such as the spatial tactics in adult male cheetahs, which first are floaters and then, if successful, territory holders (Melzheimer et al., 2018).

Heterogeneity in detection probability is inherent to many animal populations (Lebreton et al., 1992), and examples include any species with both resident and transient or nomadic individuals, such as bottlenose dolphin *Tursiops truncatus* (Conn et al., 2011), brown hyena *Hyaena brunnea* (Mills, 1990), coyote (Larrucea et al., 2007), and many bird species including blackcaps *Sylvia atricapella* (Belda, Barba, & Monrós, 2007) and Eurasian reed warbler *Acrocephalus scirpaceus* (Clavel, Robert, Devictor, & Julliard, 2008). However, capture–recapture models assume a homogenous detection probability of individuals for population estimates (Krebs, 1999). Here, we have demonstrated the importance of modeling heterogeneity in detection probability associated with spatial tactics of male cheetahs when estimating abundance. We conclude that mixture models are most appropriate for heterogeneity in detection probability and have the advantage of requiring no prior information regarding individuals. This gives them potential application for a wide range of species for which attributes effecting detection probability, such as sex, are unknown for each individual. We recommend the application of mixture models to other species with intrasexual behavioral differences which are likely to result in heterogeneity in capture probability, particularly in situations in which model results can be compared to known abundances.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

SE and JM conceived the idea. MF and JM collected the data. SE and MF analyzed the data. SE wrote the manuscript. BW gave valuable input to the manuscript. All authors read and approved the final manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Supplementary Material

Figure S1: Detection histories for each territory. Each line represents an individual, with territorial males labelled as 'T' and floater males labelled as 'F'. '1' represents a sampling occasion in which that individual was detected and '0' represents a sampling occasion in which the individual was not detected.

Territory A

1111101 T;

0100011 F

1001111 F

0010110 F

1000000 F

0001000 F

0001000 F

1001011 F

0100000 F

Territory B

1111111 T

0000100 F

1111011 F

0000010 F

1000011 F

0010000 F

0100001 F

Territory C

1111111 T

0011000 F

1100000 F

1111000 F

1110000 F

1100000 F

0000001 F

Territory D (identity of territorial and floaters was unclear)

1000001

0010000

1101000

1010001

0110000

0000100

Territory E

1111111 T

1010010 F

0101000 F

0010100 F

0000010 F

Supplementary Material

Table S1: Comparison of the true abundance of territory holders and floater male units with the top model performance estimating male cheetah abundance. Spatial tactic and mixture model were run with MARK, floater only, heterogeneity Mh (jack-knife) and heterogeneity Mh (Chao) models were run with CAPTURE.

Territory	**True abundance: territorial + floater (π)**	**Spatial tactic model: territorial (S.E., range) + floater (S.E., range)**	**Mixture model: males (S.E., range, π)**	**Floater only model: males (S.E., range)**	**M_h (jack-knife) model: males (S.E., range)**	**M_h (Chao) model: males (S.E., range)**
A	1+8 (0.89)	1 (<0.001, 1-1) + 8 (<0.001, 8-8)	9 (<0.001, 9-9, 0.61)	8 (0.77, 8-8)	22 (7.33, 14-45)	9 (0.00, 9-9)
B	1+6 (0.86)	1 (<0.001, 1-1) + 6 (<0.001, 6-6)	7 (<0.001, 7-7, 0.71)	6 (0.69, 6-6)	7 (2.83, 7-20)	12 (7.19, 8-47)
C	1+6 (0.86)	1 (0.00, 1-1) + 6 (0.00, 6-6)	7 (0.00, 7-7, 0.86)	6 (0.69, 6-6)	8 (1.33, 8-14)	7 (0.54, 7-10)
D	Total: 6 males	NA	6 (<0.001, 6-6, NA)	NA	8 (1.85, 7-15)	7 (1.87, 7-17)
E	1+4 (0.80)	1 (<0.001, 1-1) + 4 (0.00, 4-4)	5 (0.00, 5-5, 0.80)	4 (0.77, 4-4)	5 (0.73, 5-9)	6 (1.31, 5-9)

π: *probability of any individual within the population being a floater male*

Manuscript

7. Shifting cattle herds away from communication hubs of cheetahs solves the cheetah-farmer conflict

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7.1 Abstract

Human wildlife conflicts occur worldwide and often involve threatened species. Although many non-lethal mitigation solutions are available, none has previously used the biology of the conflict species itself to derive an effective and long-lasting solution. Here we demonstrate how the socio-spatial organisation of cheetahs (Acinonyx jubatus) provides the key for such a solution. Cheetahs maintained regularly distributed communication hubs, defended by territory holders and inherited from generation to generation. These communication hubs were regularly visited by non-territorial cheetahs, forming hotspots of cheetah density and consequently increased predation risk to young calves for cattle farmers in central Namibia in these areas. Shifting cattle herds elsewhere during the calving season drastically reduced cattle losses, because cheetahs did not follow herds and preyed on naturally occurring local prey species. Our approach of exploiting the biology of conflict species might inspire similar solutions for other conflict species with non-homogenous space use.

7.2 Introduction

Human wildlife conflicts (HWC) are a global challenge and likely to increase in the future (Ripple et al. 2016). In particular, carnivore species often require large ranges and are therefore expected to come under increased pressure from human population growth and concurrent loss of natural habitats (Bales et al. 2005). Contact between carnivores and humans and their livestock will increase, and so will predation on livestock (Inskip & Zimmermann 2009). Retaliatory killing of carnivores is a common response to the perceived or actual threat of carnivore predation on livestock (Clark et al. 1996, Weber & Rabinowitz 1996, Gittleman et al. 2001, Ray et al. 2005).

Many carnivore species involved in HWC are listed as vulnerable or endangered by the International Union for Conservation of Nature (IUCN) (Inskip & Zimmermann 2009). Therefore, non-lethal methods to mitigate HWC should be encouraged, such as predator-proof bomas or kraals (e.g. lions (Panthera leo) Lichtenfeld et al. 2014, cougar (Puma concolor) Mazzolli et al. 2002), livestock guarding dogs (e.g. wolves (Canis lupus) Gehring et al. 2010, cheetahs (Acinonyx jubatus) Marker et al. 2005), compensatory payments (e.g. African wild dogs (Lycaon pictus) Woodroffe et al. 2005, tigers (Panthera tigris) Karanth & Gopal 2005), beef from certified carnivore-friendly farmers (e.g. wolves Aquino & Falk 2001, cheetahs Marker et al. 2010) and translocations (e.g. brown bear (Ursus arctos) Zimmermann et al. 2003).

Although all these methods were shown to be successful in some cases, they failed in others (Inskip & Zimmermann 2009, Massei et al. 2010, Treves et al. 2016). Particularly translocations have a low success rate, with approximately only 40% of translocated feline individuals surviving for at least one year after release after a translocation (Fonturbel & Simonetti, 2011, Weise et al. 2015). Compensatory payments are often not effective, difficult to implement and often only successful in combination with other mitigation methods (Madhusudan 2003, Gusset et al. 2009, Inskip & Zimmermann 2009). Livestock guarding dogs might kill target and non-target carnivore species when defending livestock and require substantial attention (Potgieter et al. 2016). Beef from certified carnivore-friendly farmers is dependent on the market and the willingness of consumers to pay more for such meat (Marker & Boast 2015). Finally, predator-proof bomas or kraals are only appropriate for small-scale farmers who handle all of their livestock on a daily basis but are impractical for commercial farmers with several hundred heads of livestock (Mendelsohn et al. 2003).

The rapidly developing field of movement ecology and the substantial improvements of tracking devices and analysis tools (Nathan et al. 2008, Kays et al. 2015, Wilmers et al. 2015) have a large potential for the development of new and innovative approaches for conservation (Allen & Singh 2016, Tucker et al. 2018). In the context of HWC, collaring and tracking of conflict species is often mentioned as a possible mitigation tool, although examples of successful applications are rare and typically limited to geofencing and early warning systems (Wall et al. 2014, Weise et al. 2019). These systems are mainly technical applications and warn the livestock owners or herders of an approaching carnivore, requiring them to be on continuous standby in order to respond quickly (Wall et al. 2014, Weise et al. 2019). Here we present a new method that provides a highly effective and long-lasting solution to mitigate a widely known HWC. We use an in-depth understanding of the spatial movements and socio-spatial organisation of a carnivore species, the cheetah to experimentally test a research-based modification of livestock management that substantially reduced livestock losses on commercial farmland in central Namibia.

Conflicts between farmers and cheetahs are well documented and various non-lethal mitigation methods have been attempted in the past. Some focus on changing the perception of farmers towards cheetahs through education, others on direct protection of livestock with the help of bomas and/or livestock guarding dogs and others by removing “problem animals” and translocating them to another location (Marker & Boast 2015). None, however, has used information on the socio-spatial organization of the conflict species itself to derive an effecting and long-lasting HWC solution.

Cheetahs have an interesting social system in that males either operate on their own or live in coalitions of two or three males. Any such social unit either holds a small territory or roams as “floaters” over large home ranges (Caro 1994, Melzheimer et al. 2018). Females also roam across large home ranges, either on their own or with dependent offspring. In the Serengeti National Park (NP) in Tanzania, East Africa, the territories of males cover on average 48 km2 if calculated as a minimum convex polygon (MCP) encompassing 95% of all locations and the home ranges of floaters 777 km2 (95% MCP, Caro 1994). On commercial farmland in Namibia, southern Africa, territories of males comprise on average 379 km2 (95% MCP) and home ranges of floaters 1595 km2 (95% MCP, Melzheimer et al. 2018). Home ranges of females in the Serengeti NP covered on average 833 km2 (Caro 1994), in Namibia 650 km2 (Melzheimer et al. 2018). Territorial cheetah males regularly scent mark prominent landscape features, mainly conspicuous trees but also termite mounts and rocks, with urine and faeces to advertise their territory ownership (Caro 1994, Melzheimer et al. 2018). Competition for territories is high amongst males and fights over territories often result in the death of the territory holder(s) or their challenger(s) (Caro 1994, Melzheimer et al. 2018). This suggests that territories contain valuable resources such as preferred access to females or prey animals (Caro & Collin 1987, Caro 1994, Melzheimer et al. 2018).

In this study, we first show that the small cheetah male territories are distributed in a regular pattern across the landscape (see results, Figure 1). The territories are not contiguous with each other but are separated by a surrounding matrix of “no man’s land”, i.e. land not defended by any cheetah. This results in farms containing cheetah territories, or parts of it, and farms not containing cheetah territories (see results, Figure 1). Because cheetah males fight over territories, we expect that the location and shape of the territory remains approximately constant across successive territory holders. If so, this means that the same farms contain (or do not contain) cheetah territories over many cheetah generations and that the respective farm owners have the highest (or lowest) conflict with cheetahs. If territories remain stable over time, we also expect that the marking locations are traditional, "culturally inherited" sites used by several generations of territory holders.

Home ranges of floaters overlapped substantially with each other and encompassed two or three territories (see results Floaters visit the territories within their home ranges frequently to sniff, but not scent-mark, marking locations during one or two days before they moved onto the next territory (Melzheimer et al. 2018). If floaters started challenging the territory holders to take over the territory, they also began to exhibit marking behaviour at the marking locations (Melzheimer et al. 2018).). Marking locations were typically located in the core area of the territories (see results), defined by the 50% kernel density estimator (KDE50) of the GPS locations ("fixes") of the territory holder. The home ranges of females also overlapped with several territories, but they visited the marking locations less frequently than the males (Caro 1994, see results). Since males of both tactics and females visit the core areas of the territories we termed these areas "cheetah communication hubs". These hubs are information centres with the dual function of territory defence and information exchange on a local population level (Darden et al. 2008).

The core areas are local hotspots of cheetah activity and density as a result of the constant presence of the territory holders and the frequent visits of up to four floater units (Melzheimer et al. 2018). Each floater or floater coalition spent a considerable amount of their time in the communication hubs (see results) and we assumed that the frequency of hunting is positively correlated with the time spent in the area. Taking the duration of the visits, the frequency of the visits and the number of visiting floaters into account, the density of kills should be substantially higher within the hubs than in the surrounding matrix. If these areas are used for cattle herds with calves under 6 months of age, then cheetah hubs would be hotspots for cheetah-farmer conflicts. Thus, farmers containing a full or part of a cheetah hub on their farm should face higher cattle calf losses than farmers not containing a cheetah communication hub on their farm. Furthermore, we would expect that cattle calf losses can be substantially reduced when breeding herds with young calves are shifted away from cheetah hubs. If cheetahs in hubs do not follow cattle herds to their new location (“camp”), then this simple management adjustment is the key to substantially reduce farmer-cheetah conflict in central Namibia.

7.3 Results

Distribution of communication hubs and overlap with farms. Within the study area, we identified 28 cheetah male territories. The 28 corresponding cheetah communication hubs (i.e. KDE50 of territory holders) had an average size (± standard deviation (SD)) of 41.3 ± 24.7 km2 (95% confidence interval (CI): 50.5 km2, 32.2 km2, Figure 1). The distribution of the cheetah hubs was significantly more regular than expected, i.e. overdispersed, on a scale of 15 - 20 km (range of radius R, Figure 2). The average distance between centroids of neighbouring cheetah hubs was 22.9 ± 4.0 km (95% CI: 21.6 km, 24.3 km, n = 38). Six territory holders owned two territories temporarily. Most of them defended both communication hubs over many months but eventually gave up one of them.

We collected data on movements of the majority of visiting floaters from 20 directly neighbouring communication hubs, thus used only these hubs for further analyses (Figure 6). This core study area covered 10,552.5 km^2 and encompassed 278 farms (Figure 1). The 20 hubs covered a total area of 764.9 km2, or 7.2% of the core study area. The 278 farms within the core study area had an average size of 45.8 ± 20.7 km2 (95% CI: 43.3 km2, 48.2 km2). Of those, 89 farms (32.0%) contained a cheetah hub or parts of a cheetah hub with a median overlap of 6.5 km^2 (Figure 3a) and the median of the portion of overlap between hub and individual farm was 13.1% (Figure 3b). In five of the farms, the hubs covered >50.0% of the farm (Figure 3c).

Stability of core areas of territories and used marking locations over time. During the study period, six territories changed ownership several times (n2generations = 2, n3generations = 2, n4generations = 4, Table 1, example Figure 4 a). The average of the overlap of the core areas between two successive territory holders was 71.0% (Table 1). The centroids of the KDE50 of consecutive territory holders were on average 1.9 km apart (95% CI: 0.9 km, 2.9 km, n = 16). In four cases, the new territory holders shifted the core area by more than 3.0 km (average = 4.8 km) (Figure.5). If these cases were omitted from the analyses, the average distance between centroids was 0.9 km (95% CI: 0.5 km, 1.4 km, n = 12).

Incoming territory holders typically used the same marking locations as the previous owner (Figure 4 b-d). Most of these marking locations were located within the communication hubs (Figure 4 b-d).

Utilisation of communication hubs by floaters and females. Floater units (i.e. solitary floaters or coalitions) frequently visited the communication hubs within their home ranges, which showed substantial overlap between each other (Figure 6 and 7). Floater units visited on average 2.9 ±

1.1 hubs (95% CI: 2.3, 3.6, n = 14, Figure 6 and 7) and spent on average 28.6 ± 14.5% (95% CI: 20.3%, 37.0%, n = 14) of their time inside these areas. In comparison, communication hubs comprised on average 9.1 ± 3.4% (95% CI: 7.2%, 11.1%, n = 14) of the home range areas of the floaters. Their time spent in communication hubs indicated a strong preference for these areas (paired t-test, $P < 0.001$, n = 14).

Females visited on average 3.9 ± 2.8 communication hubs (95% CI: 1.8, 5.9, n = 10) (Figure 8) and spent on average 4.0 ± 2.6% (95% CI: 2%, 6%, n = 10) of their time inside the hubs. In comparison, the communication hubs comprised on average 5.7 ± 3.1 % (95% CI: 3.5%, 7.9%, n = 10) of the home range areas of the females. Their time spent in the communication hubs indicated an avoidance of these areas (paired t-test, $P < 0.032$, n = 10).

Density of floaters in and around communication hubs. Within each hub, there were territory holders present (solitary or coalitions) plus a varying number of floater units (solitary or coalitions) visiting the hub. The density of floater units decreased exponentially with increasing distance from the border of the hubs (Figure 9).

Losses of cattle calves. Farmers with at least an area of 7 km^2 of the farm (the median for affected farms) overlapping with a cheetah hub experienced substantial losses of cattle calves (Table 2). The highest losses were as high as 33 calves per year. Once farmers adjusted their farm management by shifting cattle herds with suckler cows and calves away from the location of known cheetah hubs, the number of calves lost to depredation by cheetahs decreased substantially (Wilcoxon signed-ranks test, $P < 0.027$, n = 6, Table 2). None of the cheetah hubs shifted when the farmers shifted their breeding herds away from the hubs. With a price for a weaner of approximately 300 Euros, the observed losses prior to management adjustments reached in some cases several thousand Euros per year, and in the most affected farms up to 11,100 Euros, a substantial loss in earnings.

7.4 Discussion

Human wildlife conflicts (HWC), particularly human carnivore conflicts, are globally widespread. Many non-lethal mitigation methods have been tried. Common methods are predator-proof bomas for livestock, livestock guarding dogs, compensatory payments for losses, beef from certified carnivore-friendly farmers, translocations of "problem animals" and geofencing (Zimmermann et al. 2003, Karanth & Gopal 2005, Marker et al. 2005, Marker et al. 2010, Lichtenfeld et al. 2014, Weise et al. 2019). Here we demonstrate a new approach based on the socio-spatial organisation of the conflict species, the cheetah, and show that on farmland in central Namibia livestock losses were drastically reduced when breeding herds were kept away from areas of high cheetah activity and density. Such areas are the cheetah communication hubs, i.e. the core areas or KDE50 of the territory holders, which encompass numerous marking locations patrolled and marked at high frequencies by the territory holders and visited regularly by floater units which spent considerable time in the communication hubs.

High vs. low predation risk areas provide key to avoid livestock losses. If breeding cattle herds are unwittingly kept within a cheetah communication hub, losses of calves are substantial. Due to the high local density of all cheetah individuals using the hub, the resulting local predation risk is also high. Although cheetahs do not preferentially select livestock species as prey (Marker et al. 2003a, Wachter et al. 2006, Voigt et al. 2013, Voigt et al. 2014), they will readily prey on cattle calves when available because they are relatively naïve and easy prey. If the suckler cows are moved away from the hubs into other cattle camps of the farm, the losses declined drastically, because cheetahs do not follow the breeding herds. They rather prey on naturally occurring local prey species such as juvenile eland (Taurotragus oryx), greater kudu (Tragelaphus strepsiceros), red hartebeest (Alcelaphus buselaphus), gemsbok (Oryx gazelle) and adult warthog (Phacochoerus africanus), springbok (Antidorcas marsupialis), duiker (Sylvicapra grimmia), steenbok (Raphicerus campestris) and scrub hare (Lepus saxatilis, Marker et al. 2003a, Wachter et al. 2006, Voigt et al. 2013, Voigt et al. 2014). These prey species are distributed rather evenly throughout the year across the farmland in central Namibia. With grass and water being available across the farmlands, wildlife prey of cheetahs do not migrate but are stationary, resident prey (Lindsey 2011).

These findings have important implications. First, the key insight is that (1) there are “problem areas”, the cheetah communication hubs, rather than “problem cheetahs” and (2) the matrix surrounding the cheetah hubs is a relatively safe area to keep the suckler cows with the calves. Cheetahs occurring in a “problem area” and killing livestock might still be perceived as “problem animals”, but such individual cheetahs are not problem animals in the sense of habitual livestock killers (Marker et al. 2003b).

Depredation risk by cheetahs in the matrix between the hubs does exist and farmers lose calves to cheetahs also in these areas. However, the losses are much lower and typically in a range acceptable to most farmers. In particular, cheetah females use the matrix between the communication hubs. Females are solitary or with their offspring and roam in central Namibia in large home ranges of 650 km2 (Melzheimer et al. 2018), encompassing approximately 14 farms. They use their entire home range and thus in principle distribute their potential depredation impact across a large area. Nevertheless, females with offspring can remain for several weeks in a relatively small area of their home range (Caro 1994), hence inducing locally and temporally aggregated cattle calf losses to particular farmers. An adjustment of breeding herd management might also be possible in such cases but female movements are less predictable than male movements. Detailed knowledge of the location of the communication hubs and the safer surrounding matrix is the ultimate key for the success of our mitigation solution in the farmer-cheetah conflict.

Long-term adjustment of breeding herd management. A successful implementation of the knowledge on cheetah hub locations into the grazing management of breeding herds requires enough alternative grazing grounds on the farm. An economically effective rangeland management ensures that all areas are grazed according to their capacity without over-utilizing the vegetation. This can be challenging even without cheetah hubs adding another management dimension to consider. In order to make use of cheetah hubs for grazing, the hubs should be used for grazing by adult cattle or oxen. The larger this area is, the more difficult it becomes for a farmer to adjust the grazing management. Large overlap areas were relatively rare in our study area, with only five farms having an overlap of more than 50%. It is not possible to set a threshold for a critical overlap area of a cheetah hub with the farm, because the remaining available grazing area depends on the farm size, the grazing capacity, the grass quality, water availability, habitat and geographic characteristics of the farm, road accessibility and infrastructure of camps on the farm. In difficult cases, additional management measures might be required, such as supplementary feeding of the herds in safe areas of the farm or some form of cooperation with neighbouring farmers of their matrix areas during the calving season. It is therefore appropriate to develop for and with each farmer a tailored solution for his farm. This is particularly important when cheetah hubs have unconventional shapes and consist e.g. of two poles. Although this research-based approach is time intensive, it is a sustainable and long-lasting solution, because we could show that the locations of the cheetah territories and resulting hubs are stable over time. Similarly, Caro (1994) reported for the Serengeti NP that the territories remained stable after a change in territory ownership.

There is also anecdotal evidence from farmers that cheetah territories are stable over time. Some farmers containing a cheetah hub on their farm reported that some cheetah marking trees on their farm were already known by their fathers, grandfathers and great-grandfathers. Their ancestors tried to reduce the number of cheetahs on the farm not only by killing cheetahs, but also by cutting their marking trees. As is well known in the farmer community, neither approach reduced the perceived number of cheetahs on the farm. This is consistent with our results, because a cheetah communication hub contains a high number of marking trees and the removal of some trees will likely intensify the use of other marking trees or activate new marking trees or other conspicuous marking sites such as termite mounts or even human made structures such as water basins. Because cheetah males queue for territory ownership, the direct elimination of territory holders will likely increase the turnover of territory holders and therefore cheetah activity in the communication hubs (Melzheimer et al. 2018), a counterproductive development from a livestock predation point of view.

Fine-tune adjustment of breeding herd management. Although the locations of the cheetah communication hubs generally remained stable over time, we observed a few small scale shifts of the centroids between consecutive generations of territory holders. Depending on the farm logistics and characteristics, such a distance might indicate a laborious change in the adjustment of the handling of the breeding herds. An average farm in central Namibia of 45.8 km2 has a diameter of 6.8 km if shaped as a square, thus a shift of a cheetah hub centroid by a few kilometres might be challenging to handle. This would be another important reason not to induce a pre-term change in territory ownership by killing the territory holders but to maintain the status quo as long as possible. Nevertheless, changes in territory ownership do regularly occur through fights of cheetah males, thus ideally, at least one cheetah per known cheetah hub should be monitored over long periods, preferably over many years, to provide data for regular adjustments of the grazing management of breeding herds.

Predicting locations of yet unknown cheetah hubs. The home ranges of floaters encompass several communication hubs, which they visit on a frequent basis. If floaters frequently visit an area not yet identified as a cheetah hub and at a distance of approximately 20 km from a known cheetah hub, it is highly likely that this cluster of GPS fixes represents an additional cheetah hub (Figure 7). Such clusters and the regular distribution of the cheetah hubs across the landscape allows to predict new, not yet known or investigated hubs.

Significance of cheetah territories and their distribution. Cheetah territories are important communication areas (Caro 1994, Melzheimer et al. 2018). Territory holders frequently visit and mark the marking locations in the core area of their territories to claim ownership, whereas floaters only sniff at the marking locations during their frequent visits (Melzheimer et al. 2018). Females visit the marking locations in the male territories only rarely (Caro 1994, Edwards et al. 2018). The high activity in the territories and the heavy fights over territory ownership implies that territories contain valuable resources for males, most likely preferred access to females or prey animals (Caro & Collin 1987, Caro 1994, Gottelli et al. 2007). A previous study on paternity analyses did not clearly reveal whether territory holders or floaters had a higher reproductive success (Gottelli et al. 2007). However, encounters between females and males resulting in successful reproduction were not linked with the spatial movements of the animals.

Availability of easy-to-kill prey animals such as cattle calves is unlikely to be the underlying factor which determines the location and distribution of male territories in Namibia, because cheetahs do not follow the cattle breeding herds when they were shifted. Locally naturally occurring wildlife prey species are distributed approximately evenly across the farmland, because they can move freely between most of the farms and the widely distributed water places on farms discourage large scale migration movements (Lindsey 2011).

The average distance between centroids of neighbouring cheetah hubs was 22.9 ± 4.0 km and spacing was significantly regular resembling an ideal free distribution (Fretwell 1972). The surrounding matrix of “no man’s land” is not defended by any male, but used mainly by females to raise their offspring and floaters to travel from one territory to another (Caro 1994). Also in the Serengeti NP, the distance between the centroids of the territories was approximately 20 km (estimated from figure 8.5 in Caro 1994).

Some territory holders temporarily owned two territories. This likely increases their access to preferred resources but might also require additional investment in defending the hubs. Most territory holders in our study held both communication hubs over many months and eventually gave up one of them. Caro (1994) described similar incidences of territory holders in the Serengeti NP. However, in areas with low cheetah density, it might be feasible for cheetah males to own two territories over substantial time periods.

Cheetah aggregations described in other studies. Several previous studies described the occurrence of specific areas with high local individual and population densities (Durant 1998, Muntifering et al. 2006, Broekhuis & Gopalaswamy 2016). These studies did not focus on the conceptual socio-spatial organization of cheetahs and its potential for mitigation methods of HWC. A study on spatial movements of cheetahs in north-central Namibia reported on high-use and low-use areas by cheetahs on farmland (Muntifering et al. 2006). The high-use areas were characterised by greater visibility, more grass cover, more abundant prey and shorter shrub vegetation. The study was conducted on three farms with GPS data from four male units and three females, with all data pooled together. As the spatial distribution of the high-use areas across the three farms was not depicted, it is unknown whether the high-use areas corresponded to the hubs described in our study.

Another study reported cheetah aggregations in the Serengeti NP where prey species accumulate during the large-scale migration of herbivores in the Serengeti ecosystem (Durant

1998). Cheetahs occurred temporarily in large numbers within a few kilometres from each other when prey availability was high, particularly Thomson's gazelles (Eudorcas thomsoni). These "temporary hotspots" (Durant et al. 2007), however, are substantially different from the cheetah hubs describe here.

A relatively recent study in the Maasai Mara landscape in Kenya also described "hotspots" of cheetah densities (Broekhuis & Gopalaswamy 2016). The study estimated cheetah densities by conducting a survey in the study area by car and using a spatially explicit capture-recapture (SECR) method. The estimated posterior density of cheetahs resulted in areas with high densities (hotspots) and low densities. Interestingly, the areas with high densities (n = 7) were distributed in a regular pattern with distances of approximately 20 km. It is unknown whether these areas correspond to the territories in our study and the one in the Serengeti NP (Caro 1994), because the areas included pooled sightings of territory holders, floaters and females, and the sex ratio in study population was biased towards females with approximately five females to every one male. Irrespective of whether the hotspots describe in Broekhuis & Gopalaswamy (2016) and the cheetah hubs in our study correspond to each other, the use of SECR models to estimate density of cheetahs is questionable. These models are based on the assumption that the probability of detection decreases with movement away from the centre of a home range (Royle et al. 2014). This assumption is met for territory holders and females, but not for floaters, that encompass in their home range several territories of territory holders (Edwards et al. 2018). For such a system, we showed that the most useful models are heterogeneity models (Edwards et al. 2018).

Mitigation solutions for HWC with different constellations. The here presented key to drastically reduce livestock losses in sustainable way by adjusting the management of breeding herds is tailored for the HWC between cattle farmers and cheetahs. It takes into account the unique socio-spatial organization of cheetahs that we have shown to be spatially stable over time. Not all farmer in Namibia are cattle farmers, some keep additionally or exclusively valuable game species (Marker-Kraus et al. 1996). Game farmers who keep particularly valuable game species on their farm, erect high game fences of approximately 3.2 meters in height. These game fences are typically permeable for cheetahs, either by using holes dug by borrowing species or by squeezing themselves between the wires. The loss of a calf of a roan antelope (Hippotragus equinus) and sable antelope (Hippotragus niger) can reach up to 10,000 Euro. Game farmers are therefore highly intolerant towards cheetahs that entered their game camps and usually use lethal methods to solve this conflict. Collaboration between game farmers and researchers is likely to be fruitful because knowing the location of a cheetah hub before erecting game fences to keep valuable game will prevent future losses and conflict with cheetahs. When the game fence has already been erected and encloses a cheetah hub or part of it, the most successful approach might be to add an electrified wire at the bottom of the fence. The fence needs to be controlled regularly for holes to ensure keeping the cheetahs out which are en-route to their traditional marking locations.

Other carnivore species than cheetahs obviously have different socio-spatial organizations and their occupied area rarely contains “no man’s land” that is not defended by any animal of the population. For these species other mitigation solutions are needed, but our approach of closely investigate the biology of the carnivore species and to closely collaborate with the people affected by the HWC might inspire new and conceptually similar solutions.

7.5 Methods

Study animals. We captured, immobilised and collared the cheetahs as described in Melzheimer et al. (2018) and Thalwitzer et al. (2010). If males were part of a coalition, we captured also the other coalition members. We fitted only one coalition partner with a GPS collar and the other(s) with a VHF collar or they were not collared, because we previously showed that the coalition partners always stay together (Melzheimer et al. 2018). Only fully grown, adult cheetahs entered the analyses of this study. This were 56 male units (42 units of territory holders, 14 units of floaters) and 10 females, collared between 2008 and 2018 in central Namibia.

We fitted the animals with accelerometer-informed GPS collars (e-obs GmbH, Grünwald, Germany) that recorded GPS fixes every 15 minutes when the animal moved and every 360 minutes when animal was resting. As soon as the animal started moving again, the higher schedule was triggered again (Brown et al. 2012). On average, the collars recorded 46 GPS fixes per day and the gaps where filled using the last known position when resting started. Battery lifetime of these GPS collars lasted up to 36 month, but collars were exchanged earlier when animals were recaptured to extend information of the animals. Six cheetahs were fitted with a GPS collar taking only two fixes per day during high activity times (Vectronics Aerospace GmbH, Berlin, Germany). GPS data were retrieved through regular aerial tracking flights and the spatial tactic of the males identified as described in Melzheimer et al. (2018).

We defined the core are of the territory using the 50% kernel density estimator (KDE50) which represents the area in which an animal spends 50% of its time. Because KDE50 is sensitive to the number of fixes (Kolodzinski 2010), we used for all territory holders only the last full year of GPS data. Territory holder tend to decrease the frequency of excursions with increasing length of tenure. KDE50 estimates of young territory holders with rather short tenure in territoriality are typically larger (see Figure 1 e.g. hub 7, 17 and 25 vs 5, 6 and 16).

All spatial analyses except of the distribution of the hubs where calculated in RStudio (RStudio Team 2016) using codes of the rhr package (Signer & Balkenhol 2015) for KDE and MCP calculations.

Study area. Central Namibia is characterized by thornbush savannah and is partitioned in approximately 1000 privately owned farms. The main farming type is cattle ranching with a stocking density of 0.12 km2 per large livestock unit. A farm has an average size of approximately 45 km2, thus a farm contains on average 375 cattle, and is fenced along the entire border (Mendelsohn 2003). Farms are further divided by fences into camps with access to water from boreholes. Cattles are regularly shifted from one camp to another to ensure that they graze in an optimal manner across the farm.

Game species such as the greater kudu, red hartebeest, gemsbok, warthog, springbok, duiker and steenbok are common on the cattle farms and cattle fences are constructed in a way that allows these species to move freely. Few farmers erected high game fences (approximately 3.2 meters) that prevent the movement of bigger species, but typically allow smaller mammals (including the cheetah) to pass underneath the fence. An unknown number of leopards (Panthera pardus) and brown hyenas (Parahyaena brunnea) also occur, but lions and spotted hyenas were extirpated on commercial farmland in the beginning of the last century (Shortridge 1934, Joubert & Mostert 1975, Griffin 1998).

Spatial distribution, inheritance and utilisation of the cheetah communication hubs. To investigate whether the spatial pattern of all cheetah hubs was regularly distributed, we used the L-transformation of Ripleys'K function using the program Programita (Wiegand & Moloney 2014). As we did not know all hubs in the modelled rectangular grid (Figure 2(a)) we implemented a null model based on a heterogenous Poisson process and used a moving window with a fixed bandwidth of 30 km. Hence, patterns may only be interpreted up to a radius of 30 km (Wiegand & Moloney 2004). To estimate the average distance between neighbours we measured the distance between centroids of neighbouring hubs.

To determine the average overlap of the core areas between successive territory holders, we determined first the average overlap between successive territory holder (two, three or four generations, Table 1) of the same communication hub (n = 6), averaged within each hub and then between hubs to provide one value.

The utilisation of the communication hubs was measured by determining the number of GPS fixes inside and outside the hubs. To determine whether cheetahs preferred or avoided the hubs, we compared the ratio of the utilization inside and outside the hubs with the expected ratio given by the area of the hubs compared to the entire home range of each individual within the study area. For this analysis we used the black polygon in figure 1 encompassing the 20 cheetah hubs for which we had best information.

Identification of marking trees. Marking trees were identified using the spatial data of territorial males which produced clusters of GPS locations, because such trees were visited frequently (Melzheimer et al. 2018). These clusters were visited in the field to verify that they were actively used marking trees. We also visited systematically every tree outside one of the territories (territory 6 in Figure 1) within a radius of 20 km and until the border of the next territory in the north-east (territory 25 in Figure 1). Since we did not find any tree with cheetah faeces on it, we assumed that this was true also for the rest of the territory surrounding matrix.

Determination of losses of cattle calves. We asked the farmers of the Seeis Conservancy (n = 27) once a year how many cattle calves they have lost within the past year. All calves had an identification number and were recorded in a logbook. Farmers counted the calves when they shifted the herds within the farm from one camp to another, when the calves were ear-marked or needed veterinary services such as vaccinations. The value of a calf during the study period was approximately 300 Euros depending on market and exchange rate fluctuations.

Data analysis. Lilliefors tests revealed that floater and female fixes inside and outside hubs were normally distributed and data sets were compared using a paired t-test. All other data were not normally distributed and thus Wilcoxon signed-ranks tests were used (Hollander et al. 2014). All test were conducted with SYSTAT 13.0 (Systat Software Inc., Richmond, VA, US), and results are reported as means ± S.D. with 95% confidence limits.

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7.7 Figure legends and figures

Figure 1. Location and extent of 28 cheetah communication hubs (i.e. 50% kernel density estimator (KDE50) of GPS fixes of the territory holders). Different colours indicate different cheetah hubs. In seven cases the KDE50 revealed two neighbouring poles within individual hubs, indicated by the same colour. Eight communication hubs were omitted from the analyses of the visitations by the floaters because not all floater units visiting the communication hubs were fitted with a GPS collar. The black polygon encompasses the remaining 20 cheetah hubs and represents the core study area of 10552.5 km^2. Grey polygons represent farm borders.

Figure 2. Modelled L-transformation of Ripleys' K function. (a) Centroids of used hubs in the rectangular grid used for the calculations. **(b)** L-transformation of Ripleys'K function across an increasing radius with the lower and upper envelopes. A null model was used based on a heterogenous Poisson process and a moving window with a fixed bandwidth of 30 km.

Figure 3. Farms affected by cheetah communication hubs. (a) area (km^2) and **(b)** percentage of area affected by the cheetah hub across the 89 farms. **(c)** number of farms affected by the area of communication hubs.

Figure 4. 50% kernel density estimator (KDE50) areas of consecutive territory holders. (a) The four KDE50 areas of the territory holders of communication hub 16 (see Fig. 1 for hub number) and the corresponding centroids depicted as dots. The temporal order of the territory holders was from black to yellow to blue to red. Green stars represent marking locations, which were typically located in and around the KDE50, i.e. communication hub. **(b) – (d)** Movement paths of the yellow, blue and red territory holders. Green stars represent marking locations.

Figure 5. Shifts of 50% kernel density estimator (KDE50) areas between consecutive territory holders. The four KDE50 areas of the territory holders of **(a)** communication hub 24 and **(b)** 21 (see Fig. 1 for hub number) and the corresponding centroids depicted as dots. The temporal order of the territory holders was from black to yellow to blue to red. Green stars represent marking locations.

Figure 6. Home ranges of floaters show a wide overlap between individuals. Home ranges drawn as 95% minimum convex polygon (MCP95) to allow comparison with Caro (1994).

Figure 7. Movement path of floaters visiting the communication hubs of territory holders. (a) Two floater units (pink and blue lines) oscillating between four and three cheetah hubs respectivley. The black circle marks a currently unknown hotspot indicated by the frequent revisitations of the blue floater unit. The yellow lines represent the movements of the territory holder of communication hub 6 (see Fig. 1 for hub number). (b) Movements and visitations of the marking locations of all animals within the hub. Grey polygons represent farm boarders.

Figure 8. Movements of a cheetah female in relation to communication hubs. Lilac coloured lines represent movement path during four years. Cluster in the south of the range indicates a lair where the female spent most of her time during the first two month after birth. For location and numbers of communication hubs see Fig. 1.

Figure 9. Density of cheetah males in relation to the distance of communication hubs. Densities of floaters were calculated in buffers around the communication hubs and plotted over distance measured from the border of the hub. Density is standardised to the average density across the total core study area.

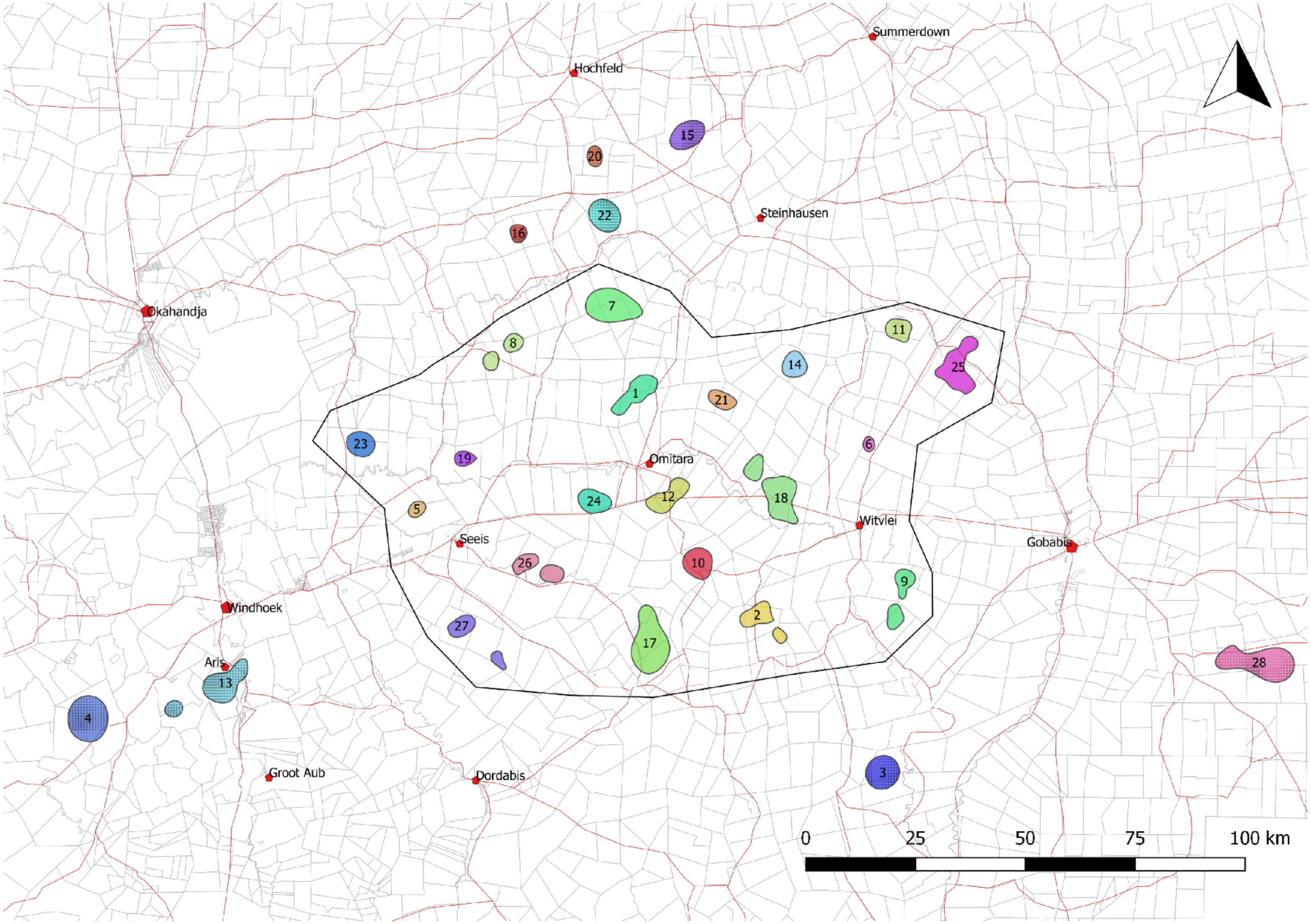
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Figure 1.

Figure 2.

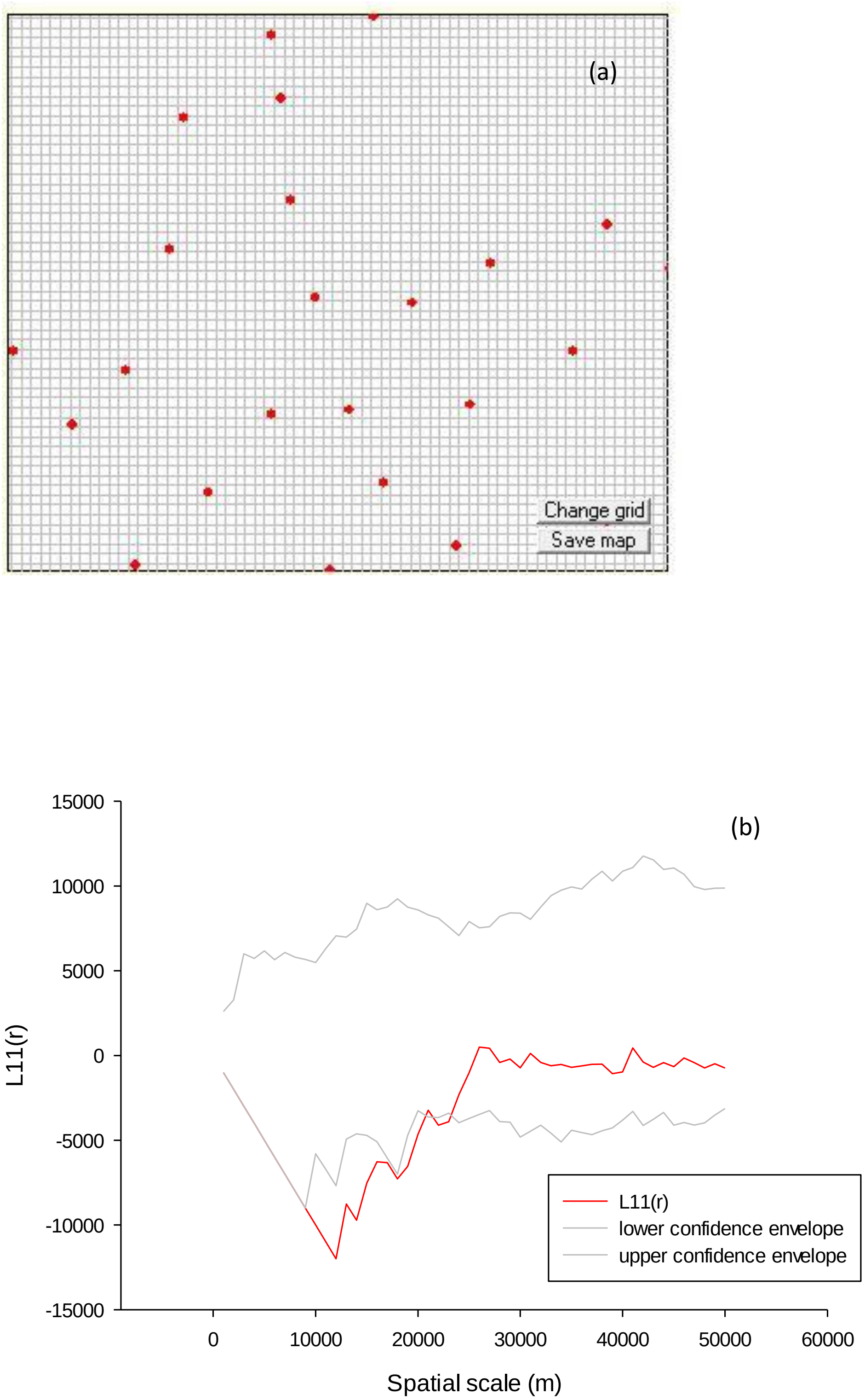
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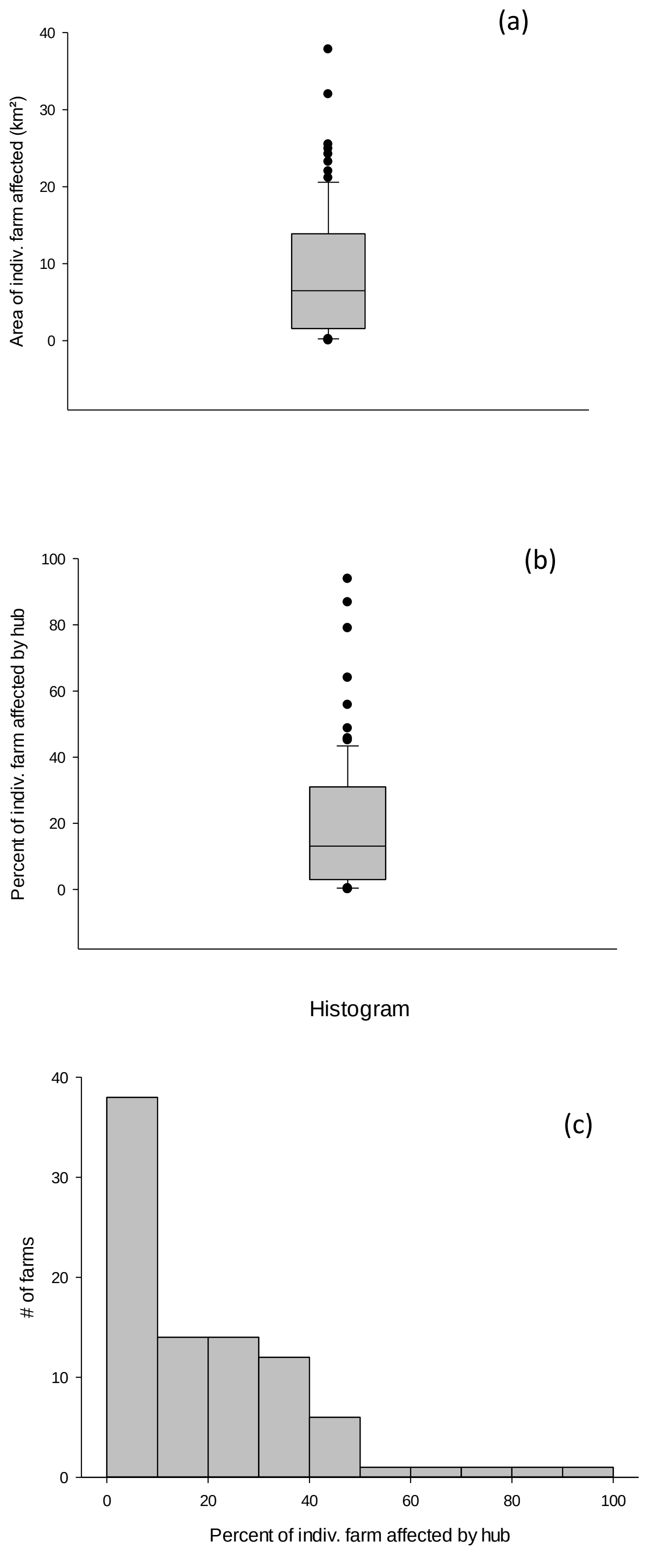
Figure 3.


(a)
Area of indiv. farm affected (km²)
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10
0
(b)
Percent of indiv. farm affected by hub
100
80
60
40
20
0
Histogram
(c)
# of farms
40
30
20
10
0
0
20
40
60
80
100
Percent of indiv. farm affected by hub

Figure 4.

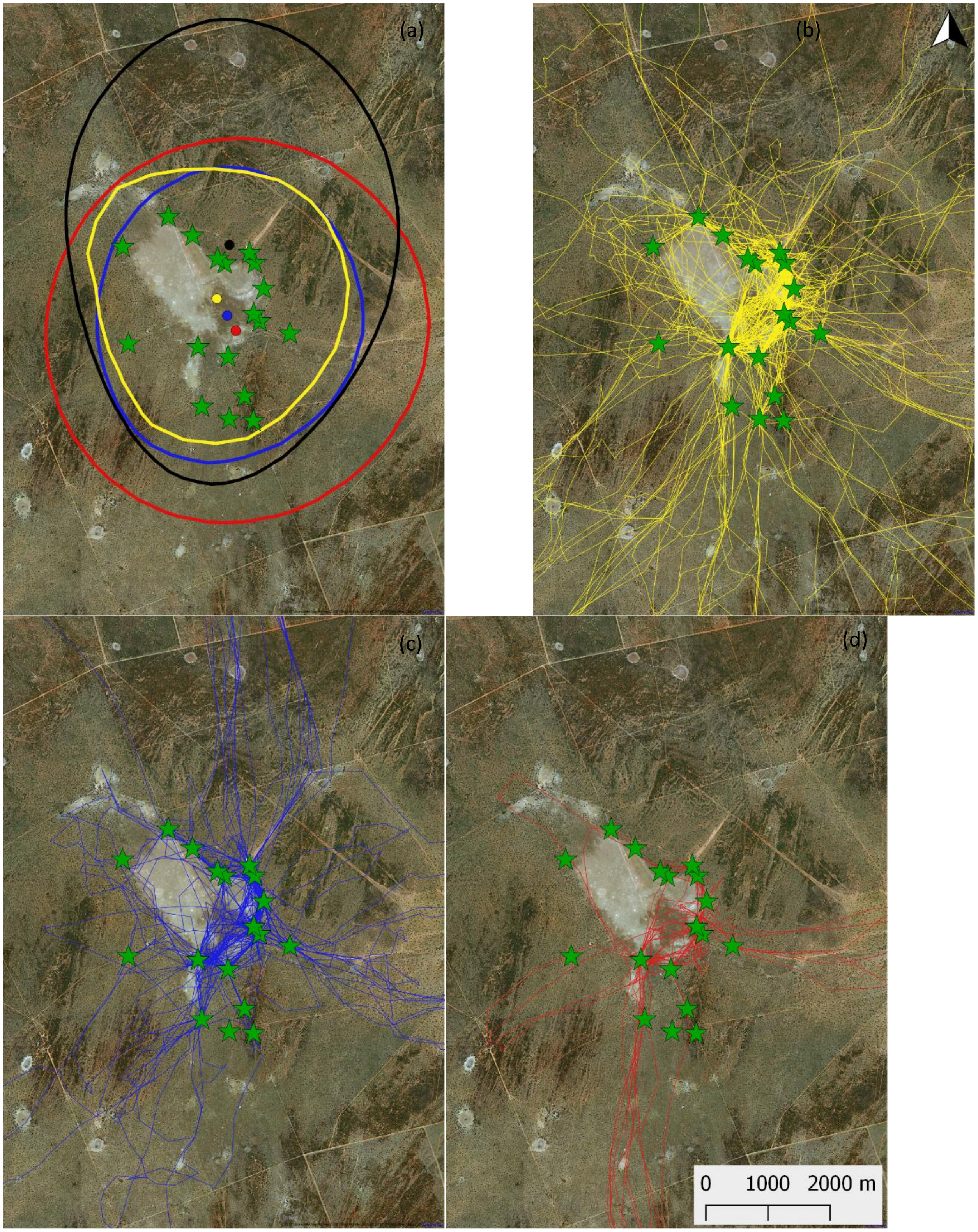

Figure 5.

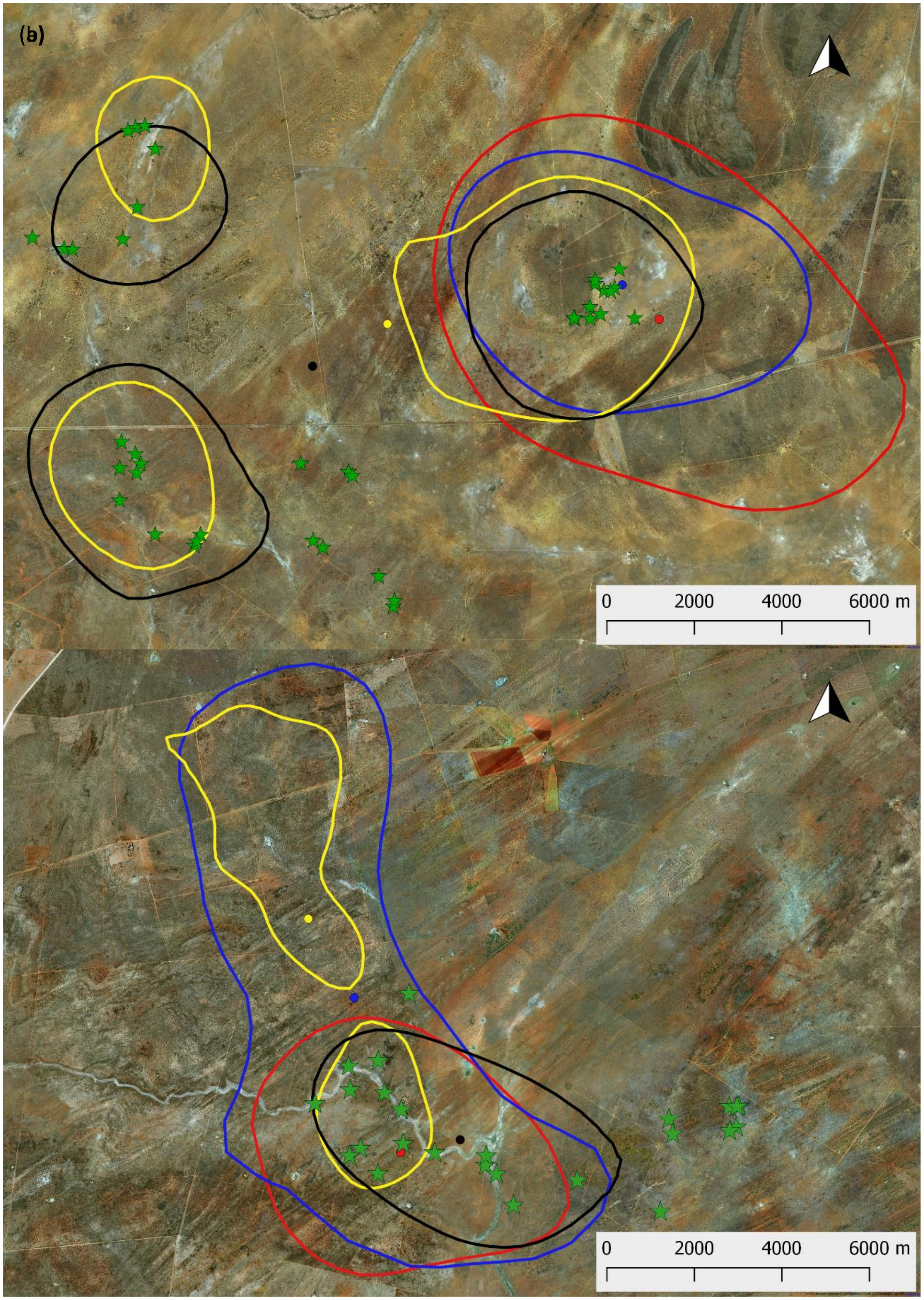

Figure 6.

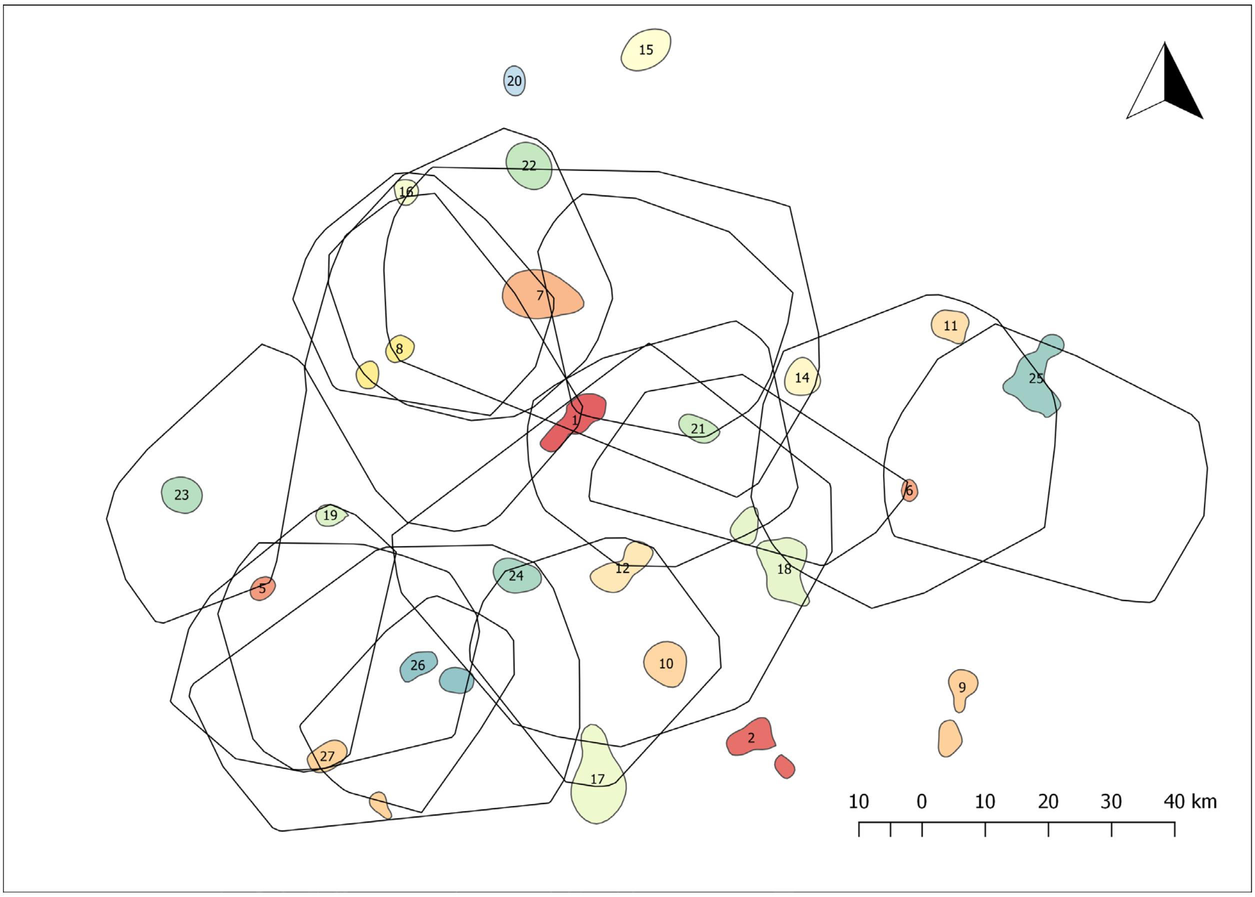
15
20
22
16
7
11
8
25
14
1
21
23
6
19
12
18
24
5
10
26
9
2
27
17
10 0 10 20 30 40 km

Figure 7.

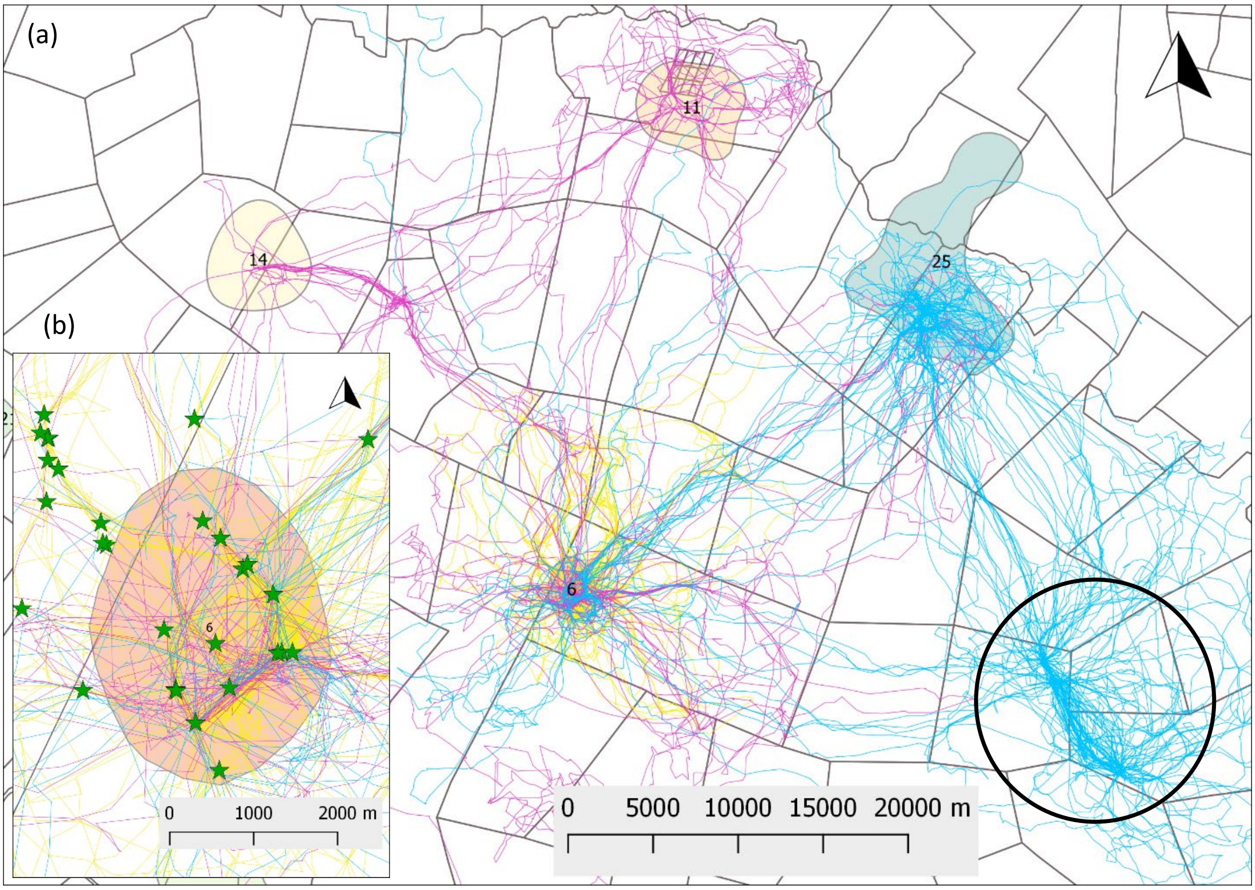

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Figure 8.

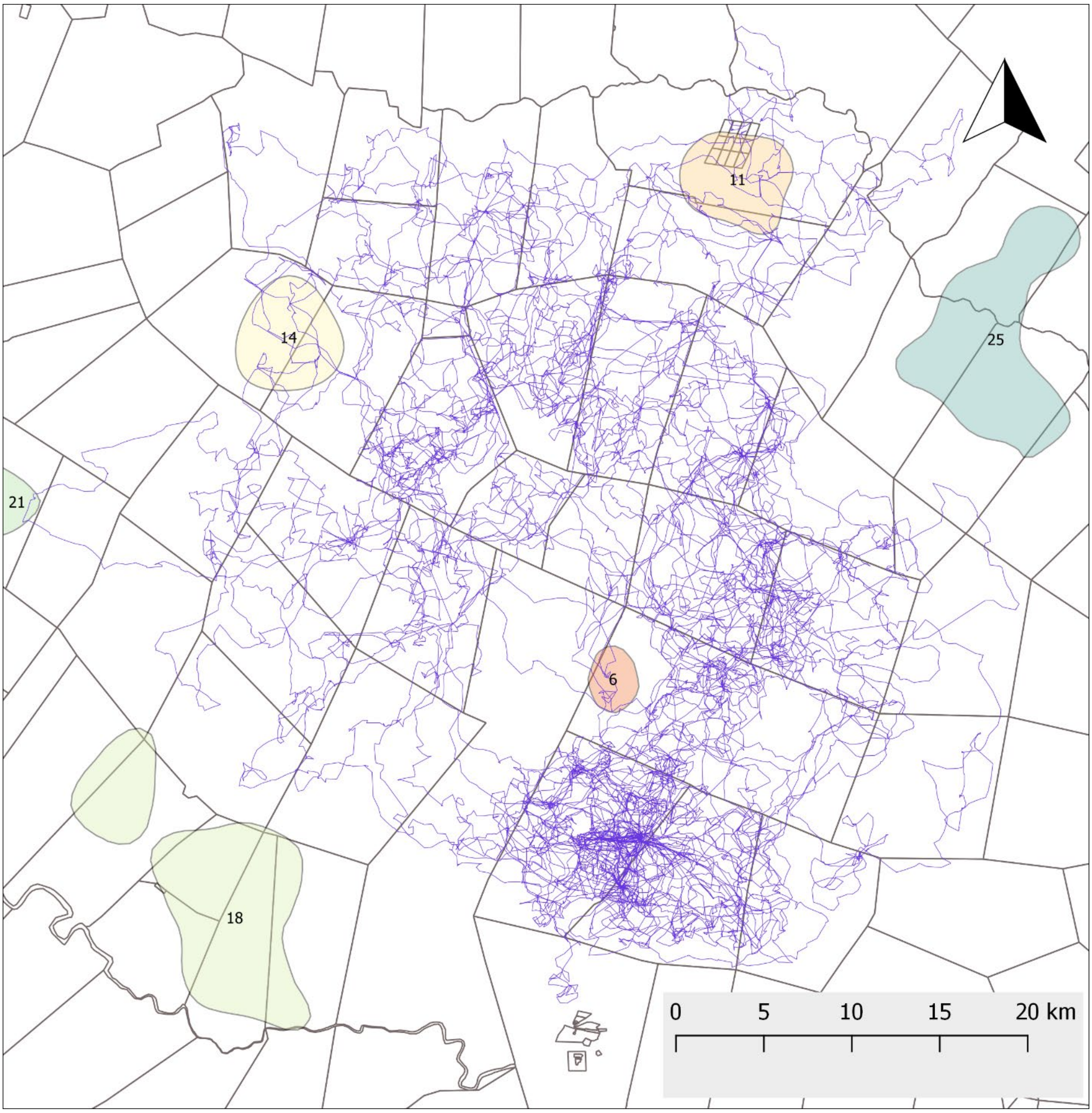

Figure 9.

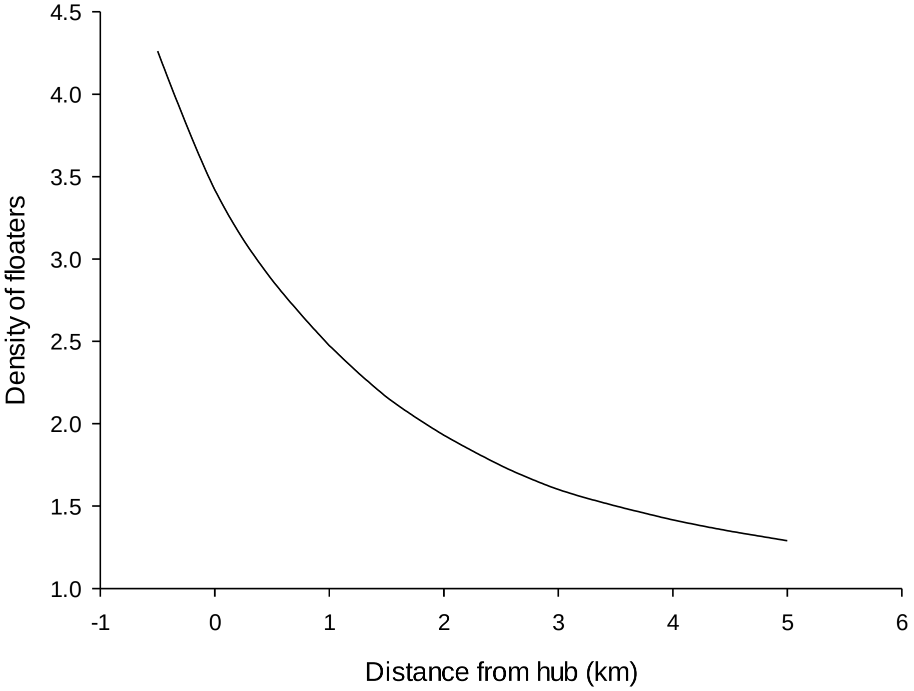
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Density of floaters
-1
0
1
2
3
4
5
6
Distance from hub (km)

Table 1. Overlaps between the kernel density estimators (KDE50) of consecutive territory holders. Overlap is calculated comparing the KDE50 of the succeeding territory holder (B) with the one from preceding territory holder. For numbers of communication hubs see Fig. 1.

Hub ID	Animal ID	First GPS fix	Last GPS fix	Duration (d)	Overlap B-A (%)	Distance between centroids (m)
16	P033	15.11.2005	01.03.2008	837		
	P068	10.03.2009	22.10.2013	1687	100	907
	P144	15.03.2017	09.07.2017	116	86	308
	P128	14.12.2017	22.01.2018	39	53	260
21	A077	07.04.2009	14.04.2013	1468		
	A133	16.12.2013	19.05.2014	154	31	5530[1]
	A161	22.05.2014	25.12.2017	1313	33	1966
	A246	10.12.2017	25.01.2019	411	93	3334[1]
6	A043	26.11.2006	14.11.2011	1814		
	A111	09.11.2011	27.09.2017	2149	82	121
	A238	31.08.2018	06.02.2019	159	54	728
5	W032	29.06.2008	18.08.2008	50		
	Aju11	10.12.2008	17.01.2010	403	100	1610
	W057	05.07.2013	22.08.2015	778	57	451
	W061	26.03.2017	25.01.2019	670	36	590
24	W053	02.01.2012	11.05.2013	495		
	A155	08.01.2014	17.08.2014	221	77	1978
	A172	13.03.2016	29.08.2018	899	60	5447[1]
	A255	25.08.2018	07.01.2019	135	54	1173
7	A133	04.12.2012	30.06.2013	208		
	P145	29.07.2018	05.12.2018	129	100	898
4	K010	06.03.2016	24.09.2017	567		
	K012	15.07.2018	25.01.2019	194	73	4400[1]

[1] core area shifted > 3000 m

Table 2. Losses of cattle calves due to depredation of cheetahs prior and after adaption of management to the locally high cheetah densities in the hub. Hub 16 affects two neighbouring farms. y-2: two years before experimental shift of suckler cow herds was first implemented; y-1: one year before experimental shift of suckler cow herds was first implemented; y+1: one year after experimental shift of suckler cow herds was first implemented. n.a. = not available

Hub No	Farm area affected by hub (km²)	Year (y) of start of trial	# of calves lost in y-2	# of calves lost in y-1	mean annual losses before shifting suckler cows and calves out of hub	# of calves lost in year y (start trial)	# of calves lost in y+1	Mean annual losses after shifting of suckler cows and calves out of hub
6	6.9	2007	23	16	19.5	0	2	1
8	7.6	2010	n.a.	13	13	0	0	0
9	12.2	2008	9	7	8	1	2	1.5
14	17	2008	6	15	10.5	3	5	4
16	7.2	2004	20	20	20	5	5	5
16	7.1	2008	20	20	20	5	5	5

8. GENERAL DISCUSSION

The general objective of this thesis was 1) to investigate in detail the socio-spatial organization of free-ranging cheetahs in Namibia, where one of the largest remaining populations occurs, 2) to test the performance of several capture-recapture models which allow for heterogeneity in detection that take into account the socio-spatial organization of Namibian cheetahs to reliably estimate abundance and density of the cheetah population, and 3) to use all this information to develop and experimentally test a non-lethal mitigation strategy to reduce the ongoing human-cheetah conflict in non-protected areas. By observing and measuring the outcome of the implementation of a research-based mitigation strategy, the ultimate objective was to contribute to the conservation of this threatened species.

8.1 Spatial tactics of cheetah males represent life-history stages

In Chapter 5, I examined whether the socio-spatial organization of cheetahs described in the 1990s in the Serengeti NP (Caro 1994) is unique to Tanzania. No other study since Caro (1994) described two spatial tactics of cheetah males as consisting of territory holders and floaters, with floaters fighting territory holders to obtain these small territories (Broomhall et al. 2003, Marker et al. 2008a, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). This was surprising because holding a territory is an evolutionary advantage as it results in preferred access to females and fights for territories in cheetahs are well known (Caro and Collins 1987, Caro 1994). In a first step, I tested predictions derived from the Serengeti cheetahs with long-term CRP data from cheetahs in Namibia and confirmed that the socio-spatial organization in Namibia is the same as the one described in the Serengeti.

Territories of territory holders and home ranges of floaters were much larger in Namibia than in the Serengeti NP, with territories being 379 km^2 in size and home ranges of floaters 1595 km^2 (in the Serengeti NP they were 48 km^2 and 777 km^2, respectively, Caro 1994). Competition over territories was also high, suggesting that territory holders have preferred access to females, and attempts of floaters to take over a territory ended mostly with the death of either party. Hence, we concluded that territories are highly valuable also for Namibian cheetah males and floaters queue to take over a territory. It is therefore likely that also in Namibia the two spatial tactics of males represent two successive life-history stages. The Namibian floater males were fully grown with established, stable home ranges, not dispersing males looking for a new area to settle down. Females had large home ranges (650 km^2), similar to the ones in the Serengeti NP (833 km^2, Caro 1994) and encompassed several male territories. Thus, also the social and sexual relationships between males and females is most likely similar in the two study populations.

Previous studies categorized the males a priori into solitary males and males in coalitions (Broomhall et al. 2003, Marker et al. 2008a, Houser et al. 2009, Marnewick and Somers 2015, Mills et al. 2017). Since both territory holders and floaters consist of solitary males and coalitions, the two spatial tactics were not detected. When I re-analyzed the published data from another long-term study in Namibia (Marker et al. 2008a), I detected the same socio-spatial organization in the dataset of Marker et al. (2008) as in the Serengeti and in our data.

The chances for floaters to successfully take over a territory were higher when their group size was larger than that of the territory holders. In central Namibia, coalitions consist of two or three males and floaters in such coalitions had good chances to take over a territory previously occupied by a solitary male or a coalition of two males. Once floaters successfully took over a territory, their body mass index (BMI = mass / body length^2) increased substantially in subsequent months. This resulted in territory holders having a higher BMI than floaters. The higher BMI, however, did not prevent solitary territory holders to lose their territory against a coalition of two floaters, i.e. group size was more important to win a fight than body condition.

This socio-spatial organization has several implications for the conservation management of free-ranging cheetahs. There are farmers who capture cheetahs at marking trees on their farm and call animal rescue centers such as the “Cheetah Conservation Fund” requesting them to fetch the cheetahs and translocate them to another area – or else they will kill the animals (Marker et al. 2003a, Marker et al. 2008a). The centers often accept the request but rarely collect information on the fate of the cheetahs in the new area, for instance by tracking the translocated and released individuals with a GPS collar (Marker et al. 2003a, Marker et al. 2008a). A recent study investigated the fate of such cheetahs and showed that most animals returned to their original place or were killed on the farm where they were released (Weise et al. 2015). Territorial males might return to their original area to quickly re-occupy and defend the territory against floaters, whereas floaters might stay in the new area and establish a large home range encompassing several territories. When cheetahs are captured at marking trees in territories, the most likely individuals to be trapped are territory holders as they visit the marking trees most frequently (Chapter 5 and 6). Thus, it is likely that most translocated cheetahs are territory holders that will typically attempt to return to their original territory as quickly as possible, typically turning the effort of translocation into a probable failure. It therefore might be useful to determine before translocation whether the captured cheetah is a territorial male or a floater. Chapter 5 documented that there are at least two reliable biological markers to quickly identify the spatial tactic of a male. The first uses its mass and body length to calculate its BMI. Territory holders have a higher BMI than floaters (mean ± standard deviation (SD): 29.7 ± 2.4 and 25.8 ± 1.8, respectively). The second marker is the behaviour of the cheetah in the trap when approached by a person. Territory holders mostly attack and hiss, whereas floaters mainly exhibit anxious behaviour and retreat to the other end of the trap.

Some farmers with high livestock losses might decide to kill the cheetahs in the trap. Since these cheetahs are likely to be the territory holders, such a removal is likely to accelerate the rate of turnover of territory ownership. This in turn is likely to result in a higher cheetah activity on the farm, increasing the conflict with the farmer and thus resulting in the opposite effect than the intended one. Such a scenario was shown with cougars (*Puma concolor*), when the removal of territorial males stimulated the immigration of young cougars, which increased livestock predation (Peebles et al. 2013). Similarly, territorial Eurasian lynxes (*Lynx lynx*) killed in their territory were replaced so quickly that there was no decrease in livestock losses (Herfindal et al. 2005). A recent review on lethal and non-lethal methods to decrease livestock predation identified several non-lethal methods that were effective in the USA and Europe (Treves et al. 2016). It is therefore wise to invest in the identification and implementation of new non-lethal mitigation strategies for the human-cheetah conflict on Namibian farmlands (see Chapter 7).

8.2 Best capture-recapture models for cheetah allowing for heterogeneity in detection

The unique socio-spatial organization of the cheetah has implications for several other research fields and methods, including abundance and density estimates. The most common methods to collect the relevant data and derive density estimates are camera traps and the application of capture-recapture models to the resulting data set, respectively (Karanth and

Nichols 1998, Marnewick et al. 2008, Sollman et al. 2011, Wilting et al. 2012, Sollmann 2018). These models are based on several assumptions which need to be met in order to produce reliable estimates (Pledger 2000, Sollmann et al. 2011, Sollmann 2018). One of these assumptions is a homogenous detection probability across the individuals (Krebs 1999, Pledger 2000). If this is not the case, then classes of individuals of similar detection probability have to be identified and these groups incorporated into models allowing for heterogeneity in detection (e.g. Krebs 1999, Pledger 2000, Sollmann et al. 2011, Boulanger et al. 2014). For these models, an important parameter is the frequency of recaptures. Only datasets with a high number of recaptures will give robust estimates with small confidence intervals. Hence, camera traps need to be placed at locations were individuals frequently pass through (Soisalo and Cavalcanti 2006, Brassine and Parker 2015). Previous studies on cheetah abundance and density estimates did not account for the social-spatial organization of cheetahs because they did not recognise the system, thus violating the assumptions of the models (Marker et al. 2008b, Marnewick et al. 2008, Boast et al. 2015). This resulted in biased and unreliable estimates (Portas et al. 2017).

Chapter 6 tested the performance and usefulness of four types of capture-recapture models allowing for heterogeneity in detection to estimate the abundance of cheetah males in Namibia. The four types were (a) a spatial tactic model, (b) a mixture model, (c) a floater-only model, in which only floaters were included in the detection history and (d) the traditionally used heterogeneity M_h model with the jackknife and Chao estimators. Mixture models do not require the spatial tactic of each male and produce a probability of any individual in the population to be a floater. Four models were ran in several combinations for the four types of heterogeneity capture-recapture models: (i) the null model in which all capture and recapture probabilities are equal, M_o, (ii) the heterogeneity model with two mixtures, each of equal capture and recapture probabilities for territory holders and floaters, respectively, M_h, (iii) the behavioural model with one mix of different capture and recapture probabilities but territory holders and floaters having the same capture and recapture probability, M_b, and (iv) the behaviour and heterogeneity model with two mixtures of capture and recapture probabilities, plus a behavioural response which considers a differential response if the individual has been previously captured, M_{bh}, i.e. trap-happy or trap-shy (Anile et al. 2012).

The performance of the models was determined by comparing the produced abundance estimates with the true abundance of cheetah males in five well-known territories. True abundance was known because of camera trap studies at frequently used marking trees that produced a complete list of individually known cheetahs that visited these territories. Such trees were identified with GPS data of territory males, which were shown as clusters of locations on a map. These marking trees were visited in the field and the ten trees with the largest number of fresh faeces were chosen to monitor with camera traps. To verify that all floaters were captured on the camera traps, GPS data of floaters were used. All floaters were captured with camera traps every time they visited the marking trees of a territory, thus the detection probability of floaters at marking trees was 100 %. True abundance in a study area is often not known, thus performance and precision of abundance models cannot be compared with these numbers and cannot be assessed for their suitability. Our study design was therefore perfect for such a comparison.

The spatial tactic, mixture and floater only models all correctly estimated male cheetah abundance in the five territories, whereas the heterogeneity M_h models were less reliable. The poor performance of this commonly used heterogeneity M_h model was also recognized for other large carnivore species (Grey and Prun 2012), thus previous abundance estimates of cheetahs (Marker et al. 2008b, Marnewick et al. 2008) produced with this model are likely to be biased. Concerning precision, the spatial tactic and mixture models showed a similar performance, with each top model showing a standard error (SE) of less than 0.001. Such precision has not been previously possible for cheetah data. For example, two studies using the heterogeneity M_h model estimated an abundance of seven males with a SE of 1.93 and a range of 6 - 14 males (Marnewick et al. 2008) or an abundance of five males with a SE of 1.36 and a range of 5 - 11 males (Belbachir et al. 2015).

Spatial models and mixture models are therefore both appropriate to estimate abundance of cheetahs. However, the advantage of mixture models is that they do not require prior information of the spatial tactic of each male which might not always be available. They are therefore also robust when the identity of the territorial male is unclear, which was the case in one of the five territories. In this territory, two different male coalitions were scent marking, probably being in the process of sorting out territory ownership. However, the ability of mixture models to correctly estimate the probability of being a floater was inconsistent. Thus, to determine the number of floaters it is recommended that all individual encounter histories are compared with each other to identify those individuals with a high frequency of detection (= territory holders) and those with a lower frequency of detection (= floaters) rather than rely on the produced abundance estimate.

The calculation of abundance in territories is the first vital step in producing population estimates across landscapes and to monitor trends in the population at a larger spatial scale. The movement of floater males between multiple territories needs to be considered for the next steps when conducting population estimates. In this study, floaters visited two or three different territories, thus models calculating population estimates need to incorporate the average number of territories visited per floater and the available space for territories per region. Females visit marking trees in the territory only rarely, thus cannot be reliably estimated with this study design. However, currently there are no identified places or areas which are known to be frequently visited by females. To estimate population sizes, I therefore suggest to assume a sex ratio of 1:1 and double the estimate produced for males with the mixture model.

Chapter 6 concludes that mixture models are most appropriate for heterogeneity in detection probability and have the advantage of requiring no prior information regarding individuals. This gives them the potential application for a wide range of species for which attributes affecting detection probability, such as sex, are unknown for each individual.

8.3 Novel and successful mitigation strategy for human-cheetah conflicts

Cheetahs are one of nine felid species for which conflict with humans is of great conservation concern (Inskip and Zimmermann 2009). Human-cheetah conflicts are widespread in Namibia and affect commercial livestock farmers, hunting operators and subsistence pastoralists. Central Namibia, where most cheetahs occur (Hanssen and Stander 2004, Portas et al. 2017), is divided into freehold farms. These farmers typically own or have access to box traps and guns, and some of them are responsible for a large number of killed cheetahs (Marker et al. 2003a, Weise et al. 2017). It is important to develop successful conflict mitigation strategies for these farmers, because the future survival of the Namibian cheetah population is literally in their hands.

During the last decades, several conflict mitigation methods were tested and/or are in place in Namibia (Dickman et al. 2018). Examples are the deployment of livestock guarding dogs, translocations, removing "problem cheetahs" to permanent captivity and beef produced on certified carnivore-friendly farms (Marker et al. 2003a, Marker et al. 2005, Maclennan et al. 2009, Marker et al. 2010, Marker and Boast 2015, Weise et al. 2015, Potgieter et al. 2016). While all these methods were successful in some cases, they failed to solve the conflict in others (Marker and Boast 2015, Weise et al. 2015, Potgieter et al. 2016). None of these measures considered the space use of cheetahs to solve the problem by making use of the insights generated by understanding the movement ecology of the species.

Chapter 7 followed a novel approach by taking into account the socio-spatial organization of cheetahs and adjusting farm management to take into account the activity and social centres of cheetahs, which are the territories of the males. I first presented the distribution of the territories across the farmland. Because of the long-term and intensive fieldwork of the CRP from the Leibniz-IZW, we know all territories in the study area. Similar to the Serengeti NP, the territories were not directly contiguous (Caro 1994). The average distance between the centroids of the territories was 23 km and the territories were located in a regular distribution with an average core area of 41 km². The territories, and particularly the core area of the territories with the marking trees, were characterised by high cheetah activity. The territory holders spent a lot of time patrolling and marking at marking locations. In addition, the floaters regularly visited the marking locations as well, oscillating between the core areas of the territories and spending approximately 30 % of their time inside these areas (Caro 1994, Chapters 5, 6 and 7). In contrast, the matrix between the territories was characterised by low cheetah activity. Floaters basically only travelled through this matrix en-route to the next territory, typically oscillating between three territories all the time and spending two to three days in each of them before they moved on to the next one. In contrast, females spent most time in the matrix and actively avoided the territories, however they rarely but regularly visited the marking locations.

The core areas of the territories are communication hubs for the cheetah population resulting in a high activity and density of cheetahs inside these hubs.

The regular distribution and spacing of hubs resulted in some farms overlapping with a cheetah hub whereas other farms are situated in the matrix. Since the core areas of the territories exhibited the highest cheetah activity, these areas represented the local risk hotspots for livestock losses. Farmers who reported high or low livestock losses were indeed those who did or did not have a hotspot on their farm, respectively. It is therefore essential that the exact knowledge about the location of the hub on a farm is integrated into the management and grazing plan to ensure that suckler cows with calves younger than approximately six months of age are kept away from high risk areas. Calves older than six month of age are less vulnerable to predation an rarely attacked by cheetahs once they have passed this threshold. Cattle herds can be easily managed within the farm, because each farm is divided into numerous camps. Cattles are regularly shifted from one camp to another to ensure that grazing pressure is distributed evenly across the farm. During such shifting operations, farmer have the opportunity to count their cattle and detect losses. Famers containing a cheetah hub on their property should keep the breeding herds as far away as possible from the hub to minimize the predation risk for the calves.

Chapter 7 further demonstrated that territories did not shift when livestock animals were moved away from the hub, which was an initial concern of some collaborating farmers. Neither did territory holders conduct excursions to the shifted cattle herds nor did floaters follow the herds. Cheetah males seem to hunt those animals locally available, i.e. livestock animals if present and otherwise naturally occurring wildlife species. Farmers who adjusted their farm management to the spatial organisation of cheetahs substantially reduced their livestock losses. Because floaters and female cheetahs with their offspring roam in the matrix outside the hubs, losses cannot be completely avoided but can be minimised on an acceptable level.

An early study of the CRP determined the diet composition of cheetahs using undigested prey remains in scats collected from marking trees (Wachter et al. 2006). The study revealed that livestock comprised only 4 % of the diet. The work in this thesis showed that scats on marking trees only originate from territorial males since only they mark trees (Chapter 5 and 6, Caro 1994). Unfortunately, records of livestock presence or absence are not available for the dates of scat collection for this study. It is therefore not known whether the low percentage of livestock in the diet was because of a lack of available cattle in the hub or a preference for other prey species. It is likely that other studies on cheetahs' diet included scats collected from marking trees and thus might report a diet biased towards territorial males (Marker et al. 2003b, Boast et al. 2016).

In Chapter 7, I further demonstrated that consecutive territory holders typically used the same marking locations and therefore the core area of the territories remained stable. This is consistent with reports from some farmers who knew the marking trees from their fathers and grandfathers who in turn already had conflicts with cheetahs in earlier days. Some farmers even cut down several marking trees in an attempt to reduce the cheetah population on their farm. This had little effect since the cheetahs simply started to use trees in the neighbourhood of the cut-down trees or made use of any other prominent landmark in the vicinity such as termite mounts and man-made structures such as water troughs. As a consequence, the area of high predation risk for livestock on a farm is highly consistent over time and therefore its implementation into the livestock management is a long-lasting mitigation strategy for farmers.

Although the hubs were distributed in a regular pattern across the farmland by an average distance of 23 km, the precise location of a hub needs to be individually determined for each affected farm, ideally by deploying GPS-collars on cheetah males. If a GPS-collar is fitted to a territory holder, the data will provide a detailed insight into the respective territory and its marking locations. This information is most useful to the affected farmer as it provides many details and a high resolution data of cheetah activity inside the communication hub. If the collar is fitted to a floater, the information is collected at a landscape level indicating all neighbouring hubs. This type of data was used to slowly increase our study area and make sure no hub was missed. Camera traps placed at frequently visited marking trees will indicate how many floaters visit the hub, providing additional information on predation risk.

To develop a livestock management plan, farmers were provided with data on the movements of the cheetahs on their farm. This sensitive information could potentially have been misused by farmers as it would have facilitated any attempt to capture and kill cheetahs in a systematic way. However, none of the farmers did so, probably because they knew from previous years that the elimination of cheetahs does not reduce their livestock losses and that they gain more from knowing the whereabouts of the cheetahs and adapt their livestock management in an appropriate manner. It is also likely that farmers changed their perception towards cheetahs because they received a tool to actively handle and minimize the conflict. To develop the described mitigation key required a lot of patience from the farmers, particularly in the beginning of the project. They had to agree to release captured cheetahs with a collar, instead of killing them or requesting for a translocation. They then had to wait approximately six months until a reasonable number of GPS-fixes was collected. This cooperation was only possible because of the mutual trust the CRP carefully built and maintained throughout the years with the farmers. This thesis therefore highlights the importance of long-term projects in conservation science and the importance of close and trustful collaboration with stakeholders.

I conclude that the described individually farm-tailored livestock management plans are a highly effective and sustainable mitigation strategy to reduce the long-lasting farmer-cheetah conflict in Namibia. It takes the socio-spatial organization of the cheetah into consideration and thus solves the conflict from a biological point of view. This new approach is likely to be adaptable to other study areas and potentially solve the farmer-cheetah conflict at a larger spatial scale.

8.4 Conclusion and perspectives

In this thesis, I investigated the socio-spatial organization of free-ranging cheetahs in Namibia. I demonstrated that the system described in the 1990s in the Serengeti NP with males operating two distinct spatial tactics representing two life-history states (Caro 1994) was not unique to Tanzania, but does also exist on farmland in Namibia. Other studies categorized cheetah males as solitary males or males in a coalition, rather than territory holders and floaters and thus were unable to detect the true socio-spatial organization of cheetahs. These studies probably used the categories of solitary males or coalitions because males can be allocated quickly to either category, whereas the identification of the spatial tactic requires GPS data of approximately three months. Since competition over territories is very high and territory holders have preferred access to females, it is likely that this system also operates in other study populations. I demonstrated this for another study in Namibia (Marker et al. 2008), and my findings could be extended in the future to additional studies by re-analyzing also their data.

Another follow-up study, which is on the way within the CRP, are paternity analyses to verify that territorial males have a higher chance than floaters to sire offspring. This required genetic samples of cubs and as many potential fathers as possible – a data set available in the CRP (Palmegiani et al. in prep.). Also, the investigation of the movements of females will be highly interesting to learn when and how often females visit the hotspots (Palmegiani et al. in prep).

The presented key to mitigate the farmer-cheetah conflict is highly successful for livestock commercial farmers. However, for hunting operators and farmers keeping and/or breeding valuable trophy animals the shifting of animals away from the hubs is not possible. Naturally occurring species that are valuable for trophy hunting such as greater kudus or gemsbok move freely on the farms and cannot be moved easily. Highly valuable species that are imported from other countries such as roan (*Hippotragus equinus*) or sable antelopes (*Hippotragus niger*) are kept in large enclosures surrounded by electrified fences. As long as these fences are intact and the enclosures free of cheetahs when built, the animals are safe. However, when electricity is interrupted and/or warthogs dig a tunnel beneath the fence, cheetahs can enter. The owners have no tolerance in these cases because the trophy of such a species can yield up to 20,000 Euros. Solutions for these farmers might be a full surveillance system of the enclosure or a shift of the entire enclosure away from the hotspot. If the enclosure is not yet built, it can be planned in such a way that the information of the location of the hotspot is incorporated.

With the knowledge of the best performing heterogeneity model, it is now possible to produce meaningful abundance and density estimates for cheetahs. We did this in a preliminary study in four different habitats in Namibia, resulting in density estimates of 0.1 – 0.4 adult cheetahs/100 km^2 in the sandy and gravel desert areas, 0.6 adult cheetahs/100 km^2

in a grass and dwarf shrubland area and 1.1 adult cheetahs/100 km^2 in the Kalahari thorn bush savannah in central Namibia, where the long-term CRP of the Leibniz-IZW has its main study area (Portas et al. 2017). This study demonstrates that densities substantially differ between habitats and that extrapolations of density estimates for one habitat to other habitats are not advisable. I therefore suggest to conduct additional density estimates in other main habitat types in Namibia and to extrapolate the generated values only then to the entire country. Similar estimates could be conducted for other countries to create a basis for population trend studies in southern Africa, the stronghold for the global cheetah population.

Since female cheetahs are only rarely captured at marking trees in male territories, it would be valuable to find out more on the movements and whereabouts of females. Currently, the number of females is assumed to be similar to the number of males when population estimates are conducted. For future models and estimates it would be useful to have own data of females.

8.5 References

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9. CURRICULUM VITAE

For reasons of data protection,

the curriculum vitae is not included in the online version

10. PUBLICATION LIST

10.1 Journal Publications

Costantini D, Czirják G, **Melzheimer J**, Menges V, Wachter B. 2019. Sex and species differences of stress markers in sympatric cheetahs and leopards in Namibia. Comp. Biochem. Physiol. -Part A Mol. Integr. Physiol. 227: 8–13.

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10.2 Book Chapters

Marker L, Schmidt-Küntzel A, Portas R, Dickman A, Good K, Hartmann A, Cristescu B, **Melzheimer J**. 2018. Capture, Care, Collaring, and Collection of Biomedical Samples in Free-Ranging Cheetahs. In: Cheetahs: Biology and Conservation. Elsevier, p 457–469.

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11. INNOVATIONS/PATENTS

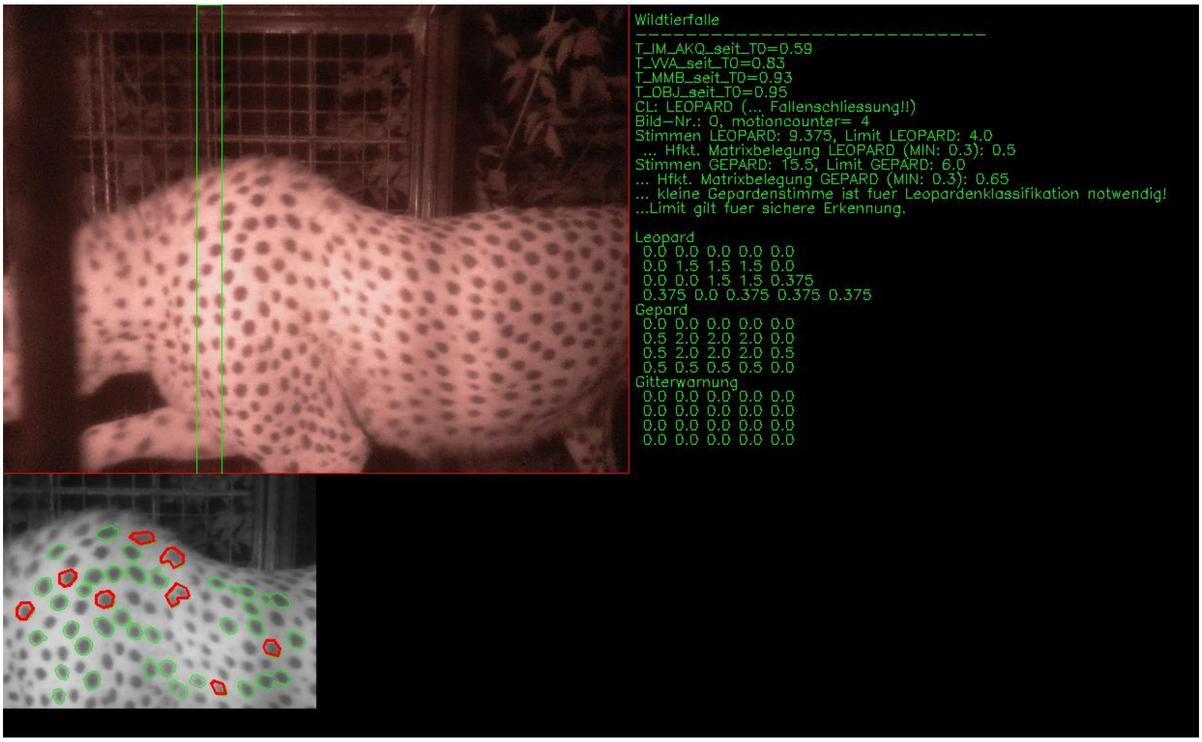
Within the framework of the CRP and the fieldwork to this dissertation the author and his colleagues developed a fully automatic trap to selectively live capture target animals. The trap is equipped with a micro-computer running an artificial intelligence to detect species-specific coat patterns, with a two way GSM and GPRS communication modem, satellite communication, various sensors, a fast and noise-reduced electro-magnetic trigger mechanism, a M2M communication to transmit a photo of the captured animal and an independent back up system with own power supply for maximal user safety and animal welfare. The invention has fundamentally changed the fieldwork and increased access to study animals even in very remote areas (Figures 1-5). The invention has been registered as “Arbeitnehmererfindung” “EM14 IZW-2” and patent is pending.

Figure 1: Boxtrap with sensors mounted in the white boxes on the sides of the trap. Black box contains 12V battery and the circuit board (see Figure 2) in a water proof housing.

Figure 2: Circuit board running an artificial intelligence with a GSM-modem.

Figure 3: Setup in the field, white box on the top of the tree is the GSM antenna.

Figure 4: The author sending test commands via GSM-network to the trap. Solar panels supply power and charge the 12V battery.



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Wildtierfalle
----------------------------------
T_IM_AKQ_seit_T0=0.59
T_VVA_seit_T0=0.83
T_MMB_seit_T0=0.93
T_OBJ_seit_T0=0.95
CL: LEOPARD (... Fallenschliessung!!)
Bild-Nr.: 0, motioncounter= 4
Stimmen LEOPARD: 9.375, Limit LEOPARD: 4.0
 ... Hfkt. Matrixbelegung LEOPARD (MIN: 0.3): 0.5
Stimmen GEPARD: 15.5, Limit GEPARD: 6.0
... Hfkt. Matrixbelegung GEPARD (MIN: 0.3): 0.65
... kleine Gepardenstimme ist fuer Leopardenklassifikation notwendig!
...Limit gilt fuer sichere Erkennung.

Leopard
 0.0 0.0 0.0 0.0 0.0
 0.0 1.5 1.5 1.5 0.0
 0.0 0.0 1.5 1.5 0.375
 0.375 0.0 0.375 0.375 0.375
Gepard
 0.0 0.0 0.0 0.0 0.0
 0.5 2.0 2.0 2.0 0.0
 0.5 2.0 2.0 2.0 0.5
 0.5 0.5 0.5 0.5 0.0
Gitterwarnung
 0.0 0.0 0.0 0.0 0.0
 0.0 0.0 0.0 0.0 0.0
 0.0 0.0 0.0 0.0 0.0
 0.0 0.0 0.0 0.0 0.0
```

Figure 5: Decision of the artificial intelligence based on pattern recognition on a photo of the passing cheetah. Assessment of pattern and decision whether or not to close the trap is executed within 0.2 seconds.

12. SELBSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit selbständig und ohne unzulässige Hilfe oder Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe.

Berlin, den 28.02.2019

Jörg Melzheimer