


# 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<sup>2</sup>), which were regularly visited by females whose range sizes were much larger (mean 833.0 km<sup>2</sup>; Caro 1994). Adult males that did not hold a territory (floaters) roamed over large ranges with a size (mean 777.2 km<sup>2</sup>) 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 1987a, 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 male 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 1987b). When coalition size was reduced, the remaining male(s) eventually lost their territory to larger coalitions (Caro and Collins 1987b). 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 Thälwitzer 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 expect 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 submitting 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<sup>2</sup> per flight in a study area of approximately 40,000 km<sup>2</sup> (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 on-board 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  $381.8 \pm 414.4$  d (mean  $\pm$  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

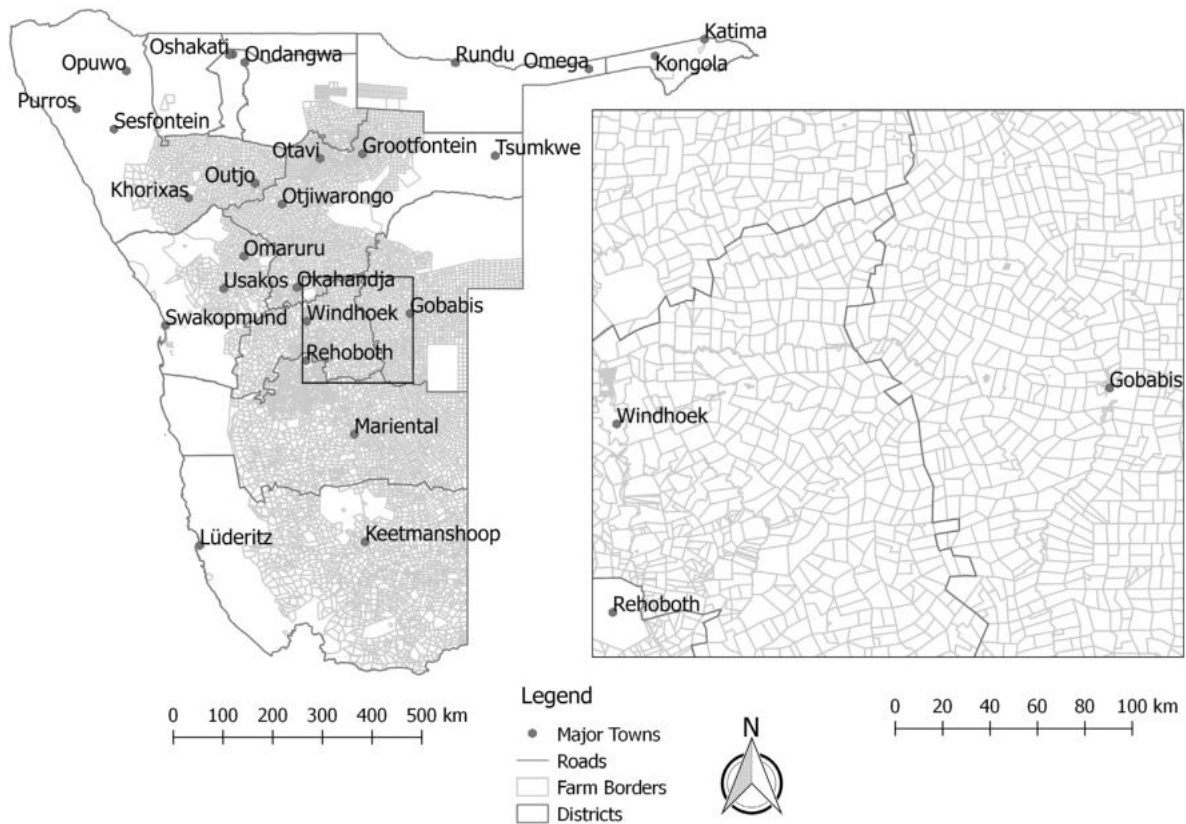


Fig. 2. Location of study area of approximately 40,000 km<sup>2</sup> on farmland in central Namibia.

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<sup>2</sup>, 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 <sup>2</sup> ) | 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 <sup>2</sup> ) | 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 mounds, 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 HyperFire™ 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<sup>2</sup> (kg/m<sup>2</sup>). For the statistical comparisons of BMIs of territory holders and floaters, we averaged the values of coalition members to avoid pseudo-replication. 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

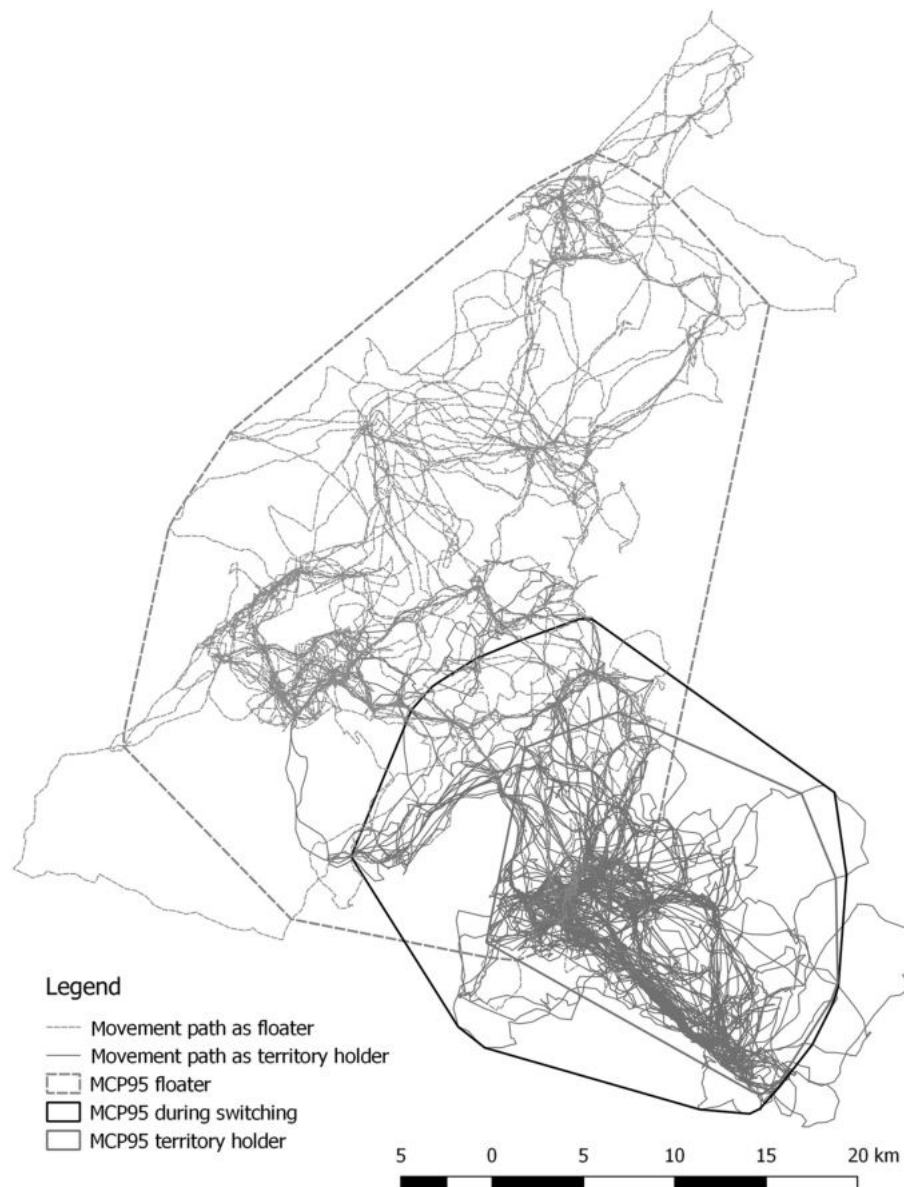


Fig. 3. Example of the home range and movement paths of a male that switched from a floater, covering 1116 km<sup>2</sup> during 357 d, to a territory holder covering 289 km<sup>2</sup> during 443 d.

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  $\pm$  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  $379 \pm 161 \text{ km}^2$  (95% confidence interval [CI]:  $313 \text{ km}^2$ ,  $441 \text{ km}^2$ ,  $n_{\text{sol}} = 13$ ,  $n_{\text{co2}} = 11$ ,  $n_{\text{co3}} = 4$ ) or ranged over large areas of  $1595 \pm 1131 \text{ km}^2$  (95% CI:  $1156 \text{ km}^2$ ,  $2033 \text{ km}^2$ ,  $n_{\text{sol}} = 20$ ,  $n_{\text{co2}} = 6$ ,  $n_{\text{co3}} = 2$ , Table 2, Mann–Whitney  $U$  test,  $U = 10$ ,  $P < 0.0001$ ). Stable HRs of cheetah females had intermediate sizes of  $650 \pm 278 \text{ km}^2$  (95% CI:  $507 \text{ km}^2$ ,  $793 \text{ km}^2$ ,  $n = 17$ ), 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  $43.0 \pm 86.1$  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  $24.8 \pm 48.6$  occasions, or a marking rate of 0.9 trees per day and territory. In contrast, none of the other males ( $n_{\text{sol}} = 5$ ,  $n_{\text{co2}} = 1$ ) 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<sup>2</sup> 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<sup>2</sup> 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:  $n_{\text{ter}} = 20$ ,  $n_{\text{flo}} = 7$ , solitary males:  $n_{\text{ter}} = 17$ ,  $n_{\text{flo}} = 32$ ,  $n = 76$ ,  $P = 0.001$ ; 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  $29.7 \pm 2.4$  (range 24.2–34.3) than floaters with  $25.8 \pm 1.8$  (range 21.9–29.4, *t* test,  $t = 7.98$ ,  $n_{\text{ter}} = 26$ ,  $n_{\text{flo}} = 50$ ,  $P < 0.0001$ ; Fig. 4, Table 2). The BMI of males increased significantly after they became territory holders, from  $27.3 \pm 1.3$  to  $30.3 \pm 2.6$  (Wilcoxon signed-ranks test, exact  $n = 7$ ,  $P = 0.016$ , Fig. 5). The average time elapsed between both measurements was  $27.5 \pm 12.5$  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:  $n_{\text{pro}} = 34$ ,  $n_{\text{anx}} = 19$ ,  $n_{\text{amb}} = 23$ , floaters:  $n_{\text{pro}} = 15$ ,  $n_{\text{anx}} = 29$ ,  $n_{\text{amb}} = 18$ ,  $n = 138$ ,  $P < 0.05$ ), 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

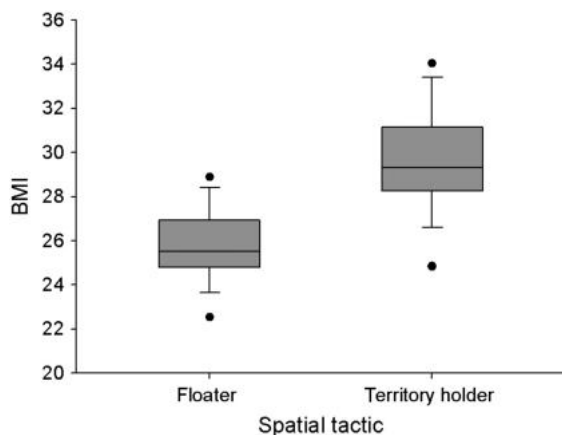


Fig. 4. Body mass index (BMI) of floaters and territory holders.

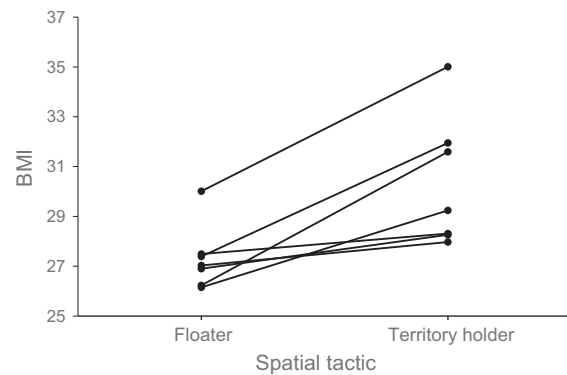


Fig. 5. Comparison of the body mass index of males that switched from floater to territory holder.

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.

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<sup>2</sup>) and males in coalitions (range 385 to 3403 km<sup>2</sup>; 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<sup>2</sup> for assumed territory holders, that is, with no behavioral support of territoriality, and 2300 km<sup>2</sup> 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<sup>2</sup>) 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<sup>2</sup> ( $n = 5$ ) and of the assigned floaters 1710 km<sup>2</sup> ( $n = 6$ ). 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<sup>2</sup> (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<sup>2</sup> (Mendelsohn et al. 2003). With a mean HR size of 1595 km<sup>2</sup>, 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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