# Namibian Journal of Environment Volume 5

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# Detection success of cheetah (*Acinonyx jubatus*) scat by dog-human and human-only teams in a semi-arid savanna

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## ABSTRACT

The cheetah (*Acinonyx jubatus*), like many other terrestrial large carnivores, exhibits elusive behaviour, occurs in low numbers over large home ranges, and has experienced population decline and range contraction. Therefore, long-term conservation strategies are needed which rely on accurate ecological data. Surveys using scat collection and analysis can generate these data and using scat detection dogs (*Canis familiaris*) is an effective method to gather scat samples. However, transect dimensions, local weather conditions and vegetation can influence the scat detection success. We conducted an experiment evaluating the influence of these factors on a scat detection dog-handler team, to assist the planning of optimal survey designs. We placed cheetah scat along transects of varying sizes established in different vegetation conditions and recorded environmental parameters during searches. Additionally, we evaluated the dog's performance compared to that of human searchers on one identical set of transects. The dog had an average detection rate of 45% and an accuracy rate of 100% over all trials. Increasing search time and decreasing transect width had the strongest positive influences on the detection rate. If transect dimensions did not exceed 100 m in length and 25 m in width, the dog achieved a detection rate of 93.3%, resembling the effective search area. We found no significant influences of weather conditions and vegetation cover. Human searchers achieved a detection rate of 22% and an accuracy rate of 55% compared to a 75% detection rate and 100% accuracy rate for the dog on the identical transects. To increase sample return, we recommend the calibration of study designs for individual dog-handler teams, as well as more frequent use of scat detection dogs for surveying populations of rare carnivores.

**Keywords:** canine; carnivore survey; cheetah; conservation; detection dog; Namibia; non-invasive survey; scat; wildlife monitoring

## INTRODUCTION

Many large carnivores are elusive, occur in low numbers and roam over large home-ranges, which makes it difficult to monitor their population status (Becker *et al*. 2017). The cheetah (*Acinonyx jubatus*) is a prime example of such a carnivore, with home-range sizes on Namibian farmlands averaging 1 651 km² (Marker *et al*. 2008): 379 km² for males with stable home-ranges in the form of small territories, 1 595 km² for males ranging over large areas and 650 km² for females (Melzheimer *et al*. 2018). With the majority of their population living on livestock farmland (Marker-Kraus & Kraus 1994), cheetahs are unique among predators in southern Africa in that they sometimes benefit little from protected areas (Cristescu *et al*. 2017). Nonetheless, on farmland, the potential for human-wildlife conflict is high, leading to death or persecution of the animals (Marker *et al*. 2003a) with an effective annual removal of 0.59 individuals per 100 km² over all ages and sexes (Weise *et al*. 2017).

To assist carnivore conservation and management, ecological data including population density, habitat use, home-range size, and resource use information is needed and predator scat surveys can facilitate these outcomes (Wasser *et al*. 2004; Davidson *et al*. 2014). Additionally, scat can provide species and gender identification (Harrison 2006; Hollerbach *et al*. 2018), as well as insights on reproduction and health (Rolland *et al*. 2006). Scat samples can also be used to determine a predator's diet which is a vital tool to evaluate human-wildlife conflict situations (Marker *et al*. 2003b).

Scat of territorial male cheetahs can be found close to and on scent marking areas that are prominent landmarks such as trees ('play trees'), termite mounds or rocks (Caro 1994). When those are known, the collection and identification of cheetah scat from territorial males is feasible, but female individuals and non-territorial males will likely remain undetected (Melzheimer *et al*. 2018). These latter samples are essential to achieve a dataset not limited by the hierarchy and spatial tactic of an individual cheetah or a specific gender, making it necessary to find samples away from scent marking areas.

Scat detection dogs (*Canis familiaris*) have been shown to efficiently find scat samples in a minimally invasive fashion, and thus their use is becoming popular in modern research (Beebe *et al.* 2016). Scat detection dogs have been used to find scats from a variety of species including bobcats (*Lynx rufus*) in North America (Harrison 2006), bush dogs (*Speothos venaticus*) in South America (Matteo *et al.* 2009), Eurasian lynx (*Lynx lynx*) in Europe (Hollerbach *et al.* 2018), non-human primates in Asia (Orkin *et al.* 2016), koalas (*Phascolarctos cinereus*) in Australia (Cristescu *et al.* 2020) and Cross River gorillas (*Gorilla gorilla diehli*) in Africa (Arandjelovic *et al.* 2015), but the effort and costs involved in using detection dogs are often higher compared to other survey methods or human searchers. Long *et al.* (2007a) calculated an average of US$ 153 per site when using hair snares, US$ 214 when using camera traps, and US$ 316 when using a leased detection dog to survey carnivores. In another study costs per scat sample were US$ 1479 when using a dog and only US$ 224 when using human searchers (Arandjelovic *et al.* 2015). However, this cost can be offset by an increased sample detection rate (Rolland *et al.* 2006; Arandjelovic *et al.* 2015) and more precise sample identification (accuracy rate) (Cristescu *et al.* 2015). Because funding resources are often limited in conservation research (Orkin *et al.* 2016), studies need to be designed to promote the potential of the individual dog-handler team (MacKay *et al.* 2008). Therefore individual working characteristics need to be identified in field experiments mimicking real search conditions, to quantify the search area where detection and accuracy rates are high (Reed *et al.* 2011). The aim of a study defines the rates necessary, for example, if the goal is to detect presence of a common species a lower detection rate can be tolerated (MacKay *et al.* 2008), while eradication of invasive species may rely on 100% detection rate (Glen & Veltman 2018). Important variables impacting the effectively searched area are the perpendicular distance from a transect line to a detected target (detection distance) (Glen & Veltman 2018), the distance from the start of a transect to a detected sample, and the search time per area (Bennett *et al.* 2020).

Detection dogs may also be influenced by local weather conditions, such as wind direction, wind speed, temperature and humidity (Wasser *et al.* 2004; MacKay *et al.* 2008; Kapfer *et al.* 2012; Beebe *et al.* 2016). These factors influence the scat, for example temperature affects bacterial activity leading to an increase or decrease of the amount and diffusion of odour (Wasser *et al.* 2004) while they also affect the dog, for example low humidity can cause dry nasal tissue leading to a reduced scenting ability (MacKay *et al.* 2008). Wind is considered important because the scent cone leading to the scat can be diffused and therefore impact the detection distance (MacKay *et al.* 2008). Vegetation structure is another important aspect as it affects the dispersal of scent (Wasser *et al.* 2004) and the ability of the dog-handler team to manoeuvre in the search area (Leigh *et al.* 2015). Closer investigation of those factors has been suggested (Long *et al.* 2007a; Reed *et al.* 2011), but to date the amount of research quantifying them is limited (Nussear *et al.* 2008; Reed *et al.* 2011; Leigh *et al.* 2015).

Dogs can find more samples in a shorter period of time (Oliveira *et al.* 2012) and are more accurate in identifying the species that deposited the scat than human searchers (Cristescu *et al.* 2015). Humans tend to search where higher sample abundance is expected, such as scent marking areas. This can lead to a bias in the spatial coverage of the search area and towards individuals with different spatial tactics (Arandjelovic *et al.* 2015). The collection of cheetah scat around marking areas is not sufficient to display the entire population in an area and therefore samples need to be found away from marking areas. It is therefore of particular interest to test scat detection dogs in comparison with human searchers in their ability to find those samples.

We conducted an experiment to assist with calibration of field efforts for detecting cheetah scat in a savanna system in north-central Namibia and to test the hypotheses that: (1) transect dimensions impact the detection rate, (2) an experienced dog can achieve stable detection rates under changing weather and vegetation conditions, and (3) a scat detection dog outcompetes humans when searching for scat.

## METHODS

### Study Area

The study area was located 45 km east of Otjiwarongo in north-central Namibia (20.436S, 17.100E) (Figure 1). The habitat is classified as semi-arid thorn bush savanna with an annual rainfall of approximately 400 to 500 mm (Buyer *et al.* 2016). More than 90% of the precipitation occurs in the hot wet season (15 September to 14 April) (Marker *et al.* 2008). We conducted our study in the cold dry season (15 April to 14 September) between 28 July and 25 August 2017. Lower temperatures increased the daily working hours of the dog, and the activity of dung beetles, which are known to remove the samples, was reduced (Becker *et al.* 2017). High precipitation rates can destroy scats (Arandjelovic *et al.* 2015), therefore the dry season with lower temperatures and nearly no rainfall provided ideal circumstances for our investigation.

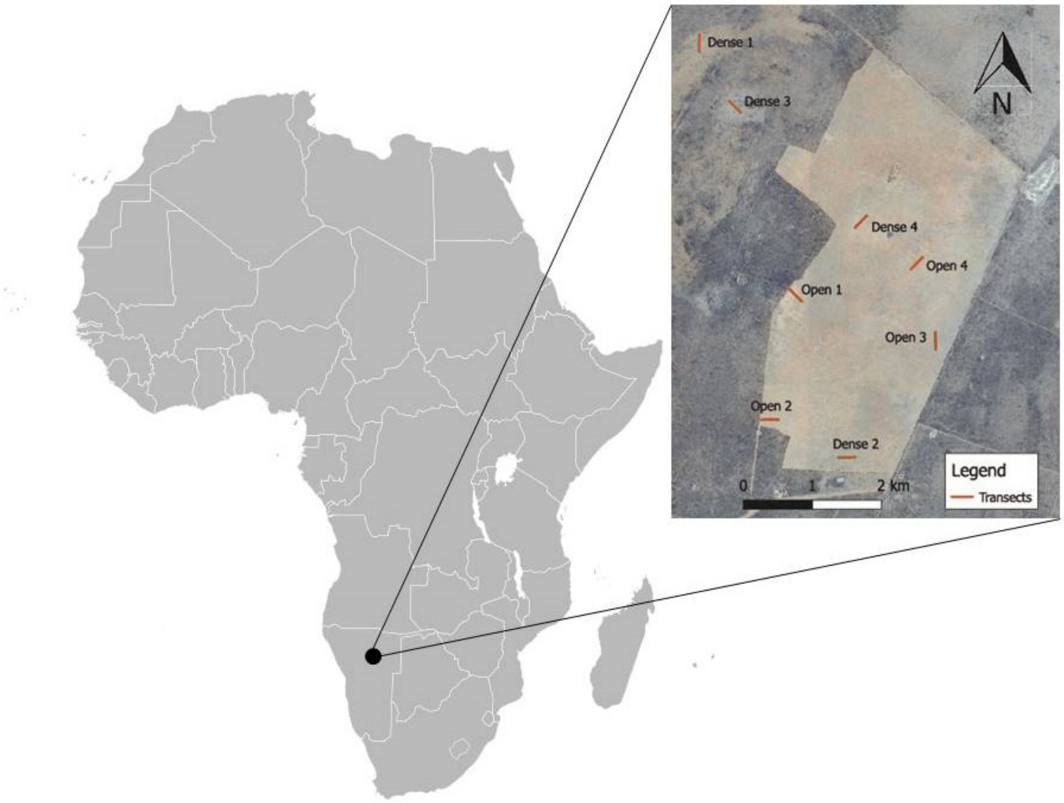

***Figure 1**: Study area (farm Elandsvreugde) with the locations of the four transects in dense vegetation and the four transects in open vegetation that were searched by the human-dog and human-only team.*

## Transects

We established eight transect lines (Figure 2, Table 1), four in open/low, predominantly grassy vegetation and four in dense/high vegetation. To find five randomly deposited cheetah scats, each transect was searched over four trials by a human-dog team and in one additional trial by human searchers (Table 1). The directions of the transects were fixed but their starting points were selected at random. They ran North to South, East to West, North-East to South-West and South-East to North-West to ensure working under variable wind directions. Transects were located approximately 1 540 m above sea level and their difference in elevation was negligible. The distance between transects was more than one km (mean ± SD; 1.26 ± 0.49 km) to prevent scent spreading across transects, assuming that average detection distances for dogs on terrestrial surfaces are below that threshold (Cablk *et al*. 2008; Leigh *et al.* 2015). Subsequent searches on transects were conducted at least two days (6.58 ± 2.04 days) after previous searches to reduce the presence of scent from sample remains. Transects were 250 m long but the search area changed with their strip width (Table 1), which is defined as the maximum distance where samples were deployed, perpendicular to both sides of the transect line. The first and second trial had a strip width of 50 m leading to a total search area of 2.5 ha (big transects), the third trial had a strip width of 25 m leading to 1.25 ha of search area (medium transects), and the fourth and the fifth trial had a strip width of 12.50 m leading to 0.63 ha of search area (small transects).

***Table 1:** Experimental design with the dimensions of the cheetah scat detection transects and search area, the number of transects per habitat type, the search team and the resulting total number of searches for each trial.*

| Trial ID | Total transect width [m] | Search area [ha] | Number of transects in open habitat | Number of transects in dense habitat | Search team | Number of searches |
|---|---|---|---|---|---|---|
| 1 | 100 | 2.50 | 4 | 4 | Human-dog | 8 |
| 2 | 100 | 2.50 | 4 | 4 | Human-dog | 8 |
| 3 | 50 | 1.25 | 4 | 4 | Human-dog | 8 |
| 4 | 25 | 0.63 | 4 | 4 | Human-dog | 8 |
| 5 | 25 | 0.63 | 4 | 4 | Human-only | 8 |

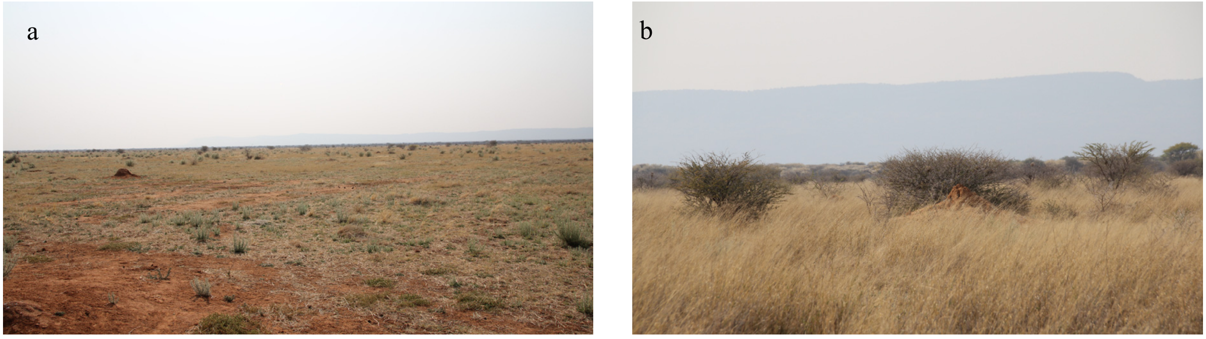

***Figure 2:*** *Examples of cheetah scat detection transects: (a) an open habitat transect characterised by bare soil and sparse vegetation, and (b) a transect in dense habitat characterised by a higher and denser grass layer with some bushes/trees.*

### Samples

Fresh target samples (~24 hours old) were collected from 13 captive cheetahs at the Cheetah Conservation Fund (CCF). Each sample consisted of a complete excrement and therefore differed in shape, size and consistency. Cheetahs were fed raw donkey (*Equus asinus*) or horse (*Equus ferus caballus*) meat with predator powder (©Health Tech Laboratories) supplement providing vitamins and minerals. Cheetahs of different age, sex and status of relatedness were chosen to reduce the effect of single odour components associated with an individual (Smith *et al*. 2003). Samples were collected with single-use gloves and immediately placed into separate, sealable plastic bags to be frozen. Freezing conserves the odour pattern (Goss 2019), but the process of thawing might influence the scent of the samples (MacKay *et al*. 2008). We decided to freeze to reduce the influence of different ages of the collected samples, as was also done by other authors (Reed *et al*. 2011; Oliveira *et al*. 2012). The transects were not cleared of existing scats from large carnivores present in the study area such as leopard (*Panthera pardus*), brown hyaena (*Parahyaena brunnea*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*), which acted as natural non-target scats. We avoided establishing transects near cheetah play trees to minimise the likelihood of encountering wild cheetah scat.

### Sample placement

The orienteer, wearing single-use plastic gloves, placed five scat samples per transect. The location of each sample was created randomly, using the research tool 'random points inside polygon' with no set maximum distance between the points in a GIS (QGIS Development Team 2016), inside a buffer which differed in size depending on the trial. The fourth and the fifth trials, which acted as the comparison between human searchers and the dog, were conducted with the same locations to eliminate bias due to sample positions. Coordinates were uploaded into a GPS (Garmin GPSMAP 60CSx) allowing placing the sample at the correct position, however, the inaccuracy of a GPS can lead to a bias in the target's position (MacKay *et al*. 2008). The orienteer walked randomly over the whole search area reducing the chance for the dog to follow his footsteps to the targets (Leigh *et al*. 2015). Placement was done within 7 to 24 (17.1 ± 4.82) hours before the trial began, to reduce the presence of human scent and to allow the scent of the scat to disperse. The time we chose exceeds the time used in another similar study (Reed *et al*. 2011).

### Human-dog team

The human-dog team consisted of the dog, the dog handler, and the orienteer. The dog was an experienced, ten-year-old, male border collie that had been trained for his first two years of age on frozen cheetah scat, and was used for field searches in the study area for the next six years. His training followed the general principles in this field of research (Wasser *et al*. 2004; MacKay *et al*. 2008). The dog displays an indication behaviour, sitting, to communicate the detection of a target scat to the handler, and is then rewarded with a play session. The dog's drive and focus on the task aids quick learning and successful identification of target and non-target samples. For two years before this study, the dog was used regularly for short training sessions but not for field searches. The dog was handled by CCF's scat dog handler and trainer, who had two years of experience working with detection dogs in the private security sector. Orientation and data collection were carried out by the lead author.

### Trial procedure

We conducted trials on three sequential days, followed by a one-day break to rest the dog. Trials took place from 06h00-10h00 and 15h00-18h00 to avoid the hottest time of the day. The dog walked off leash in front of the handler. To mimic field conditions, the dog handler was only given the transect direction and no time limit; therefore, the handler decided independently how much time was spent on each transect, defined as 'search time'.

The trial procedure followed the general strategy in this field of research (Wasser *et al.* 2004; Long *et al.* 2007b; Nussear *et al.* 2008). The handler sent the dog in specific directions or walked with the dog to either side of the transect line to make sure the dog covered the area sufficiently. The orienteer stayed a few metres behind the dog handler and kept the team on track using a handheld GPS (Garmin GPSMAP 60CSx). If scat was detected, the dog sat and waited for the handler to arrive and check the scat sample. If the handler approved the dog's findings, the orienteer marked his position on the transect line and approached the team. Once the orienteer confirmed the scat as a target sample, the dog was rewarded with a short playing session and the orienteer collected the scat. The team then returned to the marked point on the transect line and continued with the trial. Each trial ended when the team reached the end of the transect line.

Before the start of each transect, at every detected sample and at the end of each transect, the environmental variables temperature, humidity, wind speed and wind direction were recorded, using a hand held weather station (Kestrel 4500nv Pocket Weather Tracker) with a precision of one decimal unit. All variables were measured at 1.30 m height, but at the scat positions at 0.30 m height.

### Human-dog vs. human-only

The comparison between the human-dog team and the human-only team was done on one set of eight small transects. Three human participants with experience in identifying cheetah scat searched after the dog on those transects. Searcher One had worked for five years as large carnivore keeper in a safari park, Searcher Two had worked for two years analysing cheetah scat in a genetics laboratory, and Searcher Three was a qualified field guide with one year of experience. The trial procedure was consistent with the dog team's trials, but the searchers were not told if the samples they pointed out were correct until the end of the trial, to avoid influencing their search morale. No weather data was recorded because the effect on human performance was assumed negligible in the moderate weather conditions worked in (Nussear *et al.* 2008).

### Analysis

Detection rate was defined as the number of targets found, divided by the number of targets available. Accuracy rate was defined as the total number of correctly indicated samples divided by the total number of indications. The perpendicular distance from each sample to the transect line ('detection distance') and the distance from the starting point of the transect to the sample's location ('distance from start to target') were calculated using QGIS 2.18 Las Palmas.

We tested for significant differences between groups using Mann–Whitney U tests ($U$) and Kruskal-Wallis-Rank Variance Analysis with multiple *post hoc* tests ($H$), as well as correlations between variables with Spearman's Rank Correlations ($r_s$) (Bortz *et al.* 1990). All calculations were performed using STATISTICA 13.3 (Tibco Software Inc. 2017). The alpha level of statistical significance for all our calculations was set to 5% ($p < 0.05$).

## RESULTS

### Dog performance

The dog indicated 72 out of 160 possible samples at a rate of 2.3 (± 1.3) samples per transect resulting in a detection rate of 45% (Table 2). This rate differed between the transect sizes; the dog indicated 3.8 (± 0.5) available targets on the small transects (75% detection rate), 2.9 (± 0.6) samples on the medium transects (58% detection rate) and 1.2 (± 0.9) samples on the big transects (24% detection rate). The detection rate differed significantly ($H$ = 22.57, df = 2, p = 0.000; n = 32) between the big transects compared to the medium (p = 0.015) and small transects (p = 0.000), but not between the medium and the small transects (p = 0.485). The dog never indicated a non-target scat and no wild cheetah scat was encountered during the study; the accuracy rate was 100%.

The average search time over all transects was 23.0 (± 15.3) min/ha; 46.0 (± 5.4) min/ha on small transects, 25.6 (± 1.4) min/ha on medium transects and 10.1 (± 2.9) min/ha on the big transects. The search time differed significantly ($H$ = 26.23, df = 2, p = 0.009; n = 32) between the big transects compared to the medium (p = 0.009) and small transects (p = 0.000) but not between the medium and the small transects (p = 0.264).

The detection (n = 72) and non-detection (n = 88) distance ranged from 0 m to 44 m and differed over all transects widths ($U$ = 1409.50, p = 0.000; n = 160). Detected samples were on average 10.1 (± 9.7) m away from the transect line and undetected samples 22.3 (± 14.1) m. Samples were detected (n = 30) on the small transects at a distance of 5.5 (± 3.6) m and not detected (n = 10) at 9.0 (± 2.4) m ($U$ = 64.00, p = 0.007; n = 40). On the big transects, samples were detected (n = 19) at a distance of 17.7 (± 13.7) m and undetected (n = 61) at a distance of 26.7 (± 14.3) m from the line ($U$ = 365.00, p = 0.016; n = 80). A similar pattern was found for the average distance from the start to detected targets over all trials, but it

***Table 2:*** *Key values describing the performance of human-dog and human-only teams in detecting cheetah scat under field conditions, including average and total numbers for detection of target and non-target samples, and distance values for detection and non-detection of samples from the transect line and the start to the targets (means with standard deviations).*

| Transect | Trial | Number of searches | Total number of available samples | Total number of detected samples | Average number of detected samples per transect | Total detected non-target samples | Average number of non-target samples detected per transect | Average search time per transect [min/ha] | Average distance of detected targets to the transect line [m] | Average distance of undetected targets to the transect line [m] | Average distance from the start to detected targets [m] | Average distance from the start to undetected targets [m] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Big** | 1 & 2 | 16 | 80 | 19 | 1.2 (± 0.9) | 0 | 0.0 | 10.1 (± 2.9) | 17.7 (± 13.7) | 26.7 (± 14.3) | 117.0 (± 78.8) | 115.8 (± 75.6) |
| **Medium** | 3 | 8 | 40 | 23 | 2.9 (± 0.6) | 0 | 0.0 | 25.6 (± 1.4) | 9.7 (± 7.3) | 14.5 (± 8.4) | 110.8 (± 68.2) | 152.4 (± 70.0) |
| **Small** | 4 | 8 | 40 | 30 | 3.8 (± 0.5) | 0 | 0.0 | 46.0 (± 5.4) | 5.5 (± 3.6) | 9.0 (± 2.4) | 113.5 (± 69.5) | 163.6 (± 75.1) |
| **Overall** | 5 | 32 | 160 | 72 | 2.3 (± 1.3) | 0 | 0.0 | 23.0 (± 15.3) | 10.1 (± 9.7) | 22.3 (± 14.1) | 113.6 (± 70.7) | 128.3 (± 76.1) |
| **Human** | 5 | 8 | 40 | 9 | 1.1 (± 1.0) | 7 | 0.9 (± 1.4) | 40.6 (± 2.3) | 6.3 (± 3.7) | 6.4 (± 6.4) | 124.0 (± 87.0) | 127.0 (± 70.5) |

was only found significant on the small transects (*U* = 84.00, p = 0.041; n = 40), with a detection distance of 113.5 (± 69.5) m and a distance for undetected samples of 163.6 (± 75.1) m. The average distance for undetected samples increased with decreasing transect width but was only found significant between the big (n = 61) transects compared to the grouped small and medium (n = 27) transect (*U* = 554.50, p = 0.015; n = 88). It was 163.6 (± 75.1) m for the small transects, 152.4 (± 70.0) m for the medium transects and 115.8 (± 75.6) m for the big transects. The effective searched area (Box in Figure 3) was 100 m in length and 25 m in width where the dog achieved a detection rate of 93.3%, and an accuracy rate of 100%.

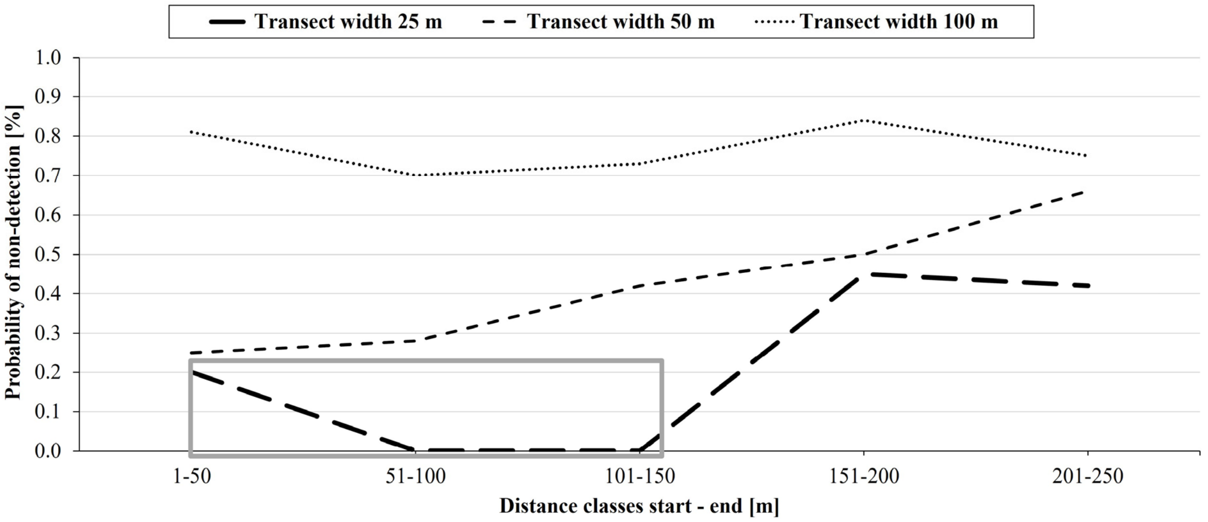

***Figure 3:*** *Probability [%] of non-detection for scat samples at different transect widths (small, medium and big) dependent on the distance from the start point to the samples; box indicates a 93.3% detection rate.*

***Table 3***: *Environmental factors (windspeed and direction, temperature and humidity) measured at the start and end of the transects at chest height and at dog nose height (0.3 m) at every detected sample (means with standard deviations, minima and maxima).*

| | **Temperature [°C]** | | | **Humidity [%]** | | | **Windspeed [m/s]** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Average** | **Min.** | **Max.** | **Average** | **Min.** | **Max.** | **Average** | **Min.** | **Max.** |
| **Transect (1.3 m height)** | 23.9 (± 4.4) | 5.4 | 32.1 | 18.0 (± 6.0) | 0.2 | 37.9 | 1.4 (± 1.0) | 0.1 | 3.7 |
| **Scat (0.3 m height)** | 23.9 (± 5.2) | 2.6 | 31.8 | 19.0 (± 7.0) | 9.1 | 37.8 | 1.5 (± 1.1) | 0.1 | 4.9 |

### Weather and vegetation

Environmental values measured at the beginning and at the end of the transect, and at the scat positions are listed in Table 3. None of the environmental factors nor the vegetation categories had a significant influence on the detection success of the dog (*H*, *U*, $r_s$, $p \geq 0.05$).

### Human vs. Dogs

The dog detected 30 samples at a rate of 3.8 (± 0.5) samples (75% detection rate) per transect, while humans found 9 samples at a rate of 1.1 (± 1.0) samples (22% detection rate) per transect ($U = 1.00$, $p = 0.001$; $n = 16$) (Figure 4). The dog never indicated a non-target scat, while humans indicated 7 non-target scats, resulting in 0.9 (± 1.4) false indications per transect, and an accuracy rate of 56%, compared with 100% for the dog. Both teams spent similar time searching (46 min/ha and 40.6 min/ha, respectively). There was no statistically significant influence of vegetation on the performance of human-dog or human-only teams (*U*, $p \geq 0.5$).

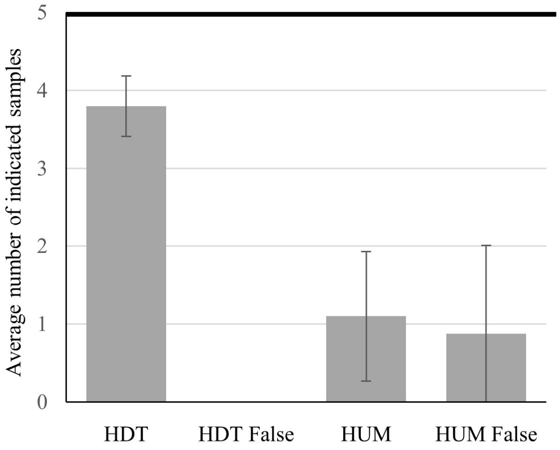

***Figure 4:*** *Average number of detected target and non-target (false positive) scat samples by the human-dog team (HDT) and the human-only team (HUM) per transect; line indicates the maximum number of available targets; error bars indicate the 95% confidence interval.*

## DISCUSSION

### Dog performance

The tested dog-team reached 93.3% detection and 100% accuracy rate under transect dimensions of 100 m in length and 25 m in width, which we consider the effective search area. Transect dimensions drastically influence the performance of a scat detection dog but can be calibrated to achieve a higher detection success; this proved our first hypothesis. This experiment was executed with only one dog and the impact of the individual might change results drastically. However, our results align with those found by other authors.

### Detection rate

Although the overall detection rate in this study of 45% is low compared to most previous research showing 68% and 77% (Reed *et al*. 2011), 83% and 87% (Leigh *et al*. 2015) and 97% (Cristescu *et al*. 2015), the highest rate of our dog, 75% on the small transects, is within those ranges. One study showed a lower overall detection rate of 29% (Oliveira *et al*. 2012), These results are difficult to compare as they did not follow a common testing design and information on training, age of dog and experience of the team was not always communicated (Oliveira *et al*. 2012; Cristescu *et al*. 2015). Our dog was ten years of age and had been performing short training sessions in the year before the experiment. A decrease in drive and agility, which are known as key characteristics for the success of a scat detection dog (MacKay *et al*. 2008) had been observed due to his age. Additionally, this study was the first time this human-dog team worked together and therefore they might perform better once a familiarity is established (Smith *et al*. 2003). Together with the transect width, the target abundance also differed, because we always placed five samples independent of the transects' width. This led to increasing target abundance with decreasing transect size. To avoid that, we would either have to deposit more samples on the big transect, which was not feasible in the given time frame, or less on the smaller transects, which would have made it difficult to draw sound statistical conclusions. We believe that the transect size had a stronger influence on the dog's performance than the target abundance, even though we cannot prove that statistically. If the motivation resulting from reward shows a stronger impact on the dog's performance than we observed, the orienteer should place training scats while searching, to keep the dog's search morale high, even if scat is encountered at a very low rate (MacKay *et al.* 2008).

### Search time

The search time had the strongest positive influence on the dog's detection rate and was chosen by the dog handler. The handler decided when the area is covered sufficiently (MacKay *et al.* 2008); we did not set a time limit as it is not advisable to interfere with the dog-team's work (Wasser *et al.* 2004). Also, we wanted to study the team under real working conditions, where time limits are usually not applicable (Hollerbach *et al.* 2018; Cristescu *et al.* 2020). The handler spent a similar time on each transect independent of its width, leading to lower search time per ha on the big transects. We assume that an increased search effort would have led to higher detection rates increasing the effective search area. Dog errors are often due to handler errors (Wasser *et al.* 2004), which stresses the importance of a well-functioning team with an experienced handler (Orkin *et al.* 2016). Our handler was a professional dog handler and trainer but was not experienced with the search system applied in this investigation. Other researchers successfully recruited dog handlers from different backgrounds, for example police, after some initial training (Arandjelovic *et al.* 2015), or had dogs trained by the military police (Oliveira *et al.* 2012). We recommend further exploring the utilisation of handlers and dogs from different backgrounds but emphasising the importance of intense training to reduce errors (MacKay *et al.* 2008).

### Accuracy rate

The 100% accuracy demonstrated by our dog is above the rates given by other authors ranging between 64% (Clare *et al.* 2015), 60% and 85% (Vynne *et al.* 2011), 72% (Harrison 2006) and 81% (Orkin *et al.* 2016). These accuracy rates are often based on genetic analysis of scat (Smith *et al.* 2003; Harrison 2006; Long *et al.* 2007b; Clare *et al.* 2015) and researchers may discard samples that can not be genetically assigned to a particular species (Long *et al.* 2007b), which makes it impossible to calculate exact accuracy rates. For example, Smith *et al.* (2003) found an accuracy rate of 100% for each of the five dogs used in their investigation, but DNA could not be extracted from all the scats. Long *et al.* (2007b) only analysed samples that were promising for species identification and over 38% of the samples failed to extract DNA. Exact accuracy rates can only be calculated from an experimental study where the exact number of target samples is known or when genetic analysis is 100% successful.

We did not deposit non-target samples, but scat of other large carnivores acted as natural non-target samples. Our dog was initially trained on frozen samples which were also used in this experiment. Temperature affects bacterial activity in the scat (Wasser *et al.* 2004) and freezing/thawing might influence the odour pattern. It is possible that non-target samples manipulated identical to the target samples might have influenced the accuracy of the dog. Freezing conserves the odour pattern (Goss 2019) and if the dog is only trained on 'fresh' samples it might not have generalised older samples (Leigh *et al.* 2015) which could also affect the accuracy. Additionally, the diet of the captive animals differed from the wild, which introduces another source of difference in scent between training samples and wild samples (MacKay *et al.* 2008). We recommend that future studies deploy non-target samples that were manipulated identically to the target samples to test for the dog's accuracy.

We did not observe the dog ground scenting a certain path (MacKay *et al.* 2008), therefore assume that the accuracy rate was not influenced by scent trails left behind during sample placement. The random movement while deploying the samples and the time elapsed between placing and searching were therefore sufficient.

### Detection distance

We found that indicated samples were closer to the transect line than undetected samples and that this distance increased with transect width. The latter is intuitive as samples were on average further away as the transect width increased, so this is not necessarily a trend linked to the dog's performance. It is important to keep in mind that the distance analysed is the perpendicular distance from the transect line to the sample, not the distance from where the dog caught the scent, indicated by a change of behaviour, which could therefore differ (Reed *et al.* 2011). The average value over all transects of 10.1 m is comparable to the distances found by other authors ranging from 4.8 m (Ralls & Smith 2004), 7.2 m (Oliveira *et al.* 2012) to 9.6 m and 10.4 m (Reed *et al.* 2011). Studies that measured the detection distance, indicated by a change of behaviour, give average values of 13.9 m (Cablk *et al.* 2008), 12.9 m and 15.4 m (Leigh *et al.* 2015). Despite our dog's age and lack of field searches before the investigation, the distance values align with other studies. Therefore, we must assume that these values are accurate despite the variation given by the individual teams and should be considered when planning search efforts.

The average distance from the start to undetected samples increased with a decreasing transect width, and the difference between detected and undetected samples was most prominent on the small transects. Considering that transects differed in their width but not in their length these findings have practical application. By working a smaller width, the dog is also able to work a longer transect effectively (Box in Figure 3). One reason for the decrease of detection rate could be fatigue, as an increase in panting reduces the dog's scenting ability (Smith *et al.* 2003). Motivation might also decrease over time and distance (MacKay *et al.* 2008). Cristescu *et al.* (2015) investigated the effect of the distance from the start to a target and did not find a negative trend like we did; however, their transect length was only 25 m. Our findings show that the transect width and length influence the detection success. We recommend that transect dimensions should be kept small. Using dogs that exhibit a high drive and a high accuracy rate will allow researchers to use larger dimensions without diminishing the effectiveness (Beebe *et al.* 2016).

### Weather and vegetation

We found no significant effects of vegetation and weather parameters, supporting our second hypothesis that an experienced dog can compensate for varying environmental conditions. One explanation is that we chose the cooler time of day and year for our experiment. Also, the vegetation categories were different but showed an overall similar character as this displayed the real search environment. Testing under extreme weather and vegetation conditions might have revealed thresholds that limit the dog (MacKay *et al.* 2008) therefore studies should always be designed in a way that supports the dog rather than restrict it (Reed *et al.* 2011). Working under real field conditions helped us develop reasonable transect dimensions. Dog and handler were not restricted to the transect line, and the dog worked off leash which allowed the dog to catch wind from different angles and for the handler to send the dog anywhere over the search area. It is therefore advantageous to allow the dog this freedom of movement (MacKay *et al.* 2008). Our findings are supported by other authors who also did not detect a significant influence of wind on the detection success working under comparable conditions (Long *et al.* 2007b; Nussear *et al.* 2008; Reed *et al.* 2011; Leigh *et al.* 2015).

### Human vs. dog

In our study, the dog detected 3.5 times as many samples as the human searchers did while never indicating a non-target scat, proving our third hypothesis that dogs are more effective when searching for scat. Our findings align with previous research investigating the detection of bird/bat carcasses around wind turbines, in which dogs indicated 96% and 75% of the available targets and humans indicated 9% and 20% (Paula *et al.* 2011; Mathews *et al.* 2013). Other studies reported the same trend (Cablk & Heaton 2006; Kapfer *et al.* 2012), while some found equal detection rates for dogs and humans (Nussear *et al.* 2008; O'Connor *et al.* 2015), but no research was found that showed humans to perform better than dogs. When dogs are used to detect scat by smell a clear advantage, regardless of the target species, is observed (Arandjelovic *et al.* 2015), since humans can only detect scats by sight (Smith *et al.* 2003) and this can be difficult because of the often similar colour of the soil, the target samples and the vegetation cover.

Our human searchers reached an accuracy rate of 56% because they also found natural non-target scats from other carnivores. This is consistent with previous research, showing a 153% increase in accuracy by dogs compared to humans (Cristescu *et al.* 2015) and only 45% genetically proven accuracy by humans compared to 81% by dogs (Orkin *et al.* 2016). The ability of humans to identify scat is limited, especially when differentiating between scat with similar morphological appearance (Matteo *et al.* 2009).

We did not deploy scats at potential marking sites such as trees, which are more intensely searched by humans than by the dog, as observed in our study and mentioned by other authors (MacKay *et al.* 2008; Arandjelovic *et al.* 2015). This might have increased the chances for humans to detect samples, but we wanted to test the ability of human observers to find samples randomly in the landscape.

Considering both detection and accuracy rate, we found that the human-dog team was both more efficient and more accurate than the human-only team. Therefore, we highly recommend the use of scat detection dogs to increase the sample detection rate and decrease false sample identification, especially when samples independent of marking sites are needed.

## CONCLUSION

Changes to the search area, as exemplified by our experimental manipulation of transect widths, have a strong influence on the detection rate, therefore search designs should be calibrated individually for each dog team. Scat detection dog surveys should report in detail the characteristics of the survey design and methodology, including but not restricted to season, time of the day, transect dimensions, and search time. Detection dogs can work with constant success under variable environmental conditions related to vegetation structure and microclimate in a semi-arid savanna. The advantages of detection dogs are not only a higher sample return but also an increased accuracy in target identification.

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# Of teeth and claws: Taking stock of carnivore research in the greater Etosha landscape

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## ABSTRACT

The Etosha National Park and its surrounding areas in northern Namibia have been the focus of research for more than a century, yielding a great amount of environmental and ecological knowledge. The results have appeared in different forms and formats, and these are stored in numerous repositories, many of which are difficult to access. This limits distribution and effective use of existing knowledge about specific topics and biological taxa, whilst also constraining the opportunity to identify future research priorities. In this study, we assessed published and unpublished accounts to compile an overview of previous mammalian carnivore research in the greater Etosha landscape – one of the few remaining large sub-Saharan areas (> 69,000 km$^2$) with a nearly intact carnivore guild. Of the 644 carnivore-related documents we found, 139 studies met our inclusion criteria. From these, we identified trends emerging from spatial, temporal, species, authorship, and topic patterns, whilst also digitising source materials and creating an annotated bibliography that is being made available to others. Our synthesis of carnivore research revealed several historical biases in terms of: i) where carnivore studies occurred (mainly within National Park boundaries); ii) which species were studied (mostly large-bodied, charismatic animals, especially the lion *Panthera leo*); and iii) which research themes and topics prevailed (mostly ecology topics focussing on occurrence, diet, and demographics). We also found that carnivore research output has been declining during the last three decades and this was accompanied by a shift in lead authorship from government-employed researchers to external investigators. We use our results to provide a stimulus for re-focusing future carnivore studies. We encourage similar syntheses and stock-taking of what is known for other taxa and topic areas, stressing the importance of preserving historical knowledge and making it accessible.

**Keywords:** bibliography; Carnivora; Etosha National Park; Namibia; predator; protected area; research history; synthesis

## INTRODUCTION

The Etosha National Park (hereafter ENP) in northern Namibia is an example of a large African conservation area with a long and well documented history in research and monitoring. For nearly six decades, numerous studies covering a wide range of topics have been conducted in and around ENP. Fields of study have included, among many others, the measuring of soil and water characteristics, surveys to estimate animal numbers, wildlife natural history, rainfall patterns, disease investigations, and factors affecting large animal movement patterns. Most of the resulting data, stored as hard copies at the Etosha Ecological Institute (hereafter EEI), were either compiled as internal reports, peer-reviewed publications, book chapters, academic theses, or conference proceedings.

The EEI, which opened on 1 April 1974 (Berry 1997), is responsible for securing and disseminating scientific data generated in ENP. Since the inception of the EEI, a large amount of information has been collected and substantial technological advances made to improve data collection, analyses, and interpretation. This assisted science-based decision-making in ENP. However, unless a centralised data repository for the safe storage, management and dissemination of all current and historic data is established, there is a risk of losing a wealth of institutional knowledge due to generation overturn among researchers and changes in knowledge distribution technologies and formats. In addition, the availability of historic knowledge is often constrained by inaccessible data repositories or incompatible formats, which can be difficult and time-consuming to reconcile and standardise in digital format. The latter is a prerequisite for accessing and distributing knowledge on a global scale.

Mammalian carnivores are the focus of extensive research across the world, mainly because their importance in ecosystem functioning is increasingly recognised (Ripple *et al*. 2014). The greater Etosha landscape is no exception, and structured carnivore research began as early as the mid-1960s, with the first published report assessing the population sizes of lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), and (Cape) wild cat (*Felis lybica/silvestris*) in 1972 (Reid 1972). In addition, this landscape provides a representative example of global conservation

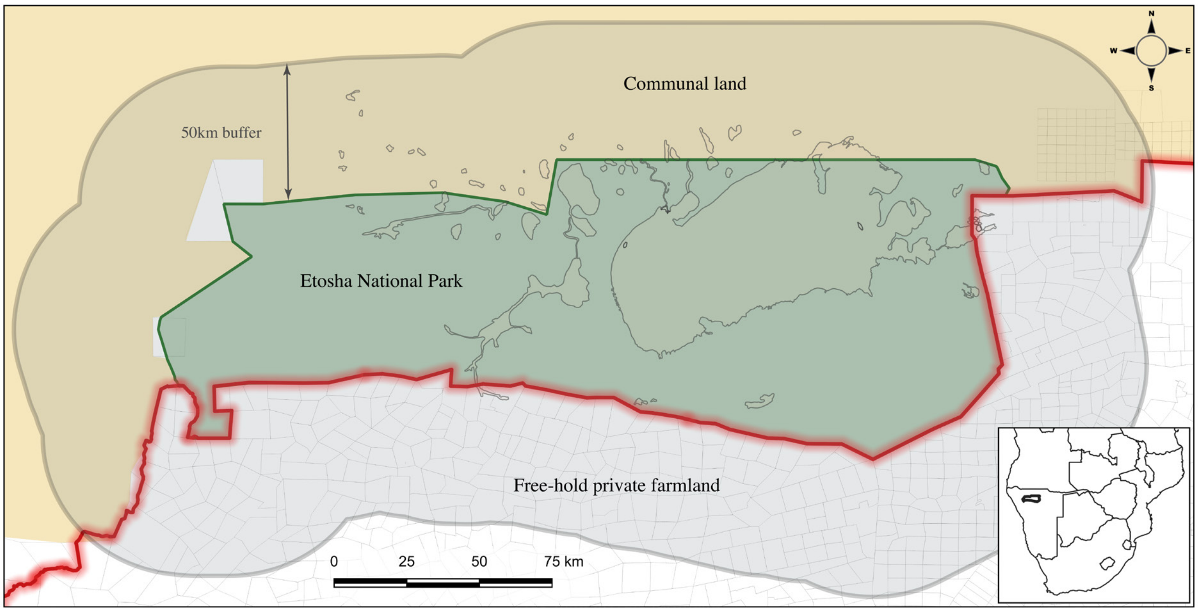


***Figure 1**: Extent of the carnivore research study area in northern-central Namibia. Our focal area encompassed 69,092 km$^2$, including 23,163 km$^2$ of free-hold, multi-use farmland, the state-protected Etosha National Park measuring 22,904 km$^2$, and 23,025 km$^2$ of multi-use communal lands. The red line shows the veterinary cordon fence. The inset shows the focal area's location in the southern African sub-region.*

challenges, with a core protected area surrounded by a matrix of human multiple-use systems. It is internationally recognised as one of the last conservation areas in sub-Saharan Africa with a largely intact predator guild (Wolf & Ripple 2017). Despite the local extinction of African wild dogs (*Lycaon pictus*) in the 1980s, ENP still supports source populations of five large carnivore species, including lion, leopard (*Panthera pardus*), cheetah, spotted hyaena (*Crocuta crocuta*) and brown hyaena (*Parahyaena brunnea*), as well as an associated range of medium-sized meso-carnivores. This provides a rare opportunity to study functional guilds and trophic interactions between predators and their prey populations.

Our goal was to write an overview paper, with a focus on the mammalian carnivore guild occurring in the greater Etosha landscape, whilst also creating an annotated bibliography and making materials available to others as a digital library. Our motivation to conduct this work stemmed from the global importance of long-term carnivore research and conservation, as well as the availability of numerous publications and unpublished reports. The value and impact of similar reviews was illustrated by Balme *et al.* (2014), in their paper on drivers determining priorities for leopard research and conservation.

We structured our work as a synthesis of available materials, with the intention of summarising and condensing existing information, identifying patterns and trends, and highlighting research gaps to stimulate future studies.

## METHODS

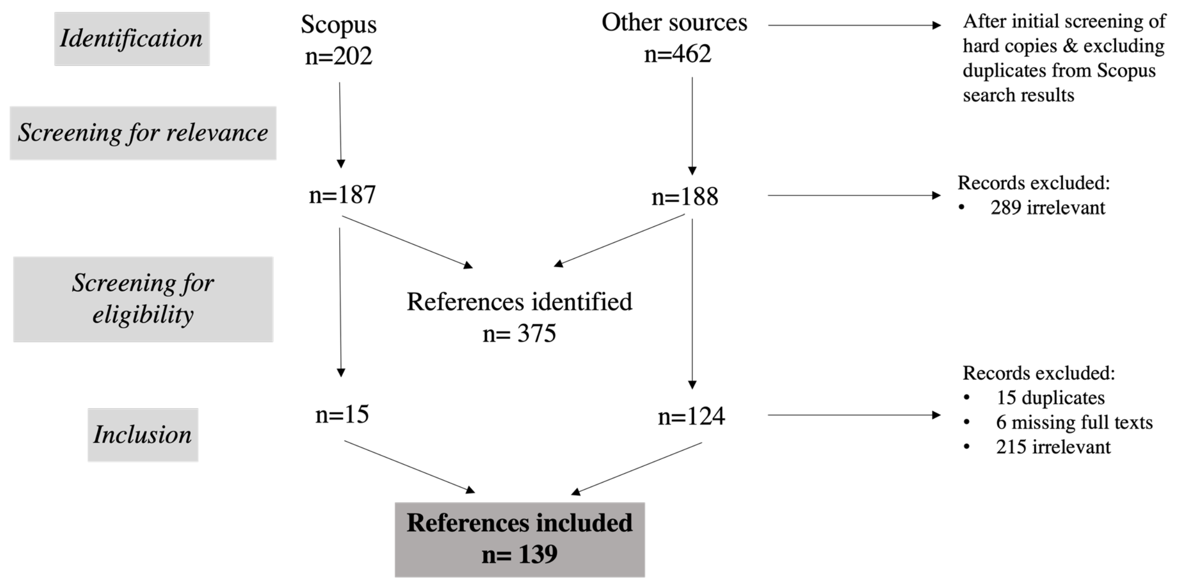
### Scope

The focal area was defined as the greater Etosha landscape in northern Namibia, including the ENP and an arbitrarily defined 50 km buffer around its current boundaries (Figure 1). This 69,092 km$^2$ landscape encompasses three main land tenure system at nearly equal area proportions, being: 23,163 km$^2$ of free-hold, multi-use farmland to the South and East of ENP, the state-protected ENP of 22,904 km$^2$ in its centre, and 23,025 km$^2$ of communal, multi-use residential and farmland to the West and North of ENP (Figure 1). Any historical carnivore research in this area, even if only partly overlapping with it, was considered for inclusion.

Sayer (2018) emphasised the aim of considering the entire historic account of literature. Hence, we had no temporal exclusion rule, assessing documents published during the last 110 years, with contents dating as far back as the 19th century. Our synthesis focussed on large-bodied mammalian carnivores, including lion, leopard, cheetah, spotted hyaena, brown hyaena and African wild dog as well as medium-sized carnivores, including honey badger (*Mellivora capensis*), black-backed jackal (*Canis/ Lupulella mesomelas*), serval (*Leptailurus serval*), and caracal (*Caracal caracal*). In our search, we considered species' Latin names, their vernacular names and common synonyms, and also spelling variants in different languages (Appendix 1), including documents in English, German and Afrikaans.

## Material sources

Materials were retrieved through structured searches from a broad spectrum of published and unpublished sources, whilst also obtaining materials opportunistically, for example from research colleagues. Structured carnivore literature searches were carried out between April and October 2020. First, we conducted a detailed abstract, title and keywords search using the SCOPUS online database on 16th April 2020. Our primary search terms included: "hyaena/hyena", "lion", "leopard", "cheetah", "wild dog", "badger", "jackal", "serval", and "caracal" and each of these was paired with the secondary search term "Namibia". In addition, we browsed the entire holdings of Etosha Ecological Institute's research archives, manually extracting relevant files. We also searched for materials in Google Scholar, the open online repository of Namibia's Environmental Information Service (www.the-eis.com) and the Digital Cat Library of the IUCN/SCC Cat Specialist Group (http://www. catsg.org/catsglib/index.php). Full publications lists of Namibia's research titles: Madoqua, Roan News, Cimbebasia (journal of the State Museum, Windhoek) and Mitteilungen der Wissenschaftlichen



| | | |
|---|---|---|
| **Journal articles** | 15 | 55 |
| **Magazine** | - | 2 |
| **Newspaper** | - | 1 |
| **Presentations** | - | 3 |
| **Reports** | - | 49 |
| **Thesis** | - | 7 |

| | Applied research | Ecological research | Method development | TOTAL* |
|---|---|---|---|---|
| PA | 33 | 92 | 21 | 117 |
| Free-hold private farmland | 22 | 34 | 6 | 47 |
| Communal land | 13 | 16 | 1 | 23 |
| TOTAL* | 44 | 107 | 21 | 139 |

* The total number of studies for themes and location differ from the overall number of studies assessed, as each reference could qualify for multiple themes and locations.

***Figure 2**: Flowchart outlining the source material review and selection process, including the distribution of eligible references in terms of reference type, research type, and study location. Out of 664 carnivore-related documents initially identified, 139 references were included in the synthesis. Most references were peer-reviewed journal articles (50.4%) and reports (35.4%). The majority of research was conducted within Etosha National Park (84.2%) and focussed on ecology topics (77.0%). Appendix 2 and Appendix 3 provide the full account of references included and six items for which full texts were not accessible.*

Gesellschaft (Namibia Scientific Society's periodical newsletter) were screened, as well as de Waal's (2002) large predator bibliography and the bibliography of the Northern Namibian Environmental Project (Ministry of Environment and Tourism in Namibia 1997). Finally, we conducted a tri-lingual abstract, title and keyword search of the library holdings of the Namibia Scientific Society (https://www.namscience.com/library). Search terminology was consistent across all sources.

We considered any document format, digital and print, including peer-reviewed research articles, book chapters, academic theses, grey reports, policy documents, unpublished research reports, conference proceedings, presentations, posters etc. Since we were primarily interested in compiling a bibliographical overview of previous scientific studies, only materials with an obvious research element, those containing original data and an analysis thereof, be they descriptive and/or inferential, were considered. We excluded popular science articles or news materials that only described studies and/or their results. To avoid pseudo-replication, we removed duplicate publications of the same studies and assessed the contents of sequential documents (e.g., interim project progress reports), in both cases only including the most comprehensive study account in our review, usually the latest or final version, though not always (n = 2). Raw data accounts as well as documents only containing general correspondence about research projects, project proposals, meeting minutes, and any other documents not providing original data and some form of formal analysis thereof, were rejected. Figure 2 outlines the literature search and selection process, including sample sizes and general results.

### Processing and analysis

For processing and future reference, all relevant materials were digitised, imported into a Zotero literature database (https://www.zotero.org), from which we created an annotated bibliography in Excel format that contains publication and content details, as well as the source of materials. For each document matching our search criteria, we read the full account and, if also matching our inclusion criteria, the following information was extracted: author(s) and document title, year of publication, publication title, volume and issue, page numbers, DOI, and source URL. We categorised studies by type of publication such as *peer-reviewed journal article*, *report*, *academic thesis*, *book chapter*, *poster*, *conference paper*, *presentation*, and *magazine/newspaper article* and also by broad theme, being: *applied research*, *ecological research* or *methods research* (Table 1). Based on the study's specific objectives and the data and analyses contained, materials were categorised by study focus and specific topic (Table 1). Neither

***Table 1:*** *Study themes and specific topics used for literature categorisation.*

| **Broad theme** | **Examples of data contained, or analyses performed** |
|---|---|
| Applied research | Management investigations, e.g., translocations, population control measures, human-carnivore conflict topics |
| Ecological research | Natural history investigations, e.g., population demographics or spatial ecology studies |
| Methods research | Methodology studies involving carnivores as experimental units, e.g., development of immobilisation procedures |
| **Study topic/focus** | |
| Distribution | Presence-absence and occurrence surveys |
| Population | Abundance, density, population trends |
| Demographics | Group size, group composition, sex ratios, age classes |
| Mortality | Numbers and causes |
| Physiology | Organism and body part functioning |
| Reproduction | Litter size, gestation period, birth interval |
| Feeding ecology | Diet composition, preferences, hunting |
| Spatial ecology | Home range size, movements, habitat selection |
| Behaviour | Communication, activity budgets, behaviour patterns |
| Interactions | Inter- and intra-specific interactions |
| Genetics | Genetic relatedness, population genetics, heredity |
| Disease | Parasites, pathogens, clinical manifestation |
| Human-carnivore interactions | Conflict, tourism, fences, trophy hunting, utilisation |
| Management | Population control, translocation, policies |
| Immobilisation/Anaesthesia | Darting and restraint methods, testing of immobilisation technology and chemicals |
| Other | Any other contents not fitting the above categories |

broad themes nor specific topics were mutually exclusive. In case of any uncertainty during literature categorisation, we used a double-observer rule for theme and content decisions.

For each reference, we extracted information about the focal species, the year(s) of data collection, geographic details, land tenure and land use information provided for the study area, as well as the specific data contained, such as any empirical information presented about carnivore group size, group composition, home range size etc. (Table 1). Finally, each document's reference list/bibliography was scanned to identify additional research items of interest.

We summarised results by the number of relevant, non-duplicate references (i.e., unique research items), rather than by the number of original studies because several long-term studies resulted in multiple publications with different study foci, results, and analyses. Furthermore, some publications contained cross-sections of the data and results obtained from multiple studies. We employed mainly descriptive statistics to analyse spatial, temporal, authorship and content patterns and trends. Since data categories were not mutually exclusive, for example a study being carried out across more than one land tenure category, the sum of relative proportions presented may exceed 100%. Results were temporally binned by decade, using the year(s) of data collection for categorisation, as opposed to publication date. Studies that spanned multiple decades were included in each. We sourced average adult female body mass estimates of the focal species from Skinner and Chimbimba (2005) and Estes (1991) using estimates from study sites nearest to ENP. We processed and analysed data with Microsoft Excel, JMP Pro v15 (SAS Institute Inc. 2020) and R v4.0.2 (R Core Team 2020).

## RESULTS

### Overview: effort and valuable references

Our initial search yielded 664 carnivore-related documents for assessment, of which 375 were screened for eligibility. A total of 139 (37.1%) documents met the selection criteria and were included in the synthesis (Figure 2, Appendix 2 and Appendix 3). As a key product of this work, we created a digital, annotated bibliography of the final 139 references (Appendix 2), containing publication details as well as the information on broad study themes and specific topics, the focal species studied, study duration, and study area. Since about half of all full texts are not freely available online (n = 70; 50.4%), the bibliography also contains details of where these items can be sourced.

We found 13 references (9.4%) that were included but reported insufficient detail on the dates of data collection. Similarly, 49 references (35.3%) reported only a vague description of the study area such as "*Etosha National Park*", without providing further detail on specific locations or sample origin. One reference reported results for "*hyaena*", without providing clarity which species was studied. This reference was, therefore, excluded from species-specific analyses. Except for two references (1.4%) that were published in German, all materials included in the final analyses were published in English. In addition to focusing on at least one of our ten species of interest, three references also presented results on aardwolf (*Proteles cristata*), and one reference bat-eared fox (*Otocyon megalotis*), Cape fox (*Vulpes chama*), and African wild cat (*Felis silvestris*), respectively.

### Temporal distribution and authorship

The carnivore documents we assessed dated back into the 1910s, with some reported contents extending into the late 19th century. However, structured carnivore research in the greater Etosha landscape only commenced during the second half of the 20th century (Figure 2). We found a clear increase in research output beginning in the 1960s, with a peak in the 1980s, followed by a subsequent decline from the 1990s until present (Figures 3a and 3b). There were 21 references (15.1%) reporting research results based on data collected for 10 years or longer, predominantly during the 1960s-1990s. A total of 288 authors contributed to the 139 references, with ENP staff Philip Stander (n = 23, 16.5%) and Hu Berry (n = 15, 10.8%) contributing to most references overall. Another three independent researchers each contributed to 8-11 references respectively, equivalent of > 5% of all references. The majority of authors (n = 258, 89.6%) contributed to one or two references. Overall, first authorship was approximately even between government employees (n = 66, 47.5%) and external researchers (n = 71, 51.1%) but relative contributions varied strongly over time (Figure 3a). Whilst first authorship could not be ascertained for two items (1.4%), government-employed researchers (Ministry of Environment, Forestry and Tourism including EEI staff) led carnivore publications for three decades (1960s-1980s). This trend reversed post-independence (1991) with external researchers gradually replacing them as lead authors, and most recently appearing as first authors on > 90% carnivore references (Figure 3a). Of the 139 references, 72 (51.8%) were peer-reviewed research articles and book chapters, 61 were grey literature (43.9%), whilst the remaining six (4.3%) were academic theses (Figure 3b). The latter contributed least to overall research output in terms of absolute numbers, but not necessarily in terms of the knowledge gained.

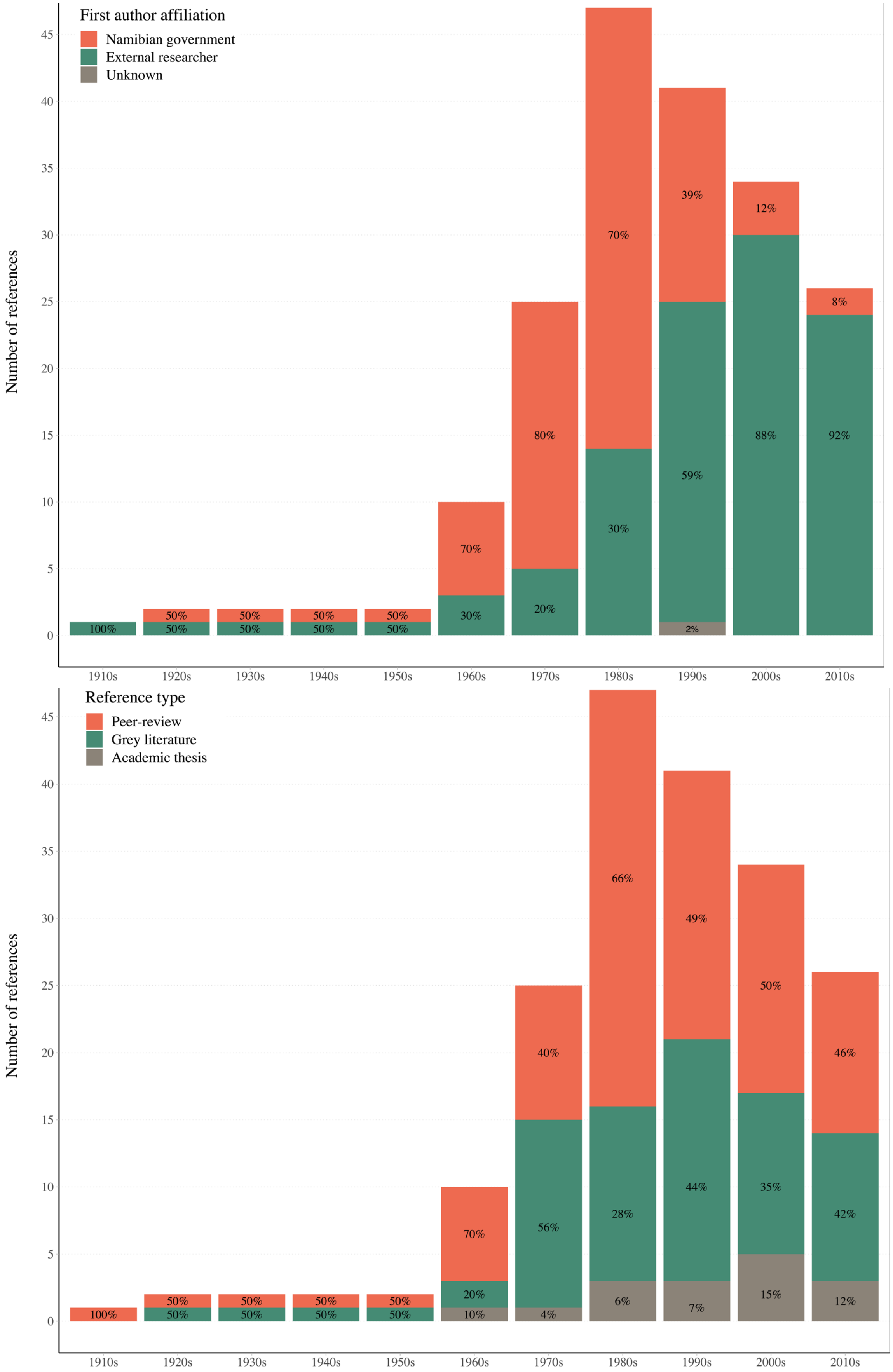


***Figure 3:*** *Temporal distribution of research reference first author affiliations between 1910 and 2010 (3a; top) and reference types during the same period (3b; bottom). The results demonstrate an increasing trend in carnivore research between the 1960s and 1990s, with a peak in the 1980s and a subsequent decline until present. The leading role of Namibian government researchers in carnivore publications reversed post-independence, gradually being replaced by external researchers (3b). Academic studies became more prevalent since the 1980s, coinciding with a substantial and continuous decrease in peer-reviewed publications and growing contribution of grey literature publication formats (3b).*

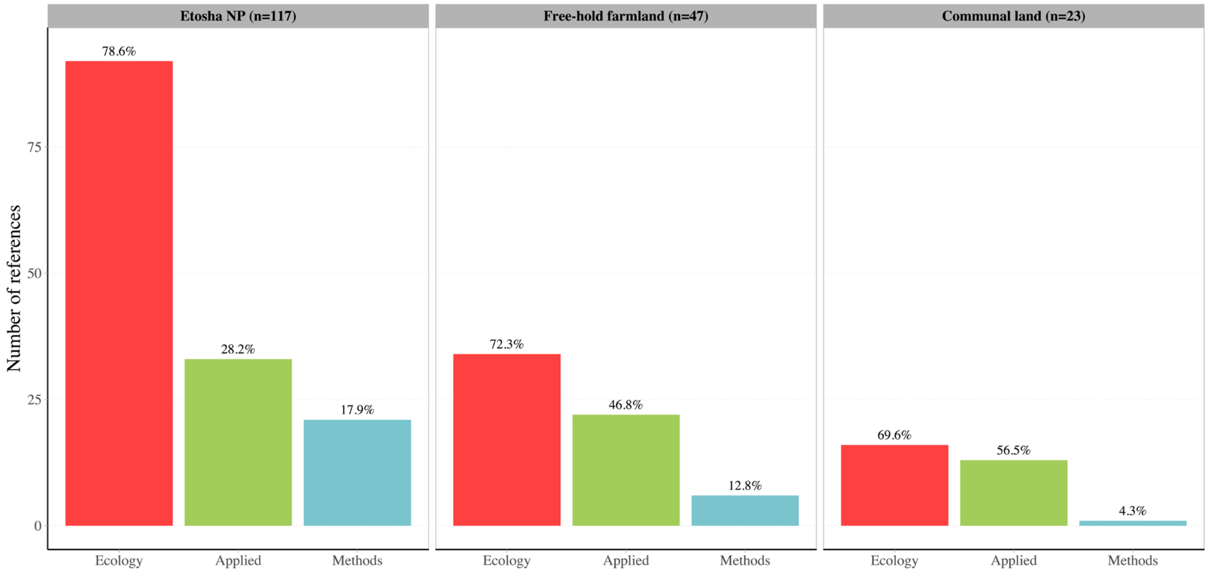


***Figure 4:*** *Graph showing the relative contribution of different study themes to all publications across the three main land tenure systems. Proportions reveal a clear prevalence of ecology studies across all land tenures and a strong overall bias toward studies being carried out in Etosha NP. Theme categories were not mutually exclusive; each reference could qualify for multiple categories. Thus, the sum of relative proportions may exceed 100%.*

## Spatial distribution and research themes

Although the three main land tenure systems contributed to the focus area almost equally in terms of area (Figure 1), there was a significant bias ($\chi^2 = 77.268$, $p < 0.00001$) toward carnivore research inside ENP (n = 117, 84.2%), followed by private, free-hold farmland references (n = 47, 33.8%), and lastly communal lands (n = 23, 16.5%, Figure 2 & 4). The bias toward the protected area held true for all ten focal carnivore species (Figure 5). Irrespective of land tenure, there was also a clear, significant bias in terms of broad research themes ($\chi^2 = 67.098$, $p < 0.00001$), with references predominantly comprising of ecology studies (n = 107, 77.0%), whereas only 44 references (31.7%) contained a focus on applied carnivore management, and 21 references (15.1%) included a methods component (Figures 2 & 4). Ecology was the dominant broad theme for any of the focal species, with a minimum relative contribution of 66.7% for caracal and, in some cases featuring as a focus in 100% of references (for serval and honey badger, Figure 5). Conversely, methods references consistently had the lowest contribution to research output per species (< 10%) and four species (brown hyaena, honey badger, caracal, and serval) had no references entailing a methods development component (Figure 5). Most references (n = 110, 79.1%) dealt with a single research theme, whilst 25 references (18.0%) had a dual theme focus, and four references (2.9%) covered all three research themes. Influenced by several human-carnivore conflict studies outside ENP, the relative proportion of applied management studies was considerably higher on private, free-hold farmlands (46.8%) and highest in communal lands (56.5%, Figure 4). Methods studies predominantly occurred in ENP (Figure 4), with a particular focus on lion and African wild dog (Figure 5), and mainly including population control via contraception (lion) and the development of chemical immobilisation procedures. Methods references had a higher relative contribution on private, free-hold farmlands when compared with communal areas (Figure 4). Large-bodied carnivores generally had a higher proportion of applied studies, although this was not apparent for the spotted hyaena (Figure 5). Caracal and black-backed jackal had the highest proportions of applied references amongst the medium-sized carnivores.

## Species and study topics

There was a strong bias in terms of species coverage in carnivore research (Figure 6). Overall, the majority of references (n = 97, 69.8%) focussed on a single species only, 11 references (7.9%) focussed on two species, and 31 (22.3%) focussed on three or more species simultaneously. The most common combination of any two species was lion-spotted hyaena (n = 29, Appendix 2). Research predominantly focussed on large-bodied carnivores, with at least one of the six species featuring as the focal species in 128 (92.1%) of all references (Appendix 2). A Spearman's rank correlation analysis revealed a significant association between species' average adult female body mass and relative contribution to all references ($S = 61.686$, $R_{ho} = 0.626$, $p = 0.0263$, $n = 10$), suggesting that research focus was indeed biased toward the larger, charismatic species. This bias was mainly driven by

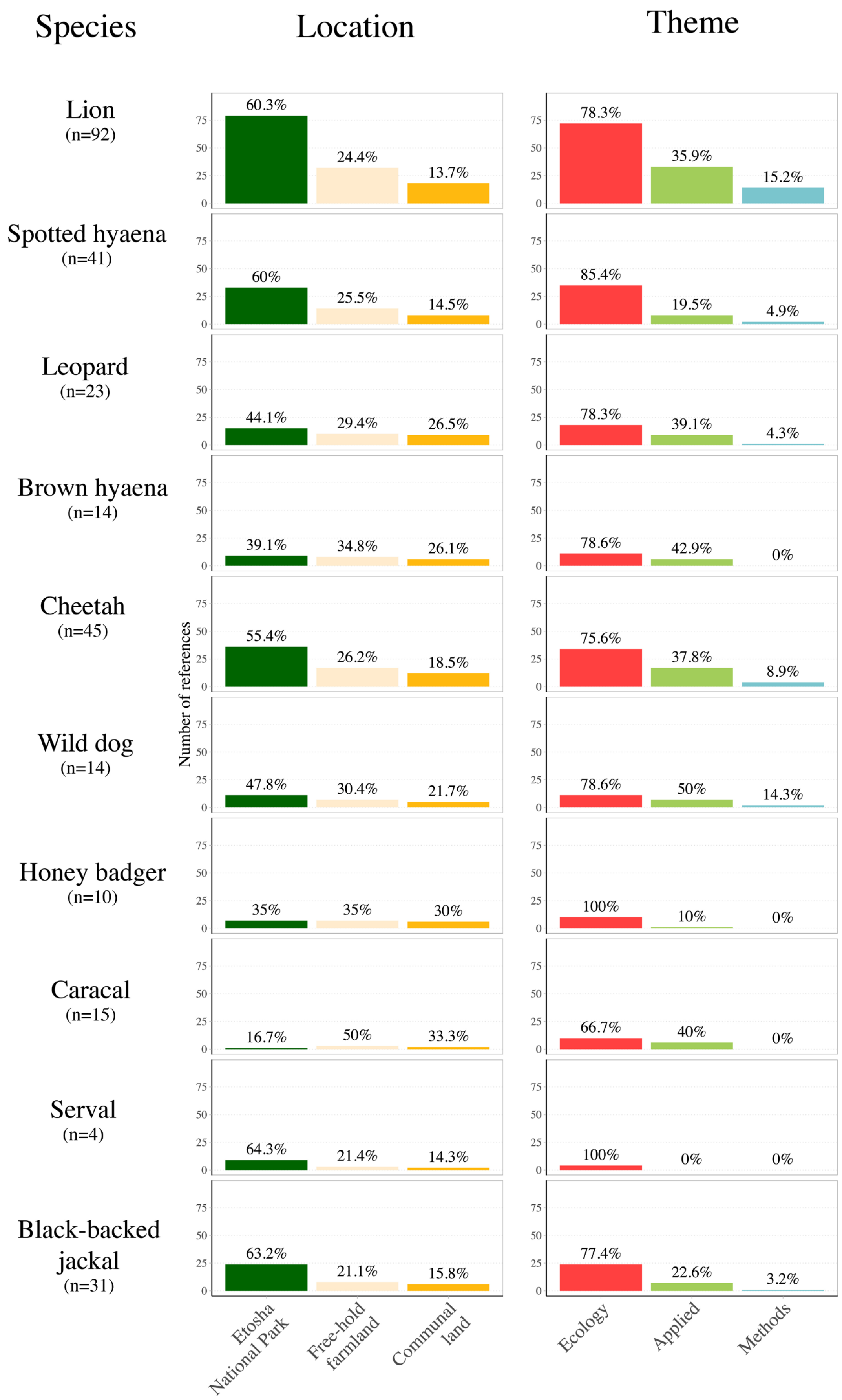


***Figure 5:*** *Relative proportions of references for the three main study themes and different land tenures for each carnivore species. Panels are scaled to the number of references. Neither broad research theme nor land tenure categories were mutually exclusive and, thus, the sum of relative proportions may exceed 100%.*

a strong research focus on lion, which was a focal species in 92 references (66.2%), thus featuring more than twice as often as any other carnivore, followed by cheetah (n = 45, 32.4%), and spotted hyaena (n = 41, 29.5%, Figure 5). Of the larger carnivores, brown hyaena and African wild dog were least studied, with 14 references each (10.1%, Figure 5). The most commonly studied medium-sized carnivore, and fourth most studied species overall, was black-backed jackal with a total of 31 references (22.3%, Figure 5). The other six species each featured in < 17% of references, with serval having the lowest representation of 2.9% (n = 4). Other medium-sized carnivores, such as caracal and honey badger, only appeared in 15 references (10.8%) or less (Figure 5).

We identified 15 main topics in the carnivore research literature (Table 1) and 52 references (37.4%) focussed on a single research topic, 43 (30.9%) contained two topics, 19 (13.7%) covered three topics simultaneously, with the remainder of references (n = 25, 18.0%) addressing four topics or more. Lion, cheetah, and spotted hyaena were the only species with references containing results on all topics, and despite its current absence from the region of interest, African wild dog references covered all topics but one (i.e., reproduction, Figure 6). Our species-topic matrix revealed largest research gaps for leopard and brown hyaena as well as the four medium-sized species, of which black-backed jackal had the broadest topic coverage (Figure 6).

Historically, there has been a clear bias toward species distribution, population size and human-carnivore interaction studies, whereas more recently evolved fields of research inquiry and topics requiring sophisticated analytical methods such as genetics, physiology, reproduction, and guild

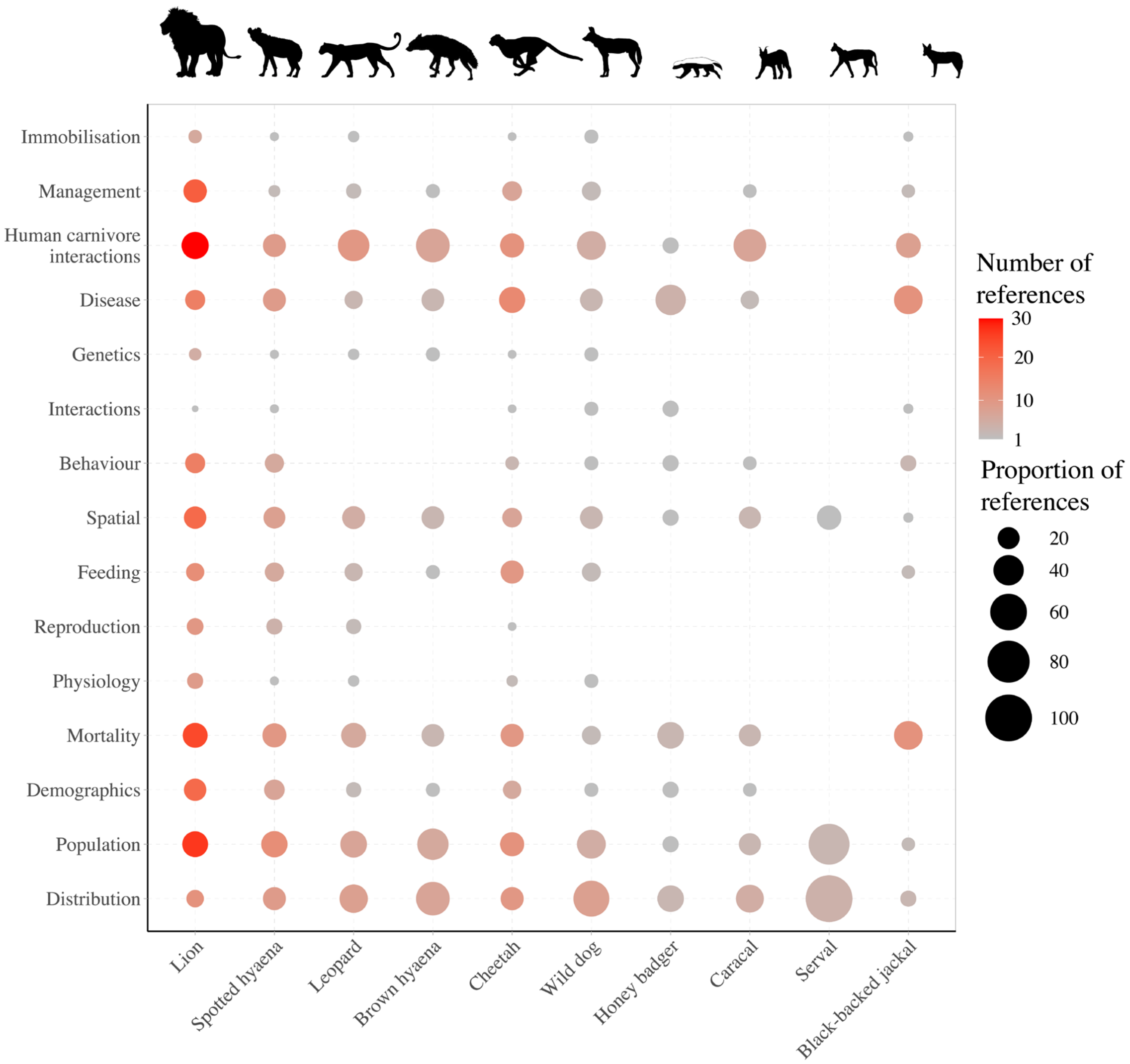


***Figure 6****: Matrix showing the relative distribution of specific study topics across all species and their relative contribution to all references for each species. Node size reflects the relative proportion each topic contributes to all references for each species whilst colour intensity signifies the number of references available for each species-topic node. Topic categories were not mutually exclusive; each reference could qualify for multiple categories. Thus, the sum of relative proportions may exceed 100%.*

interactions have received much less attention (Figure 6). Except for lion and spotted hyaena, very little is known about the detailed demographics of carnivores in this landscape, and their behaviours (Figure 6). Carnivore occurrence, abundance (also local density) and movements were the only topics studied across all ten focal species, followed by mortality investigations, conflict surveys, and disease topics (Figure 6). The most frequently studied diseases were anthrax, feline immunodeficiency virus, and rabies (Appendix 2). Conflict studies often were descriptive, including investigations into livestock predation incidence, human perceptions of carnivores and evaluation of specific conflict management approaches such as the efficacy of translocations (Appendix 2). Human-carnivore interaction topics (n = 25) almost exclusively focussed on the damage caused by carnivores outside ENP (92%), particularly lion, with very little attention given to the values or benefits derived from carnivores in this landscape (16%). Methods studies were dominated by the development of chemical immobilisation procedures and contraception (Appendix 2).

## DISCUSSION

The creation of an annotated digital bibliography of 139 key references applicable to carnivore research in the greater Etosha landscape has provided a good foundation to enable users to conduct literature searches, identify research gaps and prioritise future research directions. All key references, including those formerly in paper format, have been digitised and are available in a standardised format. This adds value in facilitating and improving accessibility, dissemination and safe keeping of records in a centralised repository at the EEI. We are confident that the synthesis and analyses of available materials were rigorous enough to the extent that the observed patterns and interpretation thereof yield an accurate reflection of the long-term trends in carnivore research.

The establishment of a permanent research section in 1965, which consisted of a veterinarian and two biologists, followed by the formal opening of the EEI in 1974 (Berry 1997) contributed greatly to stimulating carnivore research in ENP. Multiple factors, including an emphasis on focal species research by individual government-employed researchers dedicated to carnivore research were responsible for the observed increase in research output during the 1960s and 1980s (Figure 3a). Importantly, during the latter period, government-employed researchers were actively encouraged to register for postgraduate degrees at Tertiary Institutions, which promoted collaborative research projects and increased output of peer-reviewed publications. Notably, the majority of peer-reviewed publications on carnivores could be attributed to only two government deployed researchers. The 1990s heralded a period of significant transition when Namibia gained its independence. Subsequently, staff re-structures, accelerated turnovers in staff, coupled with a diversification of research priorities were contributing factors to the observed decline in peer-reviewed publications by government-employed researchers specifically (Figure 3b). The decline in output, with a noticeable lag, was also evident amongst external researchers. Irrespective of author affiliation, the temporal decline in research output is continuing.

In general, the decline in research output over time, combined with a paucity of studies in communities surrounding ENP, calls for a need to initiate and expand research activities to communal and private lands. Taking cognisance of the larger human multiple-use system, such studies would cement the role of ENP, both as source of, and a safeguard for, carnivore populations, whilst also determining its importance in providing functional connectivity with other carnivore habitats in the geographic region. Etosha, as a National Park and important carnivore refuge, hosts a large diversity and abundance of carnivores. Therefore, the main functions and priorities of government-employed researchers were aligned to support research and monitoring programmes within the boundaries of ENP. This is evident from the study distribution pattern we found (Figure 4), which clearly illustrates a bias towards work within ENP boundaries as opposed to private and communal lands where most studies were restricted to conflict assessments.

The long-term trends and patterns across themes, species, and study topics (Figures 5 and 6) indeed correspond with global carnivore research patterns (Brooke *et al*. 2014). In southern Africa, ENP is the most important formal conservation area for carnivores in a semi-arid ecosystem. Although challenging, opportunities do exist and should be actively pursued to improve the functional connectivity of the greater Etosha landscape with other conservation areas located to the West and to the North-West into Angola, such as Iona NP. If this can be realised, the resultant joint management of resources across the existing boundary of ENP, would have a beneficial impact on carnivore conservation. The strong historic focus on a few charismatic large-bodied species, with particular emphasis on lion, likely reflects their public appeal and their immediate relevance for park management in terms of tourism value, impact on other species and, not least, conflict implications (Figure 5). Large species are also easier studied than cryptic smaller ones and usually attract more funding for research.

Our results provided a valuable platform to identify and highlight selected gaps in our current knowledge of carnivores in the greater Etosha landscape. Our main purpose in elucidating these is to provide the stimulus to promote and sustain long-term research across this area. Future research foci may, for instance, include:

a) Identifying and quantifying both the ultimate and proximate drivers of carnivore fitness in this landscape, in terms of distribution and abundance, to ensure long-term species persistence.
b) Although 27 disease studies have already been published, some of which ranged among the longest carnivore studies ever conducted in ENP, and more are currently underway, their emphasis was mostly on the prevalence and clinical manifestation of three diseases: rabies, anthrax, and feline immunodeficiency virus. Given an intensifying interface between wildlife, people, and domestic animals world-wide, disease studies may expand to include the role of carnivores and their parasites as disease reservoirs and vectors. Such studies would also help with disentangling the complex effects of changing habitats and climate on disease incidence and prevalence.
c) To date, carnivore studies in the greater Etosha landscape have largely been of descriptive nature, and with a general focus on ecology and natural history, especially occurrence, abundance, diet, and movements patterns. Considering the complex challenges that protected areas and carnivores face (Ministry of Environment and Tourism 2015, Di Minin *et al.* 2016), it is expected that mechanistic and predictive studies will play a more prominent role in future, along with the increasing application of sophisticated methods such as conservation genetics.
d) Currently, very little is known about carnivore physiology, behaviour, and communication, for instance, and how these might influence, or be influenced by, intra-guild processes. An increasing appreciation of the trophic complexity of carnivore landscapes (Montgomery *et al.* 2019) further suggests that future research should focus more on animal-environment interactions as well as trophic dynamics. Accordingly, greater importance should be placed on studying intra-specific and intra-guild interactions including both apex and meso-predators.
e) A progression from simply documenting and describing carnivore impacts on land users around ENP to strategic, experimental testing of human-livestock-carnivore coexistence strategies (van Eeden *et al.* 2018) that acknowledge the dynamics and complexity of conflict. This also reflects the need to incorporate detailed information on livestock, stimulating a more holistic approach to conflict investigations (Weise *et al.* 2019).
f) Considering the economic importance of carnivores for eco-tourism in southern Africa (Maciejewski & Kerley 2014, Van Der Meer *et al.* 2016), current research should be expanded to include positive and negative influences of tourism and other forms of commercial land use on carnivores and their management. Such studies should extend beyond ENP boundaries to represent the variety of stakeholders that benefit or accrue costs from carnivores, such as human settlements with livestock holdings, private tourism reserves and communal conservancies, or livestock and game ranches. Similarly, anthropogenic influences on carnivores and their habitat associated with tourism, such as the development of artificial waterholes and fencing deserve greater research attention.

However, none of the above-mentioned suggestions should occur at the expense of detailed biological investigations and natural history research, as these form the foundation of our understanding of how carnivores utilise their environment and adapt to special circumstances. We also regard the importance of long-term research as a crucial prerequisite for addressing these knowledge gaps. Long-term ecological studies contribute to an understanding of how species and ecosystems respond to a spatially and temporally changing environment. Studies conducted over prolonged time periods can reveal important patterns and provide insights into ecological processes that would otherwise go unnoticed (Hughes 2013, Taig-Johnston *et al.* 2017, Melzheimer *et al.* 2018). In reference to the long-term anthrax research programme in ENP, Carlson *et al.* (2018), illustrated the importance of an interdisciplinary approach where key advances have been made in exemplifying the complexities of the enzootic process. Lindenmayer *et al.* (2012) identified five key values of long-term ecological studies, which are:

“(1) quantifying ecological responses to drivers of ecosystem change;
(2) understanding complex ecosystem processes that occur over prolonged periods;
(3) providing core ecological data that may be used to develop theoretical ecological models and to parameterise and validate simulation models;
(4) acting as platforms for collaborative studies, thus promoting multidisciplinary research; and
(5) providing data and understanding at scales relevant to management, and hence critically supporting evidence-based policy, decision making and the management of ecosystems”.

In recognition of the value of an interdisciplinary approach (Carlson *et al.* 2018) as well as applying the key values identified by Lindenmayer *et al.* (2012), we believe that a long-term carnivore research programme in the greater Etosha landscape should be implemented and encouraged. The management of such an initiative, where data are gathered on a variety of topics by different institutions over decades, is challenging. Both private and government institutions thus play a crucial role in leading and coordinating research effort, in fostering collaborations, in archiving the data collected, in synchronising efforts across time and organisations, and in providing directions for future research. Given the global importance of Etosha as a carnivore stronghold, Namibia, through the EEI, is ideally placed to stimulate, facilitate, and strengthen long-term carnivore studies in collaboration with local and international partners.

The scope and focus of this synthesis should further be expanded by consolidating information from literature sources with the great number of raw data accounts, many of which have yet to be analysed and published, that different organisations have gathered for future in-depth meta-analyses. Detailed topic- and species-specific reviews of the existing contents and results would provide additional important insight into the current state of knowledge.

In conclusion, we encourage similar stocktaking and synthesis exercises for other biological taxa and research topics with a long research history in ENP, as well as for other similarly important carnivore strongholds with historical data such as the Serengeti NP in Tanzania, or Kruger NP in South Africa. Specifically, with regards ENP, the EEI archives hold a tremendous amount of environmental information that extends far beyond the field of carnivore research, some of which has yet to be analysed comprehensively. Preserving this existing knowledge and merging it with information gathered by other organisations is a priority. No less important is to ensure that the information is readily available, which provides prospective studies with a comprehensive overview of historical work conducted. It also enables a rare and valuable perspective on how changes have occurred in this landscape for carnivores, and the ecosystem with all its components. Ultimately, this could drive the identification and prioritisation of future studies.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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# *Euryops walterorum*, a declining restricted-range endemic of the Greater Gamsberg

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*This paper is dedicated to the memory of Dr Thorsten Neckel, astronomer, friend, father and inspirer of this long-term initiative to monitor the population of one of Namibia's very special endemic species on the Greater Gamsberg. Dr Neckel passed away on 8th August 2020.*

## ABSTRACT

*Euryops walterorum* is a perennial shrub, endemic to an extremely limited habitat on the plateau of the Greater Gamsberg. The population of this endemic has been shown to be in decline since the early 1980s. The Gamsberg plateau is identified as one of the world's best astronomical observatory sites and has been used as an astronomical base since 1971. Due to its position and favourable atmospheric conditions, the establishment of the Africa Millimetre Telescope is planned here. This development may adversely affect the population of *Euryops walterorum*. In this paper we present information on the ecology and habitat of this plant. We also speculate on possible reasons for the population's decline. Based on this, we propose a long-term monitoring programme on the population health of this restricted-range endemic, as well as further measures for the conservation of the species. Preliminary results from the initial survey show the population stands in their habitat are unevenly distributed and most monitoring plots contained about two plants or less, and many had none. From the current plot data, the estimated total number of mature plants on the plateau was calculated to be about 22 000. Based on the observed reduction in population, as well as both the extremely small Extent of Occurrence and Area of Occupation, the conservation status of the species has been reassessed following IUCN Red List Criteria, and found to be Critically Endangered B1 ab(iii,iv) + 2ab(iii,v).

**Keywords:** endemic plant; conservation status; *Euryops walterorum*; Gamsberg; monitoring; Namibia; restricted range

## INTRODUCTION

At an altitude of 2 347 m, the Greater Gamsberg (Figure 1) is one of the famous landmarks of Namibia. It is located at the edge of the Namib Desert in the Khomas Highland, about 120 km southwest of Windhoek. The plateau harbours a very special plant which, due to the seclusion of the mountain, few people have ever seen: *Euryops walterorum* Merxm. (Figures 2a and 2b). This species is a restricted-range endemic to the Gamsberg plateau (Nordenstam 1966, 1968, Loots 2005). The plateau covers an area of about 220 hectares (Carr & Strohbach 2019, Strohbach 2021), making this an extremely limited habitat. Because of the unique species composition and dominance by *Euryops walterorum*, Strohbach (2021) described the vegetation of the plateau as a unique vegetation association, being the *Digitario erianthae–Euryopietum walterorum.* This association is characterised by the presence of *Panicum lanipes, Euryops walterorum, Eriospermum bakerianum* subsp. *bakerianum, Hypertelis salsoloides, Boophone disticha, Eragrostis nindensis* and *Digitaria eriantha*.

The first herbarium specimens were collected in 1891 by Fleck, followed by Schwerdtfeger in 1953, Merxmüller in 1957 and Nordenstam in 1963 (Nordenstam 1968). Merxmüller described it as a new species in 1955 and named it after the botanists Prof. H. and his wife Dr E. Walter (Giess 1984). In 1963, *E. walterorum* grew in abundance on the stony, flat plateau (Nordenstam 1968), but Giess (1984) observed a severe decline of about 75% of the population in 1983.

Due to its altitude, the dry and clear atmosphere, the very dark night sky and excellent astronomical observation results, the Gamsberg plateau is identified as one of the world's best observatory sites and an astronomical station was built on it after the plateau was bought by the Max Planck Society in 1970 (Elsässer 1989). In 2017, the Netherlands's Radboud University pronounced its intention to construct the planned Africa Millimetre Telescope (AMT) on the Gamsberg plateau (Falcke 2020). Since January 2019, access to the plateau has been restricted only to Max Planck Society partners and

***Figure 1**: The north-western aspect of the Greater Gamsberg. The plateau is the habitat of the endemic shrub* Euryops walterorum*. Towards the left margin of the image, the Lesser Gamsberg with its tiny plateau is visible.*

closed to the public (Lemke 2019). Comments on the Environmental Impact Assessment for the proposed establishment of the AMT on Gamsberg were made as part of an Environmental Impact Assessment feedback session in January 2019 at the Namibian Scientific Society in Windhoek. At this meeting, the need for protecting the species from the construction work was stressed and an alternative AMT site was proposed on a different plateau area outside that of the *E. walterorum*'s habitat. A botanical specialist study is part of the EIA, has highlighted the threat to the *E. walterorum* population and made management recommendations. This includes the search for alternative sites.

However, the apparent long-term decline of this limited population and the added pressure that the proposed AMT project will impose, warranted further investigation of the ecology and population dynamics of *E. walterorum*. As a means of obtaining baseline data for this species, studying population dynamics and exploring population trends over time, the National Botanical Research Institute initiated a long-term monitoring project, in cooperation with the Namibia University of Science and Technology (Carr & Strohbach 2019).

## *EURYOPS WALTERORUM* IN A PORTRAIT

*Euryops walterorum* is one of about 100 *Euryops* species, which mostly occur in Africa, with two species known from the Arabian Peninsula (Ali *et al.* 2016). Most species are confined to southern Africa (Devos *et al.* 2010). The genus *Euryops* in Namibia is common in the southern part of the country, where it is mainly restricted to higher mountainous regions (Nordenstam 1969).

A full description of the species was provided by Suessenguth & Merxmüller (1958) and Nordenstam (1968). *Euryops walterorum* is described as a vigorous glabrous shrub without a subterranean caudex, moderately branching from the base, with erect or ascending branches (Figure 2a). The flowering period with lots of yellow capitula (Figure 2b) starts in mid-winter, generally in July, during the dry period.

Based on morphological characteristics, *Euryops walterorum* seems closely related to *E. lateriflorus*, *E. sulcatus*, *E. ciliatus* and *E. empetrifolius*, the last three of which also have ciliolate leaf-margins. The closest relative appears to be *E. empetrifolius*, which likewise has discoid or shortly radiate capitula. *Euryops walterorum* differs from the latter species mainly by its bigger capitula and larger leaves (Nordenstam 1968). No genetic evidence is available to substantiate these observations, though (Devos *et al.* 2010).

### Evolution and endemism in the context of the prehistoric formation of the Greater Gamsberg Mountain plateau

As *E. walterorum* is found only on the Greater Gamsberg plateau (Nordenstam 1968), the question of its origin comes into focus. The endemism can be explained by an insight into the geological formation of the Gamsberg. The present-day Gamsberg formed on intrusive granites, which formed on the southern

***Figure 2a:*** *(left) A mature individual of* Euryops walterorum *in February 2020.* ***Figure 2b:*** *(right)* Euryops walterorum *with buds and capitula (flowerheads) in July 1995.*

edge of the Damara Orogen. Uplift of this orogen formed a high plateau, which was systematically eroded until only the granites remained. Throughout the Karoo sedimentation, this massif remained an island, only to be covered by sands later during the Karoo sedimentation period (Schneider 2004). These sands were partially blown together to form dunes or washed into shallow depressions about 130 million years ago. This wide, sandy plain was not much higher than the sea level at that time, far from its present height (Wittig pers. com. 2020). This is shown by angular holes, up to five cm in size, in the Gamsberg quartzite: Judging by cast rubber fillings, these holes originate from weathered gypsum roses from that period and indicate brackish water (Wittig 1976). At roughly the same time, the African continent began to separate from the South American part of the Gondwana supercontinent. This break-up resulted in the upliftment of the southern African subcontinent through tectonic effects which led to the formation of the Great Escarpment, also in Namibia (Schneider 2004). Over time, the sands solidified into hard quartzite layers forming large table mountains (Schalk 1983). These included the Mount Etjo and Waterberg further north, with the Gamsberg plateau forming an isolated, southernmost occurrence of the Etjo Sandstone (Schneider 2004). By gradually breaking off at the edges (Figure 3a), erosion changed the shape of the table mountains (Schalk 1983) and split the Lesser Gamsberg from the early Gamsberg plateau (Schneider 2004). It is still clearly visible that the same plateau once covered both mountains if observed from a distance (Wittig pers. com. 2020) (Figure 3b).

Nordenstam (1969) regarded the genus *Euryops* as an old and widespread member of the African flora, which differentiated in the Paleogene, about 66 million to 23 million years ago. Recent genetic investigations estimate that differentiation between different clades and species of this genus started some 39 million years ago (Devos *et al.* 2010). This implies that the predecessor to the genus *Euryops* likely already populated the former Gamsberg area during the formation of the Great Escarpment. Through erosion, this population became isolated from other populations further south, and started evolving to the present-day restricted-range endemic species. Unfortunately, *E. walterorum* has not been included in any phylogenetic studies yet (cf. Devos *et al.* 2010, Ali *et al.* 2016), thus its evolutionary history remains unclear. As the Gamsberg plateau was much larger once, the species may also have had a larger habitat, which possibly included the present-day Lesser Gamsberg. Today, the Lesser Gamsberg forms a small plateau remnant with an eroded, unsuitable habitat and no evidence of *E. walterorum*. It is thus likely that the species disappeared from there a long time ago.

## GROWING CONDITIONS ON THE GREATER GAMSBERG

### Climatic conditions

No weather stations have been installed on the Greater Gamsberg. This means that there are only general climatic data available for the area between the Khomas Highland and the Namib Desert (e.g. Mendelsohn *et al.* 2002). Here the mean annual precipitation is indicated as being between 200 and 250 mm, with a coefficient of variation (CV) of over 50%. Orographic effects of the high plateau are not taken into account.

The development of the CRU-TS 4.03 data set makes modelled historical climatic data available (Harris *et al.* 2014). A down-scaled version of these data, ranging from 1961 to 2018, is available for further climatic studies via the WorldClim data system (Fick & Hijmans 2017). The data have a spatial resolution of 2.5 geographical minutes, or roughly 4.2 x 4.6 km. From these data, monthly historical data have been extracted for the Gamsberg plateau, and have been used to construct climate diagrams (Figure 4). Mean annual precipitation is 287 mm, however, with a high variability (CV of 39.7%).

As the Gamsberg plateau is about 450 m higher than the ground level on the east side and about 1 100 m higher on the west side (Schalk 1983), a strong orographic effect exists. This is especially evident after good rains over consecutive days when the cool and humid plateau can be observed to be covered by clouds in the morning (Figure 5a and 5b), forming a dense fog (Figure 5c), while the sky in the vicinity of the mountain is clear and sunny. In addition, ambient temperatures on the plateau appeared to be several degrees lower compared to the surrounding plains and especially the land below the escarpment to the west. These conditions of lower temperature and higher humidity on the plateau could be a distinct advantage for *E. walterorum* to survive on the Gamsberg.

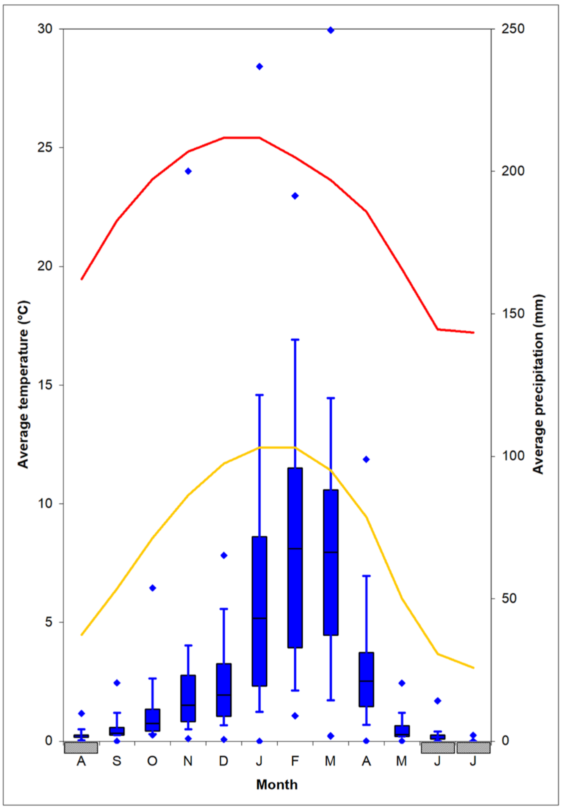

***Figure 4:*** *Climate diagram for the Gamsberg plateau, based on CRU-TS 4.03 data (1961 – 2018) from WorldClim (Fick & Hijmans 2017). Rainfall is indicated as Box-and-Whisker boxes; there the boxes represent the 2nd and 3rd quartile, and the whiskers the 10th percentile (lower whisker) and the 90th percentile (upper whisker). Absolute minimum and maximum precipitation values are indicated as diamonds. The average minimum temperature is indicated as a yellow line, the average maximum temperature as a red line. Frost can occur in the shaded months June, July and August.*

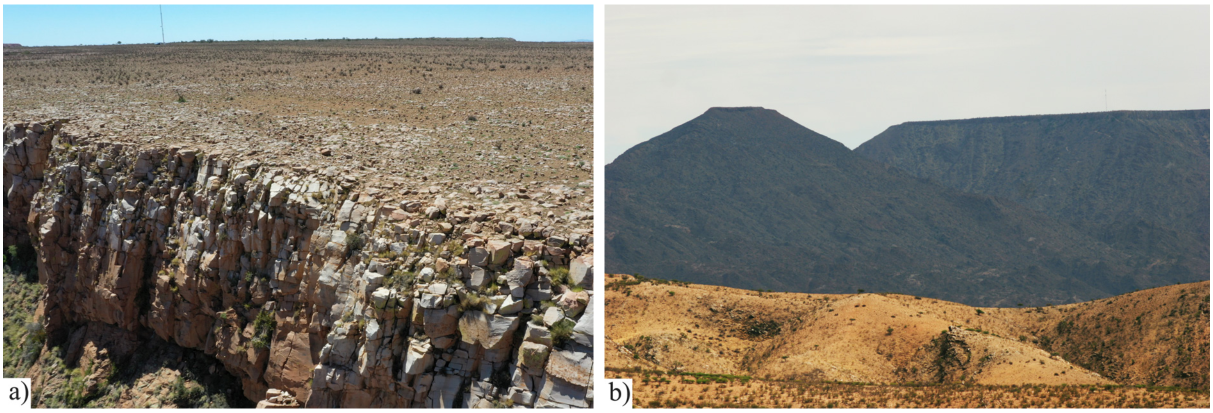

***Figure 3a:*** *(left) The Greater Gamsberg plateau with its 25 to 30 m thick quartzite layer of flat-lying rocks. The edges are eroded and have been breaking off continuously for millions of years (Schalk 1983).* ***Figure 3b****: (right) Lesser and Greater Gamsberg seen from the north east at a distance of 18 km. Both plateaus were once part of the same mountain. This is indicated by nearly the same plateau height of the Greater (2 347 m) and Lesser (2 326 m) Gamsberg (Schalk 1983).*

***Figure 5a:*** *(top left) The cloud covered plateau after exceptional rain in August 1998, seen from the plain south of the Gamsberg.* ***Figure 5b:*** *(top right) The cloudy plateau, as often seen during a good rainy season, recorded from Farm Hakos, about 18 km north east of the Gamsberg, on 1 March 2020 at 09h18. (Photo by Hakos Webcam (Straube et al. 2019)).* ***Figure 5c:*** *(bottom) Dense fog on the plateau in March 2000 enclosed and moistened* Euryops walterorum.

Additionally, casual observations showed the formation of ephemeral wetlands on the plateau. During good rainy seasons in the 1970s, large areas on the plateau were flooded by rain to form pools and puddles, with frogs and fish soon appearing. The frogs came out of cracks in the ground and the fish hatched from eggs in the soil laid by the previous generation (T. Neckel pers. com. 1994). As late as March 2000 (Figure 6a) croaking frogs could be heard from the puddles on the soaked, loamy soil of the plateau after heavy rain. These temporary wetland biotopes have probably been forming for a very long time during good rainy seasons. *Euryops walterorum* plants associated with those areas were observed to be especially lush (Figure 6b), and this points to the possibility that the species may have originated from cooler, more humid conditions.

## Observations on autecology and population dynamics

We observed the population intermittently as follows: from 1994 to 1998 on an annual basis, continuing with observations in the years 2000, 2007, 2017 as well as in 2019 and 2020. The following discussion is largely based on these observations.

The species is probably out-crossing (Nordenstam pers. com. 1998). This is confirmed as no seeds were found on shrubs flowering outside the main flowering season, whereas shrubs flowering simultaneously during the season, growing in close proximity (Figure 7), produced plentiful seeds. As many shrubs died over the last almost 50 years, the population density declined and the chances of shrubs in the surrounding area flowering at the same time became less. Additionally, flower production seemed to be minimal or entirely absent after a previously poor

***Figure 6a:*** *(left) After heavy rain in March 2000, the plateau was saturated with water and widely covered by puddles.* ***Figure 6b:*** *(right) Flooded areas in March 2000 within the habitat of* Euryops walterorum*, where plants' condition was especially good.*

rainy season. Similar patterns have been observed with e.g. *Acacia mellifera*, which also only produces viable seeds after normal or good rainy seasons (Joubert *et al.* 2013).

*Euryops walterorum* seeds and seedlings needed prolonged wet conditions during the rainy season and additional rainfall outside the rainy season for germination and establishment. Seeds germinated after three to five days on wet soil and grew quickly. Survival in their first year depended on water reserves in the soil after an adequate rainy season. This was confirmed by observations in July 1995, when, after frequent and good rainfalls until May, many new seedlings were found on the plateau. One year later, however, due to a poor following rainy season in 1996, most of these were found to be dead. From 2017 onwards seedlings were rarely found. The rainy seasons of recent years were poor, characterised by low precipitation and several weeks of dry spells between rainfall events (Figure 11a). In February 2020, after good rainfalls of December 2019 and January 2020, at least one location with some new seedlings was found. Cocoons of insects were found inside the capitula of a considerable number of *E. walterorum*, which may have played a role in the poor seed production. These insects are still to be identified.

***Figure 7:*** *During the flowering period in July 1995, yellow flowering shrubs on large expanses of the plateau indicated the extent of the* Euryops walterorum *population.*

*Euryops walterorum* was observed to be able to survive the annual dry period without damage. During a prolonged drought resulting from a delayed or insufficient rainy season, leaves became notably drier and turned to pale green or yellow. After subsequent rainfalls most terminal leaves turned green again and branch tips continued forming new ones. However, this regeneration of the foliage, observed on a regular basis in the past, appears to have diminished from 2017 onwards. Instead, there were many shrubs without leaves, or only brown leaves falling off. Many dead shrubs were still firmly anchored in the ground and may have been standing for years.

***Figure 8:*** Euryops walterorum *grew in abundance on the Gamsberg plateau in 1971. (Photo by T. Neckel).*

***Figure 9:*** *Between 1971 and 2019, large parts of the* Euryops walterorum *population have died. This photograph was taken in February 2019 at the same location with the same viewing direction as the one in Figure 8. (Photo by A. Burke).*

## Population decline

In April 1963, *E. walterorum* was found to be abundant in large patches on the plateau, although it did not cover the entire area (Nordenstam pers. com. 1998). This was verified by the astronomer Dr Thorsten Neckel in 1971 and in later years. His photograph taken from the astronomical station in 1971 (Figure 8) shows a vigorous population. Neckel found a considerable part of the population to be dead in the early 1980s (T. Neckel pers. com. 1994). Giess (1984) confirmed this when he visited the Gamsberg in 1983 and roughly estimated a decline of about 75%, as a result of the prolonged drought (Botha 1998). The population did not increase after the loss in 1983, but remained stable (T. Neckel pers. com. 1994). In 1994, Christine Treichel visited Neckel on the Gamsberg for astronomical work and was inspired by him to start her own observations on *E. walterorum* and to continue observations during visits in subsequent years. In 2017, after an absence of ten years, Treichel found an additional, large

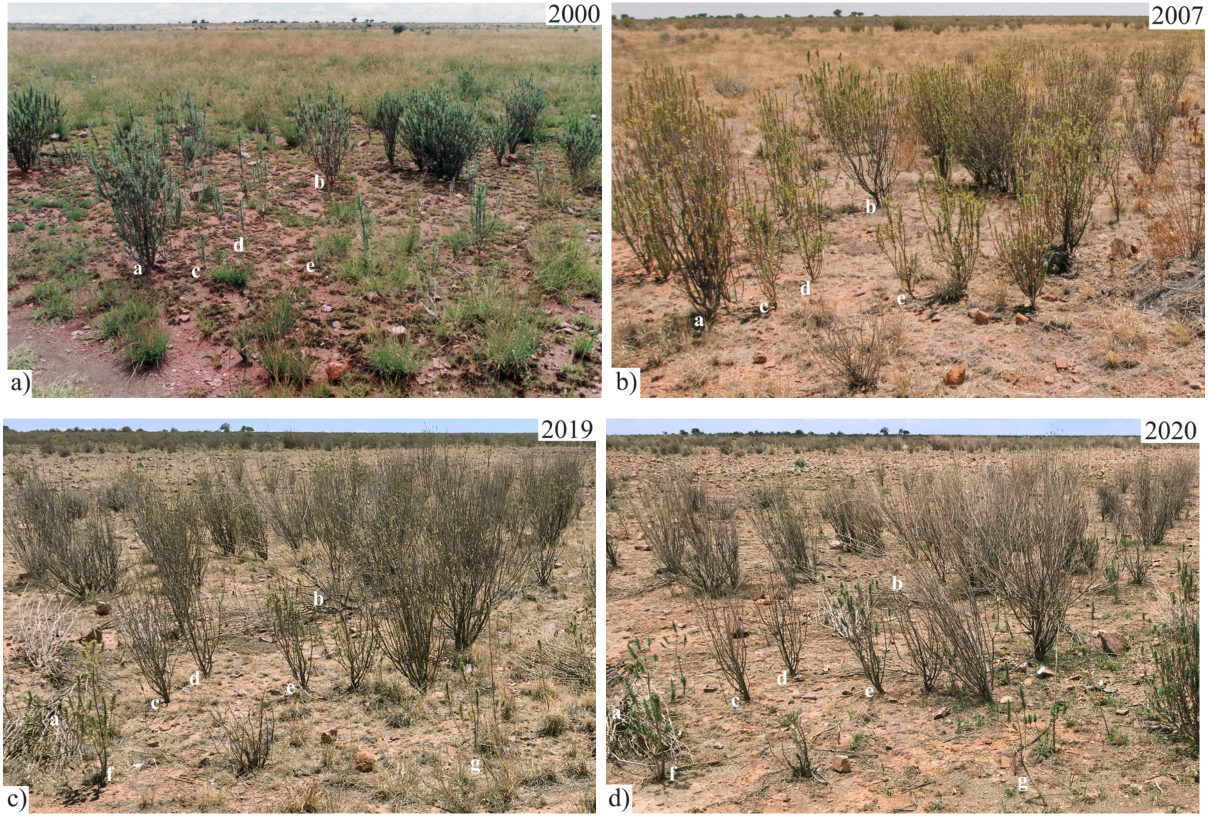

***Figure 10:*** *Repeat photograph series of* Euryops walterorum *from a fixed position over the last 20 years. (a) (top left) March 2000, (b) (top right) January 2007, (c) (bottom left) February 2019, (d) (bottom right) February 2020. For illustration, some exemplary shrubs were marked with letters on the photos: Plants a and b, which already were mature in 2000, grew by 2007, but were found to be dead and fallen over in 2019. Plants c, d and e, which were juvenile in 2000, matured by 2007, but had not significantly grown by 2019. In 2019, c and d were found to be dead whereas e was still alive in 2019 and 2020. There was some recruitment in 2019, as can be seen by markers f and g.*

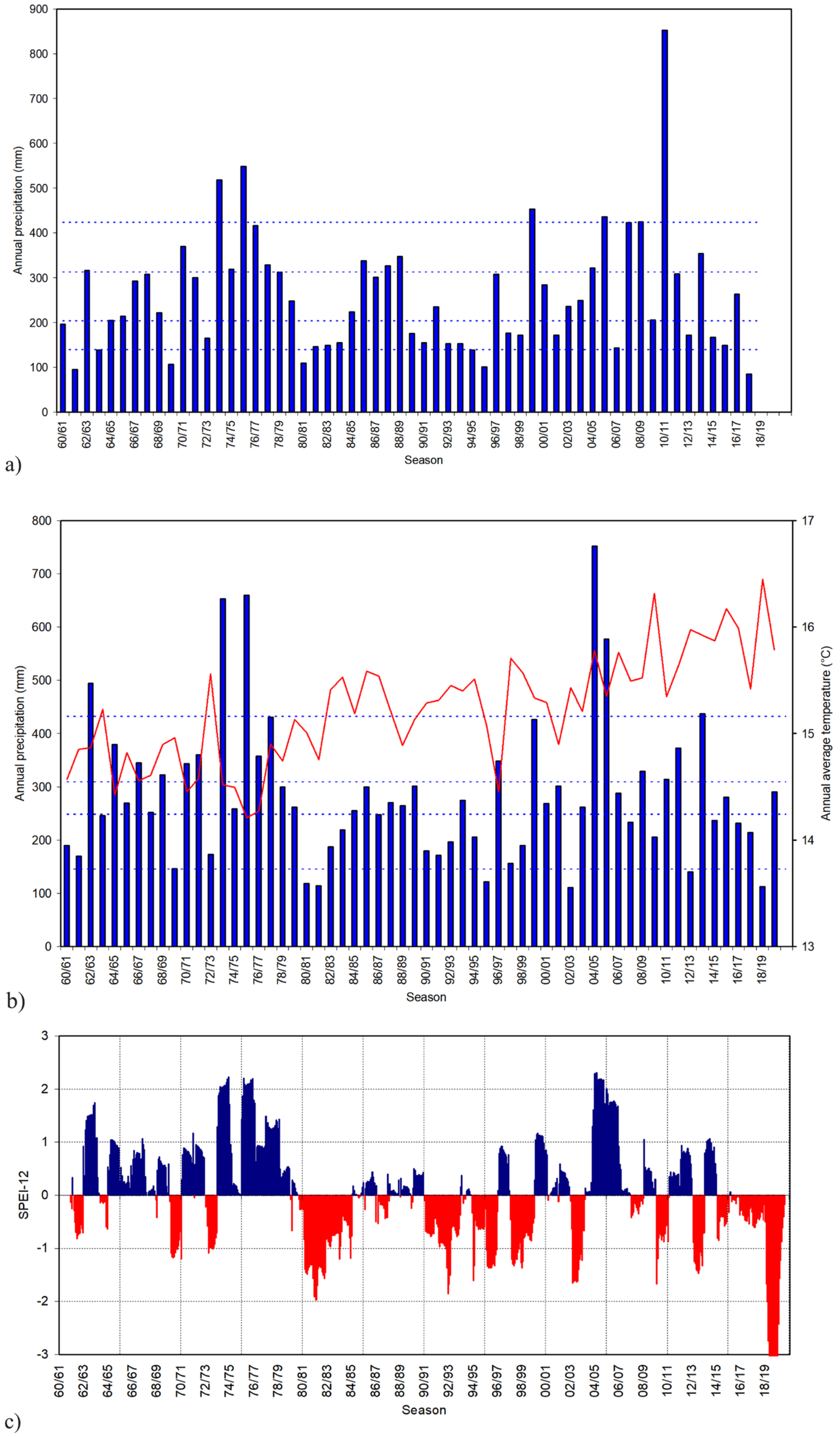

***Figure 11:*** *Long-term climatic trends for the general Gamsberg region. (a) (top): Rainfall observations at Hakos to the north east of the Gamsberg (Straube et al. 2019). This is used to verify general trends of modelled data for the Greater Gamsberg. (b) (middle) Annual rainfall (blue bars) and average annual temperatures (solid red line) for the Greater Gamsberg, based on modelled data from WorldClim and MeteoBlue. For both these graphs, the stippled lines represent the following: from the bottom: 10th percentile of long-term annual rainfall; 40th percentile, 70th percentile and 90th percentile. Seasons with less than the 10th percentile of rainfall are considered as extreme drought years, seasons with less than the 40th percentile as drought years, season with between the 40th and 70th percentile annual rainfall are considered as normal, above the 70th percentile as wet and over the 90th percentile as extreme wet (Botha 1998). (c) (bottom): SPEI index for the Greater Gamsberg, calculated from the same modelled data as used in Figure 11b. For all graphs, the annual values were calculated as seasons from August to July each year, not as calendar years.*

portion of the remaining population to have died. In 2019, this reduction was estimated to be 25% to 30% of the remaining population. In comparison to Neckel's photograph from 1971, another photograph taken in 2019 at the same location and in the same viewing direction by Burke (Figure 9), clearly shows the extent of the decline over the past almost 50 years, with the population having become thinned out and even partly disappearing from the plateau.

Repeat photographs from a fixed position, covering the years between 2000 and 2020, show the process of decline, which is prevalent on large parts of the plateau (Figure 10).

### Possible causes of the decline

The reasons for the apparent decline during the past almost 50 years are not yet understood. Beside the observations starting in 1994, satellite images and meteorological data analysed by the authors point to several possible factors that could be mutually reinforcing and may be responsible for or contributing to the perceived reduction and continuing decline. Possible reasons might be the following:

1. Giess (1984) reported a decline of 75% of the population of *E. walterorum* after the drought in the early 1980s. Based on this report, we obtained modelled historical climate data (1961 – 2018) from WorldClim (Harris *et al.* 2014, Fick & Hijmans 2017) for the Greater Gamsberg. These data were augmented with data from MeteoBlue for the 2018/19 season (meteoblue AG 2020), which is not yet included in the WorldClim data set. The WorldClim data set has a spatial resolution of 2.5 geographical minutes (roughly 4.2 x 4.6 km), whilst MeteoBlue only presents their data in a spatial resolution of 30 x 30 km (or quarter degree cells). The basic trends shown by these data were verified against rainfall measurements from the nearby farm Hakos (1 813 m above sea level, about 18 km north east of the Greater Gamsberg) (Figure 11a) (Straube *et al.* 2019). Although not exactly matching, general trends in terms of drought- and wet spells are repeated between Hakos and the Greater Gamsberg, indicating the validity of the modelled data. The quality of in-between seasons, however, varied greatly from each other, likely due to the down-scaling algorithm used by WorldClim (Fick & Hijmans 2017), taking the altitudinal difference also into account (i.e. the orographic effect of the high plateau). The long-term rainfall and mean annual temperature trends at the Greater Gamsberg (based on WorldClim data) are presented in Figure 11b. The quality of the season is indicated on the graphs as four horizontal lines, representing the 10th, 40th, 70th and 90th percentile. All seasons with a total precipitation between the 40th and 70th percentile (at the Greater Gamsberg 261 and 303 mm precipitation annually) are regarded as 'normal', all seasons with a total precipitation below the 10th percentile (less than 166 mm) are regarded as extreme droughts, whilst all seasons with more than the 90th percentile precipitation (more than 429 mm) are regarded as extreme wet seasons (Botha 1998). (For Hakos, the 10th percentile is at 139 mm, the 40th percentile at 203 mm, the 70th percentile at 312 mm and the 90th percentile at 423 mm precipitation annually.) Based on the modelled WorldClim and MeteoBlue data, a Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano *et al.* 2010) was calculated for the Greater Gamsberg. The SPEI was accumulated for 12 months, thus indicating the quality for any particular month in relation to the quality of the entire season (SPEI-12). The SPEI-12 clearly indicated wet and dry spells (Figure 11c).

The dense population in 1971, as depicted in Figure 8, could be the result of a series of near-normal or above-normal rainy seasons between 1962/63 and 1970/71. Only one drought year was recorded in 1969/70, but was followed by an above-normal season in 1970/71 (in which the picture of Figure 8 was taken). During this period, average temperatures also stayed fairly moderate. The recorded decline in 1983 (Giess 1984) could have been the result of three drought seasons after each other, with two extreme drought years in 1980/81 and 1981/82 (Figures 11b and 11c). During this period, the average temperatures also started rising. With a series of near-normal years between 1984/85 and 1989/90, the population would have stabilised, but not been able to expand. Another prolonged drought period between 1989/90 and 1998/99 would have potentially reduced the population further. A fire in 2016 (see below), coupled with a series of dry years starting in 2013 and cumulating with the severe drought in 2019 (Figures 11b and 11c), could have been the cause for the low population density recorded in Figure 9. The dry conditions were aggravated by a steadily rising average temperature (about 1.6 °C between 1961 and 2020, based on a linear regression of the mean annual temperature ($r^2 = 0.59$), Figure 11b), resulting in higher potential evapotranspiration (PET) and thus a higher net water deficiency. From this it is clear that the shrubs, even though being perennial, are relatively short-lived and the population highly reactive to the quality of the season. Projected long-term climate changes for southern Africa are thus likely to further negatively impact this population.

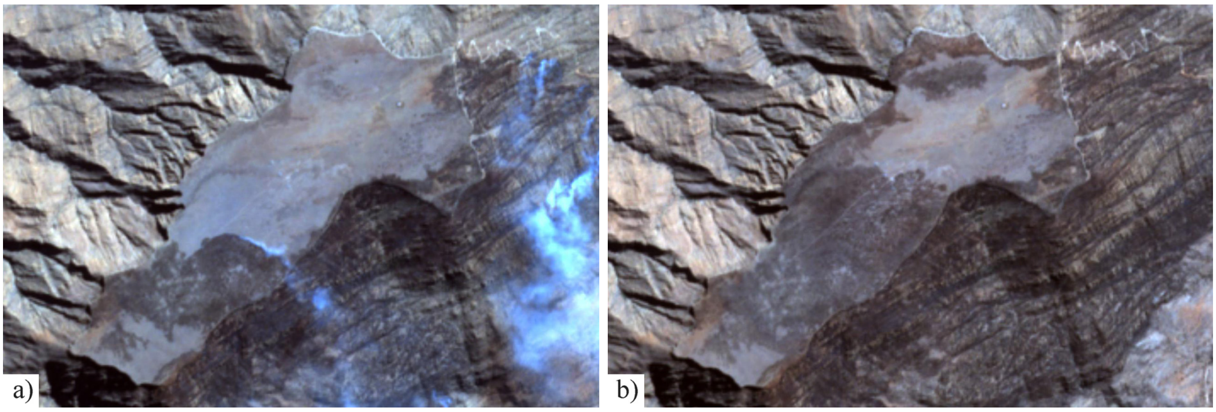

***Figure 12:*** *Progress of the bush fire on the Gamsberg plateau and slopes in August 2016, recorded by the Sentinel-2A satellite. The Gamsberg areas impacted by the fire were (a) (left) on 20 August 2016: The southern plateau, the south-eastern and eastern slopes and the eastern plateau edges, (b) (right) on 30 August 2016: The southern and central plateau, the entire edges of the north-western, northern and north-eastern plateau, a part of the northern plateau, and the eastern and northern slopes. Image sources: Sentinel-2A, Tile T33KXQ dated 20 August 2016 (left) and 30 August 2016 (right). Downloaded from https://scihub.copernicus.eu.*

2. A fire was recorded on the Gamsberg in August 2016, being the only recorded fire during the period November 2000 and June 2020, as evident from the MODIS burned area mapping tool (Giglio *et al.* 2018). This fire started on the south-eastern side of the Greater Gamsberg on 19 August 2016, and spread onto the southern plateau, the south-eastern and eastern slopes and eastern plateau edges over the subsequent day (Figure 12a). It further spread onto the central plateau and the northern edges and was extinguished by local farmers before reaching the astronomy base, leaving most of the northern part of the plateau untouched (Figure 12b). Impacts on the vegetation like charred and burned *E. walterorum* shrubs in the station area and burned *Acacia hereroensis* trees near the northern edge of the plateau, were still visible during a field visit in 2019. Overall, the long-term fire risk for the Gamsberg area is regarded as low (Le Roux 2011).

3. A high mortality rate in older shrubs may have led to a significant decline in the population size, which in turn resulted in reduced seed production or seedling establishment.

4. As the species is out-crossing, the population decline may have led to diminished pollination and seed production and this in turn would have led to a reduction in recruitment, which finally appeared to lead to a further shrinking of the population size.
5. Other species could have colonised the habitat of *E. walterorum*. *Eriocephalus dinteri* especially can be regarded as a competitor to *Euryops walterorum*, but the dense perennial grass sward dominated by *Digitaria eriantha* could be competing for moisture resources (Strohbach 2021).
6. Pests could have weakened the population through herbivory and inhibiting seed formation.

## THE NEED FOR MONITORING OF *EURYOPS WALTERORUM*

The possible effects of climate change as well as the impacts of infrastructure developments are expected to result in a continuing decline of this population, leading to a detrimental effect on the population's viability with extinction in the wild as a possible outcome in the foreseeable future. As there are no empirical data confirming any of the trends observed in the population on the plateau, a long-term monitoring initiative has been initiated by a consortium consisting of the National Botanical Research Institute (Ministry of Environment, Forestry and Tourism), the Biodiversity Research Centre of the Namibia University of Science and Technology, as well as independent lay botanists with a special interest in the project. This initiative is endorsed by the Max Planck Society as the landowners.

The aims of this initiative are:

- to establish a baseline data set on the present-day population
- to establish a monitoring system to monitor the population dynamics in relation to climatic trends and anthropogenic impacts
- to establish a conservation strategy for *E walterorum*, both *in situ* and *ex situ*.
- to determine inter-population genetic relationships (one population or two populations on the northern and southern side of the plateau?)
- to determine phylogenetic relationships with other species of the genus *Euryops*.

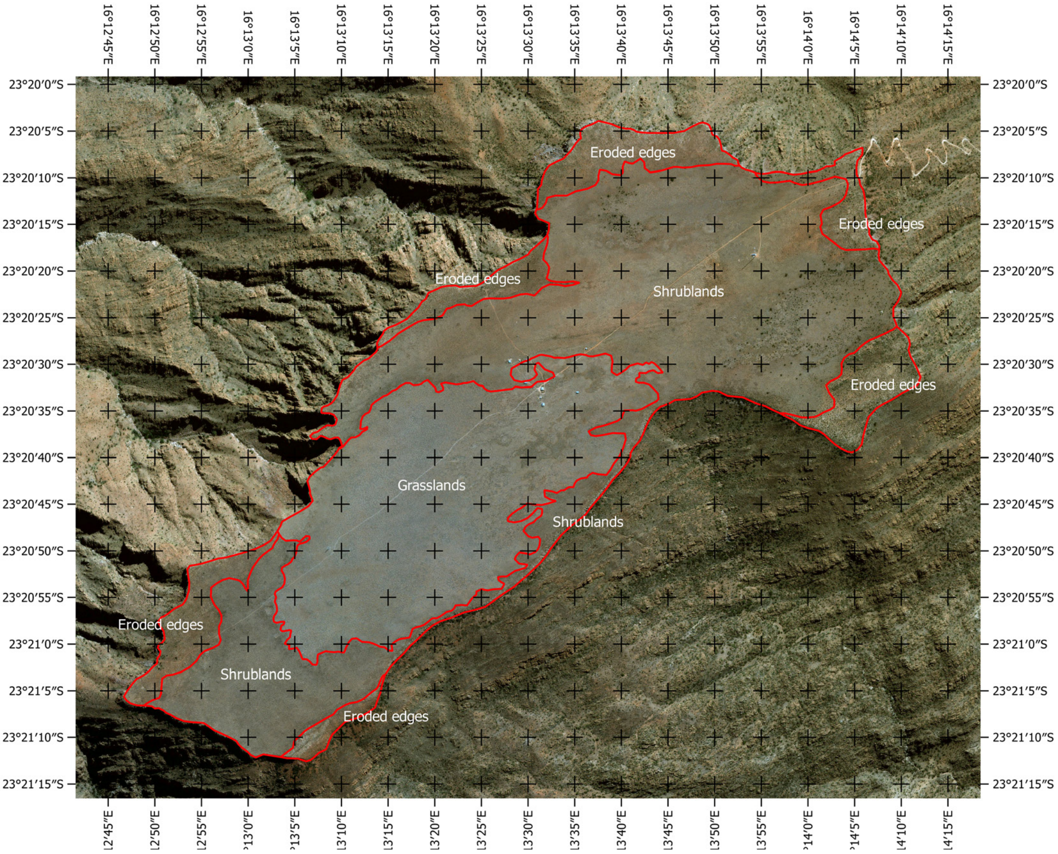

***Figure 13***: *Habitats identified and delineated on the Gamsberg plateau, using Google Earth and Microsoft Bing imagery. The shrublands represent likely* Euryops walterorum *habitat.*

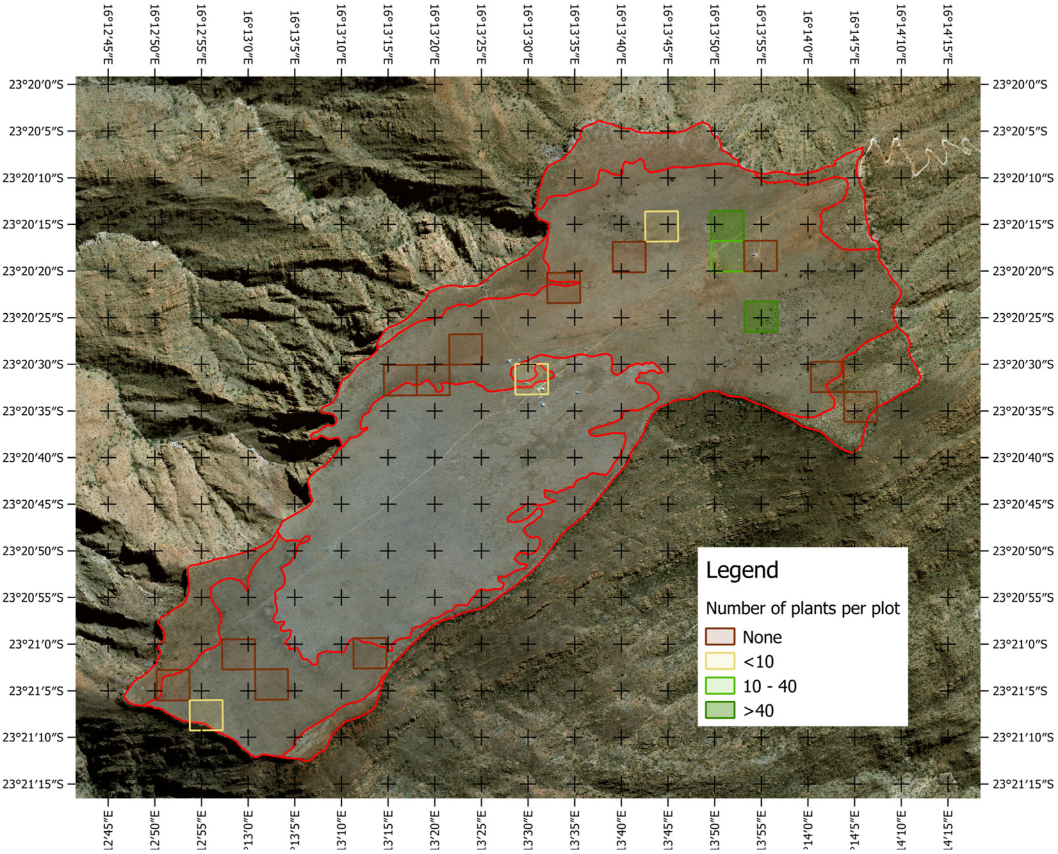

***Figure 14***: *Surveyed densities of the* Euryops walterorum *population.*

An initial survey to estimate the population density of *E. walterorum* and obtain baseline data for future monitoring was done during field visits in November 2019 and February 2020. A series of permanent monitoring sites, their lay-out and position pre-determined in a stratified randomised manner following the scheme of the Biodiversity Observatories (Jürgens *et al.* 2012), were set up.

The proposed long-term monitoring programme for *E. walterorum* is described in online Appendix 1.

## ESTIMATE OF PRESENT POPULATION OF *EURYOPS WALTERORUM*

Based on the two field visits during November 2019 and February 2020, we can describe the population of *E. walterorum* as follows:

1. The species' occurrence is restricted to the shrublands along the northern, eastern and southern parts of the plateau (about 110 ha), with none occurring in the central grassland, nor along the boulder-strewn eroded edges of the plateau (Figure 13). Within the shrublands, the stands are unevenly distributed.

2. It was evident that the population on the northern and eastern part of the plateau showed a larger amount of live plants than on the southern part of the plateau. This is possibly due to the fire which occurred in 2016 on the southern part of the plateau (Figure 12), but could also have resulted from uneven rainfall distribution over the plateau.

3. In an attempt to explain the difference in habitat, two soil samples were taken from the upper soil layer (10 to 20 cm) at the astronomical station in the shrubland where *E. walterorum* grows, as well as from the survey beacon in the grassland, where it does not occur. The samples were analysed for texture and nutrient values, using standard procedures (Carter & Gregorich 2008). The preliminary soil analysis of shrubland and grassland indicated that the sandy loam was very low in organic material (< 1.5% of organic content). At both locations nitrogen was very low (< 85 mg / 100 g of soil), therefore magnesium (> 57 mg / 100 g of soil), manganese (> 75 mg / kg of soil) and iron (> 95 mg / kg of soil) were very high and the pH value (6.1) was slightly acidic. There were no evident differences between the sites to explain the absence of *E. walterorum* in the grassland.

4. A basic descriptive analysis was done with the collected data and displayed in a geographical information system (GIS) map (Figure 14). In a few plots, over 50 individual plants were counted, but most plots had about two plants or less, and many had none. This is in stark contrast to previous observations, which showed a far denser and far more vigorous population (Figures 8 and 10). Most plants were between 50 and 100 cm high. From the current plot data, the estimated total number of mature plants on the plateau was calculated to be about 22 000.

## CONSERVATION STATUS AND STRATEGY

The conservation status of *E. walterorum* on the global IUCN Red List is currently published as 'Least Concern' (LC), reflecting the last global assessment (Craven 2004, IUCN 2012). As a consequence of the apparent threats to the species, resulting in population reductions and decline in the past and foreseen in the future, a review of the conservation status is required and was carried out by the National Botanical Research Institute. *Euryops walterorum* occupies an extremely small Extent of Occurrence (EOO) and Area of Occupancy (AOO). Past reductions in the number of plants were reported as significant and climate data recorded over at least 60 years, suggest a significant plausible threat from the effects of climate change, resulting in a continuing decline in the number of mature individuals and the quality of the habitat. The construction of the planned AMT in the future is predicted to result in further population reduction. The single sub-population is also viewed as a single location because of the significant plausible threats, which limit the spread of the risk of extinction. Although the species qualifies for the Vulnerable D2 category as well as VU A3c and Endangered A2c and A4c, the higher category of Critically Endangered applies in the B category because of the small EOO, AOO, number of locations and the continuing decline in the quality of the habitat and number of mature individuals. The preliminary conservation status is therefore given as CR B1 ab(iii,v) + 2ab(iii,v). The assessment was done using the IUCN categories and criteria (IUCN 2012, IUCN Standards and Petitions Committee 2019) and entered onto the IUCN Species Information System (SIS), from where it will be published as part of the next IUCN global Red List, after a review process approves the assessment.

As a conservation measure, the *ex situ* growing of plants from seeds is planned. This is meant to complement *in situ* conservation measures, aid in preserving a portion of the gene pool and maintain a fallback population of mature plants in case the conditions on the Gamsberg plateau continue to deteriorate. Additionally, excess seeds will be deposited in the National Plant Genetic Resources Centre.

## CONCLUSION

*Euryops walterorum* is a national treasure, growing invisibly to the public on the hard-to-access Gamsberg plateau. The data obtained from the long-term monitoring measures that are now in place will be indispensable and instrumental in revealing population trends in time, such as a further decline in population size, or problems with germination and seedling establishment in this very limited population, and may provide imperative information for understanding and mitigating these effects. A Population Viability Analysis can be conducted once sufficient data have been collected to aid in calculating the risk of extinction.

In times of climate change and biodiversity loss it is in our hands to preserve this extraordinary species.

## AUTHOR CONTRIBUTIONS

This paper was initiated and drafted by CT. CT also contributed most of the observations and photographs on *E. walterorum*. BS developed the proposed monitoring system and field-tested this together with SC. BS also provided inputs in the sections ‘Climatic conditions’ and ‘Population decline’. SL provided structural improvements to the sections ‘Introduction’, ‘Observations on autecology and population dynamics’ and ‘Conservation status and strategy’. SC, SL and AN provided various inputs and insights in this paper.

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# A description of daytime resting sites used by brown hyaenas (*Parahyaena brunnea*) from a high-density, enclosed population in north-central Namibia

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## Abstract

Successfully conserving large carnivores requires an in-depth understanding of their habitat requirements. Ideally this includes a knowledge of the habitat types and features used as resting sites. Resting sites are an important requirement for many species, as they have the potential to influence species distribution and density. We examined the daytime resting sites used by brown hyaenas, a large carnivore endemic to southern Africa and classed as Near Threatened by the IUCN, within an enclosed reserve in north-central Namibia. Using historical spatial data from GPS collars we analysed 1 582 resting sites from nine adult brown hyaenas and classified them according to their location relative to the home range of each hyaena. We also visited a randomly chosen sub-set (n = 123) of these resting sites in the field and recorded habitat types and microhabitat features for each. Our results showed that brown hyaenas most frequently rested within the core area of their home range, most frequently in riverine habitat, followed by bush encroached habitat, and most frequently used microhabitat under a tree or bush. The fact that bush encroached habitat is being frequently used for resting is an important consideration for brown hyaena conservation. Bush encroached areas are often cleared by debushing projects in Namibia and the practice may negatively impact brown hyaenas.

**Keywords:** brown hyaena, carnivore, Namibia, *Parahyaena brunnea,* resting site

## Introduction

The conservation management of large carnivores requires a thorough understanding of their habitat requirements to be successful (Doncaster & Woodroffe 1993, Gess *et al*. 2013). Resting sites are an important requirement for many species as sleeping can be considered one of the most dangerous states of an animal's life (Lima *et al*. 2005). Animals decrease the risk of threats such as predation whilst sleeping by choosing suitable resting sites (Chutipong *et al*. 2015). The availability of sites used for resting has the potential to influence the distribution and density of a species (Doncaster & Woodroffe 1993), therefore species management plans should ensure the availability of such sites, especially for species of conservation concern.

Previous studies have shown that the selection of resting sites is far from random (Freire 2011); resting sites should provide thermoregulatory benefits, protection from the weather and protection from both parasites and predators (Endres & Smith 1993). For example, American eastern spotted skunks (*Spilogale putorius*) were found to select resting sites that had increased vegetation cover and that were structurally complex, which is believed to aid with thermal regulation and predator avoidance (Lesmeister *et al*. 2008). Similarly, American mink (*Mustela vison*) select above-ground resting sites with dense vegetation for cover (Zabala *et al*. 2007).

Larroque *et al*. (2017) found European stone martens (*Martes foina*) selected buildings for resting sites whereas sympatric pine martens (*Martes martes*) selected forest patches, while both species avoided open areas for daytime resting sites. African spotted hyaenas (*Crocuta crocuta*) were found to prefer to rest in woodland habitat with low visibility and vegetation structure which provided both shade and safety (Kushata *et al*. 2017).

Brown hyaenas (*Parahyaena brunnea*) are found throughout the southern African sub-region and are currently the rarest Hyaenidae, with fewer than 10,000 adult individuals remaining. As a result they are listed as Near Threatened by the International Union for the Conservation of Nature (IUCN) (Wiesel 2015). Threats to the species include human-wildlife conflict following real or perceived livestock predation, eradication as part of predator control programs, and to a lesser degree road traffic collisions and body parts being used for traditional medicine (Wiesel 2015). Brown hyaenas are found across a range of habitat types including savanna, scrubland, grassland, wetlands, desert and coasts (Wiesel 2015) and have been found to be flexible within their habitat use at a landscape scale (Welch *et al*. 2016). Depending on the area, brown hyaenas may be considered apex predators, for example on the coastline of southern Namibia (Wiesel 2010), or as a subordinate competitor to lions (*Panthera leo*) and spotted hyaenas in areas with an intact carnivore guild (Mills 2015).

In order to understand the habitat requirements of brown hyaenas within an inland system we examined the daytime resting sites used by a high-density brown hyaena population in an enclosed reserve in north-central Namibia. The brown hyaenas at the study site were part of an ongoing study and included nine adult individuals monitored with GPS collars. Using historical GPS data, we analysed the location of previous resting sites in relation to their home ranges, classifying them as occurring within the core area, low use area or overlap areas used by two clans. We expected that brown hyaenas would not rest within overlap areas, in order to avoid direct encounters with neighbouring clan members. We also visited a randomly chosen sub-set of resting sites in the field to record habitat and microhabitat features. Because competitively dominant spotted hyaenas are also present at the study site, we expected brown hyaenas to favour habitat and microhabitat features that provide concealment.

## Methods

### *Study site*

The study was carried out on the Okonjima Nature Reserve (ONR), a 200 km² privately owned nature reserve located approximately 50 km south of Otjiwarongo, north-central Namibia (Figure 1). The reserve is fully enclosed by an electrified perimeter fence. It receives an average annual rainfall of 450 mm that falls during the hot wet season from October to March. The vegetation is predominantly tree and scrub savanna interspersed with silver terminalia (*Terminalia sericea*) and several *Acacia* species. Perennial water is provided by a total of 18 artificial waterholes across the reserve. The ONR perimeter fence was erected in 2010 around a naturally occurring brown hyaena population that was recently estimated to occur at a density of 24.01 brown hyaenas/100 km² (Edwards *et al*. 2019). Spatial data from monitored brown hyaenas has shown the perimeter fence to be impenetrable to hyaenas (Edwards *et al*. 2020). No species management has taken place since the erection of the fence. Leopard (*Panthera pardus*) density within the reserve is relatively high, having been estimated at 14.51 adults/100 km² during a 2015-2016 density survey (Noack *et al*. 2019), compared to an estimated density of 3.60 leopards/100 km² on commercial farmlands bordering the Waterberg Plateau Park (Stein *et al*. 2011), approximately 100 km from the study site.

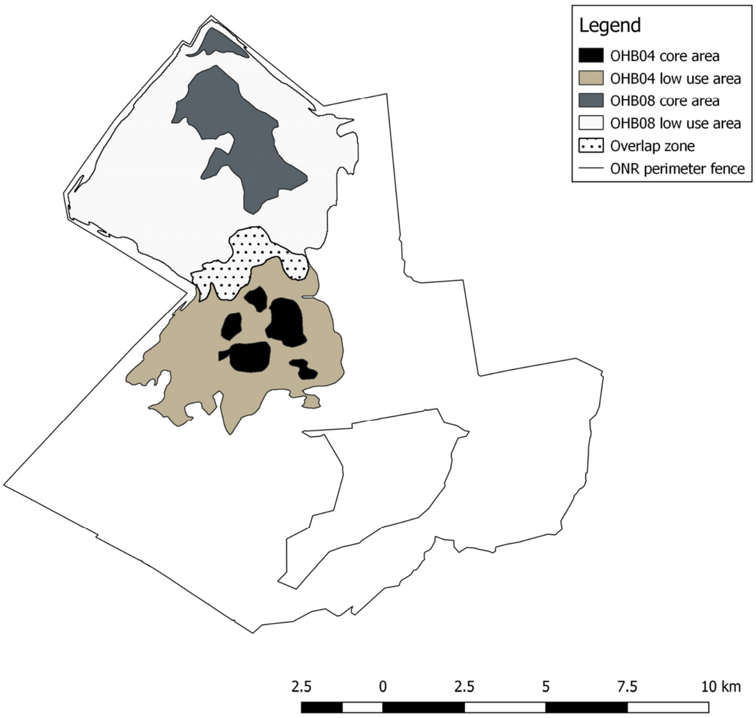

***Figure 1:*** *The Okonjima Nature Reserve study site and two example individual brown hyaena home ranges showing the core area, low use area and overlap between the adjacent home ranges. OHB-numbers refer to individual hyaenas as described in the text.*

### *GPS collars*

Between January and November 2018 a total of nine adult brown hyaenas were sedated to fit global positioning system (GPS) collars sourced from Wireless Wildlife, Potchefstroom, South Africa. For collar fitting, hyaenas were either free darted (n = 6) or captured (n = 3) in a large (approx. 2 m x 3 m) wire box trap, fully lined with industrial conveyor belt rubber to prevent the hyaena injuring itself by attempting to dig or bite at the wire. The trap was fitted with both an internal and external live feed camera and a remotely triggered door. Brown hyaenas were darted using a Pneudart projector using an average weight of 50 kg per animal for dose calculation. A combination of 125 mg Ketamine (sourced from Intersana, Windhoek, Namibia), 2.5 mg Medetomidine and 12.5 mg Butorphanol 12.5 mg (both latter sourced from Kyron Laboratories, Johannesburg, South Africa) was used. When sedation was not deep enough Ketamine at a dose of 0.5 mg/kg (approx. 20-25 mg) was intravenously injected via the saphenous vein. A minimum time of 45 minutes elapsed before the antidotes 'Antisedan' (sourced from Zoetis, Sandton, South Africa) was given at a dose of 2.5 mg intravenously and 5 mg intramuscularly, and 'Trexonil' (sourced from Wildlife Pharmaceuticals, White River, South Africa) at 12.5 mg intravenously and 25 mg intramuscularly. Because brown hyaenas are mainly nocturnal (Mills 1990) the GPS collars, from which data was remotely transferred via ultrahigh frequency (UHF) base stations and repeaters, were scheduled to provide one fix every 30 minutes at night (19h00 to 07h00 local time) and one fix every two hours during the day. Analysis of spatial data along with camera trap data from den sites revealed that individuals OHB01, OHB03 and OHB11 belonged to the same clan, and OHB07 and OHB08 to another (Table 1).

### *Brown hyaena GPS data; resting sites and home ranges*

Following Kushata *et al*. (2017) a daytime resting site, hereafter referred to as a resting site, was defined as the GPS position recorded at 13h00 on days where there was a net displacement of less than 50 m between 09h00 and 16h00. Sites were recorded between January 2018 and January 2019. As brown hyaena movement was restricted by the impermeable perimeter fence, home ranges were estimated using Permissible Home Range Estimation (PHRE) (Tarjan & Tinker 2016); for more detail see Edwards *et al*. (2020). Individuals were defined as belonging to the same clan by the repeated presence of an individual at the same communal den; for more information on communal den site monitoring see Edwards *et al*. (2020). Core areas were defined by the 50% probability kernel, and low use areas were defined as the 95% probability kernel outside of the core area kernel. Overlap areas were defined as those areas where the home ranges of two or more clans overlapped, see Figure 1 for an example. No core areas occurred in overlap zones. A total of 1 582 resting sites from nine monitored brown hyaena were analysed and assigned as falling within the core, low use or overlap area of the individual hyaena's home range by plotting resting sites and home range contours with QGIS 2.8.4 Wien software (www.qgis.org). A resting site was determined as being within an overlap zone if it fell into the overlap between an individual's home range and that of a neighbouring individual from a different clan. As home ranges from clan members had a high degree of overlap, only overlap with non-clan members was considered.

**Table 1:** *Summary of nine individual adult brown hyaenas monitored on Okonjima Nature Reserve using GPS collars.*

| Hyaena ID | Sex | Reproductive status* | GPS monitored clan members |
|---|---|---|---|
| OHB01 | Male | Unknown | OHB03 & OHB11 |
| OHB02 | Female | Confirmed | None |
| OHB03 | Male | Unknown | OHB01 & OHB11 |
| OHB04 | Female | Confirmed | None |
| OHB06 | Female | Confirmed | None |
| OHB07 | Male | Unknown | OHB08 |
| OHB08 | Female | Confirmed | OHB07 |
| OHB10 | Female | Confirmed | None |
| OHB11 | Female | Confirmed | OHB01 & OHB03 |

**Reproductive status of females only, confirmed by camera trap data of the female suckling cubs at a den site.*

A subset of 123 randomly chosen resting sites from seven monitored brown hyaenas (range 7-20 resting sites per monitored brown hyaena) recorded between January 2018 and January 2019 were visited on foot in the field to assign a habitat and microhabitat type to each. Due to time constraints the initial aim of visiting 20 resting sites for each individual could not be met, explaining the variation between individuals in the number of resting sites visited (Table 3). Resting sites were randomly chosen using the 'Random selection' feature in QGIS. Resting sites were located by loading GPS positions of resting sites into the Avenza maps application (Avenza.com) on a GPS enabled Samsung tablet. The five habitat types used were: bush encroached, mountain, open savanna, riverine and open woodland. Bush encroached habitat was defined as having dense growth of *Acacia mellifera*, *Dichrostachys cinerea* and *Terminalia sericea* with little to no grass coverage. Mountain habitat was defined as rocky areas with a higher elevation than the surrounding area. Open savanna habitat was defined as mixed woodland-grassland with spaced trees and an unclosed canopy. Riverine habitat was defined as riverbeds plus a 50 m buffer on each side. Open woodland was defined as habitat with large trees with a canopy density of 10-40%. Each resting site was also assigned to a microhabitat, these being: burrow (assumed to be originally from aardvark *Orycteropus afer* or warthog *Phacochoerus africanus*), drainage line, riverbank or under a tree/bush. A burrow microhabitat feature was assigned if the GPS position of the resting site fell within 2 m of an established burrow. A drainage line microhabitat was defined as a channel naturally cut into the ground through which water would normally flow during heavy rains. A riverbank microhabitat was defined as the sandy area directly adjoining a riverbed. The tree or bush microhabitat was assigned if the resting site fell within 2 m of the base of a tree or bush.

***Figure 2:*** *Typical riverine habitat brown hyaena resting site.*

## Results and Discussion

### *Resting sites in context of the home range*

Of the 1 582 daytime resting sites analysed 55.3% (n = 874) were located within the core area of the home range, 33.4% within the low use area and 11.4% within overlap areas. Although individual brown hyaenas showed differences in patterns of resting site locations, 77.8% (n = 7) used core areas for resting most frequently, with female OHB04 having the majority (69.8%) of resting sites in the low use area, and male OHB03 having 43.1% of resting sites in the overlap areas (Table 2).

***Table 2:*** *Resting site locations of nine individual adult brown hyaenas in relation to their home ranges on Okonjima Nature Reserve.*

| Hyaena ID | Number of resting sites | Percentage of resting sites within: | | |
|---|---|---|---|---|
| | | Core area | Overlap areas | Low use areas |
| OHB01 | 131 | 40.5 | 22.9 | 36.6 |
| OHB02 | 122 | 64.8 | 5.7 | 29.5 |
| OHB03 | 102 | 25.5 | 43.1 | 31.4 |
| OHB04 | 172 | 27.3 | 2.9 | 69.8 |
| OHB06 | 282 | 60.3 | 9.9 | 29.8 |
| OHB07 | 49 | 53.1 | 0 | 46.9 |
| OHB08 | 359 | 64.9 | 5.0 | 30.1 |
| OHB10 | 194 | 84.5 | 5.7 | 9.8 |
| OHB11 | 171 | 44.4 | 21.6 | 33.9 |
| Mean<br>(SD, 95% CI) | | 51.7<br>(18.2, 39.8-63.6) | 13.0<br>(13.1, 4.5-21.5) | 35.3<br>(15.2, 25.4-45.3) |

### *Resting site habitat choice*

Riverine habitat was the most commonly selected habitat for daytime resting (Figure 2), with a total of 41.5% of resting sites located in this habitat (Table 3). Bush encroached habitat was the second most commonly utilised with 33.3% of resting sites, followed by open woodland (10.6%), open savanna (8.9%) and mountain (6.5%) habitats (Table 3).

A one-way analysis of variance (ANOVA) test showed that significant differences existed in the percentage of resting sites found within the different habitat types (F = 5.87, d.f. = 4, $p < 0.05$). A Tukey's pairwise multiple comparison test revealed significant differences between the mountain and bush encroached habitats ($p < 0.05$) with significantly more resting sites located in bush encroached habitat; between riverine and mountain habitats ($p < 0.01$) with significantly more resting sites located in riverine habitat; between open savanna and riverine habitats ($p < 0.05$) with significantly more resting sites in riverine habitat; and between open woodland and riverine habitats ($p < 0.05$) with significantly more resting sites in riverine habitat.

***Table 3:*** *Habitat types utilised as resting sites by adult brown hyaenas within the Okonjima Nature Reserve.*

| Hyaena ID | Number of resting sites | Percentage of resting sites within each habitat type: | | | | |
|---|---|---|---|---|---|---|
| | | Bush encroached | Mountain | Open savanna | Riverine | Open woodland |
| OHB01 | 19 | 15.8 | 21.1 | 0 | 47.4 | 15.8 |
| OHB02 | 7 | 57.1 | 0 | 28.6 | 28.6 | 0 |
| OHB03 | 18 | 11.1 | 16.7 | 11.1 | 38.9 | 22.2 |
| OHB04 | 20 | 55.0 | 0 | 10.0 | 35.0 | 0 |
| OHB06 | 19 | 79.0 | 0 | 5.3 | 0 | 15.8 |
| OHB10 | 20 | 15.0 | 5.0 | 5.0 | 70.0 | 5.0 |
| OHB11 | 20 | 15.0 | 0 | 15.0 | 60.0 | 10.0 |
| Mean<br>(SD, 95% CI) | | 35.4<br>(25.5, 16.5-54.4) | 6.1<br>(8.3, -0.1-22.3) | 10.7<br>(8.6, 4.4-17.1) | 40.0<br>(21.1, 24.5-55.6) | 9.8<br>(7.9, 4.0-15.7) |

***Table 4:*** *Microhabitat types utilised as resting sites by adult brown hyaenas within the Okonjima Nature Reserve.*

| Hyaena ID | Number of resting sites | Percentage of resting sites within each microhabitat type: | | | |
|---|---|---|---|---|---|
| | | Burrow | Drainage line | Riverbank | Tree or bush |
| OHB01 | 19 | 0 | 15.8 | 0 | 84.2 |
| OHB02 | 7 | 0 | 28.6 | 14.3 | 71.4 |
| OHB03 | 18 | 5.6 | 16.7 | 5.6 | 72.2 |
| OHB04 | 20 | 0 | 0 | 0 | 100.0 |
| OHB06 | 19 | 5.3 | 0 | 0 | 94.7 |
| OHB10 | 20 | 0 | 0 | 0 | 100.0 |
| OHB11 | 20 | 5.0 | 0 | 5.0 | 85.0 |
| Mean<br>(SD, 95% CI) | | 2.3<br>(2.6, 0.3-4.2) | 8.7<br>(10.8, 0.7-16.7) | 3.5<br>(5.0, -0.1-7.2) | 86.8<br>(11.2, 78.5-95.3) |

### ***Microhabitat choice of resting site***

For all monitored brown hyaenas, both combined and individually, the tree or bush microhabitat was most commonly utilised as a daytime resting site, with 88.6% of visited resting sites being under trees or bushes (Table 4). A total of 6.5% of resting sites were located in drainage lines, 2.4% in burrows, and 2.4% on riverbanks. A one-way ANOVA showed significant differences in the number of resting sites found in each microhabitat feature category (F = 138.0, d.f. = 4, p < 0.01). A Tukey's multiple pair-wise comparison test showed that all resting sites under a bush or tree were utilised significantly more than burrows (p < 0.01), drainage lines (p < 0.01), open areas (p < 0.01) or riverbanks (p < 0.01).

## Conclusion

Understanding the habitat requirements of threatened species is a key component of any successful wildlife management planning. Resting sites are especially important as they are often required to provide protection from predators whilst animals are sleeping and have the capability to influence the distribution and even abundance of a species (Doncaster & Woodroffe 1993). By examining the resting sites used by GPS monitored brown hyaenas within an enclosed reserve we gained a greater understanding of the habitat requirements of this species. Brown hyaenas mainly rested within the core areas of their home ranges, with the exception of a possibly dispersing male who frequently rested in the overlap zones of his and his clan neighbours' home ranges. Riverine habitat, followed by bush encroached habitat were most frequently used for resting, with microhabitat under a tree or bush being most frequently used. However, as the total availability of each habitat type or microhabitat is not known, the results here do not represent habitat preferences. While preliminary, our results can be used to guide habitat management of areas wishing to conserve brown hyaenas.

Although patterns for individual hyaenas varied (range 25.5% to 84.5% of resting sites), 55.3% of all analysed resting sites were found within the core area of hyaena home ranges. Overlap areas were used least as resting sites, with just 11.4% of analysed resting sites being found within these areas. Such a result might be explained by a reduced risk of direct encounters with a neighbouring clan member, which Mills (1990) noted often result in antagonistic interactions for same sex individuals of brown hyaena. Direct encounters between neighbouring individuals on ONR may be more frequent than in open systems due to the high population density (Edwards *et al*. 2019) and the boundary fence constricting hyaena movement (Edwards *et al*. 2020). Therefore resting in core areas, which are unlikely to be used by neighbouring individuals, may decrease the risk of direct encounters or an individual being attacked by a neighbour whilst sleeping.

In contrast to most individuals, male brown hyaena OHB03 was found to frequently rest in overlap areas, with 43.1% of his resting sites found within overlap zones. During the study period this male showed frequent nocturnal excursions far into the territories of neighbouring clans and was recorded on camera traps at the communal den sites of two neighbouring clans (Edwards, in prep). In the Kalahari, Mills (1990) noted that most, if not all, males will leave their natal clan eventually. The behaviour of OHB03 coupled with his age, estimated at age class three (young adult) (Mills 1982), might suggest dispersal behaviour seeking to integrate into a new clan to become a breeding male (Mills 1990). Such behaviour might explain why this individual was frequently found resting outside of his core area.

Riverine habitat was the most frequently used habitat type for resting sites, and was used significantly more often than mountain, open savanna and open woodland. Riverine habitat on ONR typically has a dense network of large trees and bushes adjacent to the riverbed that provides both shade and concealment. Mills (1990) recorded brown hyaenas using the shade of trees and bushes as resting sites particularly in summer, because brown hyaenas with their thick and long hair may suffer from overheating otherwise. Similarly, Kushata *et al*. (2018) found spotted hyaenas selected for woodland daytime resting sites, suggesting these habitats provide the most shade and aid in thermoregulation. Despite brown hyaenas at the study site often selecting mountainous areas for den sites (Edwards, in prep), only 6.5% of resting sites were found in mountain habitat. Stratford and Stratford (2011) found that spotted hyaena on Ongava Nature Reserve, Namibia, avoid resting on hilltops, suggesting the angle of the slopes may provide little protection from the sun and further expose them to the elements. This might also explain why so few brown hyaena resting sites on ONR were located in mountain habitat.

Bush encroached habitat was the second most frequently used habitat for resting sites, being used significantly more often than mountain habitat. In Namibia, bush encroachment is known to lower the economic productivity of commercial ranchland by reducing the carrying capacity for livestock (Quan *et al*. 1994). As a result, 'debushing', the removal of unwanted bush by fire, mechanical, chemical or biological methods, is now commonplace in Namibia in an attempt to open up areas to restore grazing and thus the economic capacity of an area. In ONR debushing has been done over several years in an attempt to facilitate viewing of wildlife for tourists. However, the results of this study show bush encroached areas to be important for brown hyaenas through use as daytime resting sites. As resting site availability is known to be influential in the distribution of species (Freire 2011), it is important to ensure that suitable sites are available for species of conservation concern, therefore debushing projects may wish to consider leaving intact patches of bush encroached habitat within brown hyaena range, especially when other dense habitats are not available. Furthermore, as brown hyaenas were found to rest most often within core areas of their home range, leaving patches of bush encroached habitat within hyaena clan core areas may be especially beneficial.

Microhabitat under a tree or bush was most commonly used for resting, with 88.6% of sites being associated with this microhabitat. Mills (1990) recorded brown hyaenas selecting trees with large branches close to the ground for resting sites in the Kalahari and suggested that such sites, in addition to providing a thermal refuge, offered increased concealment from predators, which in ONR might include spotted hyaena. Spotted hyaenas have been infrequently recorded killing brown hyaenas, and non-food related interactions in the Kalahari usually involved the brown hyaena being harassed (Mills 1990). Therefore, choosing a resting site which provides concealment from spotted hyaenas will be beneficial and potentially explains the frequent use of bushes and trees.

Future studies may benefit from examining seasonal changes in habitat and microhabitat choice of resting site and use, and where possible, use larger sample sizes of brown hyaenas. Furthermore, because the factors relating to sleeping site selection may vary for a species depending on the environmental conditions and community of species in which it resides (Chutipong *et al*. 2018), repeating the study in contrasting habitats and species community assemblages will enable a more in-depth understanding of brown hyaena resting site requirements.

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# Towards understanding the presence of abundant fish in running *iishana*

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## Abstract

Although the *iishana* (seasonal watercourses) deltaic system in northern Namibia and southern Angola is usually dry, millions of fish populate the more than 100 000 km² area during high floods that occur irregularly about once in three years. The origin of the fish has been a topic of debate for a long time, including suggestions of refugia for breeding fish in the upper parts of the Mui and Cuvelai catchments, deep dams in both Angola and Namibia and fish arriving with flood water from the Kunene River. This paper discusses fish collections made during a major *efundja* (large flood with plenty of fish) in 2017 and a medium flood in 2020. The bulk of fish during major *efundja* comprise two species that were also collected in the flooding Cuvelai and in *iishana* fed from deep dams in 2020. The source of fish during medium floods is therefore ascribed to fish surviving in refugia and then breeding successfully. The fish occurring in abundance in *iishana* during major *efundja*, however, come from tributaries of the Kunene along the divide with the western *iishana*, where spawners and young fish cross the divide and migrate into the headwaters of the *iishana*. Plentiful fish during *efundja* relies on unhindered access into the *iishana*. The Cuvelai system is threatened by environmental degradation in the *iishana* region and inappropriate road infrastructure is a constraint. Fisheries activities should be regulated and cooperation between the Angolan and Namibian authorities is required to ensure the survival and continuation of fish resources.

## Introduction

The *iishana* (Oshiwambo, plural of *oshana*, shallow seasonally flowing grassy channel) of southern Angola and northern Namibia are part of the Cuvelai Drainage, a seasonal drainage wedged between the Kunene and Okavango Rivers (Figure 1). In ancient times, the upper Kunene did not flow westwards to the Atlantic Ocean but drained southwards into a former Lake Kunene, a much larger precursor of modern day Etosha Pan (Hipondoka *et al.* 2006). The upper Kunene was captured near present day Calueque by a smaller river to the west, leaving only the present Cuvelai and some branches to feed the *iishana* and Etosha (Mendelsohn and Weber 2011, Mendelsohn *et al.* 2013). Consequently, *iishana* are usually dry and only receive substantial floodwaters on average every third year in summer. Then usually bone-dry channels suddenly teem with small and some larger fish, all moving south with the slow water current. Such *efundja* (Oshiwambo, floods) are a welcome source of fish to local people; they use traditional traps and baskets and also modern nets, fykes and line and hooks to trap and catch mainly small barbs (Figure 2) and young catfish (Figure 3). During good *efundja* large numbers of fish are caught and offered for sale along roads or dried for later use (Figures 3 and 4), providing a valuable protein addition for residents.

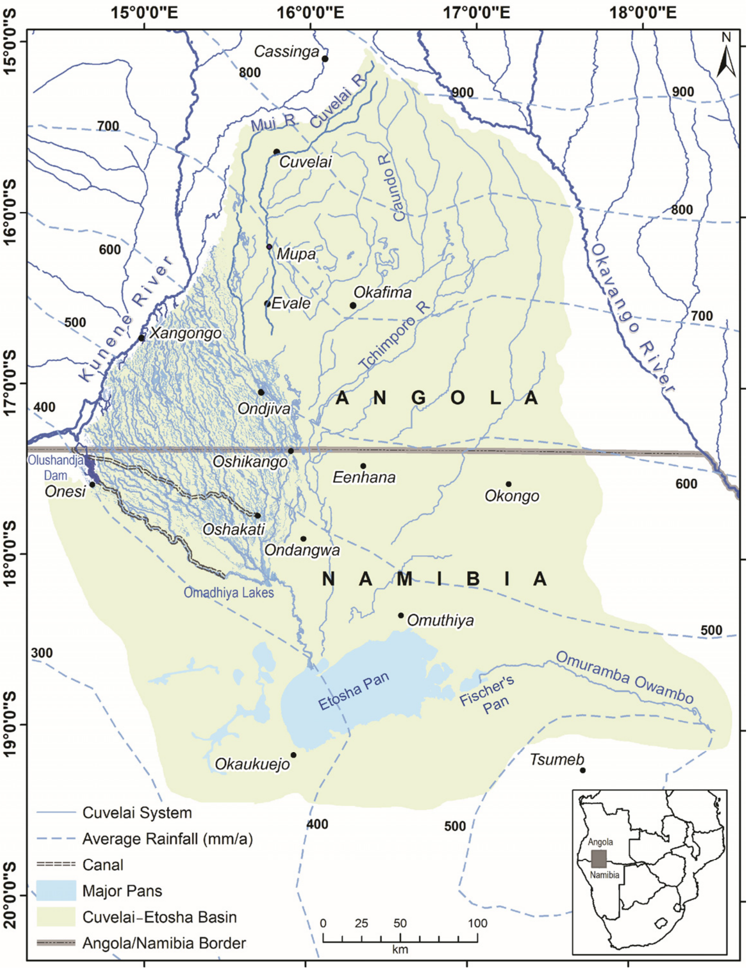

***Figure 1:*** *The Cuvelai catchment with adjacent river systems.*

***Figure 2:*** *Two barb species (*Enteromius *spp.) or* oontangu *(Oshiwambo) that form the main composition of the* efundja *catch together with catfish. These barbs are also the reason for the extremely fast growth of catfish that feed on them, reaching a length of 30 cm from December (when they hatched) to April.*

***Figure 3:*** *Catfish (*Clarias gariepinus*) or* ehepala *(Oshiwambo) from the 2020 small* efundja*, for sale along the road near Oshakati, April 2020.*

The Cuvelai is zoogeographically not completely separated from the Kunene due to a man-made canal linking the two rivers (Figure 1) (Hay *et al*. 1997, van der Waal 1991). Of the 46 fish species collected in the Cuvelai, *iishana* and canals supplying water from the Kunene to the *iishana* system, 17 are considered migrants from the Kunene via the canal (van der Waal 1991). In the southern Cuvelai the environment is saltier, drier and harsher, and there only 9 fish species are regularly found, dominated by catfish and barbs. The Cuvelai does not have any unique or endemic fish species.

It was previously assumed that the suddenly appearing fish in flooding *iishana* all come from almost permanent pools higher up in the Cuvelai River, with possible contributions by other rivers, e.g. the Mui and Chimporo in southern Angola (Figure 1), but it was difficult to understand how all *iishana* can become so quickly populated. The more than 100 *omatele* (Oshiwambo, livestock watering dams) that were built in the 1960s were then assumed to act as refugia and reservoirs for breeding fish. However *efundja* with plenty of fish also happened before these deep dams were built, and the very large numbers of fish caught during major *efundja* (Figure 4) cannot have originated from the relatively small pools and dams.

In 2017, new information was gathered of mass fish migrations upstream into small tributaries of the Kunene, originating on the divide between the Kunene and westerly *iishana* (Hipondoka *et al*. 2018). It is now understood that whereas water does not actually flow from the Kunene into the Cuvelai or its *iishana* (Stengel 1963), surface water connections are established during heavy rain and flood conditions and this facilitates the crossing of breeders and small fish from the Kunene tributaries into the headwaters of western *iishana* (Hipondoka *et al*. 2018). Because the steep tributaries of the Kunene dry up very quickly, once fish have crossed the divide they have no option of returning and follow the slow current southwards.

In February 2020 after good rain had fallen and the Cuvelai was reported to be flooding in southern Angola, an investigation was made by visiting *iishana*, tributaries on the divide between the Kunene and Cuvelai north of Ruacana, and the lower part of the Cuvelai at Mupa and Evale. A large scoop net with deep bag and 8 mm mesh size and a small seine net were used to collect fish specimens. Catches by local fishers using traditional traps and seine nets were also recorded.

***Figure 4:*** *Mass fishing activities during the large* efundja *in 2008 resulted in large scale fish sales along roads.*

## Results and discussion

Sites where surface water connections between the two river systems were possible were found (Figure 5) but due to the lack of follow-up rains no active fish migration was observed on the divide. An important find was the collection of the dominant fish species of the *efundja* (*Enteromius paludinosus*, *Clarias gariepinus* (Ekandjo 2009, van der Waal 1991)) in the flooding Cuvelai in southern Angola. *Iishana* further south in Namibia were also sampled and some fish were collected in running *iishana* that had connections with deep dams, but where the Cuvelai floods from Angola had not yet reached. Additionally, fish escaping from the overflowing Olushandja–Oshakati canal were collected. During this medium *efundja*, low numbers of fish were collected, assumed to have originated from the canal, pools and dams in which fish populations had remained after the good 2017 *efundja*.

It can now be seen that the abundant fish life of the *iishana* during efundja has multiple origins:

1. Permanent pools in the Cuvelai River in southern Angola (above Evale).
2. Semi-permanent deep livestock drinking dams (*omatale*) in southern Angola and northern Namibia.
3. The Olushandja–Oshakati canal and the canal from Olushandja down the Oshana Etaka, when they are overflowing or leaking (see Figure 1).
4. The divide area where the Kunene tributaries originate close to the top end of *iishana*. During floods and good rain periods, Kunene fish migrate upstream in tributaries to breed and disperse and they and their offspring can then reach the *iishana* and migrate downstream.

As soon as the *iishana* have filled from local rainwater, the connecting drainage lines spill their overflowing water southwards and a general southward flow starts. This flood is reinforced by floodwaters from the Cuvelai and Mui Rivers, causing stronger flows at constrictions in the channels, culverts and smaller bridges. Fishing is concentrated here and the many long fine-meshed funnel nets often completely block the passage of fish (Figure 6). During major *efundja* abundant water from upstream as well as from within the *iishana* region itself causes general overflowing and then all *iishana* become interconnected enabling fish to disperse over the entire *iishana* region.

This observed downstream migration is the opposite of the general tendency of fish to migrate upstream. There are two general upstream migration types: breeding migrations to reach the shallow vegetated inundated spawning sites of many freshwater fish species, and expansion migration, usually upstream by mainly young fish in an attempt to distribute the species higher up in the system. One of the driving forces behind the observed downstream migration in the current case is the plentiful availability of food in newly inundated areas, providing for both the smaller insect and plankton eating barbs and larger predatory catfish that also feed on them.

The Cuvelai *iishana* system is a unique ecosystem that is driven by cycles of rain and flood water. While the ancient connection with the Kunene remains intact, fish can enter the system. Fish are a valuable benefit of *efundja*. The whole system is however threatened by environmental degradation in the *iishana* region and inappropriate road infrastructure is a constraint (Figure 7).

***Figure 5:*** *On the divide between the Kunene and Cuvelai catchments, facing the Kunene, February 2020. Fish can reach these shallow standing pools if there is enough rain, and thus move into the* iishana*, breed and populate them.*

***Figure 6:*** *Nine funnel nets just below a culvert intercept fish migration, with a second and third row behind them,* efundja *2008.*

***Figure 7:*** *Two examples of inappropriately designed and seriously eroded culverts on the road near the divide, that actually overtopped during a flash flood early in the 2020 rainy season. All smaller fish and most larger fish would have great difficulty getting across these obstacles*

Furthermore, the Cuvelai drainage presents a good example of the need of cooperation between neighbouring states. The survival and continuation of fish resources in the interior of the *iishana* system in both southern Angola and northern Namibia is dependent on the protection and conservation of fish refugia populations in the Cuvelai River itself, the existence of deep dams and pools and especially on the maintenance of connectivity between the Kunene and *iishana*. It is of utmost importance that these shared water and fish resources are jointly conserved and that harvesting of the fish resources is planned and regulated.

Some suggestions that may help to promote increased fish presence in the *iishana* during floods include:

1. Modifying the road running on and near the divide between the Kunene and headwaters of the *iishana* by inserting suitable fish-friendly culverts and bridges at every drainage and stream (Figure 7).
2. Placing a ban or restrictions on netting directly at and near any man-made constriction of *iishana* and streams, including bridges and culverts. The Namibian Inland Fisheries Act of 2003 states that no fishing is allowed within 100 m of bridges and culverts; however, we have not observed its enforcement in the Cuvelai. Traditional bunds with fish traps placed in openings can however still be allowed as their effect is limited. Traditionally, local chiefs decided when fish in the *iishana* had grown big enough to be harvested. Traditional authorities and communities should again become involved in conservation of local fish life.
3. Designation of all deep dams and ponds in both countries as fish refugia, allowing fish to survive and breed early in the next rainy season.
4. Developing extensive fish farm projects through fish breeding facilities that can breed fingerlings for release in local *iishana* every year that water is present (about 2 in 3 years). In order to prevent any introduction of parasites and genetic deterioration, only locally occurring fish should be used in breeding programmes.
5. Regular monitoring for the presence of fish and managing the fish migrations so that accumulating fish life in the drainage pans of the Omadhiya wetlands can also be harvested optimally.
6. Initiating a study on the economic value of local fish in the region to motivate active management of this resource.

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# Vegetation types and structure in the Kanovlei State Forest in Namibia

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## Abstract

Vegetation mapping of the Kanovlei State Forest was carried out in 2010 using a combination of Landsat Etm+ satellite image data and field data. Eight vegetation types were identified: closed woodland, dense shrubland, mixed grass and shrubland, mixed shrubland, mixed shrubland and woodland, open woodland, shrubland, and woodland. The dominant woody species in the area were *Pterocarpus angolensis*, *Burkea africana*, *Acacia* (*Vachellia*) species, *Terminalia sericea*, *Bauhunia petersiana* and *Combretum* species. Soil types were also mapped. Most of the area is sandy soil.

**Keywords:** Kanovlei State Forest, Namibia, remote sensing, soil mapping, vegetation structure, vegetation type

## Introduction

The Kanovlei State Forest is in Namibia's Otjozondjupa region (Figure 1). It lies approximately 150 km east of Grootfontein and covers about 21 636 hectares. The area has been a protected reserve for more than 20 years and human activities have been limited in the area. This study aimed to create a detailed map of vegetation structure and communities, as well as of soil types.

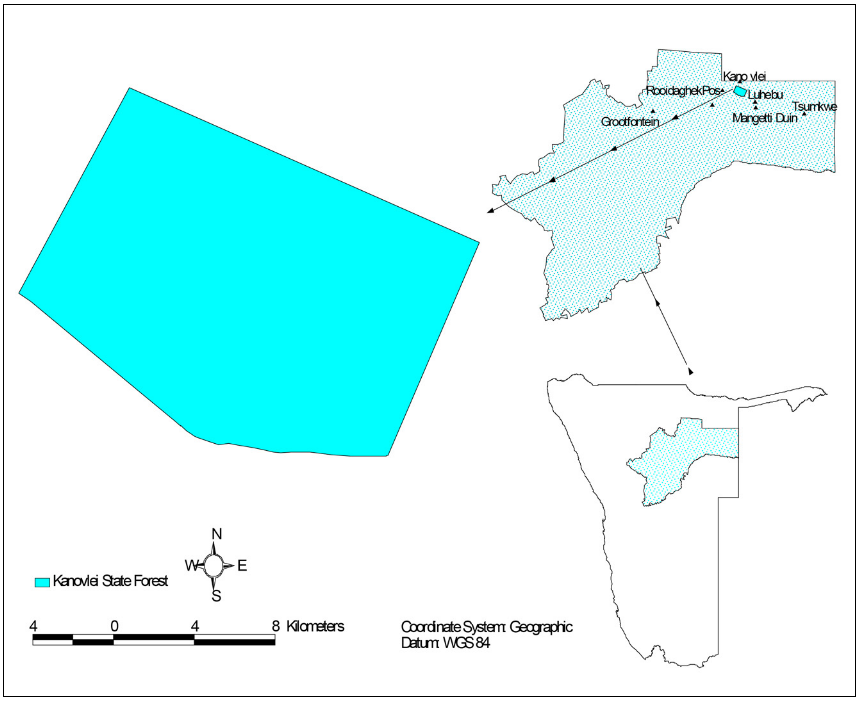

***Figure 1:*** *Kanovlei State Forest. The co-ordinates of the north-western corner are -19°14'15", 19°23'15" and the south-eastern corner is at -19°17'25", 19°36'15".*

## Methods

ERDAS IMAGINE was used for image processing, while vector data were processed and generated using ArcView GIS 3.2 (a), ARCGIS 9.3.1 and OziExplorer. Landsat ETM + (2002) images were used to allocate sample plots. A random sampling method was used to demarcate approximately 20 sample plots. Satellite images for each sample plot were printed and used in the field to identify vegetation types. Field data were recorded to match vegetation types with distinct reflectance in the image. The co-ordinates of sample points were recorded with a GPS. Vegetation type, soils and dominant plant species were recorded at each sample point.

Different vegetation cover classes were defined to reflect both vegetation structure and woody plant species dominance. Vegetation classes were then mapped using a supervised maximum likelihood classification based on training sites delimited from the field data. The classes emphasised distinct vegetation structure and community dominance.

## Results and Discussion

Eight vegetation structure classes were identified: closed woodland, dense shrubland, mixed grass and shrubland, mixed shrubland, mixed shrubland and woodland, open woodland, shrubland, and woodland (Figure 2). The closed woodland, woodland and shrubland covered most of the State Forest while the remaining classes contributed smaller proportions of the vegetation cover. No grassland areas were found.

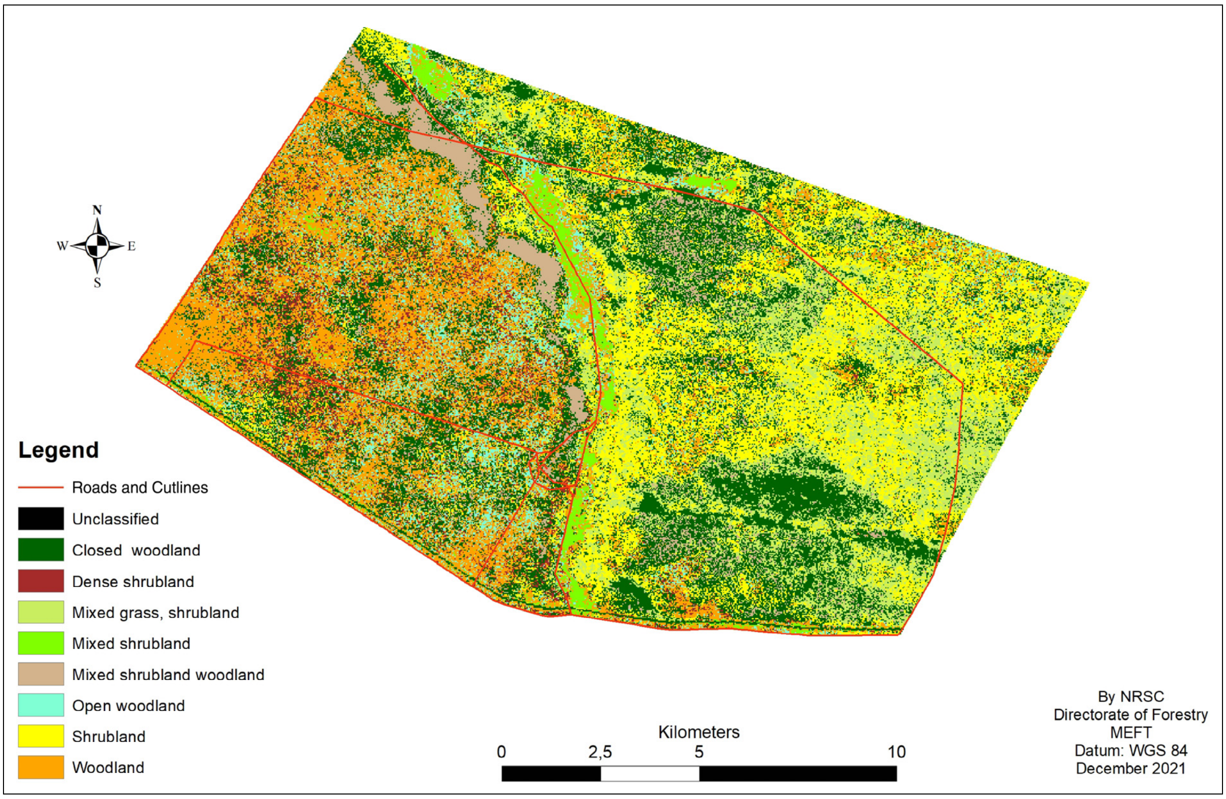

***Figure 2:*** *Vegetation structure in the Kanovlei State Forest.*

*Pterocarpus angolensis* and *Burkea africana* were the dominant woody species (Figure 3). *P. angolensis* was mostly found in the western part of Kanovlei while the eastern part was dominated by *B. africana*. Along the dry drainage lines and valleys (locally called omurimba; singular omuramba), *Acacia* spp., *B. africana* and *Terminalia sericea* were dominant while a few other areas were dominated largely by *Bauhunia petersiana* and *Combretum* spp. Other species in the area were relatively scarce and not mapped.

Much of the area consists of sandy soil while small areas along the main omuramba are comprised of sandy loam (Figure 4). Soil and vegetation types appeared to be linked. For example, *T. sericea* was normally on sandy soils. while thorny plants such as *Acacia* spp. and *Ziziphus mucronata* grew predominantly on sandy loam.

Although the mapping exercise was carried out more than 10 years ago, the results remain relevant since humans and wildlife have had little impact on vegetation resources. We encourage natural resource managers to use this baseline vegetation information to monitor the impacts of conservation and other land uses in the Kanovlei State Forest.

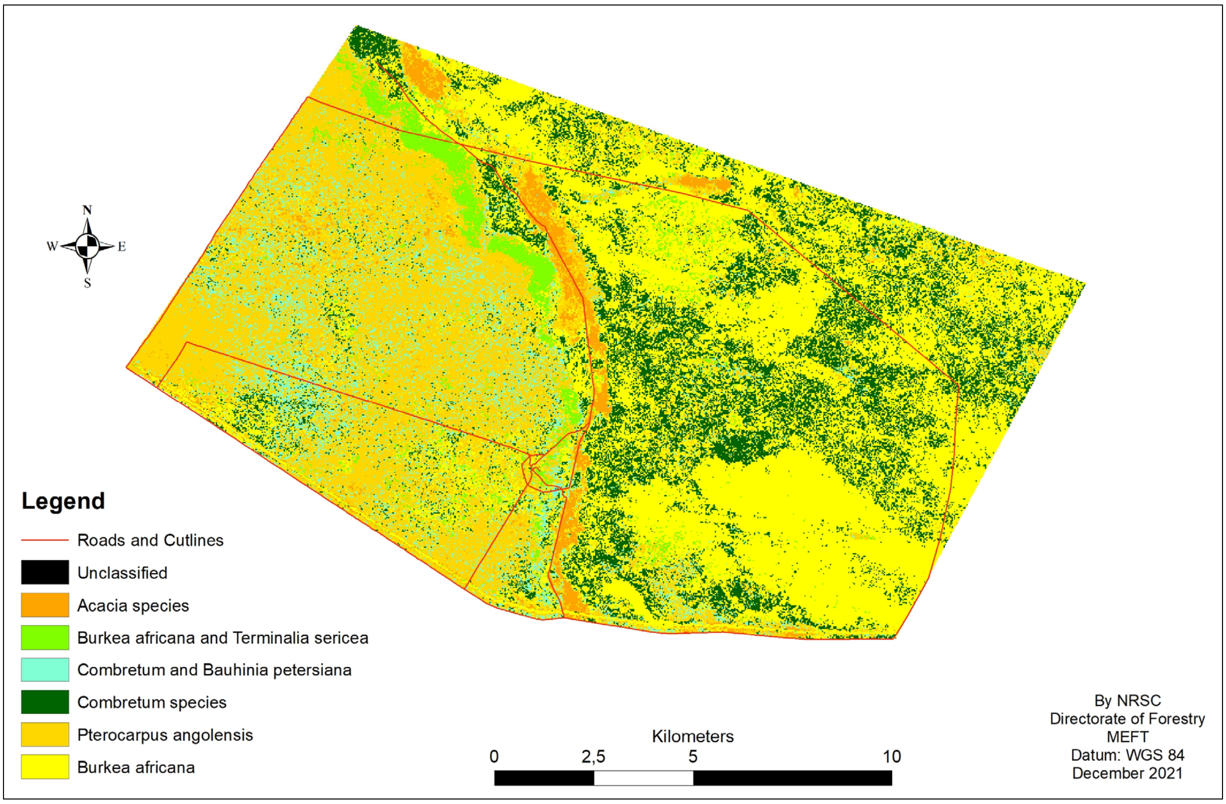

***Figure 3:*** *Dominant vegetation species in the Kanovlei State Forest.*

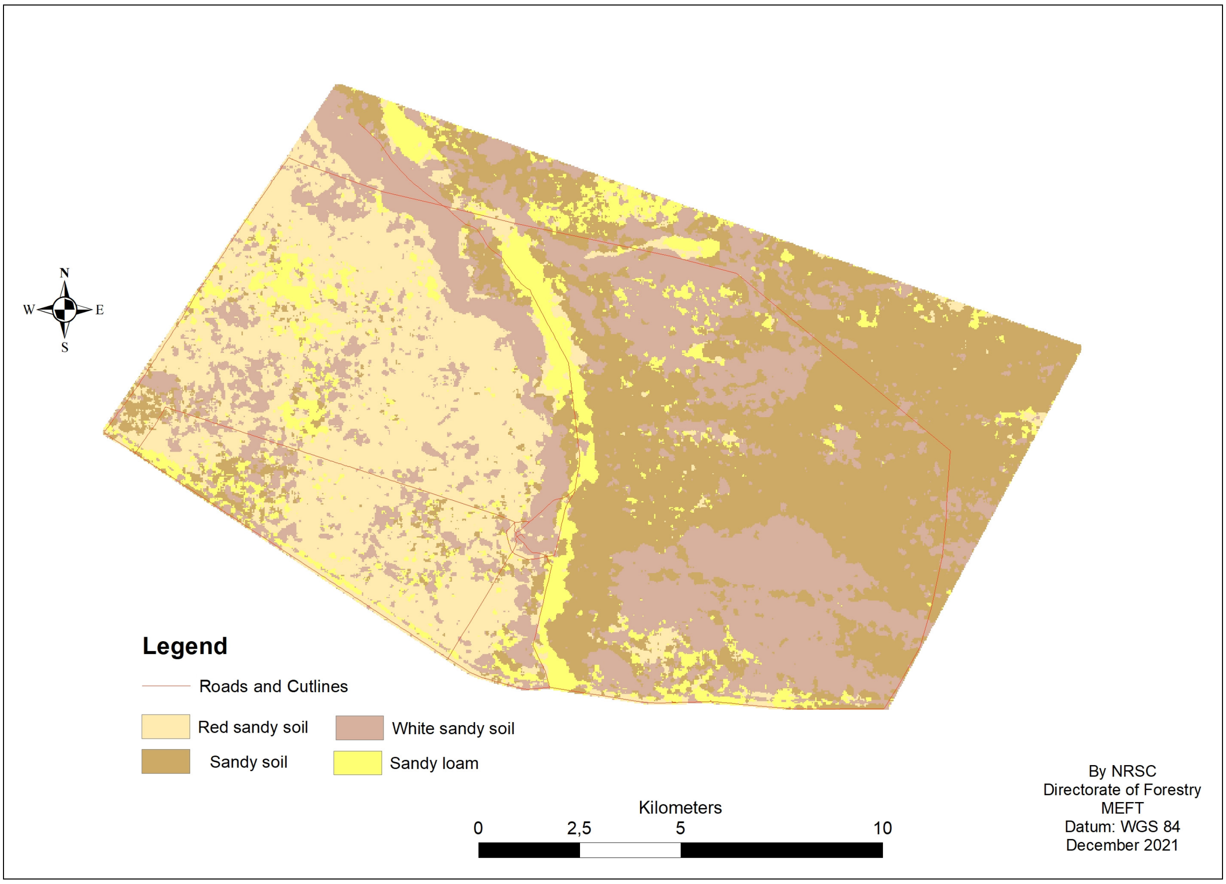

***Figure 4:*** *Soil types in the Kanovlei State Forest.*

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# Common Fiscal (*Lanius collaris*) Linnaeus, 1766: comparative biometrics, moult data and criteria for the determination of age and sex

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## CONTENTS

## ABSTRACT

We present measurement and moult data for both subspecies groups of Common Fiscal (*Lanius collaris*) that occur in Namibia: for 235 Southern Fiscals (*L. c. subcoronatus*) ringed in Namibia and nine Northern Fiscals (*L. c. capelli*) in Zambia. We compare our observations of the moult process and our records of active brood patches with previous breeding records from Namibia (Brown *et al.* 2015) to gain a better understanding of the species' annual cycle. In addition to the account of moult data in adults, we give those of first-year birds and describe in detail the plumage development through the discernible age groups: from fledgling to juvenile and immature, as well as second-year birds and adults. Furthermore, we discuss the possibility of a second generation of juvenile feathers as described in Palaearctic passerines, including the *Laniinae*, which has not yet been reported in the literature on African birds. Based on photographic evidence, we discuss the different plumages that we observed during more than 15 years of ringing. We add notes on interrupted moult, bi-focal moult, residual feathers of former plumage, recaptures and site fidelity, and precipitation and related numbers of shrikes. This monograph supplements published data and is intended to encourage further discussion and research relating to: subspecies measurements and description of juveniles of different subspecies, the different phases of feather growth of the juvenile plumage and their developmental relation to post-juvenile moult, the occurrence of residual feathers from former plumages throughout the different age groups, and the complexities concerning the overlap of moult and breeding (including double and multiple broods).

**Keywords:** age; biometrics; brood patch; common fiscal; *Lanius collaris*; moult; northern fiscal; plumage; sex

## 1. INTRODUCTION

Species and subspecies of Namibian birds are underrepresented in research and literature of southern African birds. To help address this shortcoming, we present our measurement and moult data on the Common Fiscal (Figure 1), supplementing the information available for this data-deficient species and its various subspecies. Additionally, we compare our Namibian moult records with other recorded breeding events (Brown *et al.* 2015), to place the moult process into the annual life cycle of the species.

Between 2002 and 2020 we ringed Common Fiscals and collected data on their measurements and moult in southern Africa. Our field excursions occurred mainly in Namibia, during the summer months between November to April. In this article, we present our observations on 235 Southern Fiscals (*L. c. subcoronatus*) and nine Northern Fiscals (*L. c. capelli*).

## 2. SITES AND METHODS

Our data on Southern Fiscals were collected in Namibia, mainly in the arid savanna along the eastern edge of the Namib-Naukluft Park (Farm Sphinxblick), at the Spitzkoppe, and in Swakopmund.

***Figure 1**: Adult male Common Fiscal* (L. c. subcoronatus). *Sossusvlei, October 2019. Photo courtesy of Eckart Demasius.*

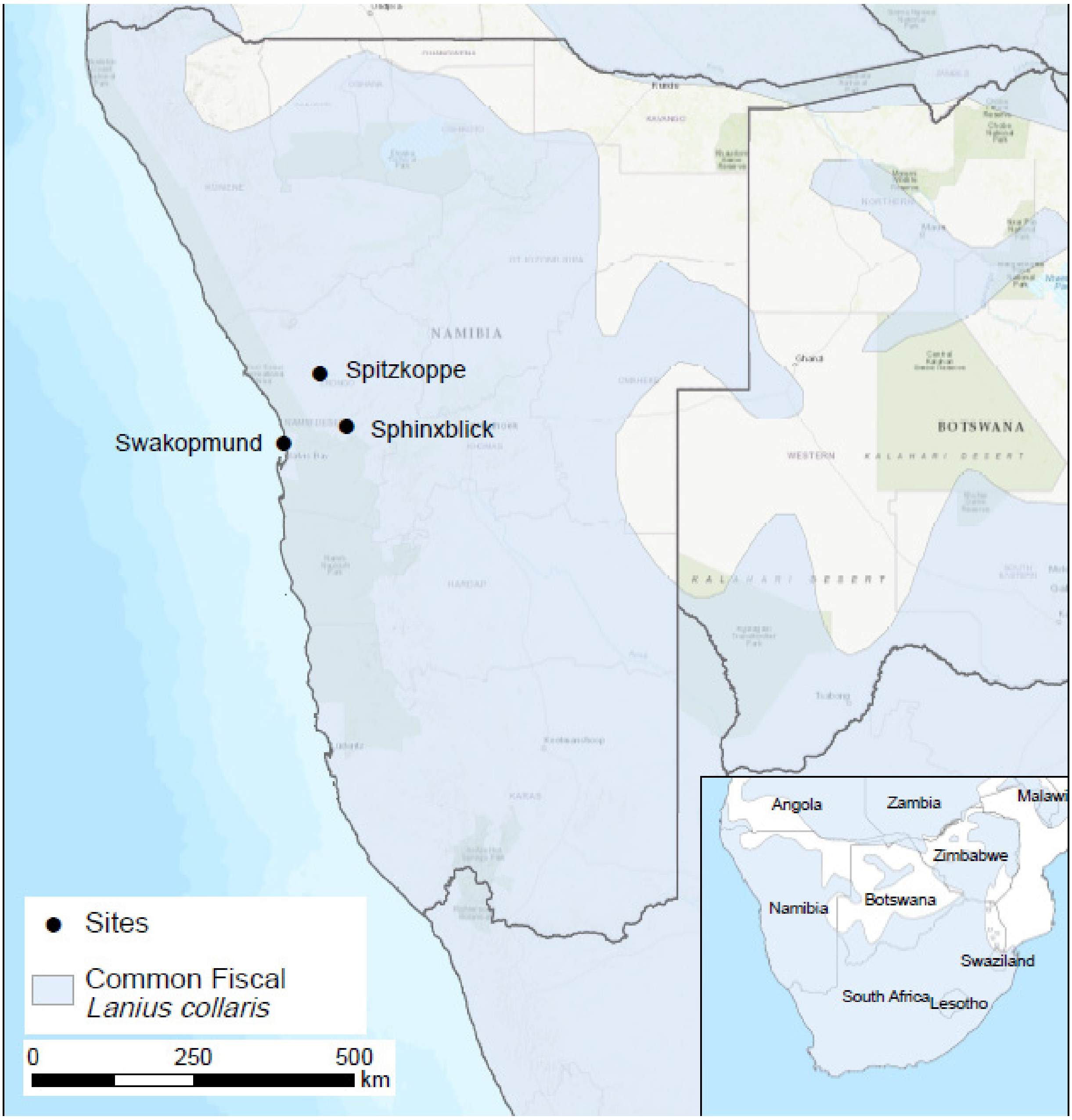


***Figure 2**: Distribution of the Common Fiscal in southern Africa, downloaded from www.iucnredlist.org on 18 May 2019. Black dots designate sites where data were gathered.*

Our data of Northern Fiscals stem mostly from north-western Zambia. If not mentioned otherwise, all photographs were taken by the authors on the Farm Sphinxblick, in the Erongo region of Namibia, and show subspecies *L. c. subcoronatus* of the Southern Fiscal. Ringing localities are presented in Figure 2 and descriptions and photos of the sites can be found in Appendix 1.

### 2.1 Distribution and Sites

Southern Fiscals were mainly ringed at the Farm Sphinxblick (Figure 3; 22°29'S, 15°27'E), at Spitzkoppe (21°50'S, 15°09'E), and a few on the artificially watered golf course in Swakopmund (22°40'S, 14°35'E) (Figure 2).

### 2.2 Bird Ringing and Measurements

Birds were ringed, measured, and moult scores were taken in accordance with the guidelines of the South African Bird Ringing Unit's (SAFRING) Bird Ringing Manual (de Beer *et al.* 2001, based on Svensson 1984). The birds' sex was determined by following phenotypical characteristics described in the common literature (i.e. Harris & Franklin 2000, Hockey *et al.* 2005, del Hoyo *et al.* 2008). The literature describing Afrotropical species reveals considerable gaps in the description of plumage through different age classes and a lack of more detailed criteria and precise terminology for ageing Namibian shrikes. Thus, we relied on the Palaearctic

***Figure 3:*** *Typical habitat at Farm Sphinxblick in the pre-Namib, a semi-arid desert and arid savanna. One Southern Fiscal is flying to the left, the other is sitting in the centre of the bush. April 2003.*

literature, as regards ageing and age development (see Appendix 2.4.4 Glossary for ageing).

## 3. CHALLENGES FACED

### 3.1 Terminology

In general, the terminology to describe the age of birds is far from consistent or clearly defined. Several core terms are used arbitrarily in both a general and a restricted sense. Terminology is not standardised and differs within Africa, but also widely between continents (see Schulze-Hagen 2019). We tried to be consistent in the use of terms and as clear as possible, mainly following Harris & Franklin (2000, pp. 50-51), Jenni & Winkler (2012), Shirihai & Svensson (2018, p. 17).

### 3.2 Age Categories in the Palaearctic and in the Afrotropical Region

The description of the age of Palaearctic birds falls into categories that follow the major seasonal changes. All Palaearctic passerines breed during (northern) summer and start moulting thereafter. Using a clear distinction of summer and winter, a clear distinction of the age differences of plumage can be made and named. Young birds can be categorised according to calendar years and, at any stage of their young lives, be clearly distinguished from adults based on plumage differences.

In the Afrotropical realm, these categories cannot be applied since breeding times of many species are variable. Breeding often takes place in December / January but can occur during all calendar months. Precipitation may trigger breeding in nomadic birds in arid environments (Dean 2004, and pers. obs.) and active Common Fiscal nests are recorded almost all year round in Namibia (see Brown *et al.* 2015 in section 4.4. Moult and breeding). An examination of the factors driving breeding needs more scientific attention. We are using the terms juvenile, immature (after the post-juvenile moult) and sub-adult for birds in their first year of life, and second year of life for birds with features that allow this specification.

### 3.3 Description

Age determination, the plumages at different ages of Namibian birds, and African birds in general, are not yet sufficiently researched and described. Stresemann & Stresemann (1966, p. 10) point out that some species display a second, and even a third, plumage before adulthood, representing immature and subadult plumages.

### 3.4 Distinction

In the literature, the two, quite distinctive, plumages of juvenile and immature birds are not being differentiated, if two different plumages are described at all (Chittenden *et al.* 2016, Dean 2005, Harris & Franklin 2000, Lefranc & Worfolk 1997, Nijssen *et al.* 2008). We observed three distinct plumages of the Common Fiscal and describe them in detail.

### 3.5 Growth Patterns

The juvenile plumage in most passerine species grows in two phases, in some species three, making it difficult to distinguish later growth phases from the post-juvenile moult. Beyond that, the post-juvenile moult can start before the juvenile plumage has fully developed (Kasparek 1981, p. 10), a feature not yet researched in African birds. Additionally, such observations are not currently found in the African literature. We describe one Common Fiscal with feathers from a supposed second phase, and one with feathers from supposedly different, yet undescribed phases (see 4.5.2 Second generation of juvenile feathers and 4.5.3 Transition to immature plumage by post-juvenile moult).

### 3.6 Moult Time Frame

The moult process is quite variable and seems to progress almost continuously in some species, in contrast to birds breeding in the northern hemisphere where there are more defined time frames for moulting. We describe several young birds in transitional plumages.

A glossary of terms is presented in Appendix 2.

## 4. SPECIES DETAILS

### 4.1 Taxonomy

In recent years, attempts to split the Common Fiscal into the Southern Fiscal (*L. collaris*) and the Northern Fiscal (*L. humeralis*) were made on the basis of distinct vocal differences (Harris & Franklin 2000a) and genetics (Fuchs *et al.* 2011). This distinction is still being discussed and, for the purpose of a clear distinction, we use the name Southern Fiscal for subspecies *L. c. subcoronatus* (our main research focus), Northern Fiscal (*L. c. capelli*) for the northern subspecies, and Common Fiscal (*L. collaris*) when we quote studies before the proposed split. Beyond that, there is much discussion and contradiction about the number of subspecies, their phenomenological expression, and their range (see Lefranc & Worfolk 1997, Harris & Franklin 2000, Fry *et al.* 2000, Dean 2005, Chittenden *et al.* 2012, Yosef & International Shrike Working Group 2019).

Following Dean (2005), the subspecies in our research area in central western Namibia would be *L. c. aridicolus*. Elsewhere (del Hoyo *et al.* 2016, Yosef & International Shrike Working Group 2019), this subspecies is restricted to the dune-fog zone of the Namib Desert in south-west Angola and north-west Namibia, located further north-west of our ringing area. We consider the studied individuals to belong to subspecies *L. c. subcoronatus*, following Yosef & International Shrike Working Group (2019) as the most comprehensive and most recently published document on the topic. Their subspecies description also best matches our field observations. See the discussion on these subspecies under "5.8. Unresolved questions" below.

### 4.2 Subspecies

Of the five southern African subspecies of the Common Fiscal, four occur in Namibia. The first three of the Namibian subspecies listed below belong to the "Southern Fiscal", and the fourth, *L. c. capelii*, to the "Northern Fiscal".

Subspecies ringed and researched in this study include:

- *L. c. subcoronatus* (Smith 1941) is reported in Namibia (excluding the coastal NW and extreme south), the extreme SE of Angola, in Botswana, SW Zimbabwe and in the north of South Africa (south to the NW Northern Cape and central Free State) (del Hoyo *et al.* 2016).
- *L. c. aridicolus* (Clancey 1955) occurs in the dune-fog zone of the Namib Desert in the SW of Angola and NW of Namibia, and
- *L. c. collaris* (Linnaeus 1766) occurs in the extreme south of Namibia, in southern, central and eastern South Africa, Swaziland, Lesotho and southern Mozambique (Maputo) (Yosef & International Shrike Working Group 2019).
- *L. c. capelli* (Bocage 1879) occurs in the extreme NE of Namibia, the distribution starting in south Gabon and southern Congo, reaching east to south of the Democratic Republic of Congo, the extreme SW of Uganda, Rwanda and Burundi, and south to Angola (except its south), Zambia and northern Botswana, possibly also to the extreme SW of Tanzania. All measurements of this subspecies were collected in Zambia.

### 4.3 Measurements

Table 1 and Table 2 present the measurements of *L. c. subcoronatus* and *L. c. capelli* respectively.

#### 4.3.1 Southern Fiscal (*L. c. subcoronatus*)

The data represent a large sample of measurements for *L. c. subcoronatus* (Table 1), which are not reported in standard publications, such as Dean (2005) or Harris & Franklin (2000). Our results confirm that variation between different subspecies plumage features is greater than size variation (Dean 2005). Our sample of *L. c. subcoronatus* was slightly lighter in weight than the nominate subspecies *L. c. collaris* (Dean 2005).

#### 4.3.2 Northern Fiscal (*L. c. capelli*)

Subspecies *L. c. capelli* did not have considerably different measurements to that of *L. c. subcoronatus* (Tables 1 and 2). Harris & Franklin (2000) noted that the Northern Fiscal's (*L. c. humeralis*) tails were consistently longer than those of *L. c. subcoronatus* of the Southern Fiscal. Our sample was too small to allow further conclusions.

### 4.4 Moult and Breeding

In Namibia, active nests of the Common Fiscal were observed during every month of the year except June (see Table 3). The young fledge at about 33 days after egg-laying, following 14-15 days incubation and an 18-19 days nestling period (Tarboton 2014).

#### 4.4.1 Moult and Breeding in Adults

##### 4.4.1.1 Moult of Adults: Post-breeding Moult

Due to the extent of breeding activity throughout most of the year, the subsequent complete post-breeding moult could be expected during all calendar months. Moult studies concerning Common Fiscals are scarce; in 22 museum specimens studied in the Eastern Cape (covering all calendar months except October and November), Craig (1983, p. 54) observed wing moult in February, March and April, suggesting a complete post-nuptial moult.

In a study of Common Fiscals in Ghana, Macdonald (1980) found breeding activity almost all year long, speculating that breeding was "suspended during the moult" (p. 69), and deduced from the observation of family groups that the Common Fiscal produced two or even three broods. In our sample, we found three peaks of moult: in February, May, and August (Table 3). Since ringing was mainly undertaken during the southern summer, our sample sizes during May and August were much smaller, limiting our results.

Over the span of 16 years, we observed that moult started in the peak months of breeding, as previously reported for Namibia by Brown *et al.* (2015). Moult in the main cohort of about 125 individuals ringed from December to March first developed slowly between December and February (with a moult score slightly above zero in December, two in January and six in February), followed by a sudden increase in March, with a moult score of 16 (Table 3). The latter moult event may be explained by a second brood and the subsequent moult.

#### 4.4.1.2 Active Brood Patches

Brown *et al.* (2015) recorded active nests almost year-round, with a peak from November to February. In our sample, females with a fully active brood patch were observed from the end of December until mid-February; one brood patch showed breeding activity starting at the end of January, and withdrawing brood patches were found both at the end of November and during first ten days of March (Table 3).

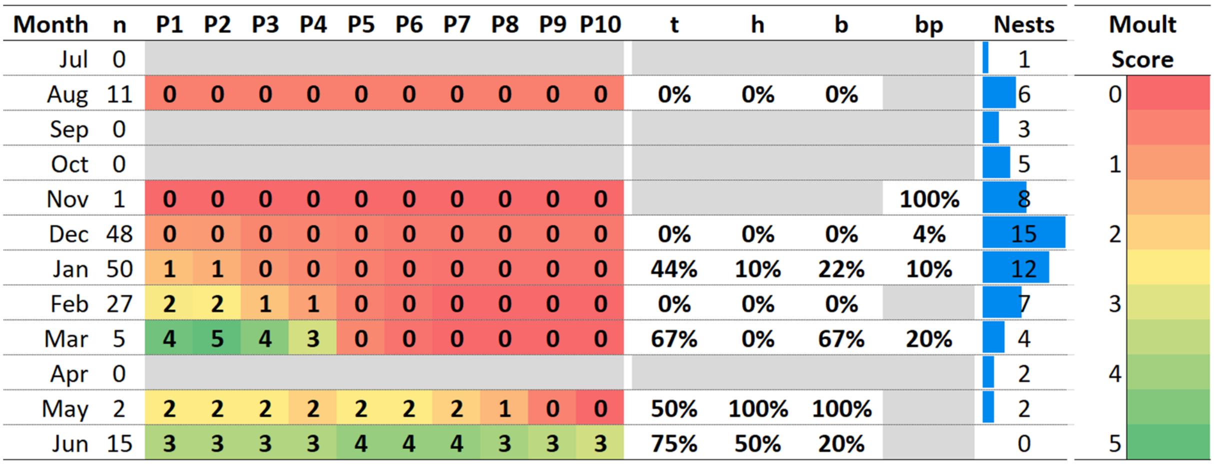
***Table 1:*** *Average adult and first-year body measurements (including standard deviation [SD], minimum and maximum) of* L. c. subcoronatus*. Measurements are grouped by age and sex of adult and first-year birds. SAFRING codes Age 5 and 6 refer to birds in their first year of life: Age 5 (0-6 months) considering birds still in mainly brown plumage, even after their post-juvenile moult; Age 6 (7-12 months) considering immature birds approaching full adult plumage.*

| **Grouping** | **Parameter** | **Wing (mm)** | **Tail (mm)** | **Tarsus (mm)** | **Culmen (mm)** | **Head (mm)** | **Mass (g)** |
|---|---|---|---|---|---|---|---|
| All adults SAFRING Code Age 4 | Mean ± SD | 97.5 ± 2.9 | 106.8 ± 5.3 | 26.8 ± 0.9 | 22.6 ± 1.4 | 43.9 ± 1.4 | 37 ± 3.1 |
| | Min-max | 90-107 | 92-118 | 24.9-28.8 | 19-26.9 | 39.8-48.6 | 29.4-51 |
| | *n* | 126 | 122 | 109 | 116 | 116 | 121 |
| Adults Unknown Sex | Mean ± SD | 100 ± 2.8 | 113 ± 2.8 | 26.7 ± 0.6 | 23.2 ± 1.2 | 44.4 ± 1.6 | 42.6 ± 4.2 |
| | Min-max | 98-102 | 111-115 | 26.2-27.1 | 22.3-24 | 43.2-45.5 | 39.6-45.5 |
| | *n* | 2 | 2 | 2 | 2 | 2 | 2 |
| Adult Males | Mean ± SD | 98.5 ± 2.6 | 108.5 ± 4.8 | 27.1 ± 0.8 | 22.9 ± 1.4 | 44.4 ± 1.3 | 37.9 ± 2.8 |
| | Min-max | 94-107 | 94-118 | 25.2-28.8 | 19.3-26.9 | 41.1-48.6 | 33.2-51 |
| | *n* | 75 | 73 | 67 | 70 | 70 | 72 |
| Adult Females | Mean ± SD | 95.7 ± 2.5 | 103.7 ± 4.5 | 26.1 ± 0.7 | 22.2 ± 1.4 | 43.1 ± 1 | 35.3 ± 2.5 |
| | Min-max | 90-101 | 92-118 | 24.9-27.4 | 19-24.7 | 39.8-45 | 29.4-40.8 |
| | *n* | 49 | 47 | 40 | 44 | 44 | 47 |
| First-year birds SAFRING Code Age 5 | Mean ± SD | 95.7 ± 5 | 100.2 ± 5.5 | 26.3 ± 0.8 | 22.1 ± 1 | 43.1 ± 1.4 | 36.7 ± 6 |
| | Min-max | 82-108 | 90-109 | 25-27.7 | 20.5-24.5 | 40.3-45.3 | 28.8-53.4 |
| | *n* | 21 | 19 | 13 | 15 | 15 | 18 |
| First-year birds SAFRING Code Age 6 | Mean ± SD | 96 ± 3.6 | 104.3 ± 5.4 | 26.5 ± 1.1 | 22.5 ± 1.2 | 43.6 ± 1.5 | 36.4 ± 3.8 |
| | Min-max | 88-106 | 92-116 | 22.1-28.3 | 19.4-25.7 | 36.6-46.4 | 29.8-58.2 |
| | *n* | 83 | 68 | 57 | 67 | 67 | 82 |

***Table 2:*** *Average adult and first-year body measurements (including standard deviation [SD], minimum and maximum) of the Northern Fiscal* (L. c. capelli)*. Measurements are grouped by age and sex of adult and first-year birds. SAFRING codes Age 5 and 6 refer to birds in their first year of life: Age 5 (0-6 months) considering birds still in mainly brown plumage, even after their post-juvenile moult; Age 6 (7-12 months) considering immature birds approaching full adult plumage.*

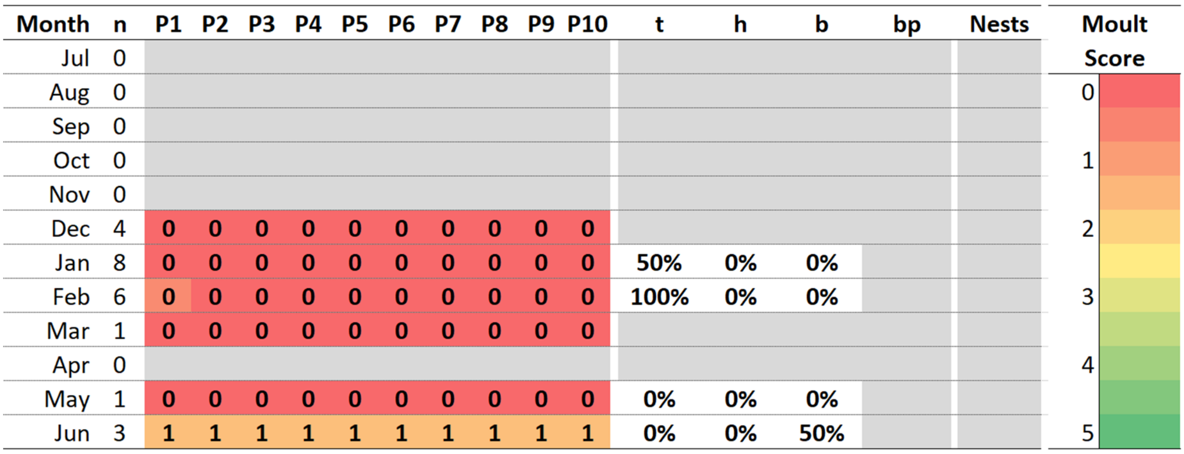
| **Grouping** | **Parameter** | **Wing (mm)** | **Tail (mm)** | **Tarsus (mm)** | **Culmen (mm)** | **Head (mm)** | **Mass (g)** |
|---|---|---|---|---|---|---|---|
| All adults SAFRING Code Age 4 | Mean ± SD | 94.4 ± 1.5 | 120.2 ± 7.3 | 25.6 ± 0.8 | 21.5 ± 0.7 | 43 ± 1.2 | 39.3 ± 1.5 |
| | Min-max | 92-96 | 112-131 | 24.7-26.7 | 20.5-22.5 | 41.9-44.9 | 38-41.2 |
| | *n* | 5 | 5 | 5 | 5 | 5 | 5 |
| Adults Unknown Sex | Mean ± SD | 93 ± 1.4 | 113.5 ± 2.1 | 25.1 ± 0.5 | 20.9 ± 0.6 | 42.2 ± 0.4 | 39.5 ± 1.6 |
| | Min-max | 92-94 | 112-115 | 24.7-25.4 | 20.5-21.3 | 41.9-42.5 | 38.3-40.6 |
| | *n* | 2 | 2 | 2 | 2 | 2 | 2 |
| Adult Males | Mean ± SD | 95.3 ± 0.6 | 124.7 ± 5.5 | 26 ± 0.8 | 21.9 ± 0.5 | 43.5 ± 1.4 | 39.2 ± 1.7 |
| | Min-max | 95-96 | 121-131 | 25.1-26.7 | 21.5-22.5 | 42.2-44.9 | 38-41.2 |
| | *n* | 3 | 3 | 3 | 3 | 3 | 3 |
| First-year birds SAFRING Code Age 5 | Mean ± SD | 90 ± 2.8 | 111.5 ± 0.7 | 25.1 ± 0.1 | 20.7 ± 0.8 | 40.3 ± 0.2 | 36.8 ± 1.3 |
| | Min-max | 88-92 | 111-112 | 25-25.2 | 20.1-21.3 | 40.1-40.4 | 35.9-37.7 |
| | *n* | 2 | 2 | 2 | 2 | 2 | 2 |
| First-year birds SAFRING Code Age 6 | Mean ± SD | 91 ± 0 | 109 ± 1.4 | 24.2 ± 1.5 | 19.7 ± 0.4 | 40.4 ± 0.9 | 37.2 ± 0.5 |
| | Min-max | 91 | 108-110 | 23.1-25.2 | 19.4-20 | 39.7-41 | 36.8-37.5 |
| | *n* | 2 | 2 | 2 | 2 | 2 | 2 |

***Table 3:*** *Extent of primary feather moult of adult Southern Fiscals. Values are average moult scores of each primary for n number of birds per month sampled. The colour gradient is shown on the side. The tail (t), head (h), body (b) and brood patch (bp) are expressed as a percentage of birds assessed showing signs of moult. Nest count values of the Common Fiscal for Namibia are taken from Brown et al. (2015). No moult records were collected during the months marked grey.*



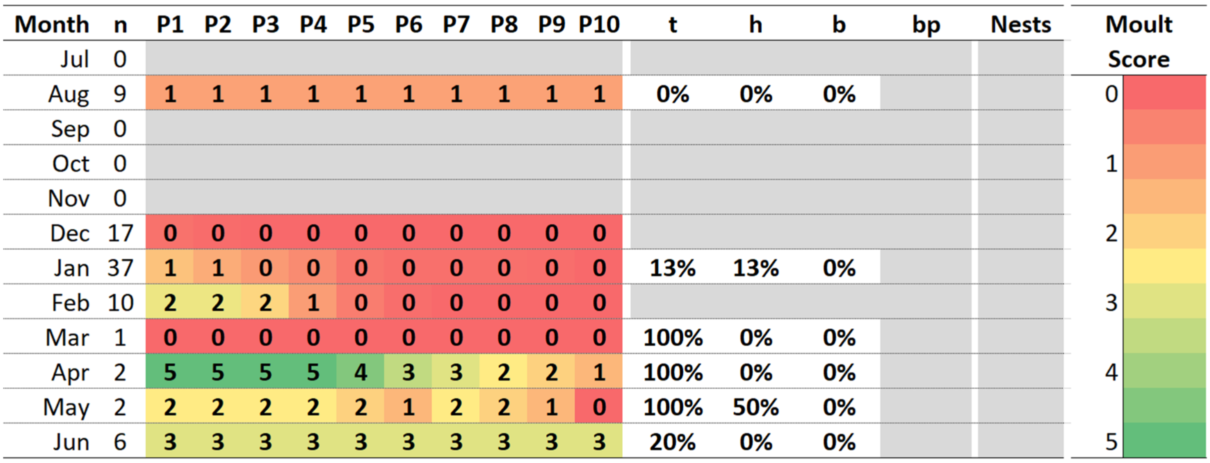
| Month | n | P1 | P2 | P3 | P4 | P5 | P6 | P7 | P8 | P9 | P10 | t | h | b | bp | Nests | Moult Score |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Jul | 0 | | | | | | | | | | | | | | | 1 | |
| Aug | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0% | 0% | 0% | | 6 | 0 |
| Sep | 0 | | | | | | | | | | | | | | | 3 | |
| Oct | 0 | | | | | | | | | | | | | | | 5 | 1 |
| Nov | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | 100% | 8 | |
| Dec | 48 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0% | 0% | 0% | 4% | 15 | 2 |
| Jan | 50 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 44% | 10% | 22% | 10% | 12 | |
| Feb | 27 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0% | 0% | 0% | | 7 | 3 |
| Mar | 5 | 4 | 5 | 4 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 67% | 0% | 67% | 20% | 4 | |
| Apr | 0 | | | | | | | | | | | | | | | 2 | 4 |
| May | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 0 | 0 | 50% | 100% | 100% | | 2 | |
| Jun | 15 | 3 | 3 | 3 | 3 | 4 | 4 | 4 | 3 | 3 | 3 | 75% | 50% | 20% | | 0 | 5 |

***Table 4:*** *Extent of primary feather moult of first-year Southern Fiscals (SAFRING code Age 5). Values are average moult scores of each primary for n number of birds per month sampled. The colour gradient is shown on the side. The tail (t), head (h), body (b) and brood patch (bp) are expressed as a percentage of birds assessed showing signs of moult. No moult records were collected during the months marked grey.*



| Month | n | P1 | P2 | P3 | P4 | P5 | P6 | P7 | P8 | P9 | P10 | t | h | b | bp | Nests | Moult Score |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Jul | 0 | | | | | | | | | | | | | | | | |
| Aug | 0 | | | | | | | | | | | | | | | | 0 |
| Sep | 0 | | | | | | | | | | | | | | | | |
| Oct | 0 | | | | | | | | | | | | | | | | 1 |
| Nov | 0 | | | | | | | | | | | | | | | | |
| Dec | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | 2 |
| Jan | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50% | 0% | 0% | | | |
| Feb | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100% | 0% | 0% | | | 3 |
| Mar | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | |
| Apr | 0 | | | | | | | | | | | | | | | | 4 |
| May | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0% | 0% | 0% | | | |
| Jun | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0% | 0% | 50% | | | 5 |

***Table 5:*** *Extent of primary feather moult of immature (SAFRING code Age 6) Southern Fiscals. Values are average moult scores of each primary for n number of birds per month sampled. The colour gradient is shown on the side. The tail (t), head (h), body (b) and brood patch (bp) are expressed as a percentage of birds assessed showing signs of moult. No moult records were collected during the months marked grey.*



| Month | n | P1 | P2 | P3 | P4 | P5 | P6 | P7 | P8 | P9 | P10 | t | h | b | bp | Nests | Moult Score |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Jul | 0 | | | | | | | | | | | | | | | | |
| Aug | 9 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0% | 0% | 0% | | | 0 |
| Sep | 0 | | | | | | | | | | | | | | | | |
| Oct | 0 | | | | | | | | | | | | | | | | 1 |
| Nov | 0 | | | | | | | | | | | | | | | | |
| Dec | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | 2 |
| Jan | 37 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13% | 13% | 0% | | | |
| Feb | 10 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | 3 |
| Mar | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100% | 0% | 0% | | | |
| Apr | 2 | 5 | 5 | 5 | 5 | 4 | 3 | 3 | 2 | 2 | 1 | 100% | 0% | 0% | | | 4 |
| May | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 0 | 100% | 50% | 0% | | | |
| Jun | 6 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 20% | 0% | 0% | | | 5 |

#### 4.4.1.3 Timing of Breeding, Multiple Broods and Moult

In his evaluation of 1147 records from south of the Kunene and Zambezi, Cooper (1971a) found only four definite examples of double and two cases of triple brooding. He concluded that there is rarely more than one successful brood per year. Cooper (in Marshall & Cooper 1969) mentions finding young birds in May and September. This could be interpreted as double brooding or indicate a long breeding period. Priest (1948) and Toschi (1950) recorded two, and Bütticker (1960) recorded two to five successful broods, the latter over a period of four subsequent years. More research is needed throughout the breeding range to clarify this question and local differences.

### 4.4.2 Moult of First-year Birds

Harris & Franklin (2000) report post-juvenile moult of the body feathers between January and June in South Africa, and wing and tail moult between February and June. Our small sample of first-year, still brown Southern Fiscals showed tail moult in January and February and some primary moult in February and at the beginning of June, corresponding to birds hatched some months before (Table 4).

In immatures, the primary moult shows three peaks: one beginning moult in August, the main cohort starting in January, and a third in May, when the former group was completing its moult (Table 5).

## 4.5 Plumage Development

We identified three distinct plumages after the nestling period: a finely barred brown juvenile plumage, a more uniform, blackish, brownish and white post-juvenile plumage that we refer to as immature plumage, and the black and white adult plumage. In a few cases, we observed a fourth, unbarred plumage after a second growth of the juvenile feathers. In the literature, the features of juveniles and immatures often seem to be merged and the term "juvenile" is being used for immature birds to distinguish a young bird from an adult. A detailed description of the development of hatchlings, including the plumage, is given in Marshall & Cooper (1969).

Like for other passerines in the region, more research is needed to describe moult processes precisely, and their corresponding phenotypes at different ages, also to clarify which specific features distinguish birds in their second year of life from fully grown adults.

### 4.5.1 Juveniles

During its 2.5 weeks as a nestling chick, the Common Fiscal grows into its adult size and acquires its first feathered plumage. As the quantity of available nutrition is limited and the growth very fast, the number of feathers is reduced to the amount necessary to cover the bird with a low density of barbs and feathers (Figure 4).

Feather quality improves with the post-juvenile moult, as shown in the comparison of a recently fledged juvenile (Figure 5A) and an immature (Figure 5B). The fluffy, "hairy" body cover is being replaced by "real" feathers, the indistinct grey barring on the chest is replaced by a light vermiculation on plain whitish underparts. The colour of the legs turns from pink to blackish, the colour of the bill from horn to blackish.

### 4.5.2 Second Generation of Juvenile Feathers

In most passerine species, the juvenile plumage grows in two (or even three) distinct and separate phases (Jenni & Winkler 2012, p. 29). This transition in feather growth is described in detail for passerines: for several warbler species observed in captivity on a daily basis (Gwinner 1969, Berthold *et al.* 1970, p. 311) and for 50 wild, resident and short and long distance migratory passerines (Dorsch 1993).

The juvenile feathers grow in veins, starting in the back and following a distinct sequence. The second and third feather sets grow in lines along the outside of these veins, adding parallel veins covering the body almost fully. "These late growing feathers were downy along the veins on the belly and chest, and contour feathers on the sides of the neck, chest and belly, and upper middle and lower back" (Berthold *et al.* 1970, p. 314).

Of the *Lanius* family, this process is known for the Lesser Grey Shrike (*L. minor*): “A second generation of juvenile feathers starts sprouting from the fourteenth day of life. This process encompasses almost all body feathers and takes at least two weeks for keratinisation” (Thiede in Bub 1981, p. 119). Our observations point toward a parallel development in the Common Fiscal, which had not previously been described.

We did not find any photographic or published documentation of this process to compare our findings. Our hypothesis is that the individual shown in Figure 7 is in transition between juvenile and immature plumages, showing two different age groups of juvenile plumage. Patches of unmarked brown feathers can be seen on the mantle, beside the barred feathers of the first phase (*cf.* Figure 4B). We hypothesise that these feathers belong to the second growth phase. At the same time, this individual is already in its post-juvenile moult. The throat and the eyebrow are in the process of turning fully white, the white wing bar is forming, and the first black lesser coverts have appeared.

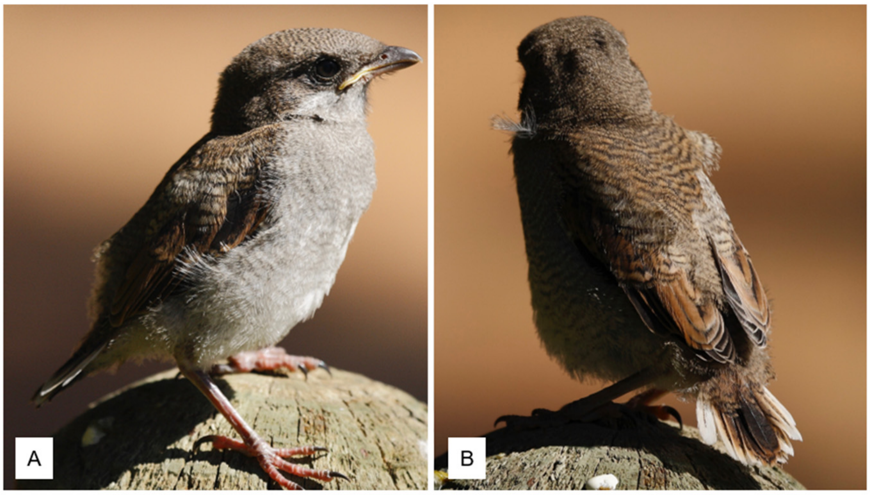


***Figure 4****: A recently fledged Common Fiscal of the subspecies* L. c. collaris *with finely barred plumage. (A) Horn coloured bill and prominent yellow gape flange, loose feather barbs and "baby face". (B) Barred back and growing wing and tail. Cape Town, October 2012. Photo courtesy of Loutjie Steenberg.*

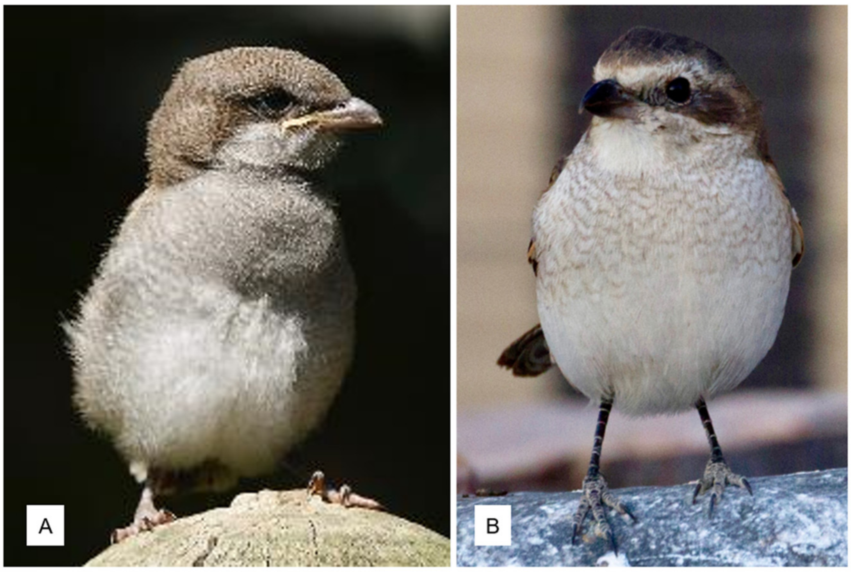


***Figure 5:*** *Comparison of juvenile and immature colouration and quality of the plumage on the chest of Southern Fiscals. (A) Juvenile* L. c. collaris *in its first plumage. Cape Town, October 2012. Photo courtesy of Loutjie Steenberg. (B) Immature* L. c. subcoronatus *after post-juvenile moult, with plain white throat and white underparts, and expressed mask and crown. Betesda Lodge, Naukluft, July 2011. Photo courtesy of Peter Lankhorst.*

***Figure 6:*** *Very young juvenile* L. c. subcoronatus *in its first plumage: (A) Close-up showing the "furry" chest, horn coloured beak, pale at the base, dark towards the tip, pink gape, no mask, and (B) plain brown nape and head (only hints of the white eyebrow), coverts edged buff with black sub-terminal band, barred rump and upper tail coverts, and brownish underparts (here upper chest visible). Farm Sphinxblick, Erongo region, December 2014.*

There is a clear difference in the colouration and quality of the feathers on the head, throat, chest and mantle, and the general impression of the young juvenile shown in Figure 6 with that of the more advanced juvenile individual in Figure 7, with feathers considered to be from the second juvenile phase. Note that similar features are still apparent in the immature birds in Figures 8 and 9.

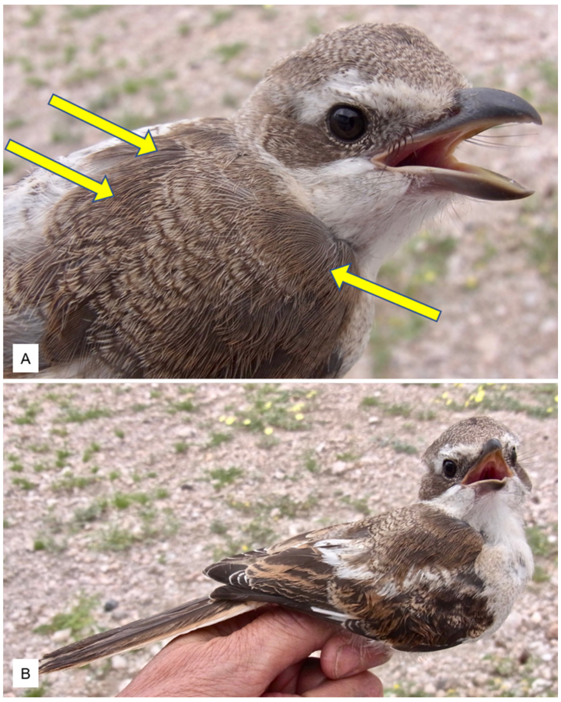


***Figure 7:*** *Common Fiscal with feathers of the two phases of the juvenile plumage and first feathers of the immature plumage. (A) Close-up showing barred feathers of the first phase, and plain brown feathers of the second phase of the juvenile plumage; tiny "tooth". (B) Uniform brown parts of the second phase on mantle and mask; white supercilium, wing bar and first blackish coverts of immature plumage; yellow-pink palate. Farm Sphinxblick, Erongo region, February 2014.*

***Figure 8:*** *Young Common Fiscal* (Lanius c. collaris) *presumably in transition to adult plumage. South Africa, February 2013. Photo courtesy of Loutjie Steenberg.*

### 4.5.3 Transition to Immature Plumage by Post-juvenile Moult

A partial post-juvenile moult in Southern Fiscals involving the body feathers, but not remiges and rectrices, starts at 2-3 months of age and is completed by 4-7 months (Harris & Franklin 2000, p. 174). As the Common Fiscal breeds almost year-round (Brown *et al.* 2015b), we expected a post-

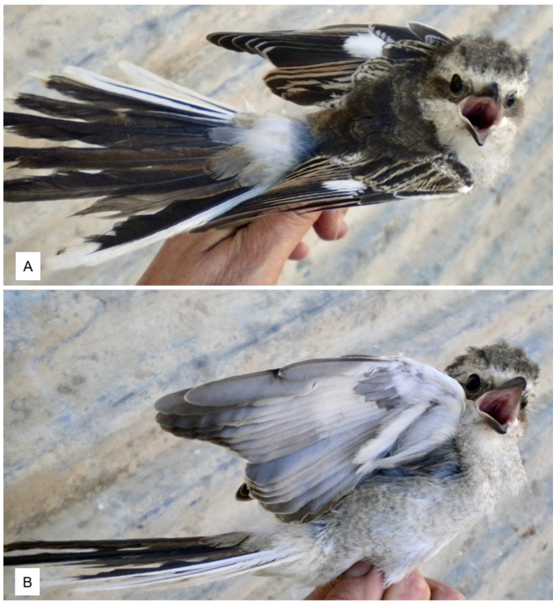


***Figure 9:*** *Complaining juvenile Southern Fiscal in transition to immature plumage: (A) throat and chest slightly barred; primaries with white tips and secondaries with buffy edges; some tail feathers replaced, now black with white tips and contrasting white edges on outer rectrices; rump turning white. (B) With fresh plain underwing, juvenile barred chest and flanks with immature white new patches. Often young birds held in the hand to be ringed complain as a defence strategy. Adults would eagerly bite. Farm Sphinxblick, Erongo region, December 2009.*

***Figure 10:*** *The wing with finely marbled inner webs at the wing patch and a first plain white, adult scapular between vermiculated juvenile ones. Moult score 0. December 2009.*

juvenile moult to occur any time of the year. However, we found in our time-restricted sample, individuals in post-juvenile body moult only from December to February (see also Cooper 1971b).

We observed that young moulting Southern Fiscals do not moult from juvenile plumage into adult plumage but go through a distinct stage of immature plumage. The transition from juvenile to immature plumage seems to be variable, as described below.

The Southern Fiscal in Figure 8 has plain colouration. We did not find any comparable appearance depicted or described in any publications. Our hypothesis is that this individual is moulting from a second, plain, set of juvenile feathers into its adult plumage. It is not an adult yet, showing a mixture of features from different age groups, but only very fine barring and without vermiculation. The plain light brown upperparts turn into (immature) grey on top of the head and in the centre of the mantle, while the beak without a visible "tooth" is still horn coloured with the lighter base of a juvenile. The wing bar is completely immature/adult white, while the visible secondary shows a broad buff fringe that is entirely black in adults. The underparts are still slightly marked, with two spots of rufous on the flanks, which can be seen in juveniles of both sexes, but consistently only in females of subspecies *L. c. subcoronatus* (see also Figure 11).

As stated by Kasparek (1981, p. 10), the post-juvenile moult can start before the juvenile plumage is fully grown. We hypothesise that this is the case with the individual shown in Figure 9 and Figure 10. It seems to moult directly from the first, vermiculated plumage into the white and blackish immature plumage, in contrast to the bird in Figure 8. Head and mantle still have the "furry" quality and the underparts are clearly barred and buff with fresh white areas. The secondaries are edged rufous-buff, the beak is blackening, apart from the base, and the palate turns pink, losing its yellow tinge.

"The partial post-juvenile moult starts on the upper- and underparts and soon includes the marginal (lesser) coverts and feathers on the head. The under and upper tail coverts, as well as the median coverts, are shed next, followed by the greater coverts and later by the alula, tertials and rectrices" (Jenni & Winkler 2012, p. 32).

This short period of post-juvenile moult at the age of 2-5 months might explain the immaculate tips of flight feathers and coverts of the wing when the first adult-like plumage starts to appear with the first pre-breeding moult (Figure 11). Here, a row of black median coverts is visible as the first sign of the starting moult.

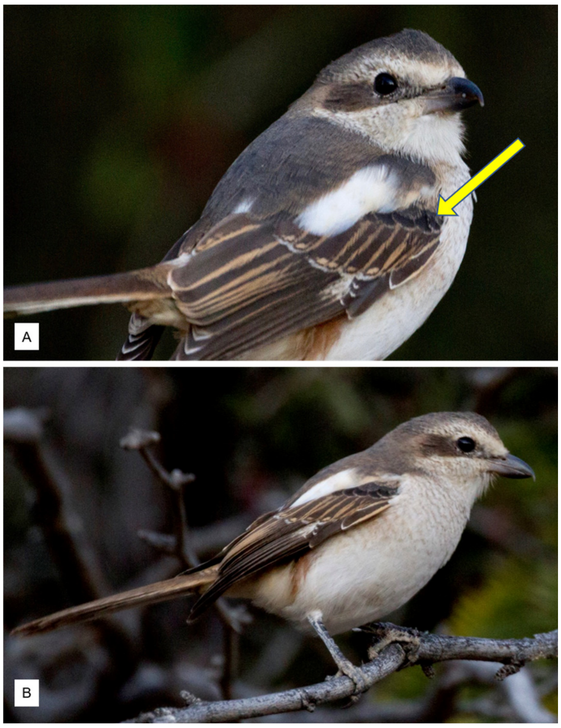


***Figure 11:*** *Upperparts (A) and underparts (B) of an immature Common Fiscal starting its pre-breeding moult into adult plumage with fresh adult black median coverts and plain white scapulars. Secondaries and greater coverts are edged rufous-buff. The plain grey mantle and crown, the brown ear coverts, the creamy underparts, and the vermiculated whitish chest are from the immature plumage. The greater coverts show a simple pattern of a rufous fringe, subterminal dot and white tip. In young birds, rufous flanks may occur in both sexes. The beak is becoming darker. Betesda Lodge, Naukluft, July 2011. Photo courtesy of Peter Lankhorst.*

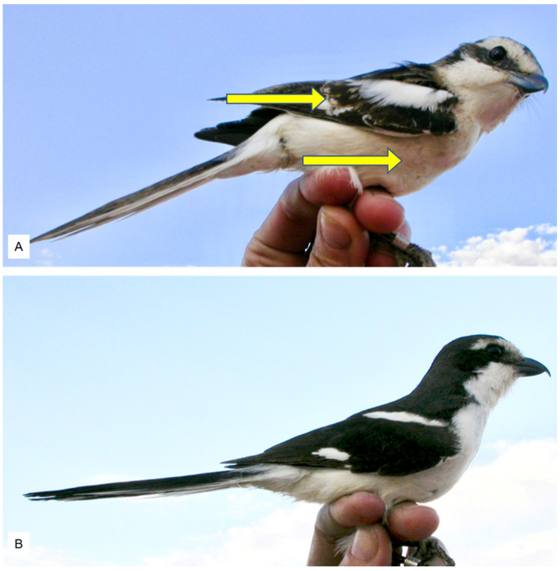


***Figure 12:*** *Comparison of immature and adult male Common Fiscals. (A) Immature male, with buff terminal spots on greater coverts, mask turning black, and a few vermiculated marks on the underparts. (B) Fully adult male, all black and white. Both Farm Sphinxblick, Erongo region, December 2003.*

### 4.5.4 Transition to Adult Plumage

During the transition into adult plumage, the last signs of immature plumage, such as vermiculated feathers on the belly, buff tips of the coverts and mixed colouration of the face mask, disappear. The bird now exhibits a clear black and white plumage (Figure 12).

### 4.5.5 Individuals in their Second Year of Life

Some second-year birds have changed entirely into a plumage resembling that of adults and only feather quality gives an indication of their age (Figure 13). We observed that some individuals in their adult plumage retain first-year feathers on the flanks (Figure 13D), the head (Figure 13C) and on the secondary coverts. Up until now, this has been described for the primary coverts and flanks of individuals of up to 18 months of age, after the immature stage and their pre-breeding moult (Harris & Franklin 2000). Rufous flanks may occur in both sexes (Harris & Franklin 2000, p. 173). Thus, the colouration of flanks alone cannot be used as a criterion to identify females reliably, but must be substantiated with other features like the grey colouration of the head and mantle in comparison with the black found in males.

Unlike the description in Harris & Franklin (2000), adult females in our sample always had plain white or slightly dull underparts. The underparts "tinged greyish with fine flecking (vermiculated)" (ibid., p. 173) belong to the immature plumage. This is apparent when comparing individuals in transition (Figures 8, 9 and 11) and second-year females (Figure 13).

### 4.5.6 Adults

Adults undergo a complete post-breeding moult with flight feathers replaced from January to April, and body feathers from January to October (Craig 1983, Harris & Franklin 2000, Dean 2005, see Table 4).

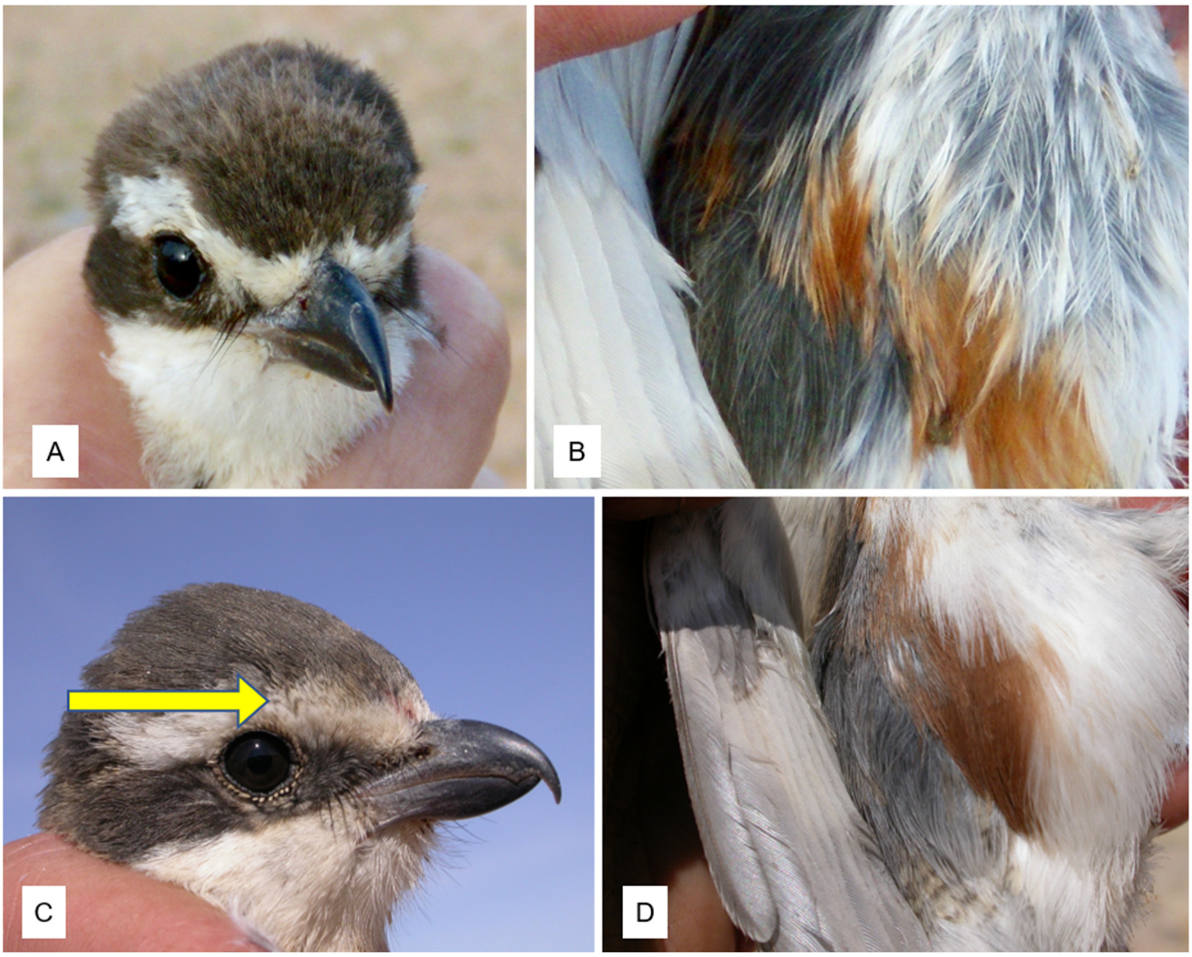


***Figure 13:*** *Second-year female. In January (A) with head moult. Note the different feather qualities between moulted forehead and un-moulted crown, blackish and compact resp. greyish and with loose barbs; (B) Flanks unevenly light and dark chestnut coloured, and chest with fewer feathers of lighter brown and of poorer quality with fewer barbs compared to the female seven months later in the year (D), January 2011. In August (C), with plain grey on the head and some residual first-year markings above the eye; and (D) uniform dark chestnut coloured sides and some barred body feathers, retained from juvenile plumage. August 2004. Farm Sphinxblick, Erongo region.*

In *L. c. subcoronatus,* the intensity of head and body colouration give an indication of the individual's sex, grey for females and intense black for males (Figure 14).

## 5. NOTES AND OBSERVATIONS

### 5.1 Interrupted Moult

On several occasions, we observed an interrupted moult in Common Fiscals. The term "interrupted moult" encompasses suspended and arrested moult. Both occur in the same sequence as a regular complete moult, but may temporarily be discontinued during migration or breeding. If the moult is suspended it will later resume, contrary to arrested moult, when moulting does not continue (Shirihai & Svensson 2018, p. 24).

During the year´s cycle, only a certain amount of energy is available for development. Both breeding and moulting are energetically demanding and, thus, rarely overlap in their timing. We found that Common Fiscals started moulting instead of breeding if there was a shortage of rain during the time of the "normal" breeding season, resulting in adverse conditions for raising chicks.

In arid environments, birds often show interrupted moult. As soon as rain falls, breeding begins. The shedding of feathers stops. Those feathers in active moult will continue to grow to their full length. Thus, the wing will show fully grown new flight feathers beside old ones of full length. We observed this over 20 years in many species, including Red-billed Spurfowl (*Pternistis adspersus*), Namaqua Sandgrouse (*Pterocles namaqua*), Cape Turtle Dove (*Streptopelia capicola*) Laughing Dove (*Spilopelia senegalensis*), Namaqua Dove (*Oena* capensis), Dusky Sunbird (*Cinnyris fuscus*) and numerous other passerine and non-passerine species.

Due to our restricted ringing season between November and March, we were not able to follow up if the moult was definitely interrupted and a new moult cycle would be started after breeding, or if the moult was resumed after a time of suspension during breeding activity.

### 5.2 Bi-focal Moult

On very rare occasions, we also recorded *L. collaris* moult at two locations of the wing at the same time (Figure 15).

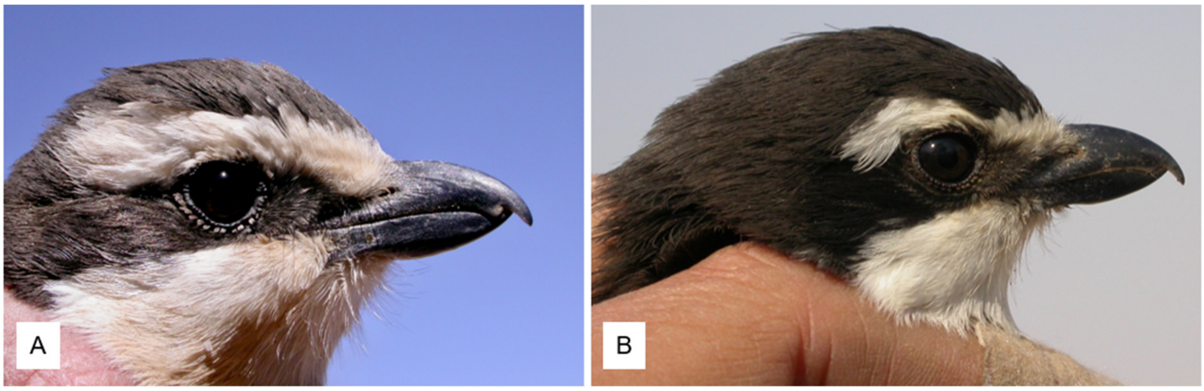


***Figure 14:*** *Colour-based comparison of both sexes of Southern Fiscal: (A) head of adult female with greyish head markings, August 2004, and (B) head of adult male with black head markings. August 2003. Both Farm Sphinxblick, Erongo region.*

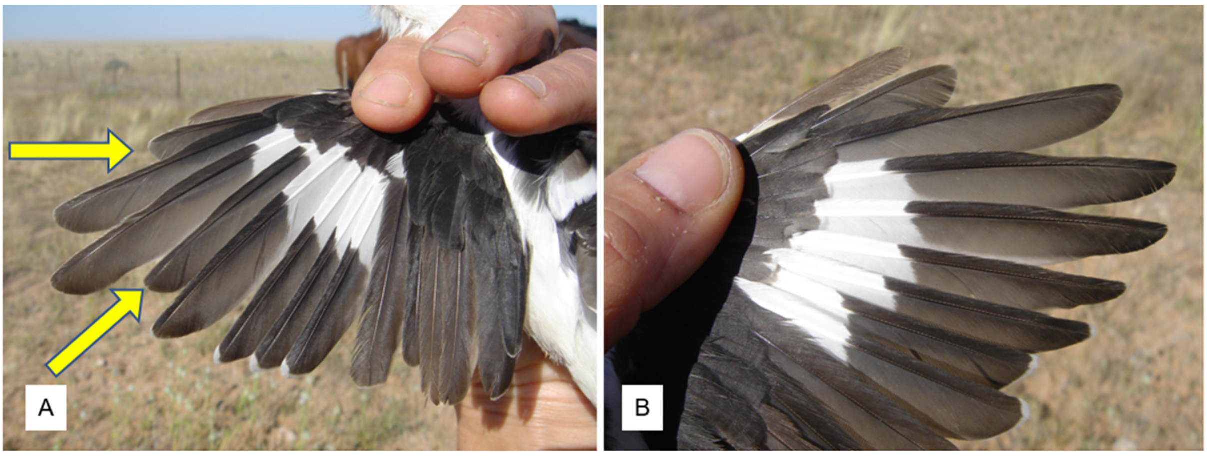


***Figure 15:*** *Exceptional moult on one individual with two moult foci on both wings: (A) left wing with primary moult score of 5555425430; (B) right wing with primary moult score of 5455555320. May 2006.*

### 5.3 Residual Feathers from a Former Plumage

Harris & Franklin (2000, pp. 173-174) point out that buff-tipped primary coverts (and sometimes rufous flanks) of the juvenile plumage are retained up to about 18 months of age. We found not only buff- or white-tipped primary coverts, but mainly greater coverts of a former plumage.

***Figure 16:*** *(A) Juvenile from Figure 5: markings on the edge of the coverts dull and little distinct. December 2014.(B) Immature after post-juvenile moult displaying three-coloured markings with light rufous, white and buff on dark coverts. January 2005. (C) Adult in its second year with white belly, fresh black greater coverts, secondaries retained from immature plumage with rufous edges and residual coverts with vermiculation. December 2003.*

***Figure 17:*** *Adult female, see rufous on flanks, with 11 primaries. The arrow marks the place between primaries and secondaries. All primaries are fully grown. January 2016.*

We surmise that a distinction must be made between residual feathers of the juvenile and the immature plumages. While juvenile greater coverts have a brownish edge, the greater coverts of the immature, post-juvenile plumage show light rufous edges on the outer vane of the feathers with dark markings and one or several vermiculated subterminal dark bars between white or buff stripes on the tips (Figure 16).

### 5.4 Eleven Primaries

Only once did we find an extra primary in both wings, with a total of 11 instead of the usual 10 primaries (Figure 17).

### 5.5 Recaptures and Site Fidelity

Out of 235 ringed individuals in our study in Namibia, 25 were recaptured (9.6%) and four were caught three times. All occurred at the same location and waterhole of the original ringing, except for two birds that moved several hundred meters. The longest tracking record for any individual in our sample was almost 8 years (14 February 2005 to 10 January 2013, SAFRING number CC70573), followed by four individuals of 6 years (19 December 2009 to 26 December 2015, SAFRING number CV25884; 11 December 2009 to 27 December 2015, SAFRING number BH22151; 19 December 2009 to 26 December 2015, SAFRING number CV25884), two with 5 and one with 4 years.

### 5.6 Parasites

Of 300 Common Fiscals we examined all over southern Africa, about 2% were infected by parasites: mites, feather flies and ticks. Two individuals in Namibia hosted great numbers of ticks: One adult in January 2006 had 20 ticks, and one juvenile in December 2014 hosted more than 30 ticks (Figure 18). We were not able to identify the species with certainty. Species identification was narrowed down to the "cattle tick" *Rhipicephalus* (*Boophilus*) *microplus* and *Hyalomma marginatum* or *H. rufipes*. All three belong to the family of Ixodidae, or 'hard ticks' that display a hard shield on the front of their body.

***Figure 18:*** *Some of the ticks removed from a Common Fiscal in December 2014.*

They feed on the blood of reptiles, mammals and birds. In a survey of ixodid tick diversity in the Etosha National Park, Namibia, twelve different species were recorded (Turner *et al.* 2017) of which only *H. rufipes* was found in birds. *Hyalomma* ticks are recognisable by their striped legs, a feature we did not observe in our sample. Thus, we assume that the species removed was *R.* (*B.*) *microplus.*

### 5.7 Precipitation and Shrike Numbers

Unlike the fluctuation of numbers of migratory Lesser Grey Shrike (*L. minor*) and Red-backed Shrike (*L. collurio*) in response to substantial rainfall arriving from the north and (especially) the east, the numbers of sedentary Southern Fiscals appeared more stable. Numbers increased a year or two following peak rains in 2007, 2010, and 2015 respectively (Figure 19), presumably due to favourable food and breeding conditions. These lags in abundance are also seen in other species, lag length depending on the size and rate of increase of prey after good rains (Chris Brown pers. com. 2021).

### 5.8 Unresolved Questions: Discussion and Distribution of Subspecies

Our main research location for Common Fiscals was in the arid savanna of central western Namibia, about 65 km SE of Usakos, 100 km east of the coast and at an altitude of 1000 m above sea level (see Figure 2). In this area, we recorded subspecies *L. c. subcoronatus*, while *L. c. aridicolus* is found in the "dune-fog zone of the Namib Desert in SW Angola and NW Namibia" (Yosef & International Shrike Working Group 2019). Fog from the Atlantic, encroaching only during distinctive weather patterns, rarely reaches the research area and is found more in the depression of the nearby Swakop River and lower lying areas descending towards the coast (Figure 20).

***Figure 20:*** *One of the rare occasions when fog occurred in the morning at the edge of our research area. Farm Sphinxblick, Erongo region, about 65 km SE of Usakos, 100 km east of the coast and at an altitude of 1,000 m above sea level, December 2009.*

One female shrike at the Spitzkoppe research site drew our attention, as she appeared particularly pale grey compared with all other Common Fiscals we had ringed in our area, just 80 km south of the Spitzkoppe (Figure 21).

*L. c. aridicolus* is considered as the palest of the subspecies (Dean 2005); see also depiction in Chittenden *et al.* (2012, p. 123), being paler and greyer above and having a whiter tail and purer silky white underparts (Yosef & International Shrike Working Group 2019). Based on plumage features, we speculate that this individual represents *L. c. aridicolus.*

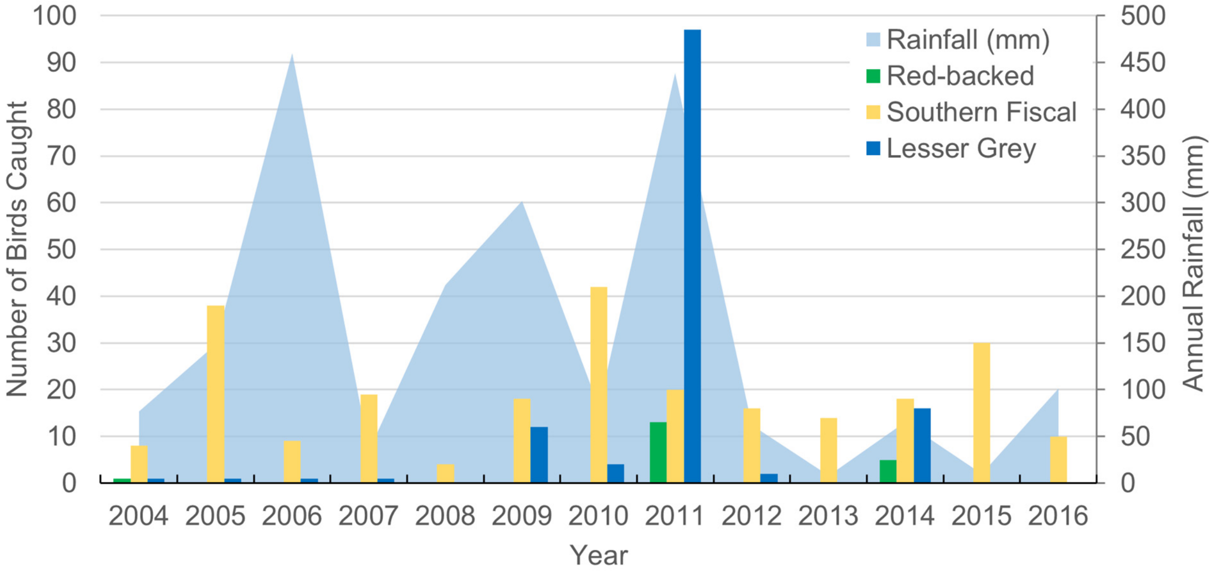


***Figure 19:*** *The numbers of Lesser Grey Shrike* (L. minor)*, Red-backed Shrike* (L. collurio) *and Southern Fiscal ringed per year in the pre-Namib savannah (22°25'S, 15°25'E) in relation to annual rainfall fluctuations. Rain data extracted by Tony Robertson from: http://earlywarning.usgs.gov/fews/product/48#download.*

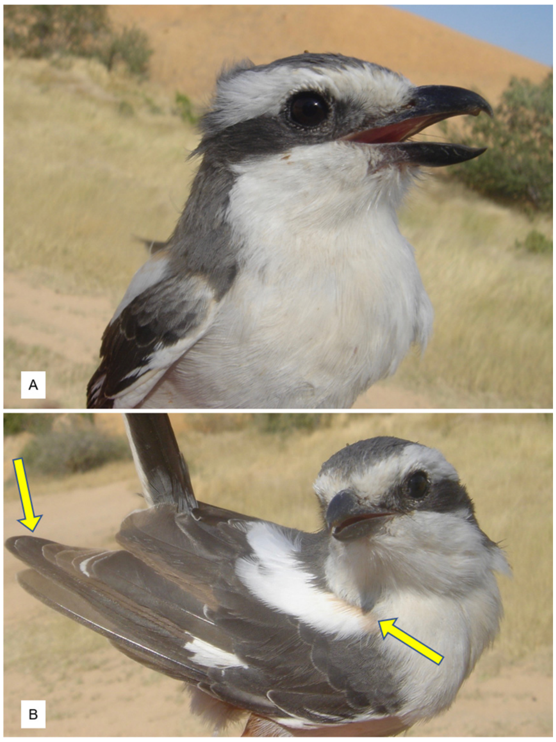


***Figure 21:** Very light grey adult showing freshly moulted, finely fringed median coverts and white edges on the alula; grey mask and neck; broad supercilium. A well-developed "tooth" points towards an adult. Also, this individual was a recapture (SAFRING BC56499). Unfortunately, no primary records could be found in the data base for this bird to be more specific about is age and possible movements. (A) Close-up. (B) It showed a few rufous feathers on the shoulder (see arrow). The moult, also, was exceptional: 0000555444, meaning that the first four innermost primaries were old, and the subsequent moult had started in the centre of the wing (see arrow). Spitzkoppe, June 2006.*

Occasionally, extensive movements of *L. c. subcoronatus* have been recorded (Forsberg 1992, Fraser & McMahon 1994, both cited in Dean 2005). It remains uncertain whether similar movements occur in other subspecies, in our case *L. c. aridicolus*, moving south through the desert to find suitable shrike habitat at the Spitzkoppe?

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## APPENDIX 1: SITE DESCRIPTIONS

The locations are sorted by country, then in alphabetical order. Site descriptions and dates are noted below each photograph.

### 1.1. NAMIBIA

1.1.1. Farm Sphinxblick, between Usakos and the Namib-Naukluft Park, Erongo region (22°29'S, 15°27'E) and surroundings.

***Landscape 1:*** *Arid plains savanna of the pre-Namib at the edge of the Namib-Naukluft Park after little rain. January 2011.*

***Landscape 2:*** *Dry riverbed in the arid savanna of the pre-Namib at the edge of the Namib-Naukluft Park. February 2017.*

***Landscape 3:*** *Arid plains savanna of the pre-Namib at the edge of the Namib-Naukluft Park following good rains. February 2005.*

### 1.1.2. Spitzkoppe (21°50'S, 15°09'E)

***Landscape 4:*** *Mountains and arid savanna. January 2011.*

***Landscape 5:*** *Mountains with sparse vegetation where water accumulates. January 2011.*

1.1.3. Swakopmund (22°40'S, 14°35'E). Artificially watered golf course in coastal desert.

**1.2. ZAMBIA**

1.2.1. Kanyama, Mwinilunga District (11°26'S, 24°39'E)

***Landscape 6:*** *Grassland with trees and bushes and riverine forest. December 2017.*

## APPENDIX 2: METHODS

For more detailed descriptions see Svensson (1984) and de Beer *et al.* (2001).

### 2.1. MEASUREMENTS

The following biometric measurements were taken:

**Wing:** Stop rule used to measure longest extent of the flattened wing (mm).
**Tail:** Rule used to measure from the tip of the rectrices to the root of the central pair (mm).
**Head:** Callipers were used to measure from the back of the head to the tip of the beak (mm).
**Culmen:** Callipers were used to measure from the skull to the tip of the beak (mm).
**Tarsus:** Callipers were used to measure from the notch of the intertarsal joint to the end of the tarsometatarsal bone, bending the foot downwards to approximately 90 degrees to the tarsus (mm).
**Mass:** An electronic gem scale was used (to the nearest 0.1 g).

For biometric measurements, recaptures are not reported.

### 2.2 MOULT

The following moult scores were recorded whenever possible:

**Active moult** of the 10 primary feathers, given by a score of 0 to 5.
**Active moult** of head, tail and body, based on absence or presence of moult (yes/no).

Whenever birds were recaptured during the same climatic season, we did not take them into account for moult scores. Recaptures after a time of one year or more were included in moult calculations.

### 2.3 SEX

Sex was determined by plumage colouration, and, if possible, cloacal shape, distance and shape of the pelvic bones, and occurrence and size of a female or male brood patch. We only considered the data of fully developed, active brood patches.

The brood patch is likely to develop shortly before incubation starts, in females always, but also in males to an extent that corresponds with their active participation in breeding. The skin of the body surface with which the adult bird has contact with the eggs, is naked and looks swollen and, as the blood vessels increase in size and number, the skin turns dark red. When the young have hatched, the area starts returning to normal conditions. The naked patch shrinks, the skin becomes paler and finely wrinkled, then dry scales appear. Shortly after the young fledge, the skin returns to normal, while the new feathering on the belly will occur only during the next complete, post-breeding moult, which might start soon after breeding (Svensson 1984, pp. 38-39, and pers. obs.).

Birds were classified as either male, female, or unknown. Due to uncertainty, those identified as ‘possibly male’ or ‘possibly female’ (as per de Beer *et al.* 2001) were grouped into the unknown category.

### 2.4 AGE

#### 2.4.1 General Determination of Age

Age was determined by plumage features (colour and pattern of feathers; moult features, abrasion, feather quality, shape of remiges and rectrices); eye colouration; beak colouration, shape and wear; gape flange colour, extent and quality; leg skin colouration and softness/dryness, and mainly by a combination of the above features.

#### 2.4.2 Additional Criteria for Ageing Young Birds

In addition to the common age markers mentioned above, young birds show subtle features that help to define their age. Considering the wide variability of individual expression, none of these features is sufficient to serve as a stand-alone criterion for accurate ageing. Nevertheless, these features considerably support the accurate ageing of individuals.

**Feather Quality**

The first plumage, in its first and second feather generation, is often still of lower quality. This reflects in higher transparency of the flight feathers and in feather shafts that are less stiff than those of adult birds. The body plumage is softer and silkier, on the head or chest fluffy (“hairy”), thinner and shorter in the neck, the barbs are looser.

**Baby Face**

The proportions of head and beak give the impression of a “baby face”.

### 2.4.3 Specific Ageing Criteria for *Laniidae*

Generally, it is assumed that it is not possible to distinguish different age groups if birds have already undergone their first complete moult. Birds with residual feathers from the juvenile plumage are an exception.

“Most juvenile Laniids are known to retain some of their greater primary coverts on the upper wing until the second complete moult” (Yosef 2008, p. 378). Examining the birds in detail, we found some individuals with single residual feathers not only on the greater primary coverts, but also in other body parts, like their flanks or on the head. We determined these birds as second-year individuals, relying on an evaluation of the quality and age of the general plumage and following ageing criteria.

### 2.4.4 Glossary for Ageing

Our glossary is a summary, among others, of Stresemann & Stresemann (1966), Bub (1981), Kasparek (1981), Shirihai & Svensson (2018). For more details, also see Jenni & Winkler (2020).

**“Adult”** describes a mature bird with clearly defined plumage. This term corresponds to the SAFRING ageing code of 4.

**“Juvenile”** refers to an individual with its first feathered plumage after down plumage, or as Pittaway (2000) puts it: “Juvenile has a precise meaning: It is the first immature plumage.” In passerines, the term “juvenile” corresponds to the SAFRING ageing code of 2. The post-juvenile moult is reputedly completed within about two to three months (Harris & Franklin 2000, p. 173), latest at 6 months of age (Dean 2005).

In the process of acquiring their plumage, birds can grow a **second generation of juvenile** or non-breeding **plumage** (Bub 1981, p. 119, Jenni & Winkler 2012, p. 29). In a more general sense, as often found in the literature, the term “juvenile” is also used to distinguish young from adult plumage.

We used the term only for birds before the post-juvenile moult.

**Post-juvenile moult** refers to the first moult of a bird, when the plumage, grown during nestling or juvenile period, is moulted. This moult may start even before the juvenile plumage has fully grown. In most *Laniinae* the post-juvenile moult is a partial moult (Cramp & Perrins 1993).

**“Immature”** describes a young bird of unspecified age, but before reaching adulthood. This term is used to describe a variety of plumage stages following juvenile plumage *sensu stricto*. It can include the juvenile stage if the accurate age is not known. In passerines, this term mainly corresponds to the SAFRING ageing code of 6 (i.e. 7 to 12 months) and 3 (immature, i.e. the recognisable age between juvenile and reaching adulthood).

We used the term only for a distinct plumage that occurs after the juvenile plumage (with its possible two or three growth phases).

**“Sub-adult”** describes the last stage of the immature plumage before reaching full adulthood.

**Calendar years and years of life**

In the northern hemisphere, moult processes are linked and related to climatic seasons: the summer season when breeding takes place and the winter season when birds possibly migrate.

In this context, **first calendar year** means from hatching, which occurs sometime during the middle of the year, to the 31st of December of the same year. **Second calendar year** means from the 1st of January of the year after hatching to the 31st of December of the same year.

During northern summer, individuals, especially the migratory ones, can clearly be categorised into these age groups by plumage features.

This classification cannot simply be transferred to Afrotropical species occurring in the southern hemisphere where the breeding season coincides with the northern winter and young birds may fledge, despite of a certain seasonality, during any month of the year. This is especially the case in areas where breeding is triggered by and depends on precipitation.

The SAFRING codes propose that ageing should be categorised by months and years of life, which often is based on estimation, following criteria such as plumage features and eye or beak colour. However, very little is known and published about the development of African birds during the first 24 months of their lives.

In general, the onset of the first complete moult occurs around the age of one year, when birds reach sexual maturity and enter the adult breeding cycle. There are, however, many exceptions to this general rule. Nomadic and smaller species in particular might complete their moult within a few months, as described for Red-billed Quelea (*Quelea quelea*) (Craig 2005) and possibly also in Lark-like Bunting (*Emberiza impetuana*) (pers. obs.). In species that display breeding plumage, the young often develop their first full adult breeding plumage after about 18 months (Kobie Raijmakers, pers. com. 1993, and pers. obs.).

According to our results and observations, the end of the **first year of life** of Afrotropical birds cannot be marked clearly using calendar terms.

We use the term **second-year bird** for individuals that are already in their (first) adult plumage but still show obvious signs of either juvenile or immature plumages, displaying characteristics that have not disappeared in a complete moult. In passerines, this mainly corresponds with the SAFRING ageing code of 7 (i.e. 1 to 2 years). Other features of ageing second-year birds, as described in sections 2.4.1 and 2.4.2, are taken into consideration to support our delineation.

In rare cases, we expect residual feathers of a former plumage to still be present during subsequent age stages, as is the case with adult Palaearctic birds, which retain individual feathers up to the second next moult cycle. This feature needs to be examined and considered case-specifically.

## 2.5 SAFRING CODES

Age 0 = Age unknown
Age 1 = Pullus
Age 2 = Juvenile
Age 3 = Immature
Age 4 = Adult
Age 5 = 0 to 1/2 year
Age 6 = 1/2 to 1 year
Age 7 = 1 to 2 years
Age 8 = 2 to 3 years
Age 9 = > 3 years