Master's thesis

NTNU
Norwegian University of Science and Technology
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Department of Biology

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Impala (*Aepyceros melampus*) responses to anthropogenic activities - An accelerometry approach in the Serengeti ecosystem

Master's thesis in Biology
Supervisor: Eivin Røskaft (IBI)
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AfricanBioServices

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Abstract

Human encroachment towards protected areas and their surroundings increases pressure on ecosystem services causing wildlife to adjust to a multitude of anthropogenic activities. In the Serengeti ecosystem, impala is subject to constant human-wildlife interactions whose nature may differ depending on the form of land-use encountered. This work examined differences in impala's behavioural patterns under contrasting contexts of anthropogenic activity: High-end tourism in Serengeti National Park and traditional pastoralism to the adjacent Loliondo Game Controlled Area. Behavioural responses were quantified using video-recordings of impala behaviour coupled with activity records measured by two-axis accelerometers. The *k*-nearest neighbours' algorithm and recursive partitioned decision trees were compared as classification methods to evaluate the ability of accelerometers to remotely identify behavioural categories. Overall high-performance metrics above 0.8 were consistently obtained for both classifiers. Behavioural categories Stationary, Feeding and Foraging were identified. Higher confidence unsupervised classifications of behavioural categories revealed impala to allocate more time to stationary behaviours in presence of pastoralists during the day, but to increase nocturnal foraging activity by 74% when comparing to touristed areas. These findings indicate adaptive responses of impalas towards different forms of anthropogenic exploitation, for which human habituation and temporal avoidance of livestock and pastoralists were suggested to be at the source of such adjustments. Furthermore, this work highlights the potential pertinence of activity sensors for their eventual use in conservation biology.

Table of Contents

I Introduction

The whole east African Rift Valley is considered to be one of the main bio-culturally diverse hotspots in the world (Sinclair and Arcese 1995, Myers et al. 2000, Mittermeier et al. 2003) and understanding not only its wildlife's habits, but its coexistence with humans, is a fundamental goal for conservation and management (Kideghesho 2008). The Serengeti National Park and adjacent management areas host countless anthropogenic activities which may have negative effects on the daily habits of numerous taxa (Dobson et al. 2010, Bartels 2016). Because of habitat loss and degradation, competition with livestock and high value as a food resource or for body parts, ungulates have traditionally been particularly threatened by human activities (Ogutu et al. 2009, Veldhuis et al. 2019), with some authors even questioning their future viability in large African protected areas (Brashares et al. 2001, Thirgood et al. 2004). Impala (*Aepyceros melampus)*, despite being one of the most abundant and widespread mammals in the system (Campbell and Borner 1995), represent the main resident species targeted for bushmeat (Hofer et al. 1996, Holmern et al. 2006), show increased sensitivity to higher trafficked roads (Lunde et al. 2016) and avoid cattle during the dry season (Fritz et al. 1996). More specifically, such disturbances are known to affect physiology and behaviour by increasing stress hormone levels (Lunde et al. 2016) and flight initiation distances (Setsaas et al. 2007), while also affecting habitat preferences in mixed ranches with domestic animals (Fritz et al. 1996). Nevertheless, their potential behavioural adjustments due to increasing human pressure are still poorly understood (Matson et al. 2005, Mulero-Pázmány et al. 2016, Jackson et al. 2017), although research in other African regions suggests an increment in nocturnal activity which may have costly consequences on fitness (Crosmary et al. 2012).

Given that human-induced environmental change affects wildlife behavioural responses (Sih 2013), the interdisciplinary approach of modern conservation science (Primack 2006) proposes the conceptual framework of "conservation behaviour" (Buchholz 2007), which builds a bridge between the interface of animal behaviour and conservation biology (Berger-Tal et al. 2011). Among other claims, such as the need of more behavioural theoretical input into conservation practices (Caro 2007), this discipline supports the argument of behaviour as a possible indicator of organismal and environmental state (Morris et al. 2009), a proxy which could be implemented in management (Kotler et al. 2007). These guidelines require that extensive data on behaviour is gathered (Lindell 2008), which is congruent with the idea of field monitoring as one of the pillars of successful conservation practices (Legg and Nagy 2006, Nichols and Williams 2006, Goldsmith 2012). However, the elusiveness and difficulty of studying certain species in their natural environment are a challenge to most current monitoring methods (Mennill et al. 2012, Connor et al. 2016) if fine scale behavioural and activity patterns need to be uncovered. While direct observations may provide important and detailed data (Rijksen 1978, Williams et al. 2006), human presence as observers may alter wildlife's natural behaviour (Schneirla 1950), and despite technologies such as camera traps reduce such confounding effects (O'Connell et al. 2010), data collection remains dependent on animals moving in front of such mechanisms (Schipper 2007).

Over the past few years, advances in radio-telemetry technologies (Cagnacci et al. 2010, Hebblewhite and Haydon 2010) have facilitated detailed and quantified studies on activity and behavioural patterns remotely (Whittington et al. 2011, Newmaster et al. 2013). Although more invasive, tools such as GPS loggers (White and Garrott 2012) and axial accelerometers (Laich et al. 2008, Brown et al. 2013) have shown remarkable potential. Axial accelerometers are a family of activity sensors that measure changes in velocity per unit of time – i.e. acceleration – relative to their neutral position when attached to a wildlife tracking collar (Hansen et al. 2007), generating a gravity measure that will vary depending on animal's posture and activity (Moreau et al. 2009). Because it is expected that each performed behaviour will have an associated scale of amplitudes of gravity measure, axial accelerometers allow researchers to identify behavioural patterns when animals are out of sight.

Among other studies, this instrument has allowed to remotely distinguish three different behaviours in sheep (*Ovis aries*) (Giovanetti et al. 2017), at least four in domestic cats (*Felis catus*) (Watanabe et al. 2005), and up to nine in human beings (*Homo sapiens*) (Foerster et al. 1999). Nevertheless, up to date reports on the use of accelerometers has mainly been of methodological nature (Moreau et al. 2009, Bidder et al. 2014, McClune et al. 2014), and few studies explore its uses for conservation besides conceptual reviews (Wilson et al. 2008, Wilson et al. 2015). As stated by Shephard and collaborators (2008); a "[…] small number of people currently use accelerometery to investigate animal behaviour, and it has not yet, to our knowledge, been directly applied to animal conservation issues” (but see Suraci et al. 2019). However, recent work, such as Brownscombe *et al.*’s (2013) on bonefish (*Albula* spp.), shows the pertinence of this device to provide ingenious management ideas, such as the use of recovery bags to mitigate predation risk in post-released angled fish.

Numerous approaches have been taken when linking activity data to discrete behavioural patterns, although the most common practice is to train a classifier by first going through a ground-truthing stage where different activity values are associated to different behaviours observed in the same time lapse (McClune et al. 2014). Even if some researchers have explored the possibility to manually interpret accelerometer signals (Laich et al. 2008, Shepard et al. 2008), the aim for this project was to automate the behavioural recognition of accelerometer data, a process that not only avoided classification subjectivity, but allowed the analysis of large amounts of data provided by modern sensors (Bidder et al. 2014). Recent meta-analysis (Gao et al. 2013, Bidder et al. 2014) and case studies elsewhere (Nathan et al. 2012, Ladha et al. 2013, McClune et al. 2014, Diosdado et al. 2015, Wang et al. 2015, Alvarenga et al. 2016) have shown that computational classifiers such as the *k*-nearest neighbours algorithm and recursive partitioned decision trees offer a good compromise between conventional implementation and high accuracy of classification. However, given the need to sample observational data to successfully complete the ground-truthing stage, current accelerometer research shows a strong bias towards the study of domestic and captive wild animals (Moreau et al. 2009, Heurich et al. 2012, Wang et al. 2015), where direct manual observations (Altmann 1974) or video recording are a significantly easier task (Campbell et al. 2013). A literature analysis conducted by Brown and collaborators (2013) shows that, up to 2013, less than 15% of all accelerometery research on animals had free-ranging wild mammals as their study species. To my knowledge, this work presents the first ever recorded attempt to remotely classify behavioural patterns in wild impala while examining the data from a conservation standpoint in the Serengeti ecosystem.

This thesis evaluated impala behaviour in the context of two different anthropogenic treatments, being recreational tourism in the Serengeti National Park and local pastoralist lifestyles in the adjacent Loliondo Game Controlled Area. Under which circumstance wildlife suffer the most severe negative impacts is subject of controversy (Roe 1997, Estes et al. 2006) given important aspects of management policy needing to collect conservation revenues (Laarman and Durst 1987, Boo 1990) while also empowering local communities (Nelson and Makko 2005, Snyder and Sulle 2011). The idea of nature-based tourism as a low source of alterations for biodiversity is now challenged in Africa and other parts of the world (Knight 2009, Geffroy et al. 2015, Gutiérrez et al. 2017, Penteriani et al. 2017), since scientific literature has traditionally focused on illegal hunting and human settlement as principal sources of animal disturbance (Arcese et al. 1995, Kaltenborn et al. 2005, Setsaas et al. 2007). On the other hand, very little is known about the relationship Maasai and pastoralist communities have with wildlife to the east of the Serengeti National Park (Goldman 2011, Msoffe et al. 2011), where "[…] poaching remains minimal" (O'Malley 2000) and animals densities for some taxa have been shown to be as high as inside of the park (Campbell and Borner 1995, Maddox 2003, TAWIRI 2010). Despite documented instances of conflict between local residents and wild ungulates, such as competition for resources with livestock (Prins 2000) or disease transmission (Ocaido et al. 1996, Bengis et al. 2002), coexistence is believed to be the general paradigm between wildlife and pastoralists to the eastern side of Serengeti National Park (Butt and Turner 2012).

By using axial accelerometers, this thesis intended to delve further into these interactions by investigating impala's behavioural adjustments in relation to contrasting anthropogenic activities. First, the suitability of axial accelerometers to remotely identify behavioural patterns from activity data in wild impala was evaluated. Then, differences in behaviour between individuals occupying a highly touristed protected area and a traditional pastoralist region were analysed through unsupervised accelerometer recordings. I predicted that: 1) Impala exposed to pastoralist activities would limit their movements and remain at rest during the peak hours of the day compared to areas with recreational tourism, given the need to decrease the temporal overlap with people and livestock. 2) Impala would make-up for this lack of diurnal activity by increasing their nocturnal movement and foraging behaviour, particularly when humans and livestock spend the night at a *boma*[1] leaving most feeding grounds available for wildlife. The research and management implications of this work were two-fold; first investigating the capacity of accelerometers to accurately identify behaviours in wild impala, and secondly showing their ability to answer conservation questions relevant to soundly managing biodiversity in east-African ecosystems.

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[1] *Boma*: Thorn-brush enclosure meant to shelter cattle from large carnivores at night.

II Materials & Methods

II 1 Study species

Impala (*Aepyceros melampus* ssp.) (Swahili: *Swala pala*) is a medium-sized antelope (40-65 kg) inhabiting the bush, woodlands and savannah borders of eastern and southern Africa (Jarman and Jarman 1973, Kingdon and Largen 1997). There are around 75,000 (± 9,000) common impala in the Serengeti ecosystem (TAWIRI 2010) with lower densities in open grasslands (Setsaas et al. 2007) such as the Southern Plains (Grzimek and Grzimek 1960). Impala are mixed feeders and have the ability to both graze and browse (Cerling et al. 2003), thus shifting forage species seasonally to ensure quality nutrition (Stewart 1971, Kos et al. 2012). Because of relative low specialization (Rodgers 1976), impala are able to maintain food resources around the year and develop large group sizes in their restrained resident home ranges (16.8 km^2) (Averbeck 2002)

Impala are socially divided in two different herd types consisting of bachelor and female family herds (Schenkel 1966), usually both roaming across territories held by solitary adult males (Jarman and Jarman 1973). It has been noted that female family herds are more cohesive than bachelor herds, where members are more independent in their activities (Schenkel 1966). Despite not sharing particular levels of relatedness or social hierarchy (Murray 1981), females in a group are believed to experience similar physiological states, body condition and a remarkable degree of synchronization (Jarman and Jarman 1973, Jarman 1974). Because of the more dependent nature among individuals of female family herds, this project decided to focus on the behaviour of female herds only, and by recording activity of one animal in the group it was assumed this to be an average measure for the whole group. Female family herds also include more individuals (Schenkel 1966) and the sex ratio in the Serengeti being skewed towards females (Setsaas et al. 2018), it was thought that this social category was the most suitable representative of the impala population in the different areas of study.

II 2 Study area

The Serengeti National Park (SNP) (14,763 km^2) and surrounding regions in northern Tanzania are unitedly known as the greater Serengeti ecosystem (Sinclair and Norton-Griffiths 1995) and constitute the general region where the study was developed (Figure 1). Recognized as a World Heritage Site by the UNESCO in 1981 (Sinclair et al. 2008), the park is the core area of the system and hosts the highest densities of impala (Setsaas et al. 2007). The SNP is a strictly protected conservation area -IUCN category II- (IUCN 1994) exclusively open to researchers, park staff, tourists and their supporting infrastructure where any form of animal husbandry or extraction of natural resources is strictly prohibited (Sinclair et al. 2008). More than 200,000 tourists visit the Serengeti annually (TANAPA 2003), which numbers are increasing rapidly leaving several million USD at the entrance gates every year (TANAPA 2005). Because of high impala densities and exclusive recreational land-use, we considered central SNP an optimal location to study the impact of tourism on impala behaviour.

On the other hand, the adjacent Loliondo Game Controlled Area (LGCA) (4,000 km^2) -IUCN category VI- bordering SNP to the east is considered a habitat and species management area where controlled and sustainable use of natural resources is encouraged following traditional methods of cultural significance when possible (IUCN 1994). In LGCA, activities such as human settlement, livestock grazing and agriculture are conducted mainly by indigenous populations of the Maasai and Sonjo groups (Ojalammi 2006) which have been inhabiting the area for centuries (Kideghesho 2008). Nomadic and semi-nomadic pastoralism is at the focus of 80% of the region’s population (Homewood and Rodgers 2004), where livestock is set to graze on pasture during the day and brought back to a *boma* in the evening (Semenye 1988, Kissui 2008). Among all management units in the Serengeti, the ones to the east are the most human-populated with overall 180,000 people living in the Ngorongoro district, which encompasses LGCA among others (Forum 2011). However, LGCA features low tourist activity, with the six main villages grossing around 110,000 USD on a yearly basis from foreign visitors (Kallonga et al. 2003). High subsistence human occupancy, low tourism and relatively high impala densities (TAWIRI 2010) were the main factors considered to choose LGCA as a region to assess the effects of human settlement and pastoralism on this species.

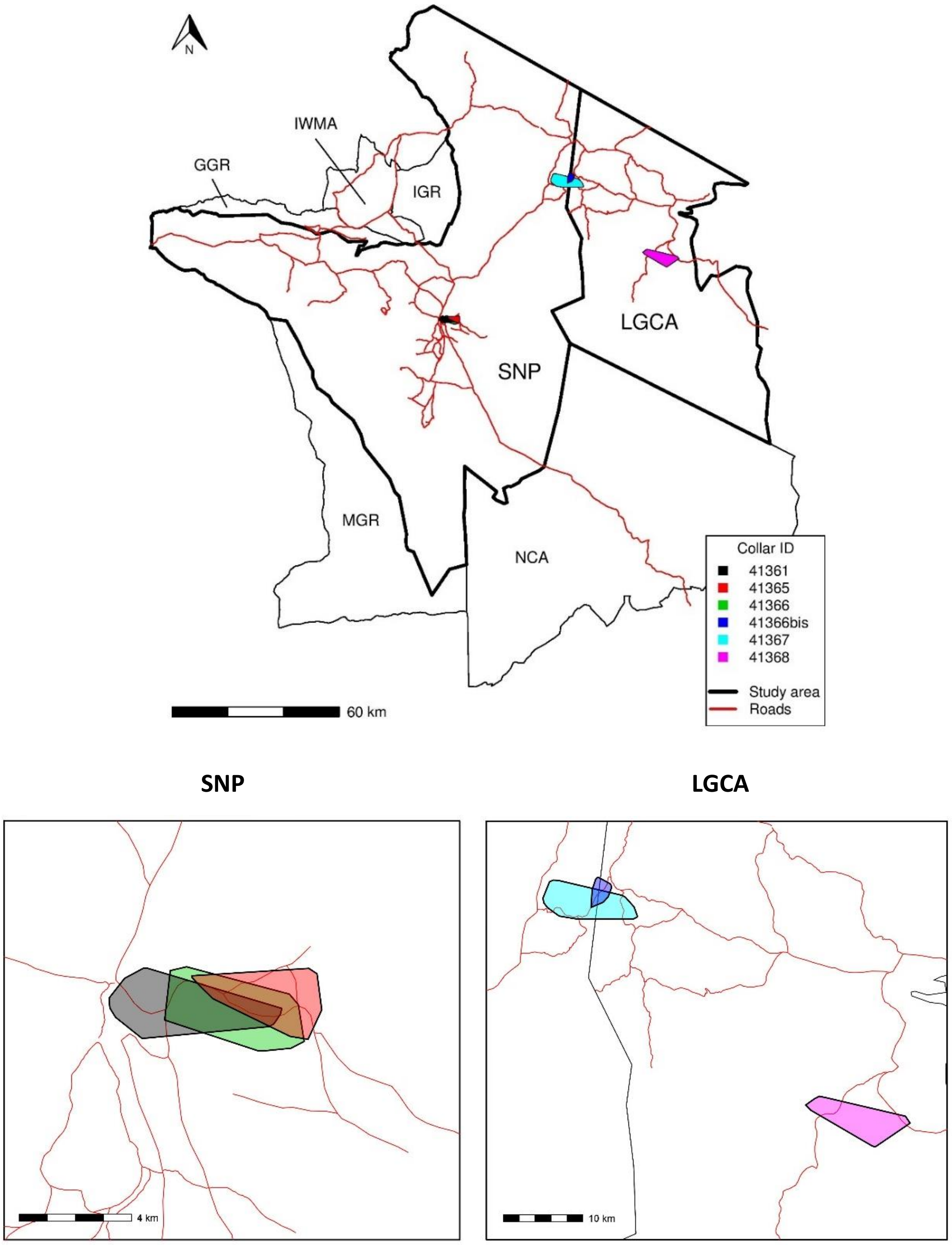

Figure 1. Top - Map of the management units constituting the Serengeti ecosystem. Bottom - Higher resolution MCP[2]s for all studied individuals in both areas of study. Abbreviations are: GGR; Grumeti Game Reserve, IGR; Ikorongo Game Reserve, IWMA; Ikona Wildlife Management Area, LGCA; Loliondo Game Controlled Area, MGR; Maswa Game Reserve, NCA; Ngorongoro Conservation Area and SNP; Serengeti National Park.

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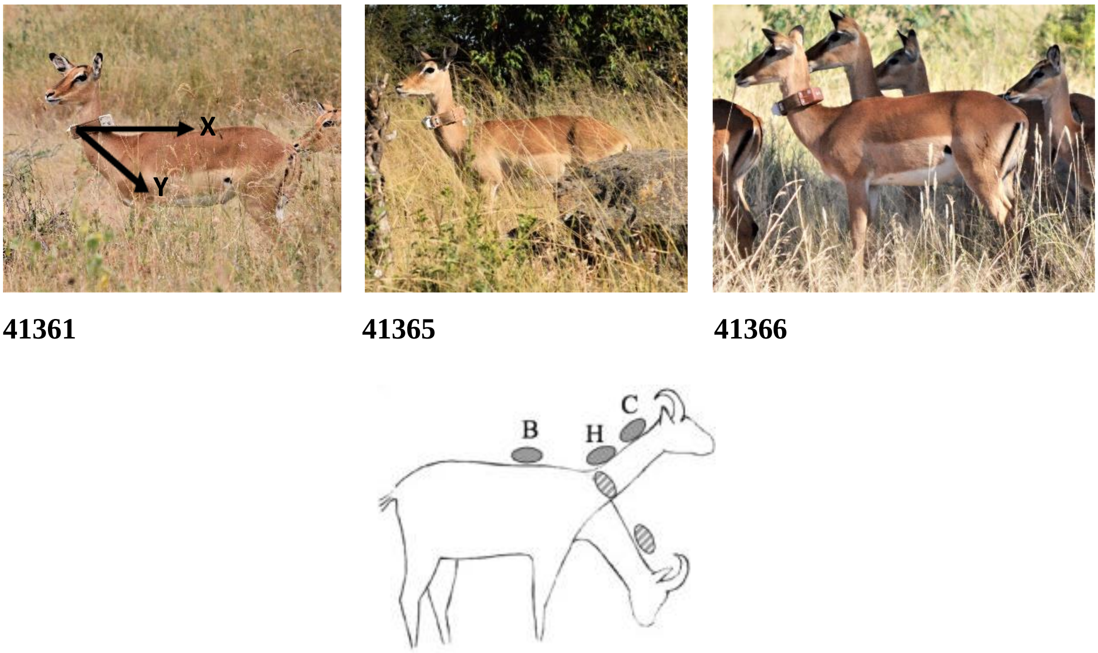
[2] Minimum Convex Polygon (MCP): Recommended measure of habitat area (IUCN 1994). Consists of the smallest polygon in which no internal angle exceeds 180 degrees containing all registered GPS positions.

II 3 Collaring and Two-Axis Accelerometers

Three adult female impala belonging to different resident herds (mean group size: $\bar{x}$ = 28 ± 14.8 SD) were equipped with GPS collars (collar identification numbers (ID): 41365, 41366, 41361; model GPS 4500 Lotek Wireless Inc., Canada) in central SNP (Figure 1). The collaring of individuals took place in June 11th (ID 41365), June 16th (ID 41366) and June 18th (ID 41361) of 2018 during the dry season. Adult individuals with good body condition were selected and slowly approached by a vehicle for immobilization using a dart containing 2 mg of etorphine and 20 mg of azaperone. Animals were down after 7 minutes approximately ($\bar{t}$ = 7 min 20 sec ± 2 min 4 sec SD) and the anaesthetic was reversed about 5 minutes later using 2 mg of medetomidine administered intravenously. Capture and handling procedures were approved and led by the Tanzania Wildlife Research Institute (TAWIRI). Collars were estimated to weigh less than 2% of the total body mass of an impala, which is under Cuthill's 5% rule of thumb to diminish abnormal effects on behaviour (Cuthill 1991). Therefore, we assumed that collared individuals didn't suffer from decreased survival when compared to the rest of the herd, and that their behaviour was consistent with other herd-mates. The collar was fitted in the dog-harness position (Figure 2) as suggested by Moreau and collaborators (2009), since this mounting system shows the highest identification scores for subtle behaviours such as head-up and down movements. Collars included a two-axis motion activity sensor – two-axis accelerometer (TAA) – recording forward and backward motions (*Surge*; X-axis) as well as sideways and rotary motions (*Sway*; Y-axis) using gravitational acceleration (Figure 2). The signal is converted to gravity units (g or m/s^2) whose raw data can be displayed graphically for further processing. Since different activity measurement modes and sampling intervals can be chosen, the sensor recorded activity measures every second on each axis (Lotek Wireless Inc. User's manual) and then averaged these readings into 80-second time intervals (i.e. epochs; option 4, Lotek Wireless Inc. User's manual). Such calibration was considered a good compromise between detail of resolution of activity and improved compatibility with already collected data in LGCA, which had a sampling interval of 4 minutes (240 seconds; collar identification numbers (ID): 41366bis, 41367, 41368; Figure 1). In LGCA, only data from the same seasonal period as collars in SNP was used, where animals were collared by TAWIRI staff in May of 2017 with the same equipment as the three females in SNP, following a similar immobilization protocol. In order to access the data gathered by the

TAA, all animals had to be de-collared and the data was manually downloaded to a computer for further analysis. The de-collaring process took place during a two month-period towards the end of the dry season of 2018 (August and September).



41361 **41365** **41366**

Figure 2. Top – Pictures, collar positions and collar ID's of the three collared individuals in central SNP. Bottom - Examples of three different mounting positions in collars equipped with TAAs. It's been shown in goats that the dog harness position (H) shows better scores when discerning between head up and down movements. Chest belt (B) and neck collar (C) positions can also discriminate between behaviours, but mostly relative to the anatomical area to which they're attached to (torso and neck/head respectively) (Moreau et al. 2009). Impala were collared using H to evaluate TAA suitability to classify behavioural categories. Image taken and modified from Moreau and collaborators (2009).

II 4 Observations and videotaping

Collared individuals in SNP were filmed using a video-camera (HC-V210, Panasonic, Japan) for ground-truthing their behaviour following the collaring procedure. Intensive observational monitoring was carried within the next few hours of immobilization to ensure a good recovery from the drug treatment (Woodroffe 2001). Film sessions to record their continuous behaviour started the day after the collaring event and lasted from 5 to 10 days per individual ($\bar{x}$ = 8 ± 2.7 SD days) for a daily average of 1 h 23 min (± 14 SD min) of footage per collared animal (Table 1). Videotaping schedules where daily in many occasions and covered dawn to dusk periods of activity (7 a.m. to 6-7 p.m.) (Jarman and Jarman 1973).

Table 1. Descriptive statistics of the videotaping sessions.

Collar ID	Start of video recording	End of video recording	Total days of recording	Total recording time	Mean of daily recording time	SD
41365	6/12/2018	6/23/2018	10	14:30:01	01:36:40	01:13:41
41366	6/17/2018	6/24/2018	9	11:27:32	01:25:57	00:52:01
41361	6/19/2018	6/24/2018	5	05:37:20	01:07:28	00:16:55
					Grand mean	**Grand SD**
					01:23:22	00:14:46

In central SNP, wild impala are habituated to human presence and thus relatively easy to observe without significantly disturbing their natural habits (Nyahongo 2008, Bejder et al. 2009). By driving on both existing tracks and roads around the area, collared individuals were slowly approached by vehicle to a short enough distance to continuously video-record their movements without causing the animal to flee. To minimize possible confounding effects of the observer on the habits of impala, film sessions only started once the animals had stopped responding to the presence of the vehicle and its passengers. This required a few trial approaches where the distance between the car and impala was varied and noted to estimate an optimal interval. Collars where equipped with a Very High Frequency (VHF) transmitter that allowed the allocation of the animals in a few minutes using an antenna and receiver. As soon as recording started, footage was time-stamped using a GPS to ensure full synchronization with the activity data gathered by the TAA. Animals where filmed for as long as possible until lack of daylight or the collared individual moving out of sight. Additional data on habitat-type, weather, group-size and composition as well as other nearby species present when filming was also gathered in a field-datasheet. To ensure that the position of the collar remained consistent throughout the ground-truthing stage, daily pictures were taken from several angles and compared within and among study animals. This is important, since displacement and/or rotation of the collar would register different gravitational measures for a given behaviour that could inhibit the automated classification of behavioural patterns (Hansen et al. 2007).

II 5 Video processing

Video footage was revised and behaviours were identified and time-stamped in chronological order (i.e. sequential analysis (Altmann 1974)) using the open-source Behavioural Observation Research Interactive Software (BORIS, version 7.3) (Friard and Gamba 2016). Discrete activities like vigilance, grazing or moving were distinguished by following previously defined behaviours (Table 2) (Setsaas 2017, Setsaas et al. 2018). This procedure led to the making of a three-column file (behaviour observed; behaviour start; behaviour finish) time-stamping all behaviours present in the video footage from start to finish for each collared individual. Poor quality recordings where the distinction of behaviours was ambiguous was not processed. Rare behaviours with little or no occurrence in the footage, and behaviours performed when the studied animal was out of sight, were categorized as *unknown*. The operation produced a dataset of n = 8 behaviours (*vigilance*, *head-up*, *grazing*, *browsing*, *moving*, *grooming*, *resting* and *fleeing*) to be correlated with activity data recorded by the TAA.

Table 2. Definitions of the behaviours observed in impala during the processing of video footage. Table taken and modified from Setsaas (2017).

Behaviour	Definition
Vigilance	Head high above the ground and examining/scanning its surroundings without feeding. Alert and actively looking around. Ears are pointed forward. The stop of ruminating activity is usual.
Head-up	Looking passively around or in front with head raised above shoulders often while ruminating. Ears are relaxed and pointed backwards or moving to avoid flies and other insects.
Grazing	Feeding with head at ground level or under shoulder height.
Browsing	Feeding with head at or above shoulders from a bush, tree or high grass
Moving	Taking more than two steps without foraging, usually with head above shoulder level.
Grooming	Scraping/scratching on the flanks and/or legs using teeth or tongue
Resting	Laying down with head-up
Fleeing	High speed running or leaping away
Unknown	Rare behavioural instances and/or ephemeral behaviours usually lasting less than 1 or 2 seconds. Can also be applied to when full or partial animal is out of sight preventing to accurately classify its behavioural activity

II 6 Time matching with data recorded by TAAs

Data downloaded from TAAs consists of a set of three main objects: For a given 80-second time interval, an amplitude value of gravity measure (i.e. activity) for the X-axis is associated along with the Y-axis. In order to time match TAA activity recordings with behavioural information from the video footage, the latter data was split into the same 80-second epochs as calibrated on the collar datasets. The duration in seconds of each performed behaviour was calculated for every time interval and the behaviour with the longest duration was established as "dominant behaviour". Its proportional duration relative to the rest of the behaviours was also noted. Due to the fact that a relatively large sampling epoch was used and impala spend most of their time standing with their head-up (Jarman and Jarman 1973), most time intervals ended with *head-up* as being the dominant behaviour. To ensure that sample sizes were as consistent as possible among dominant behaviours, the following decision rules were used to select for dominant behaviours:

1) *Head-up* was considered a dominant behaviour only if being the one and only behaviour that occurred during an 80-second time interval.
2) Even when *head-up* occurred to be the behaviour with the longest duration, it is the behaviour having the second longest duration that was established as the dominant behaviour for that time interval.
3) In case *head-up* occurred to a lesser duration than another behaviour or that did not occur at all, is the behaviour having the longest duration that was established as dominant behaviour.

II 7 Automated behavioural classification of TAA data

II 7 1 Clustering

As suggested by other studies (Brownscombe et al. 2013, Lim et al. 2018), it is expected for different dominant behaviours in the context of TAA data to group into clusters of activity depending on the nature of their movements, as they will be providing a similar spectra of gravity measure. Given the data, the most likely number of K clusters in all TAA datasets was identified using K-means clustering, a principle aiming to partition datapoints into clusters in which each datapoint belongs to the cluster with the nearest mean value, called centroid. The sum of squared distances from each datapoint to its assigned centroid was then plotted against different values of number of clusters. The optimal K number of clusters for each dataset was then selected at K = 3 for all collar ID's following the elbow method (Figure 3).

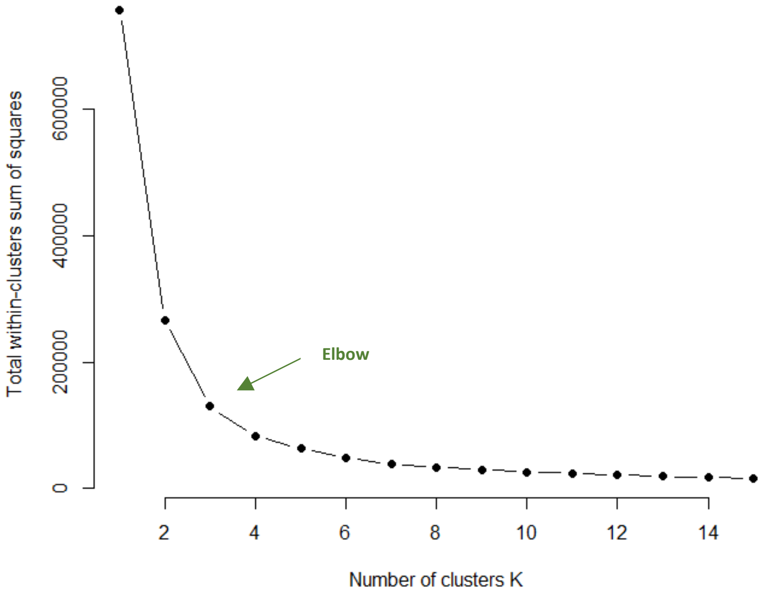


Figure 3. Graphical description of the elbow method to select the optimal K number of clusters. Among the different values of K number of clusters, one should choose one where K + 1 doesn't give a much lower total within-clusters sum of squares. It's important to note that this method allows for subjectivity relative to the choice of the researcher (Thorndike 1953).

Then, TAA and behavioural data was K = 3 partitioned following the optimal K number of clusters via the R package *dtwclust* (function: *tsclust*) using a fuzzy clustering option (Dutta et al. 2015). This provided a belonginess measure to each cluster for each epoch with associated TAA and behavioural data, the process being summarized in a partition matrix *U* following the equation (eq1) (Jang et al. 1997):

$$(\mathrm{eq1}): \; U = [u_{bj}]_{b=1\ldots c, j=1\ldots n}$$

Where u_{ij} is the value ∈ [0;1] accounting for the degree to which each dominant behaviour *b* and associated TAA values belong to the *j*th cluster. For each datapoint, the cluster with the highest *u* score was the winning cluster and was kept for further analysis.

Because up to eight dominant behaviours were defined but the data was K = 3 clustered, each cluster contained more than one dominant behaviour (Figure 4). To concretize the interpretation of the data, dominant behaviours *moving* and *fleeing* where merged together in a joined *Moving* group, *grazing* and *browsing* where combined in a *Feeding* group while the rest of dominant behaviours exhibiting little body locomotion (*head-up*, *vigilance*, *grooming* and *resting*) were appended into a common "at rest" group for *Stationary*. Based on the proportions of these three behavioural groups in each cluster, clusters were given the name of a behavioural category following the decision rules below:

1) Stationary: Cluster showing the highest proportion of *Stationary* behaviours, with the lowest proportions of *Feeding* and *Moving*. Proxy for stationary behaviours.
2) Feeding: Cluster showing the second highest proportion of *Stationary* behaviours, with the second highest proportions of both *Feeding* and *Moving*. Proxy for stationary feeding.
3) Foraging: Cluster showing the lowest proportion of *Stationary* behaviours, with the highest proportions of both *Feeding* and *Moving*. Proxy for active foraging, involving feeding and moving activities.

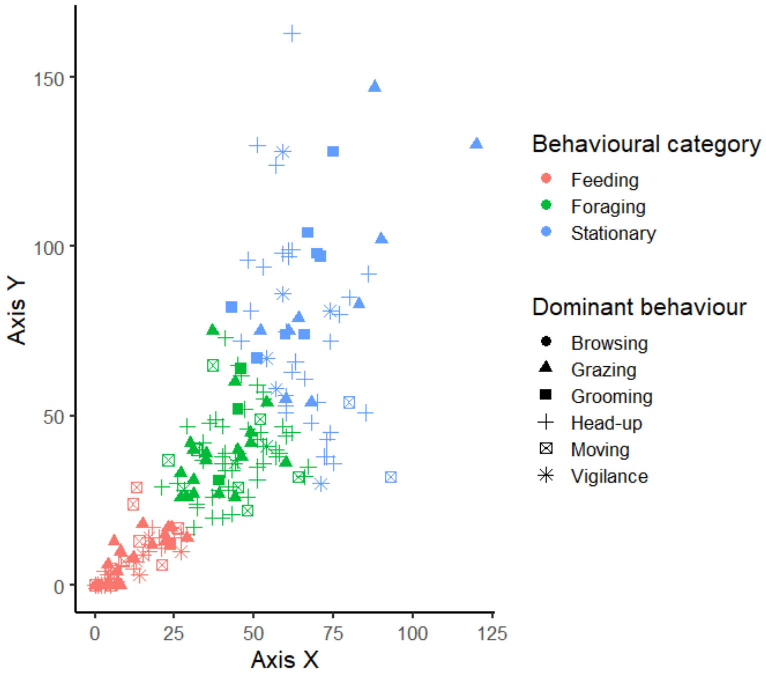


Figure 4. Example of clustered dominant behaviours based on axis values from a TAA dataset. Although clusters incorporated multiple behaviours, it was possible to distinguish among them given different proportions of dominant behaviours. Clusters were re-defined as behavioural categories.

Automated classifiers were then used to allocate a behavioural category Stationary, Feeding or Foraging to a given 80-second epoch with TAA data only. Given the relatively large sampling interval used in this study (Alvarenga et al. 2016), such clustering approach allowed to uncover differences in behavioural proportions over time, rather than discrete behaviours more suitable for smaller epochs (Moreau et al. 2009).

II 7 2 Behavioural classification with *k*-nearest neighbours' algorithm

The *k*-nearest neighbours' algorithm (*k*-NN) is a simple machine learning algorithm that will classify a test data point according to the classes of its nearest data points -or *neighbours*-. The algorithm's main parameter is the *k* number of nearest neighbours relative to the test point, whose value critically affects the categorical classification (Figure 5).

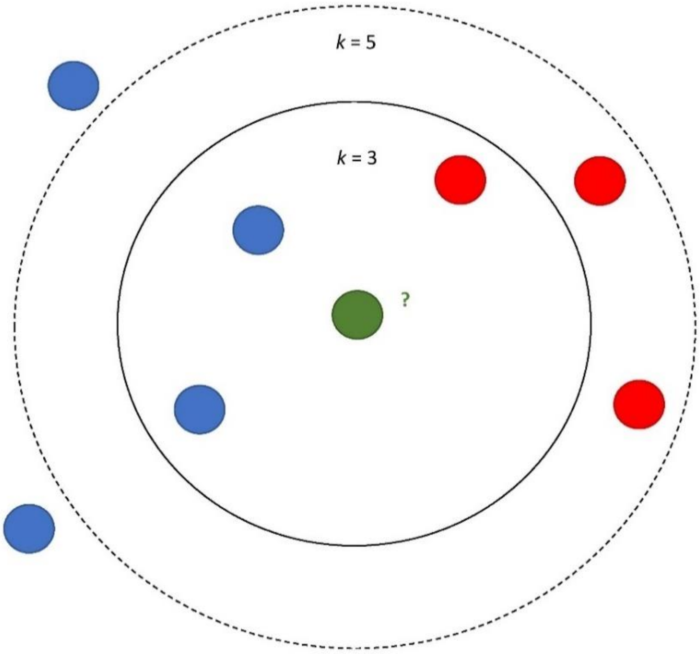


Figure 5. Illustration of the *k*-NN algorithm principle. A test point (green circle) can be classified either as a red circle or as a blue circle. When the parameter $k = 3$ (solid line), the test point will be assigned to the blue circle class since there are more blue circles than red circles among the test point 3 closest neighbours. However, if $k = 5$ (dashed line), the test point is classified as red since $n_{\text{blue circles}} < n_{\text{red circles}}$.

The class to which the nearest neighbours belongs to is set during the ground-truthing observational stage (Bidder et al. 2014), therefore acting as a training calibration set. The algorithm is available under the R package *class* and needs four main inputs in order to perform the automated behavioural classification, the two first-ones derived from the ground-truthing period:

1) A train-set: File containing TAA data from a period where the animal was observed and the performed behavioural categories for each time interval are known.
2) A class-set: File containing behavioural categories observed during the same period as the train-set. We used the winning cluster with the greatest u value as previously mentioned for each interval as an input. Both datasets 1) and 2) will allow the algorithm to associate TAA values to behavioural categories, information which will be used to classify unsupervised sensor data.
3) A test-set: File containing TAA data from a period where the animal wasn't observed, or behavioural data was not collected. This is the data the algorithm will associate to behavioural categories based on 1) and 2).
4) A k value: A user-defined constant that is used by the algorithm to select the k number of nearest neighbours to the analysed datapoint (Figure 5).

Since the k value needs to be determined by the researcher, a preliminary analysis measuring accuracy of classification with k-NN for different k values was performed instead of using a rule of thumb constant ($\text{e.g. } k = \sqrt{n_{classes}}$) as suggested in other studies (Jonsson and Wohlin 2004, Denoeux et al. 2015). Accuracy measures were plotted against different values of k, which resulted in an optimal k value selection at the elbow point (Ketchen and Shook 1996, Zhang et al. 2018). For all three collar datasets (#) # 41361, # 41365 and # 41366 this happened to be at $\overline{k}$: k = 10 ± 1 SD. The test-set used to perform this analysis corresponded to a random 20% of the supervised TAA datapoints for each collar, using the other 80% of the dataset as train-set for cross-validation. To check for compatibility across collars, among collar analysis were also performed where the whole ground-truthing dataset of one collar was used as train-set and the ground-truthing dataset from another collar was used as test-set. Then, the performance of the algorithm was evaluated via performance metrics accuracy, precision and recall (cf. II 7 4). The k-NN algorithm also outputting a minimum threshold value *prob*, all three-performance metrics were calculated for different *prob* values ∈ [0.1 - 0.9]. *Prob* represents the proportion of *k* nearest values in the train-set that belonged to the winning class (Powers 2011) and follows the equation (eq2):

$$\text{(eq2)} : \; prob = \frac{n_{winning\ class}}{k}$$

Prob was used as a threshold, were classifications made by *k*-NN that did not surpass a minimum *prob* value where discarded. Given the different nature of performance metrics, high levels of accuracy and recall were expected for low *prob* values, whereas high precision was expected for high *prob*.

II 7 3 Behavioural classification with decision trees

Decision trees, or tree classification analysis, are supervised event classifiers working through hierarchical decision rules that can either branch into another rule (internal node) or terminal rule (end node) (Figure 6).

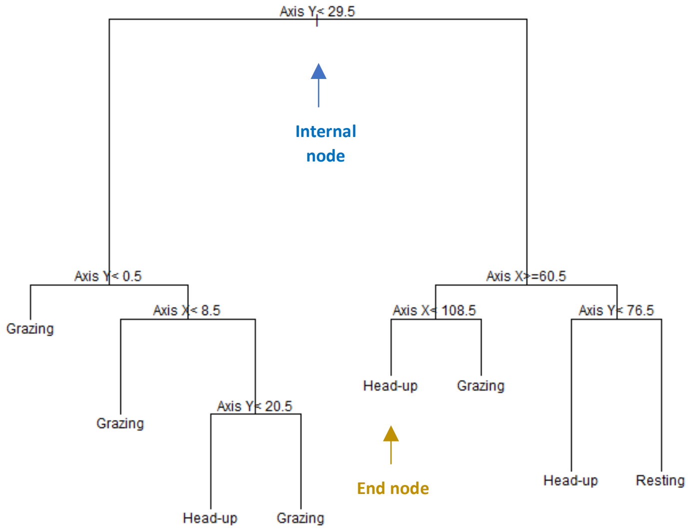


Figure 6. Example of a three-category decision tree based on values from axis X and Y. The tree is red downwards, where a split towards the right indicates a true evaluation (i.e. "if yes") of the condition stated at each node. A split towards the left indicates a false evaluation (i.e. "if no") of the condition stated at each node.

Decision trees possess great advantages in regards to other machine learning methods not only for their quick implementation (Ravi et al. 2005) but also for the interpretability of the outputted tree (Figure 6) (Nathan et al. 2012). Categorical classification trees can be grown by using the package *rpart* available in R (Therneau et al. 2015), for which the following model was implemented (eq3):

$$(\text{eq3}) : Class \sim Activity\ X + Activity\ Y$$

Here, the behavioural category *Class* is a response variable of the two axial accelerometer components *Activity X* and *Activity Y*. The algorithm uses a two-step recursive partitioning approach (Breiman 2017), where the variable best splitting the data into two groups is first calculated, which causes the data to be recursively partitioned into sub-groups until these reach a minimum size or no improvement can be made. Second, the full tree is trimmed by resampling the data via cross-validation. Contrary to *k*-NN, no preliminary parameters need to be specified besides the cross-validation split proportion. As for the *k*-NN analysis, we used the 80:20 division which is commonly found in multiple machine learning applications. Among collar analysis were also performed in the same manner as previously described and because the observed behavioural categories for *Class* were known, performance metrics to evaluate decision trees as a classification method were calculated. This allowed not only to verify the confidence and accuracy of prediction of recursive partitioned decision trees, but also to compare its performance with the *k*-NN classifier.

II 7 4 Performance metrics and evaluation

Accuracy, precision and recall measures were calculated both for *k*-NN and decision tree classifiers. Prior to this, a summary table accounting for correct and incorrect classifications needed to be constructed including the counts of true positives, false positives, true negatives and false negatives (Bidder et al. 2014), which is known in classification analysis as confusion matrix (Santra and Christy 2012). The entries of the confusion matrix have the following meaning:

- True positive (TP): Classifications that surpass the *prob* threshold and are classified correctly

- False positive (FP): Classifications that surpass the *prob* threshold and are classified incorrectly
- True negative (TN): Classifications that don't surpass the *prob* threshold and are classified incorrectly
- False negative (FN): Classifications that don't surpass the *prob* threshold and are classified correctly

Once the confusion matrix is obtained, performance metrics can be calculated as:

1) Accuracy = $\frac{TN+TP}{TN+TP+FN+FP}$ (= $\frac{n_{correct\ predictions}}{n_{total\ predictions}}$): Most intuitive performance measure. This represents the ratio of all correctly classified observations to the total number of observations.
2) Precision = $\frac{TP}{TP+FP}$: Ratio of positively classified observations that were correctly classified.
3) Recall = $\frac{TP}{TP+FN}$: Ratio of correctly classified positive observations to the total observations in an actual class.

Statistical analysis were conducted to compare mean differences in performance metrics for both methods of classification. When normally distributed and equal variance between groups, a Student *t*-test was conducted. When the variance between samples was not equal, a Welch *t*-test was used instead given that this method accounts for unequal variances (Ruxton 2006). A one-way analysis of variance (ANOVA) was used in order to test whether particular collar datasets performed better than others when used as train-sets. For all tests, the criterion of significance was taken at p < 0.05 (Siegel 1956).

II 7 5 Unsupervised classifications in LGCA and SNP

Because of differences in epochs between LGCA (4-minute = 240-second) and SNP (80-second) collar datasets, sampling intervals for # 41361, # 41365 and # 41366 were transformed to 4-minute by three-merging each 80-second time interval. Axial values were averaged, and times spent for each behavioural category were summed. The process produced three new 4-minute transformed SNP datasets # 41361´, # 41365´ and

41366´. Cross-validation within # 41361´, # 41365´ and # 41366´ and validation among datasets was performed following the same protocol as for # 41361, # 41365 and # 41366 to ensure the transformation did not decrease performance metrics significantly. Transformed datasets had three times smaller sample sizes, reason why the cross-validation split was corrected to 70:30 to increase the size of the cross-validated test-set. These three datasets were then used as train-sets to classify unsupervised TAA data from # 41366bis, # 41367 and # 41368 in LGCA from June 1st to July 31st, but also # 41361´, # 41365´ and # 41366´ from their collaring date to July 31st.

II 8 Analysis of behavioural patterns

II 8 1 Model fit

Hourly proportions of behavioural categories classified by the methods described above were compared between study areas. Data was analysed under a day (06:00-18:00 h) and night (19:00-05:00 h) partition to examine patterns of activity. Generalized linear mixed (GLM) models were fitted in order to uncover possible differences in behavioural proportions between LGCA and SNP. The response variable was the proportion of time allocated to Stationary, Feeding or Foraging behavioural categories, while area (Area: SNP or LGCA) and time of the day (Time: day or night) were included as fixed effects. To account for repeated measures on individuals, collar ID was included as a random effect. Models were formulated with and without interactions between fixed effects, and a null model only including the intercept was also tested. Five models were constructed for each response variable, totalling 15 computed models for each train-set for both classification methods, for a grand total of 90 models tested. Given that all three response variables indicate the probability of occurrence of a specific behavioural category, binomial was the most suitable distribution to use. Additionally, residuals were inspected to manually verify their normal distribution.

II 8 2 Model selection

In order to select for the best model given the data, an information-theoretical approach was followed (Burnham and Anderson 1998) by calculating Akaike's Information Criteria accounting for small sample sizes (AICc) for each model proposed (Hurvich and Tsai 1989). The model with the lowest AICc was then considered to be the model best explaining the data (Burnham et al. 2011). In cases where the ΔAICc difference between the best model's AICc and other models' AICc was ΔAICc < 2, is the most parsimonious model having the smallest number of degrees of freedom that was selected (Burnham and Anderson 1998). Although models were fitted to different datasets accounting for the different train-sets and classification methods, the same models were used to explain the proportion of all three behavioural categories across train-sets for each classifier. Hence, a mean AICc value was calculated averaging AICc's from models fitted to each train-set for each method of classification. This procedure gave the overall most parsimonious model explaining the proportion of time impala spent on a behavioural category for *k*-NN and decision trees (Grueber et al. 2011). Furthermore, the proportion of most parsimonious models for each train-set rendering the best overall model (*m*) was also taken into consideration for model selection.

III Results

III 1 *k*-NN algorithm performance

All three behavioural categories Stationary, Feeding and Foraging were detected by the *k*-NN algorithm for all six analysed datasets. Performance metrics led to high levels of mean accuracy ($\overline{\text{A}}$ = 0.886 ± 0.084 SD), precision ($\overline{\text{P}}$ = 0.906 ± 0.087 SD) and recall ($\overline{\text{R}}$ = 0.990 ± 0.017 SD) of classification within and among datasets. The minimum majority threshold *prob* associated with the highest performance metrics varied among collar datasets, although it's the lowest value of *prob* (0.1) that produced the greatest mean accuracy and recall for all datasets ($\overline{\text{A}}$ = 0.860 ± 0.024 SD; $\overline{\text{R}}$ = 1 ± 0 SD) (Table 3). On the other hand, it's the highest value of *prob* (0.9) that led to the greatest mean precision scores ($\overline{\text{P}}$ = 0.898 ± 0.018 SD) (Table 3). A trend of high mean accuracy and mean recall for low *prob* values was confirmed by a Spearman's rank correlation test ($p_{prob/\text{accuracy}} < 0.001$, $r_{prob/\text{accuracy}} = -0.925$; $p_{prob/\text{recall}} < 0.001$, $r_{prob/\text{recall}} = -0.937$). On the contrary, there was a positive relationship between mean precision and *prob* ($p_{prob/\text{precision}} = 0.016$, $r_{prob/\text{precision}} = 0.731$)

Table 3. Mean (± SD) *k*-NN performance metrics of classification and associated *prob* values when using a full dataset as train-set to classify behaviours on another dataset (*k* = 10).

prob	**Accuracy**	**Precision**	**Recall**
0.1	0.860 ± 0.024	0.860 ± 0.024	1.000 ± 0.000
0.2	0.860 ± 0.024	0.860 ± 0.024	1.000 ± 0.000
0.3	0.860 ± 0.024	0.860 ± 0.024	1.000 ± 0.000
0.4	0.860 ± 0.024	0.860 ± 0.024	1.000 ± 0.000
0.5	0.849 ± 0.030	0.858 ± 0.025	0.987 ± 0.007
0.6	0.845 ± 0.033	0.859 ± 0.021	0.960 ± 0.023
0.7	0.839 ± 0.038	0.881 ± 0.021	0.938 ± 0.028
0.8	0.825 ± 0.039	0.881 ± 0.022	0.920 ± 0.030
0.9	0.831 ± 0.032	0.898 ± 0.018	0.906 ± 0.024

Significant differences in performance metrics were found when comparing classification within a collar dataset (Table 4) versus among collar datasets (Table 5): Higher levels of accuracy (*t* = 5.712, df = 12.782; p < 0.001) and precision (*t* = 5.024; df = 12.163; p < 0.001) along with lower levels of recall (*t* = -5.190; df = 5, p = 0.003) were revealed for within collar classifications. When it comes to differences in performance of classification on other collars with varying TAA sampling intervals (80-second; 4-minute), no significant differences between original and transformed datasets were found for accuracy (*t* = -0.665; df = 9.657; p = 0.522), precision (*t* = -0.415; df = 9.615, p = 0.687) and recall (=1) (Table 5). No particular datasets performed better than others when used as train-sets to classify behavioural categories on other collars, differences being non-significant for accuracy (ANOVA: $F_{2,9}$ = 2.544; p = 0.133), precision (ANOVA: $F_{2,9}$ = 3,372; p = 0.081) and recall (ANOVA: $F_{2,9}$ = 1; p = 0.405).

Table 4. *k*-NN performance metrics for within dataset classification (*k* = 10). A cross-validation split of 80:20 was used for original datasets and a 70:30 split was used for transformed datasets.

Train-set #	Accuracy	Precision	Recall
41361	0.960	0.985	0.957
41361´	0.967	1.000	0.957
41365	0.993	0.995	0.996
41365´	0.968	0.982	0.965
41366	0.975	0.962	0.974
41366´	0.948	0.990	0.963

Table 5. Mean (± SD) *k*-NN performance metrics of classification when using a full dataset as train-set to classify behaviours on another dataset (*k* = 10). Averaged values are taken for *prob* thresholds yielding the highest performance metrics.

Train-set #	Accuracy	Precision	Recall
41361	0.865 ± 0.037	0.906 ± 0.020	1.000 ± 0.000
41361´	0.896 ± 0.108	0.921 ± 0.112	1.000 ± 0.000
41365	0.777 ± 0.105	0.798 ± 0.116	1.000 ± 0.000
41365´	0.795 ± 0.006	0.795 ± 0.007	1.000 ± 0.000
41366	0.848 ± 0.037	0.865 ± 0.046	1.000 ± 0.000
41366´	0.885 ± 0.093	0.913 ± 0.096	1.000 ± 0.000

III 2 Decision trees performance

As for the *k*-NN algorithm analysis, all three behavioural categories Stationary, Feeding and Foraging were detected by using decision trees. Performance metrics led to high levels of mean accuracy ($\overline{A}$ = 0.877 ± 0.063 SD), precision ($\overline{P}$ = 0.880 ± 0.115 SD) and recall ($\overline{R}$ = 0.851 ± 0.142 SD) for classification within and among datasets. Significant differences in performance metrics were found when comparing classification within a collar dataset (Table 6) and among collar datasets (Table 7), which translated in higher levels of mean accuracy (t = 3.371; df = 15.981; p = 0.004) and recall (t = 2.271; df = 15.992; p = 0.037) for within collar classification. No significant difference was found in mean precision of classification (t = 1.559; df = 15.953; p = 0.139) between within and among collar classification. When it comes to differences in performance of classification on other collars with varying TAA sampling intervals (80-second; 4-minute), no significant differences between original and transformed datasets were found for accuracy (t = 0.502; df = 9.316; p = 0.627), precision (t = 0.553; df = 7.081; p = 0.597) and recall (t = 1.094; df = 9.024; p = 0.302) (Table 7). No particular datasets performed better than others when used as train-sets to classify behavioural categories on other collars, differences being non-significant for accuracy (ANOVA: $F_{2,9}$ = 2.569; p = 0.131), precision (ANOVA: $F_{2,9}$ = 0.627; p-value = 0.556) and recall (ANOVA: $F_{2,9}$ = 2.339; p = 0.152).

Table 6. Decision tree performance metrics for within dataset classification. A cross-validation split of 80:20 was used for original datasets and a 70:30 split was used for transformed datasets.

Train-set #	**Accuracy**	**Precision**	**Recall**
41361	0.953	1.000	0.882
41361´	0.947	0.889	1.000
41365	0.897	0.96	0.980
41365´	0.943	0.953	1.000
41366	0.933	0.926	0.893
41366´	0.879	0.833	0.833

Table 7. Mean (± SD) decision tree performance metrics of classification when using a full dataset as train-set to classify behaviours on another dataset.

Train-set #	Accuracy	Precision	Recall
41361	0.929 ± 0.002	0.929 ± 0.030	0.949 ± 0.059
41361´	0.852 ± 0.107	0.694 ± 0.301	0.714 ± 0.274
41365	0.789 ± 0.067	0.786 ± 0.051	0.729 ± 0.008
41365´	0.823 ± 0.001	0.900 ± 0.000	0.667 ± 0.000
41366	0.869 ± 0.034	0.921 ± 0.061	0.900 ± 0.141
41366´	0.857 ± 0.042	0.912 ± 0.021	0.912 ± 0.020

III 3 Comparison between classification methods

Although within collar dataset classification for *k*-NN and decision tree methods showed non-significant differences for both precision (*t* = 2.385, df = 5.508, p = 0.058) and recall (*t* = 1.257, df = 5.430, p = 0.260), mean accuracy was found to be higher for the *k*-NN algorithm analysis (*t* = 3.13, df = 7.350, p = 0.016; Figure 7 A). On the other hand, no significant difference could be found when comparing mean values of accuracy (*t* = -0.320, df = 22, p = 0.752) and precision (*t* = 0.210, df = 18.207, p = 0.836) when collar datasets were used to classify TAA data from other collars. However, *k*-NN yielded a higher mean recall score (*t* = 4.2726, df = 11, p = 0.001315; Figure 7 B).

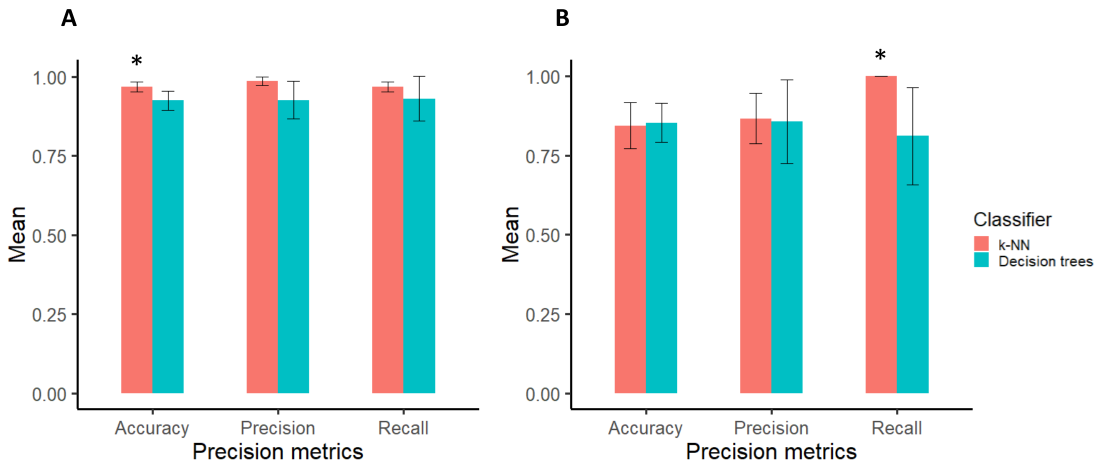


Figure 7. Mean performance metrics for both classification methods when classifying within a collar dataset (A) and among collar datasets (B). * Indicated statistical significance (p-value < 0.05).

III 4 Behavioural comparison between study areas

III 4 1 Stationary classifications

The occurrence of Stationary classifications was best explained by the additive effects of Area and Time consistently for most train-sets and for both methods of classification (Table 8a). Only when using # 41365´ as train-set and classifying TAA data with decision trees, model ~ Area + 1|ID was more parsimonious. When averaging AICc values, Stationary was best explained by ~ Area + Time + 1|ID for both methods of classification (Table 8b) and that was chosen to be the best model given the data. All three train-sets rendered the same best model when using *k*-NN (*m* = 3/3), for two out of three when using decision trees (*m* = 2/3) (Table 8b).

Table 8a. ΔAICc table using Stationary as response variable for all three transformed train-sets and both methods of classification. Bold numbers indicate the most parsimonious model and italic numbers indicate the next most parsimonious model according to an information theoretical approach. Original AICc table can be found in the Supporting Tables (ST 1a).

ΔAICc						
Train-set #	**Classifier**	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
41361´	*k*-NN	40.87	33.49	7.2	**0**	*1.92*
41361´	Decision trees	58.44	3.62	54.69	**0**	2.15
41365´	*k*-NN	51.98	3.31	48.47	**0**	2.15
41365´	Decision trees	4.85	3.86	**0.81**	*0*	2.15
41366´	*k*-NN	41.59	7.84	33.57	**0**	*1.84*
41366´	Decision trees	66.9	5.68	161.12	**0**	*1.76*

Table 8b. ΔAICc table using Stationary as a response variable when averaging AICc values among train-sets for both methods of classification. Bold numbers indicate the most parsimonious model and italic numbers indicate the next most parsimonious model according to an information theoretical approach. Original mean AICc table can be found in the Supporting Tables (ST 1b).

Mean ΔAICc						
Classifier	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**	***m***
***k*-NN**	44.814	14.881	29.747	**0**	*1.971*	3/3
Decision trees	43.397	4.387	72.207	**0**	2.021	2/3

When classifying with *k*-NN, model ~ Area + Time + 1|ID revealed a substantial nocturnal decrease in the proportion of Stationary classifications for all train-sets ($\bar{x}_{\text{day}}$ = 0.351, 95% $\overline{CI}$ [0.284 - 0.421]; $\bar{x}_{\text{night}}$ = 0.223, 95% $\overline{CI}$ [0.178 - 0.275]), which difference happened to be statistically significant for all models fitted ($z < -5.933$; p-value < 0.001) (Figure 8a). On the other hand, impala allocated twice more time to stationary behaviours in LGCA compared to SNP ($\bar{x}_{\text{LGCA}}$ = 0.416, 95% $\overline{CI}$ [0.329 - 0.509], $\bar{x}_{\text{SNP}}$ = 0.195, 95% $\overline{CI}$ [0.133 - 0.263]), which variable also happened to show statistical significance across train-sets ($z < -2.970$; p-value < 0.003) (Figure 8a). Given mean day and night differences in the time spent on stationary behaviours of 57% and mean Area differences of 113%, the additive effect of these two variables was considered biologically significant.

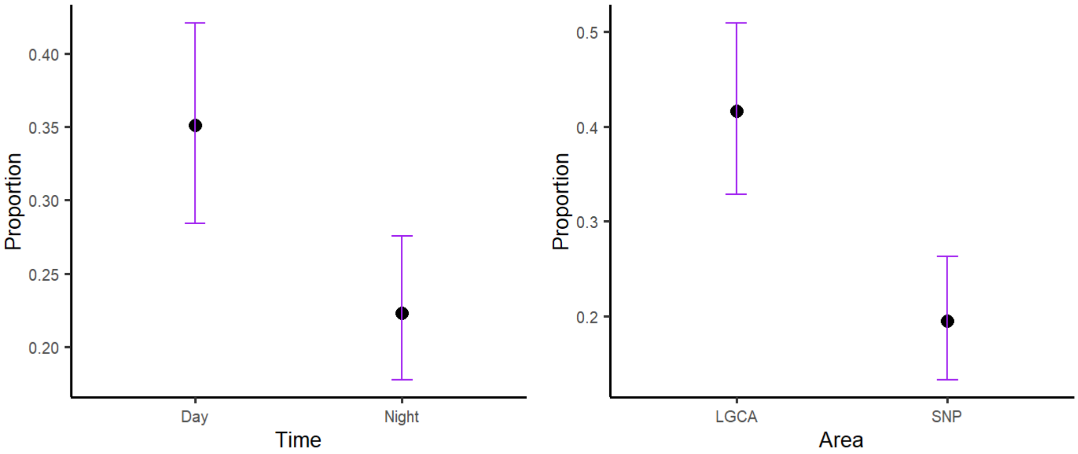


Figure 8a. Statistically significant effects best explaining the proportion of Stationary classifications in June and July using *k*-NN. Mean estimates and confidence intervals for all train-sets are plotted here.

Stationary classifications with decision trees were best explained by the same area and time additive effects, which revealed a substantial nocturnal decrease in the proportion of stationary behaviours for all train-sets ($\bar{x}_{\text{day}}$ = 0.264, 95% $\overline{CI}$ [0.189; 0.355]; $\bar{x}_{\text{night}}$ = 0.167, 95% $\overline{CI}$ [0.133 - 0.235]; $z < -6.014$; p-value < 0.001) (Figure 8b). On the other hand, the most parsimonious model explained that impala allocated up to four times more time to stationary behaviours in LGCA than in SNP ($\bar{x}_{\text{LGCA}}$ = 0.393, 95% $\overline{CI}$ [0.242 - 0.538]; $\bar{x}_{\text{SNP}}$ = 0.104, 95% $\overline{CI}$ [0.059 - 0.176]; $z < -2.970$; p-value < 0.003) (Figure 8b). Given mean day and night differences in the time spent on stationary behaviours of 58% and mean Area differences of 278%, the additive effect of these two variables was considered biologically significant.

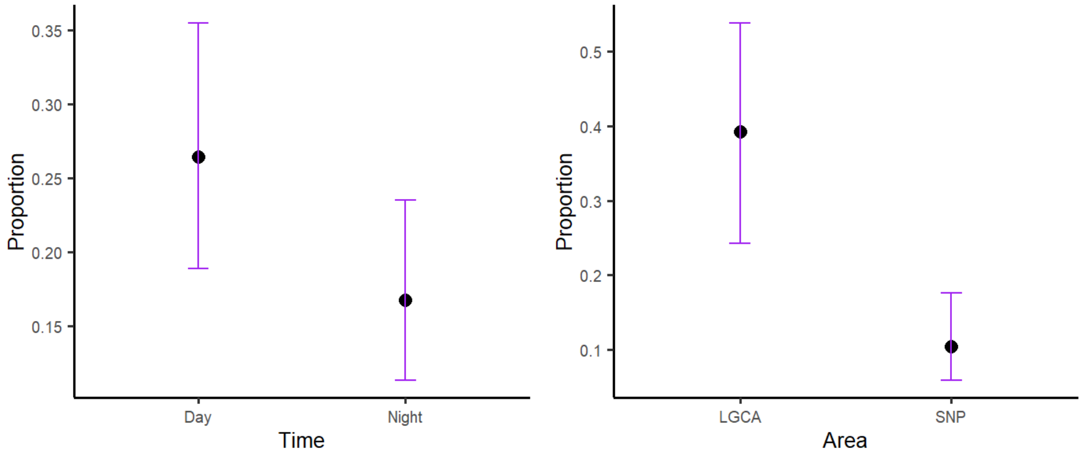


Figure 8b. Statistically significant effects best explaining the proportion of Stationary classifications in June and July using decision trees. Mean estimates and confidence intervals for all train-sets are plotted here.

III 4 2 Feeding classifications

No consensus across train-sets could be found to select the variables best explaining the Feeding classifications for both classifiers (Table 9a). When averaging AICc values, the model providing the optimal AICc proved to be different for each method of classification: The data was best explained by an Area effect for *k*-NN and by a Time effect for decision trees (Table 9b). Only one train-set out of three rendered the best averaged model for each method of classification (*m* = 1/3) (Table 9b).

Table 9a. ΔAICc table using Feeding as response variable for all three transformed train-sets and both methods of classification. Bold numbers indicate the most parsimonious model and italic numbers indicate the next most parsimonious model according to an information theoretical approach. Original AICc table can be found in the Supporting Tables (ST 2a).

				ΔAICc		
Train-set #	**Classifier**	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
41361´	*k*-NN	5.63	3.54	2.06	**0**	2.09
41361´	Decision trees	4.89	**1.9**	2.95	*0*	1.55
41365´	*k*-NN	14.68	16.46	**0**	*1.8*	3.91
41365´	Decision trees	124.65	4.3	123.26	2.94	**0**
41366´	*k*-NN	5.28	**1.5**	3.74	*0*	1.99
41366´	Decision trees	**0**	4.22	10.72	5.97	6.7

Table 9b. ΔAICc table using Feeding as a response variable when averaging AICc values among train-sets for both methods of classification. Bold numbers indicate the most parsimonious model and italic numbers indicate the next most parsimonious model according to an information theoretical approach. Original mean AICc table can be found in the Supporting Tables (ST 2b).

	Mean ΔAICc					
Classifier	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**	***m***
***k*-NN**	7.929	6.566	**1.333**	*0*	2.063	1/3
Decision trees	40.43	**0.434**	42.894	*0.22*	0	1/3

As the most parsimonious model to explain *k*-NN Feeding classifications, model ~ Area + 1|ID revealed that this classifier identified greater proportions of Feeding in SNP compared to LGCA ($\bar{x}_{LGCA} = 0.169$, 95% $\overline{CI}$ [0.130; 0.199]; $\bar{x}_{SNP} = 0.280$, 95% $\overline{CI}$ [0.232; 0.329]; $z > 2.224$; p-value < 0.026). This difference was considered biologically significant given that impala allocated an average of 65% more time to feeding behaviours in SNP than in LGCA (Figure 9a).

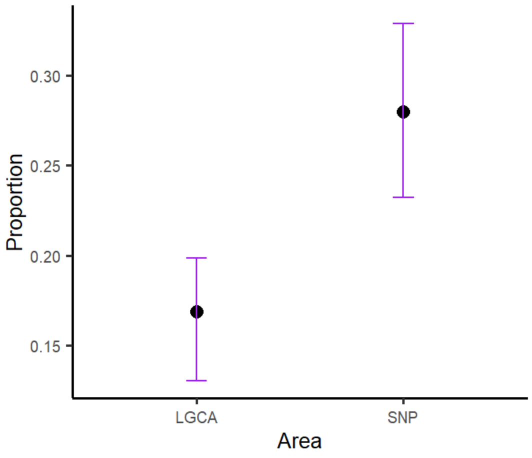


Figure 9a. Statistically significant effects best explaining the proportion of Feeding classifications in June and July using *k*-NN. Mean estimates and confidence intervals for all train-sets are plotted here.

Averaging AICc's when classifying with decision trees revealed model ~ Time + 1|ID to be the most parsimonious explaining Feeding classifications. The effect of time of the day was reported to be statistically significant for all train-sets ($\bar{x}_{day} = 0.242$, 95%

$\overline{CI}$ [0.202; 0.287]; $\bar{x}_{night} = 0.202$, 95% $\overline{CI}$ [0.166; 0.244]; $z < -2.662$; p-value < 0.007), although this only explained day and night mean differences of 20% in the proportion of time allocated to feeding behaviours (Figure 9b).

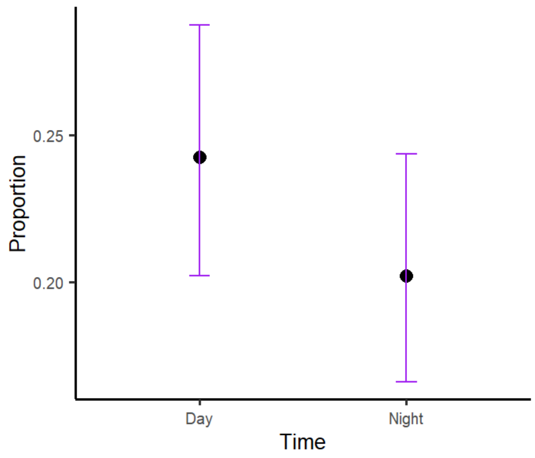


Figure 9b. Statistically significant effects best explaining the proportion of Feeding classifications in June and July using decision trees. Mean estimates and confidence intervals for all train-sets are plotted here.

III 4 3 Foraging classifications

Foraging classifications were best explained by an interaction effect between Area and Time for most train-sets and methods of classification, except for train-set # 41365´ using decision trees, where model ~ Area + Time + 1|ID had a better fit (Table 10a). When averaging AICc values, Foraging was best explained by model ~ Area * Time + 1|ID for *k*-NN, but model ~ Area + Time + 1|ID proved to be more parsimonious for decision tree classification (Table 10b). Because only one train-set ($m = 1/3$) rendered the overall most parsimonious model for decision trees and two train-sets ($m = 2/3$) rendered the next overall most parsimonious model, model ~ Area * Time was selected to be most parsimonious when classifying with decision trees.

Table 10a. ΔAICc table using Foraging as a response variable for all three transformed train-sets and both methods of classification. Bold numbers indicate the most parsimonious model and italic numbers indicate the next most parsimonious model according to an information theoretical approach. Original AICc table can be found in the Supporting Tables (ST 3a).

				ΔAICc		
Train-set	**Classifier**	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
41361´	*k*-NN	62.32	5.61	61.26	4.61	**0**
41361´	Decision trees	81.72	2.98	80.77	2.07	**0**
41365´	*k*-NN	64.33	5.2	63.58	4.51	**0**
41365´	Decision trees	83.83	2.11	82.21	**0.49**	*0*
41366´	*k*-NN	62.99	5.41	62.07	4.54	**0**
41366´	Decision trees	81.75	3.62	80.84	2.74	**0**

Table 10b. ΔAICc table using Foraging as a response variable when averaging AICc values among train-sets for both methods of classification. Bold numbers indicate the most parsimonious model and italic numbers indicate the next most parsimonious model according to an information theoretical approach. Original mean AICc table can be found in the Supporting Tables (ST 3b).

			Mean ΔAICc			
Classifier	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**	***m***
***k*-NN**	63.213	5.407	62.303	4.553	**0**	3/3
Decision trees	82.433	2.903	81.273	**1.767**	*0*	1/3

Model ~ Area * Time + 1|ID revealed that Foraging classifications using *k*-NN were best explained by the interaction between these two variables. Impala allocated a larger proportion of their time to foraging behaviours at night in both study areas for all train-sets ($z > 6.962$; p-value < 0.001; LGCA: $\bar{x}_{day} = 0.279$, 95% $\overline{CI}$ [0.192 - 0.385]; $\bar{x}_{night} = 0.453$, 95% $\overline{CI}$ [0.338 - 0.574]; SNP: $\bar{x}_{day} = 0.467$, 95% $\overline{CI}$ [0.371 - 0.566]; $\bar{x}_{night} = 0.567$, 95% $\overline{CI}$ [0.465 - 0.659]), while Foraging more on average in SNP than in LGCA ($z > 2.541$; p-value < 0.011). The interaction effect between Area and Time resulted to be statistically significant in all models ($z < -2.584$; p-value < 0.010) and given an average difference of 74% in slope steepness, impala were shown to increase nocturnal foraging behaviours by that proportion in LGCA when comparing to SNP (Figure 10a).

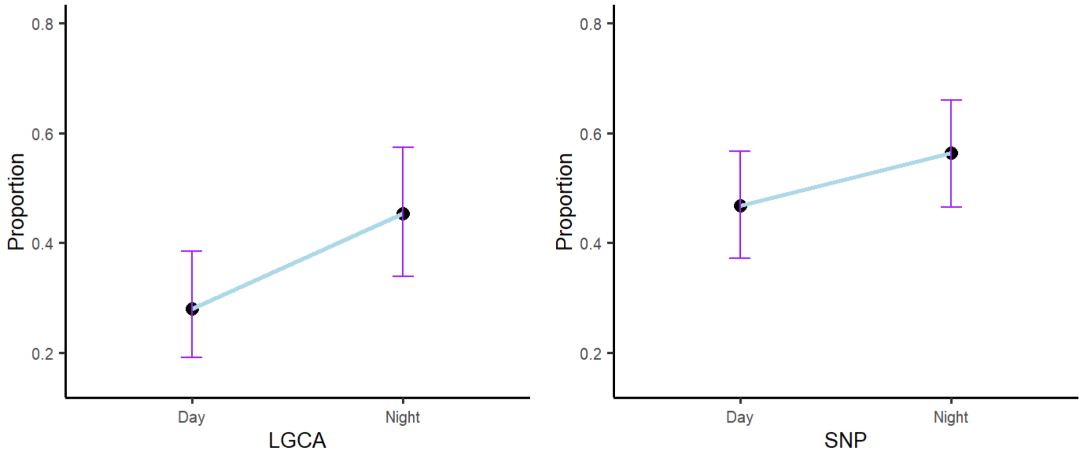


Figure 10a. Statistically significant effects best explaining the proportion of Foraging classifications in June and July using *k*-NN. Mean estimates and confidence intervals for all train-sets are plotted here. Blue line illustrates differences in slope among areas.

Foraging classifications with decision trees were best explained by the same interaction between Area and Time. Similarly, Foraging was classified more often at night in both study areas on average ($z > 7.573$; p-value < 0.001; LGCA: $\bar{x}_{day} = 0.281$, 95% $\overline{CI}$ [0.166 - 0.434]; $\bar{x}_{night} = 0.478$, 95% $\overline{CI}$ [0.320 - 0.643]; SNP: $\bar{x}_{day} = 0.486$, 95% $\overline{CI}$ [0.374 - 0.600]; $\bar{x}_{night} = 0.599$, 95% $\overline{CI}$ [0.486 - 0.706]) and impala were explained to engage in foraging behaviours more often in SNP compared to LGCA ($z > 2.541$; p-value < 0.027). The interaction effect resulted to be statistically ($z < -2.106$; p-value < 0.016) and biologically significant, given that impala increased nocturnal foraging behaviours by 74% in LGCA when compared to SNP (Figure 10b).

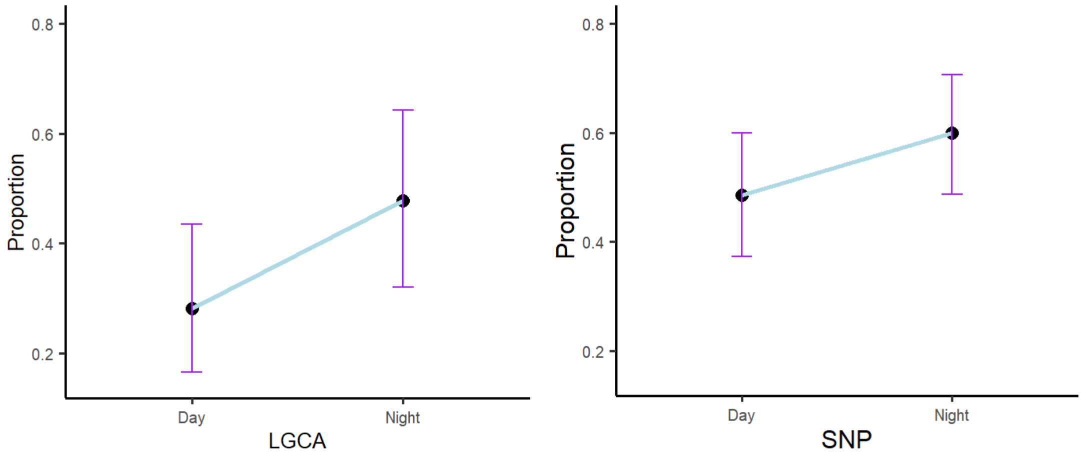


Figure 10b. Statistically significant effects best explaining the proportion of Foraging classifications in June and July using decision trees. Mean estimates and confidence intervals for all train-sets are plotted here. Blue line illustrates differences in slope among areas.

IV Discussion

IV 1 Classifier performance and suitability of TAAs

Given the high-performance metrics of classification of supervised TAA data, the current project demonstrated that *k*-NN and recursive partitioned decision trees were both suitable methods of classification to identify behavioural categories from activity data in wild impala. Although both of these classifiers rank among the easiest machine learning algorithms to implement and interpret (McClune et al. 2014, Alvarenga et al. 2016), this study proposed a comparison of their performance in an accelerometery context to study animal behaviour (Nathan et al. 2012). Both techniques provided high performance metrics consistently within and among analysed datasets, which complicated the choice of an ideal method of classification. However, *k*-NN has the advantage to output values that can ultimately be used as thresholds to refine classification performance. Because following such principle yielded higher values of accuracy for within dataset classification and higher values of recall for among train-set classification, *k*-NN was given higher confidence than decision trees when interpreting unsupervised classifications from TAA data. To its defence, decision trees had the advantage of being quicker to implement given that no preliminary parameters needed to be established, and yet still provided very high metrics of classification.

Another distinctive feature of this thesis' methodology was the relatively large sampling epochs (i.e. SNP: 80-second; LGCA: 240-second) used to measure activity in both studied areas. Recent work having examined the effect of different sampling times on classification metrics with smaller time signatures such as 3, 5 and 10 seconds found that shorter epochs don't always yield better classification results (Alvarenga et al. 2016), which was also shown in the present study: Defining behavioural categories based on the proportions of clustered behaviours in either 80 or 240-second epochs performed as good as smaller sampling intervals classified with k-NN and decision trees in other studies (cf.

Supporting Tables: ST 4). (Nathan et al. 2012, Bidder et al. 2014, McClune et al. 2014, Alvarenga et al. 2016) .

Given the high frequency of activity shifts (McClune et al. 2014) and short duration of behavioural signatures in terrestrial animals – where the fastest movements range between 0.5 and 1 second (Fehlmann et al. 2017) – longer sampling epochs don't allow to classify discrete, punctual behavioural occurrences because these are usually much shorter than such accelerometer calibrations. However, expanded settings are less memory demanding (Diosdado et al. 2015) and have the advantage to collect data for longer periods of time (Krop-Benesch et al. 2013) without significantly compromising classification performance. Research aiming to answer questions relative to long-term activity data could indeed benefit from longer epochs, as shown by Krop-Benesch and collaborators (2013) examining seasonality effects on roe-deer (*Capreolus capreolus*) or by Suraci *et al*. (2019) investigating habitat use in lions (*Panthera leo*), both using 5-minute sampling intervals for one year and six months respectively.

Successful identification of unsupervised behavioural categories was highly dependent on the ability of classification methods to perform among collars in SNP, thus both classification algorithms were trained on datasets from one impala and then validated with data from a second impala. On domestic goats, this process did not always yield consistent classification performances, where true recognition of certain behaviours – such as walking – decreased significantly from within collar calibration ($\overline{\mathrm{P}} = 0.81$) to validation on other datasets ($\overline{\mathrm{P}} = 0.28$) (Moreau et al. 2009). In this thesis, within dataset classification scores showed significantly higher metrics for accuracy and precision when using k-NN and higher accuracy and recall when classifying with decision trees. Because differences in collar position have shown to affect validation across collars (Hansen et al. 2007, Moreau et al. 2009), slightly different mounting configurations along with the natural variance of individual locomotion were considered to be the two main variables explaining differences between within and among collar-set classification of behavioural categories. Indeed, slightly lower performance metrics (but non-significantly so) for train-set # 41365´ in its ability to validate other test-sets could be related to a >90º leftwards rotation of the position of the collar in impala ID 41365 (Figure 11).

22/06/2018

23/06/2018

Figure 11. Individual ID 41365 photographed on June 22nd, 2018 (top) and June 23rd, 2018 (bottom). Note how the TAA sensor (white box) suffered from displacement when compared to its original position. By using taxa-specific equipment, such situations can be avoided.

Still, classifications among collars were consistently high and provided good confidence to identify behavioural categories in LGCA using the classification techniques analysed above, were no validation could be made given the lack of observational data in that region of study. In the same way, unsupervised behavioural classification from TAA data in SNP had to be computed for the rest of the study period after ground-truthing until July 31st, 2018. TAAs having already been shown successful to study animal behaviour in domestic ungulates (Moreau et al. 2009, Diosdado et al. 2015, Dutta et al. 2015, Alvarenga et al. 2016, Giovanetti et al. 2017), this thesis contributed evidence on the pertinence of this method to study and quantify animal behaviour in the wild.

IV 2 Impala’s behavioural adjustments to anthropogenic activities

Because behaviours that were observed during ground-truthing were concatenated into clustered behavioural categories, identified patterns corresponded to overall behavioural states within each examined epoch. Considering Stationary as a behavioural category including all static behaviours (*head-up*, *vigilance*, *grooming* and *resting*) and the smallest proportions of *Feeding* and *Moving* (cf. II 7 1), the first prediction that impala would remain at rest and allocate less time moving in LGCA than in SNP during the day was supported for both classifiers by the most parsimonious model. As a combination of intermediate *Feeding* and *Moving* (cf. II 7 1), Feeding was considered a behavioural category of stationary feeding, for which an Area effect revealed that impala spent more time under this behavioural state in SNP than in LGCA. Because Foraging was a grouped behavioural category including the highest proportions of *Feeding* and *Moving* (cf. II 7 1), this was considered a good proxy to evaluate high levels of active foraging. Although impala allocated less absolute time to this behavioural category in LGCA than in SNP at night, an Area and Time interaction revealed a significant increase in the proportion of nocturnal foraging behaviours in LGCA, thus supporting the second prediction of this thesis.

IV 2 1 Impala and tourists in SNP

Jarman and Jarman (1973) examined impala daily behavioural patterns in SNP in the early 1970’s, studying the “basic pattern of activity” via manual observations on multiple herds. Impala were noted to feed mostly at dawn and dusk, with some instances of nocturnal feeding between 23h00 and 03-04h00. Afternoon behavioural patterns were noted to be the least well-defined, generally taken up with a mixture of feeding and ruminating in which the herd may be poorly synchronized, although a well-defined period of ruminating was observed between 15h00 and 17h00 (Jarman and Jarman 1973). By visualizing hourly unsupervised behavioural classifications in SNP, some of the activity patterns described by Jarman and Jarman (1973) were seen in our data as well, such as dusk and nocturnal feeding, less defined early afternoon behaviours and a more static, ruminating period during the late afternoon (Figure 12 A).

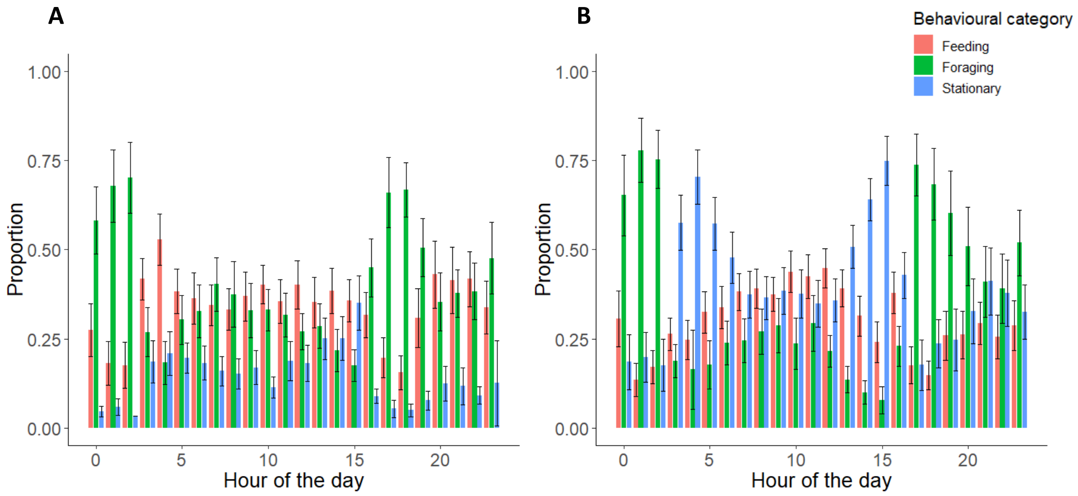


Figure 12 Mean hourly proportions (± SD) of behavioural categories for ID 41366 (A; Area: SNP) and ID 41367 (B; Area: LGCA) in June and July (ID 41366: year 2018; ID 41367: year 2017). Raw data used for modelling is displayed here. Note consistent peaks (>60%) of foraging behaviours between 00h00 and 03h00, and 17h00 for both animals. A well-defined large relative proportion of "static" behavioural categories (Feeding and Stationary) can be distinguished at 15h00 consistently across datasets. The above behavioural data for ID 41366 was classified using a proportion of # 41366 as train-set and classifying with *k*-NN. Data for ID 41367 was classified using # 41361 as train-set and *k*-NN, that being the most accurate classification method among collar datasets.

However, the proportion of behavioural categories including a feeding component (Feeding and Foraging) during early morning did not follow the trend previously described by Jarman and Jarman (1973), who defined a major peak of foraging at dawn. Rather, relatively high levels of Feeding and Foraging were classified throughout the day in all three individuals, which is not consistent with baseline observations from the previous study (Jarman and Jarman 1973). Given a fifty-year gap of historical context and the high variance in group-size of Jarman and Jarman's (1973) studied herds (twenty to 106 animals), care should be taken when comparing our behavioural data: Since impala have been noted to change their behaviour in response to human activity overtime (under manuscript, Flølo 2019), and group size is well known to affect behavioural states (Fritz and De Garine-Wichatitsky 1996, Roberts 1996), previous accounts on behavioural patterns should be seen as general descriptive guidelines of daily routines rather than validation or disproof of unsupervised TAA data classification. Instead, these differences could be explained by the strict management policies (Homewood et al. 2001) and exponential tourism (TANAPA 2005) of the past decades that have made impala highly habituated to human presence in central SNP (Nyahongo 2008), the number of visitors having tripled in the last 30 years (Eagles and Wade 2006). Given prolonged periods of contact with low-risk anthropogenic activities not followed by positive or negative reinforcements (Thorpe 1963), wildlife can become less responsive to human stimuli (McFarland 1993) which is known to alter foraging (Coleman et al. 2008, Knight 2009, Geffroy et al. 2015) and circadian habits (Wheat and Wilmers 2016). Knight (2009) suggested that this could allow for the discovery of new feeding grounds that come along with the neutralization of human predatory status, which would give animals clear road to behave bolder around people than non-habituated individuals (Lowry et al. 2013). This phenomena has been confirmed in other African ungulates such as the Günther's dik-dik (*Madoqua guentheri*) (Coleman et al. 2008), and elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) in North-America, which allocate larger proportions of time foraging when near busy touristed roads (Shannon et al. 2014).

IV 2 2 Impala and pastoralists in LGCA

Human-herbivore conflict in semi-nomadic cultures is an extensively reviewed topic in terms of competition with livestock and habitat choice (Homewood and Rodgers 1984, Du Toit and Cumming 1999), but case studies have led to ambiguous findings in regards to wild herbivore responses to people and livestock. While impala have been shown to actively avoid cattle in mixed-ranches in Zimbabwe (Fritz et al. 1996), their densities are consistently higher near pastoralist communities than in protected areas in southern Kenya (Bhola et al. 2012), indicating direct and complex interactions between wild herbivores and pastoral land-use. Most parsimonious GLM models fitted to classifications of behavioural categories revealed that impala increased their foraging activity at night in LGCA compared to SNP (Figure 12 B), suggesting that animals made-up for the lack of diurnal movement and foraging near pastoralist communities. However, such compensatory regulation was found to be only partial, given that impala in LGCA did not reach or surpass the nocturnal foraging proportions allocated in SNP. Interestingly, the proportion of time impala allocated to foraging behaviours in LGCA during the night tightly resembled diurnal foraging levels from individuals in SNP.

Nocturnal shifts in wildlife aiming to avoid potential threats is a well-known phenomenon described in landscapes were human pressure is growing (Gaynor et al. 2018) and has been noted to affect fitness-enhancing behaviours by restraining access to nutritional, water and reproductive resources (Crosmary et al. 2012, van Doormaal et al. 2015). In Hwange National Park and adjacent game reserves in Zimbabwe, Crosmary and collaborators (2012) looked at impala's nocturnal habits in relation to hunting, where opposite activity trends were observed inside and outside of the park. Animals did not use waterholes at night in protected areas, but increased their nocturnal use in hunting blocks to decrease temporal overlap with hunters (Crosmary et al. 2012). For other species of antelopes, like the sable (*Hippotragus niger*), an almost total circadian turnover was observed outside of the park, were animals rarely accessed drinking resources at daylight. These behavioural patterns resemble the results presented with this thesis, where impala remained more passive in LGCA during the main hours of the day but increased their nocturnal access to resources when comparing to individuals in SNP. Given their relatively high densities in western LGCA (TAWIRI 2010), adaptive temporal dynamics might be a key factor explaining the wide distribution of impala in pastoralist regions across east Africa (Fritz and De Garine-Wichatitsky 1996, Bhola et al. 2012).

Because it has been suggested that ungulates' ability to regulate nocturnal activity in areas with increasing anthropogenic pressure might be limited by predator density (Crosmary et al. 2012), impala in mixed-wilderness areas might be facing a diel trade-off, where being active during the day may favour human encounters, but being active at night may result in being predated given higher nocturnal predation risk (Kolowski et al. 2007, Wilmers et al. 2017). Hence, human and predator presence might drive a dynamic landscape of fear (Kohl et al. 2018) which wouldn't allow wildlife to fully compensate at night for the lack of diurnal foraging in areas hosting anthropogenic land-use (Benhaiem et al. 2008, Sunde et al. 2009, Crosmary et al. 2012). However, given the lack of recent data on large predator densities in LGCA (Maddox 2003), this remains an unsupported claim. Within restrained home-ranges, this work contributed to show that wildlife may follow a time-based avoidance strategy towards humans and livestock, in line with elusive reactions towards hunters and predators in similar land mixed-areas (Valeix et al. 2009, Crosmary et al. 2012, Gaynor et al. 2018).

V Conclusion

The double aim of this thesis, incorporating a methodological and conservation biology component, was to develop an accurate and efficient protocol able to process unsupervised TAA data remotely, which could further be used to answer ecological and conservation questions on animal behaviour. To interpret signals from activity sensors, two classification techniques were tested, and a slight preference was given to the implementation of the k-NN algorithm given more accurate performance scores. Because this method requires pre-existing observational data derived from a ground-truthing stage, such approach can be resource and time consuming given the need to collar and collect footage from a free-range individual, which has been confronted elsewhere by using captive surrogates (Campbell et al. 2013, Wang et al. 2015). Hence, the importance of training a classifier on a first collar to identify behaviours on other collar datasets cannot be emphasized enough, in case TAA data from remote individuals with lacking observational information needs to be interpreted. This process allowed to uncover differences in behavioural patterns in impala among regions hosting distinct forms of human activities, which revealed significant differences in behaviour as predicted by both formulated hypotheses: Impala remained rather passive during the day in pastoralist areas, but proportionally increased their nocturnal foraging behaviour when comparing to individuals in SNP. By contrasting these results with previous literature, the effects of tourist habituation, human and livestock avoidance and predation were discussed as possible variables explaining the observed patterns of behaviour in both areas of study. Overall, impala was found to be highly plastic in response to different anthropogenic disturbances, which could partially explain the past and present co-existence of humans and wildlife in east-African ecosystems.

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The author locating an impala herd. Fieldwork in Serengeti National Park. June 2018.

Supporting Tables

ST 1a. Model AICc scores using Stationary as a response variable for all three transformed train-sets and both methods of classification.

		AICc				
Train-set #	**Classifier**	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
41361´	*k*-NN	845.46	838.08	811.79	804.59	806.51
41361´	Decision trees	979.92	925.10	976.17	921.48	923.63
41365´	*k*-NN	972.52	923.85	969.01	920.54	922.69
41365´	Decision trees	495.38	494.39	491.34	490.53	492.68
41366´	*k*-NN	812.48	778.73	804.46	770.89	772.73
41366´	Decision trees	852.47	791.25	946.69	785.57	787.33

ST 1b. Mean (± SD) model AICc scores using Stationary as a response variable when averaging AICc values among train-sets for both methods of classification.

	Mean AICc				
Classifier	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
***k*-NN**	876.82 ± 84.503	846.887 ± 72.960	861.753 ± 92.959	832.006 ± 78.502	833.977 ± 78.663
Decision trees	775.923 ± 251.176	736.913 ± 220.436	804.733 ± 271.807	732.526 ± 220.317	734.547 ± 220.270

ST 2a. Model AICc scores using Feeding as a response variable for all three transformed train-sets and both methods of classification.

		AICc				
Train-set #	**Classifier**	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
41361´	*k*-NN	667.52	665.43	663.95	661.89	663.98
41361´	Decision trees	608.63	605.64	606.69	603.74	605.29
41365´	*k*-NN	528.62	530.40	513.94	515.74	517.85
41365´	Decision trees	1419.22	1298.87	1417.83	1297.51	1294.57
41366´	*k*-NN	715.90	712.12	714.36	710.62	712.61
41366´	Decision trees	756.89	761.11	767.61	762.86	763.59

ST 2b. Mean (± SD) model AICc scores using Feeding as a response variable when averaging AICc values among train-sets for both methods of classification.

			Mean AICc		
Classifier	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
***k*-NN**	637.346 ± 97.218	635.983 ± 94.371	630.75 ± 104.253	629.417 ± 101.417	631.48 ± 101.366
Decision trees	928.246 ± 431.609	888.25* ± 363.269	930.71 ± 429.463	888.036 ± 363.430	887.816 ± 361.041

ST 3a. Model AICc scores using Foraging as a response variable for all three transformed train-sets and both methods of classification.

		AICc				
Train-set	**Classifier**	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
41361´	*k*-NN	943.29	886.58	942.23	885.58	880.97
41361´	Decision trees	1079.66	1000.92	1078.71	1000.01	997.94
41365´	*k*-NN	958.67	899.54	957.92	898.85	894.34
41365´	Decision trees	1010.88	929.16	1009.26	927.54	927.05
41366´	*k*-NN	955.55	897.97	954.63	897.10	892.56
41366´	Decision trees	1084.10	1005.97	1083.19	1005.09	1002.35

ST 3b. Mean (± SD) model AICc scores using Foraging as a response variable when averaging AICc values among train-sets for both methods of classification.

		Mean AICc			
Classifier	**1|ID**	**Time**	**Area**	**Area + Time**	**Area * Time**
***k*-NN**	952.503 ± 8.130	894.697 ± 7.073	951.593 ± 8.274	893.843 ±7.210	889.290 ± 7.260
Decision trees	1058.213 ± 41.051	978.683 ± 42.963	1057.053 ± 41.451	977.547 ± 43.381	975.780 ± 42.259

ST 4. Performance metrics when classifying TAA data with *k*-NN and decision trees for diverse species and sampling intervals. The data below accounts for within collar dataset classification.

Species	**Classifier**	**Epoch**	**Accuracy**	**Precision**	**Recall**	**Source**
Dingo (*Canis dingo*)	*k*-NN	1	0.83	0.97	0.98	Campbell et al. 2013
Badger (*Meles meles*)	*k*-NN	1	0.71	0.95	0.99	Gao et al. 2013
Camel (*Camelus dromedarius*)	*k*-NN	0.025	0.82	0.90	0.99	Bidder et al. 2014
Sheep (*Ovis aries*)	Decision trees	3	0.83	0.83	0.79	Alvarenga et al. 2016
Sheep (*Ovis aries*)	Decision trees	5	0.86	0.79	0.89	Alvarenga et al. 2016
Sheep (*Ovis aries*)	Decision trees	10	0.83	0.87	0.83	Alvarenga et al. 2016
Cow (*Bos Taurus*)	Decision trees	0.02	-	0.82	0.88	Diosdado et al. 2015

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