

Baboon (*Papio ursinus*) group decision making at the urban edge

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Abstract

Social animals need to coordinate their group movements and make group decisions if they are to remain together. The development of urban landscapes has fragmented natural landscapes and resulted in increased human-wildlife interactions, affecting animals' decision-making. Interactions between non-human primates and people are common; high-energy foods found in urban habitats provide rich foraging opportunities for primates, increasing their growth and reproduction, but also resulting in chronic conflict with people that reduces both primate's and people's wellbeing. Understanding the decision-making dynamics of urban foraging groups will therefore inform management strategies. Here, I use high-resolution 1Hz GPS data to track the decisions of $n=13$ adults in a group of chacma baboons (*Papio ursinus*) to move into urban spaces at the edge of the City of Cape Town, South Africa. Management teams contracted by the city aim to reduce negative baboon-human interactions by herding troops away from urban areas, by targeting males that tend to lead chacma baboon troop decision-making. I find the troop shows high fission-fusion dynamics when moving into urban space. The size and composition of groups entering the urban space varies, suggesting individuals are driven by self-interests. After entering urban space, lower-ranking females spent more time in the urban space than higher-ranking individuals. Dominance rank predicted baboon's importance in the urban association network, and important individuals were more likely to lead larger group sizes into urban space. However, the alpha male was not as involved in urban association networks as predicted, with the beta ranked male being most central in the urban association network. I interpret these patterns as a consequence of baboon's response to management interventions, which focus on the alpha and their affiliates when in the urban space. The high level of fission-fusion of the troop highlights behavioural flexibility of individuals and the group in response to urban spaces and management therein.

Lay Summary

Social animals need to coordinate their movements to remain as one group. During collective movement, generally, a dominant individual will lead. Although there can be many benefits to come from group living, sometimes conflicts may occur due individuals having different needs. Therefore, social animals have evolved strategies to enable consensus under conflict of interest. An example of this is group fission and fusion. This can reduce costs to individuals as they can split off into subgroups to meet their own needs. This is a typical process for primates, and baboon species. Due to increasing development of human-modified landscapes, chacma baboons are among the species which now utilise urban food resources via urban foraging. Urban foraging events usually comprise of a subset of a whole group. Although urban foraging can bring many benefits to individuals, it can result in negative altercations and sometimes death of individuals. Management tries to reduce this by using herding the baboons out of the urban spaces, focusing on the alpha male and his close affiliates. Understanding the decision-making dynamics of these urban foraging subgroups can ensure the effective management to reduce negative human-baboon interactions, by targeting individual species which highly influence urban foraging. Here, I show the dynamics of group decisions to enter to urban space of a troop of chacma baboons residing on the urban edge of Cape Town, South Africa. I investigated the characteristics of groups entering the urban space, investigating their size, composition, and leaders. I found that the size and composition of groups entering urban space varied, and these groups did not tend to be composed of higher or lower ranked baboons. This suggests that subgroup formation occurs from individual's following their own needs and self-interests. I did find that dominant individuals turn, were often associating with others when in the urban space, and in turn these individuals associating more in the urban space had more followers when they initiated movements to enter urban spaces. However, the alpha male was less central in the urban network, with the second highest ranking male being most central. Finally, lower-ranking baboons tended to go into urban space alone or in small groups, and also spent more time in the urban space (longer events). In combination, these findings can be explained by baboon's responses to current management focused on the alpha male and close affiliates (lower-ranking individuals are less cohesive with alphas). This work highlights the high level of group fission-fusion in this group of baboons and high behaviour flexibility of its individuals.

University Declarations and Statements

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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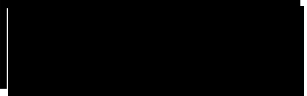
Date 16/03/2022

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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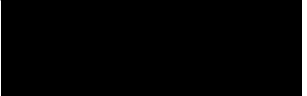
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Mres Biosciences – Statement of Expenditure

Student name: Alexie Jenkins

Student number: [REDACTED]

Project title: Baboon decision making at the urban edge

Category	Item	Descriptions	Cost*
Data storage/sharing	Hard drive	Toshiba Canvio (500GB) – portable hard drive to back up files	£66.42
Equipment	Keyboard and mouse	Microsoft keyboard and mouse set – for desk working at home during covid 19 pandemic	£48.50

*Including VAT

I hereby certify that the above information is true and correct to the best of my knowledge

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Student signature

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Statement of Contributions

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Contributor role	Persons involved
Conceptualisation	AJK, IF, AJ
Data curation	AB, AJK
Formal analysis	AJ, AJK, AB
Funding acquisition	n/a
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Project administration	AJK, IF, AJ
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Writing – original draft	AJ
Writing – review and editing	AJK, AB

Ethics Statement

The work in this thesis uses existing data collected as part of work approved by local authorities and Swansea Universities ethics committee (IP-1314-5).

Risk Assessment

Risk Assessment			
College/ PSU	COS Biosciences	Assessment Date	01/02/2021
Location	At home	Assessor	Alexie Jenkins
Activity	Desk-based research project	Review Date (if applicable)	n/a
Associated documents	<ul style="list-style-type: none"> • • 		

Part 1: Risk Assessment

What are the hazards ?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Display screen equipment	Myself	Posture problems and pain, discomfort or injuries, eg to their hands/ arms, from overuse or improper use or from poorly designed workstations or work environments. Headaches or sore eyes can occur, eg if the lighting is poor Fatigue and stress	Ensure work station is set out in a way to ensure good posture, and avoid any reflections or glare on the screen Take regular breaks from the screen	2	2	4	Review workstation assessment with Occupational Health at the first sign of any symptoms or injuries	1	2	2	
Long periods of sitting down indoors due to entirely desk based work	Myself	Muscle degeneration and lowered heart health due to less opportunity to exercise. Obesity. Fatigue, stress and depression from long periods indoors.	Get up, stretch and move around work room once an hour. During long breaks, go for walk or participate in	2	1	2					

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
			some form of exercise Eat meals away from work space.								

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
n/a	n/a	n/a	n/a

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Introduction

Social animals need to coordinate their group movements and make group decisions if they are to remain together, such as what activities to perform and when (Black, 1988), and where to travel (Stewart & Harcourt, 1994). The many benefits of group-living include reduced predation risk (Hamilton, 1971; Sorato et al., 2012), improved foraging efficiency (Stander, 1992), and improved detection of environmental gradients (Berdahl et al., 2013; Larkin & Walton, 1969). Coordinated group movement and group decisions are achieved via a variety of behavioural mechanisms. Across different vertebrate groups, it was originally thought that during collective movement, a dominant member of the group, typically an alpha male, would initiate and lead group movements (Addison & Simmel, 1980; Byrne et al., 1990; Schaller, 1965). There is evidence to support this in various taxa, for instance, in primate and canid groups, dominant individuals may more often be followed due to their strong influence over the rest of the group (Mech, 1999; King et al., 2008; Sueur et al., 2009; Bonanni et al., 2010). Thus However, recent research indicates that leadership can sometimes be more distributed (Bourjade et al., 2015), or entirely absent with all individuals in a group sharing group decisions (Conradt & Roper, 2005). Where shared decisions occur, individuals are seen to vote to indicate their preferences among alternative options, and often voting is achieved by specific vocalisations (Boinski & Campbell, 1995; Harcourt & Stewart, 1994), or stereotyped movements (Byrne, 2000; Milton, 2000). However, coordination can be difficult to achieve in heterogeneous groups (Conradt & Roper, 2009), where individuals have different requirements at different times, such as activity timing and travel destinations due to physiological needs (Clutton-Brock et al., 1982; Ruckstuhl, 1998), and these differences can lead to conflicts of interest. For example, choice of short-term travel destinations in birds, fish, and mammals can result in conflicts of interest between individuals of these taxa (Conradt, 1998; Ruckstuhl & Neuhaus, 2000). Social animals have therefore evolved a variety of strategies that enable consensus decision-making under conflicts of interest.

However, consensus may not always be reached on what direction to go or what behaviours to partake in. It can remain too costly for individuals to remain coordinated. In these cases, a process group fission can temporarily occur to limit costs to individuals (Lehmann et al., 2007). First described in hamadryas baboons *Papio hamadryas* (Kummer, 1971), this process is typical for primate species (Aureli et al., 2008). Such group fission and fusion can occur in

species ranging from Bechstein's bats *Myotis bechsteinii* (Kerth et al., 2011), to bottlenose dolphins *Tursiops aduncus* (Smolker et al., 1992) and hyenas *Hyena brunnea* (Owens & Owens, 1978). The likelihood of fission and fusion occurring increases with larger group sizes (Conradt & Roper, 2005; Focardi & Pecchioli, 2005; Kerth et al., 2011; Sueur et al., 2011) in part because individuals are unable to service social relations due to reduced time available for social interactions (Henzi et al., 1997). Therefore, kinship may be a factor driving patterns of fission-fusion, where subgroups form according to already strong affiliations, as seen in macaque species (*Macaca spp.*) (Sueur et al., 2010). Group fission and fusion can also occur to reduce travel time and feeding competition between individuals (intra competition) (Strum, 2012). For example, in chimpanzees, party sizes have been linked to food resource availability (Anderson et al., 2002; Chapman et al., 1994), and in chacma baboons, group fission has been associated to the costs of sexual competition (Ron, 1996), or when conflict over feeding location occurs between higher and lower-ranking individuals (King et al., 2008). Sometimes, group fission can be permanent.

The increasing loss of natural habitat and increased development of urban landscapes has had a powerful impact on ecosystems (Alberti et al., 2003), and resulted in decreased natural food source availability for wildlife and an increase in human-wildlife contacts (Nyhus, 2016). Generalist wildlife species may be the first to adjust to urban landscapes as they can exploit a range of food resources and may be better at recognising the risks and opportunities they may face (Sih, 2013). Long-lived, wide-ranging species with higher cognitive abilities may also be more likely to utilise these areas (Fehlmann, O'Riain, Kerr-Smith, & King, 2017; Sol et al., 2013), because it allows individuals to properly assess and remember risks related to specific locations (Fehlmann, O'Riain, Kerr-Smith, & King, 2017). Because food sources in urban areas are generally easily accessible, predictable in time and space and energy rich (Bateman & Fleming, 2012; Strum, 2010), this can make crop or urban foraging an effective strategy for wildlife, as it can lead to improved growth, reproduction and body condition (Strum, 2010), and allows for greater time allocation for other activities, such as socialising or vigilance (Forthman-Quick & Demment, 1998; van Doorn et al., 2009). When there is the option to urban forage, not all individuals in a group will partake in all urban foraging events. In savanna baboons, males were more motivated to urban forage, with females joining the urban foraging subgroups if a male they were closely affiliated with was part of the urban foraging

subgroup (Strum, 2010). In chacma baboons, recent reports have revealed that females enter urban spaces in small groups without males (Richardson, 2018).

Here, I study how individuals in a chacma baboon (*Papio ursinus*) group make decisions to use these urban spaces. Chacma baboons are well equipped to exploit urban landscapes (Hoffman & O’Riain, 2012), due to their intelligence and behavioural flexibility. The highest-ranking adult males are usually observed to have a strong influence on group decisions, as shown from work across several chacma baboon populations and environments (King et al., 2008, 2011; Stueckle & Zinner, 2008; Sueur, 2011). A strong influence of males over group decisions is similarly observed across other baboon species (olive baboons (*Papio anubis*): Ransom, 1981; Guinea baboons (*Papio papio*): Montanari et al., 2019; hamadryas baboons (*Papio hamadryas*): Kummer, 1968). However, environmental, individual, and social factors can also influence decision-making processes and leadership, hence, shared leadership has been seen in other baboon species like yellow baboons (*Papio cynocephalus*) and olive baboons (Norton, 1986; Strandburg-Peshkin et al., 2015).

When urban/crop foraging, baboons in the Cape Peninsula have been shown to use a sit and wait strategy, in which they spend most of their time out of urban space, with high energy urban foraging events being brief (Fehlmann et al., 2017). In baboons, only certain members of a troop will partake in a given urban foraging event (Warren, 2009) and therefore the group will fission, like they would in other scenarios outside of the urban space where consensus is not reached (Aureli et al., 2008). These groups urban foraging can contain less than twenty percent of the original (Schweitzer et al., 2017). Baboons foraging in urban spaces creates conflict with people, in which they are likely to be victims of human-induced harassment, injury or death (Strum, 1994; 2010). To manage these negative baboon-human interactions in urban space, on the Cape Peninsula, troops are managed by field rangers which ‘herd’ the baboons away (Kansky & Gaynor, 2000). As seen in primate populations using urban space elsewhere, negative human-animal interactions are most common amongst adult males (Marty et al., 2019; McLennan & Hockings, 2016; Strum, 2010). To reduce these conflicts, deterrence management tend to target adult males of groups (Fehlmann, 2017). On the Cape Peninsula, rangers deter the baboons from entering urban areas (van Doorn & O’Riain, 2020) and tend to focus on adult males (Kaplan et al., 2011). This strategy can be highly effective as

males drive collective movements, therefore deterrence of the males results in reduced urban space use of the majority of the troop (Bracken et al., 2021).

A proper understanding of decision-making processes of baboons when using urban space, and in particular the influence of specific individuals, will be particularly important for management policies aimed at specific groups and/or individuals (Swan et al., 2017). To study this, I focus on the behaviour and activity of a troop of baboons known as the “Da Gama” troop, in the Da Gama Park region of Cape Town. The troop are known to forage in urban space, and adults in the group were fitted with GPS tracking collars that provided high-resolution location data (1-Hz GPS data). I use these GPS data from 13 adult individuals to investigate the times at which decisions to move into urban space occur, including individual’s roles and the mechanisms involved in the movement. The troop have been shown to fission and fuse when using urban space (Bracken et al. 2021), whereby individual vary greatly in their use of the urban space use. Lower-ranking socially peripheral individuals spend more time in the urban space than higher-ranking socially connected individuals. These lower-ranking individuals entered the urban space alone or in small groups. I therefore hypothesised that the group would show high fission and fusion dynamics when entering urban space – not acting as a cohesive group, but instead splitting and entering the urban space at different times in smaller groups, and I tested a number of connected predictions:

1. As urban foraging events tend to occur earlier on in the day (Schweitzer et al., 2017), and this baboon troop are known to sleep in urban space, I expected to see a temporal component to decisions to move into urban space and predicted that most entry events into the urban space will occur earlier on in the day.
2. I expected groups which enter urban space to consist mostly of small groups, since these are less conspicuous. I expect this because entering urban environments may be more risky for individuals than foraging in “normal” foraging environments, and as there are no natural predators on the Cape which would encourage larger group formation as an anti-predator strategy (Wallace & Hill, 2012; Warren, 2009).

3. Urban foragers may be individuals which prioritise exploration over social relations (Fehlmann et al., 2020), and as lower-ranking individuals tend to avoid joining conspecifics at foraging patches (King et al., 2008), and may be more explorative as they tend to forage alone. Indeed, in this troop, lower ranked baboons use urban spaces more often than higher ranked individuals due to a combination of management and social processes (Bracken et al., 2021). I therefore expected the groups making the decisions to enter urban space to be composed of lower ranked baboons.
4. However, I predict that individuals higher up in the social dominance hierarchy would have greater influence and therefore higher ranked baboons within (sub)groups entering urban space to be more likely followed into the urban space, as in natural environment collective movement higher ranked individuals have stronger influence in decision making.

Methodology

Study site

The study site is located in Da Gama Park area (34.1617° S, 18.4054° E) on the Cape Peninsula on the South-West coast of South Africa. The Cape Peninsula spans 470km² and consists of natural habitat consisting of various habitat types including indigenous fynbos vegetation, and agricultural and urban habitat.

The Da Gama Park area consists of natural habitat, with patches of endemic mountain fynbos i.e. *Erica* spp and *Protea* spp.; (Beamish & O’Riain, 2014; van Doorn & O’Riain, 2020), and alien species of pine (*Pinus* spp.), and urban habitat, which consists of two residential suburbs: Da Gama and Welcome Glen.

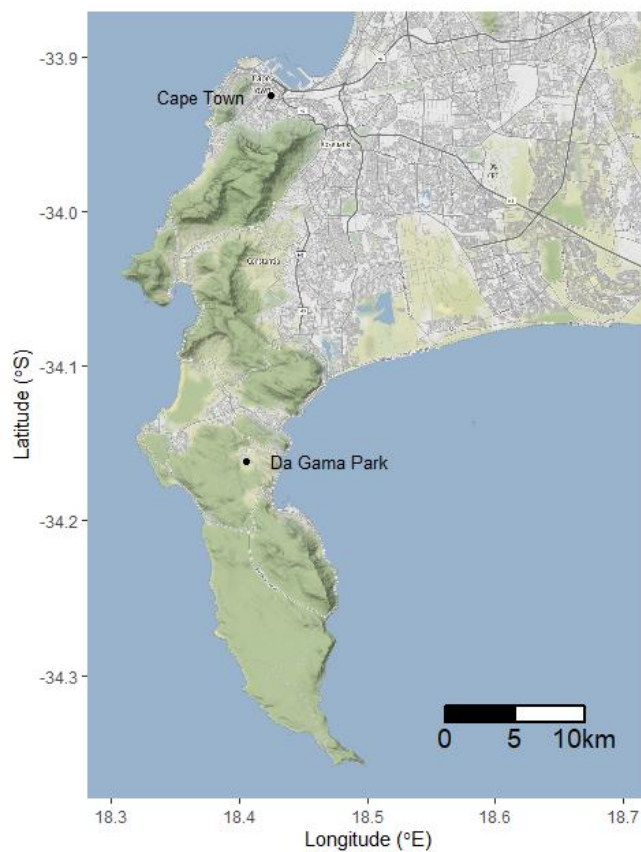


Figure 1 The Cape Peninsula. Da Gama Park (34.1617° S, 18.4054° E) is the location of the study site, which forms part of the home range of the focal baboon troop.

Study troop

There are 12 chacma baboon troops situated on the Cape Peninsula (Hoffman & O’Riain, 2011). The Da Gama troop studied here consists of 2 adult males, 19 adult females and approximately 30 infants, juveniles, or sub adults of both sexes, and were studied by Research Agreement with South African National Parks (SANParks). They range in both natural and urban environments (Bracken et al., 2021) and the urban environment provides high-energy resources from houses and food waste in addition to food sources from fruiting trees such as guava *Psidium quajava* (Hoffman and O’Riain, 2011)

Baboon GPS tracking collars

Tracking collars were constructed at Swansea University and used to track baboon movements of the Da Gama troop between 25/07/2018 and 02/08/2018. The collars were fitted by a certified veterinary surgeon when baboons were under sedation following locally approved protocols. The use of tracking collars was approved by Swansea University’s AWERB committee (IP-1314-5). Sixteen individuals were fitted with tracking collars and thirteen collars provided data that are used in this thesis: two adult males and eleven adult females. The collars weighed $\leq 2.5\%$ of the body mass of all the baboons, which is half of the 5% of body weight maximum recommended weight (Pebsworth et al., 2012).

The collars were equipped with sensors which recorded GPS (using the World Geodetic system 1984) accurate to 0-5m (depending on environment conditions, collar position on the baboon and availability of satellites; (Fehlmann et al., 2017; McCann et al., 2021). GPS fixes were recorded at 1 s sampling intervals (1-Hz) from 8:00 am to 8:00pm (SAST, UTC + 02:00) each day of the study period, for a mean \pm S.D. of 43 ± 10 days, range = 21 - 54 days (Bracken et al., 2021)

Identifying individual decisions to move into urban space

I used GPS tracked baboon movements (see above) to investigate individual and group decisions to move into the urban space. To do this, I created three datasets, a “daytime” dataset, which included GPS data between the hours of 8:00am and 6:00pm, the “all day” dataset which included the GOS data for all the recorded hours each day, ie, 8:00am to

8:00pm. The third data set, the “evening” dataset, which included the hours from after 6:00pm to 8:00pm. This was done because the hours outside of the daytime data are when the troop tended to be moving to their urban sleeping site, and so these evening hours “overestimate” urban space use (Bracken et al., 2021). Next, to record each collared baboon’s entries into the urban space, a polygon was drawn around urban space (figure 2) in QGIS and then the ‘getRecursionsInPolygon’ function, recurse package in R studio (version 1.1.2; (Bracis et al., 2018) was used to identify the times the collared baboons entered and exited this polygon. This resulted in 1791 recorded individual recursions into the urban space across the study period (for full details see: Bracken et al., 2021).

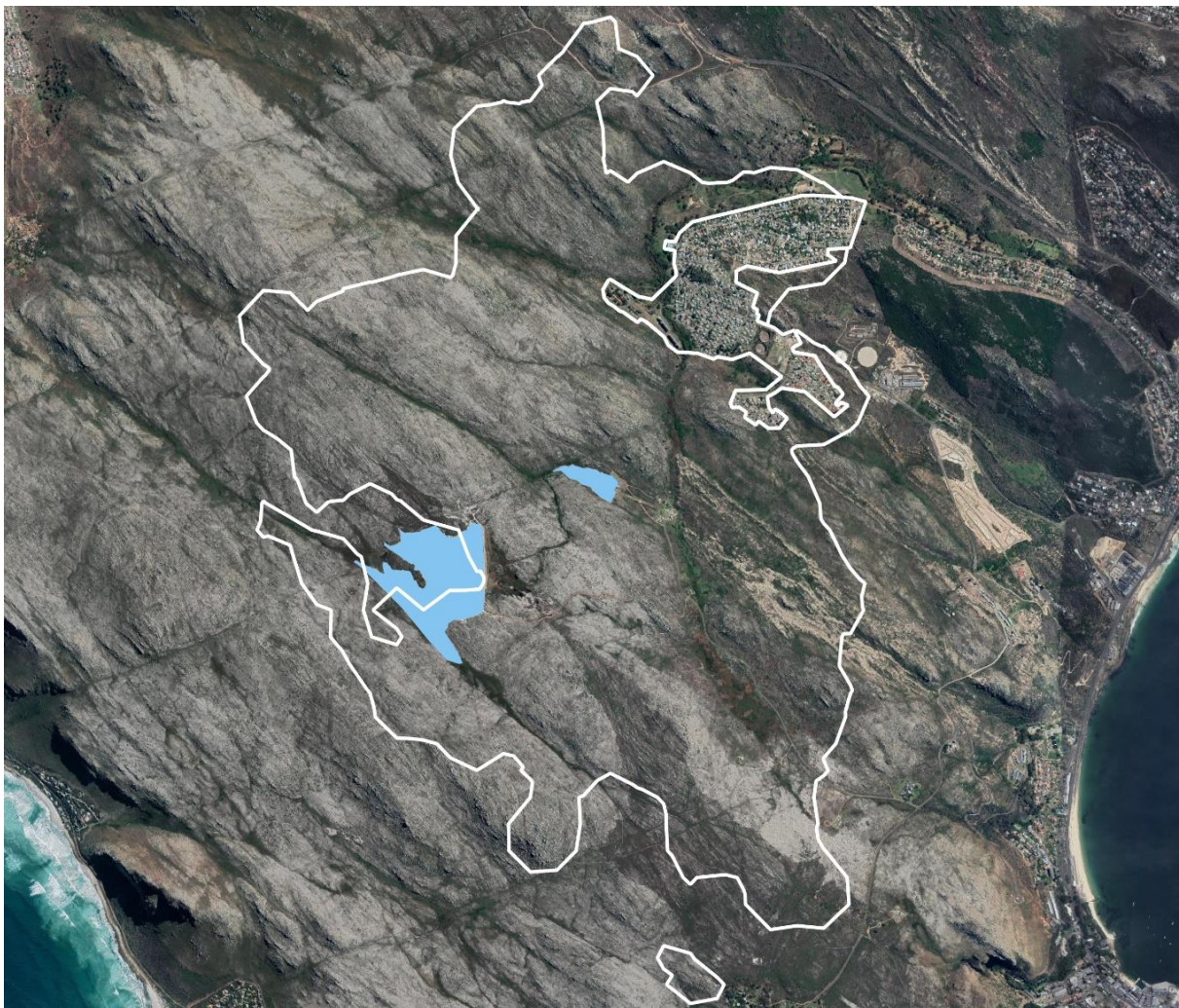


Figure 2 Da Gama troop home range (outer white outline), with urban space (inner white polygon). Blue areas represent dams in the baboon troop home range.

Identifying group decision events

To identify where one or more baboons made a decision to enter the urban space together, I first produced histograms of the individual decision data, plotting the time intervals between baboons entering urban space, and the time duration of visits to the urban space (see Appendix A).

The histograms were extremely long-tailed indicating that a lot of the entries to the urban space were clustered in time (representing a social decision) and tended to be of quite short duration. Therefore, based on these data, I decided that a decision to enter the urban space should be defined as events where a baboon remained in the urban space for at least one minute and at least one minute should have passed since the individual last entered the urban space. I defined social or 'group decisions' as instances where an individual entered the urban space less than five minutes after the previous individual had entered (Figure 3). Using these criteria, the 1791 individual entries were reduced to 703 individual entries into the urban space and of these 703 events, 117 group entry events and 88 individual entry events were recorded across the entire study period.

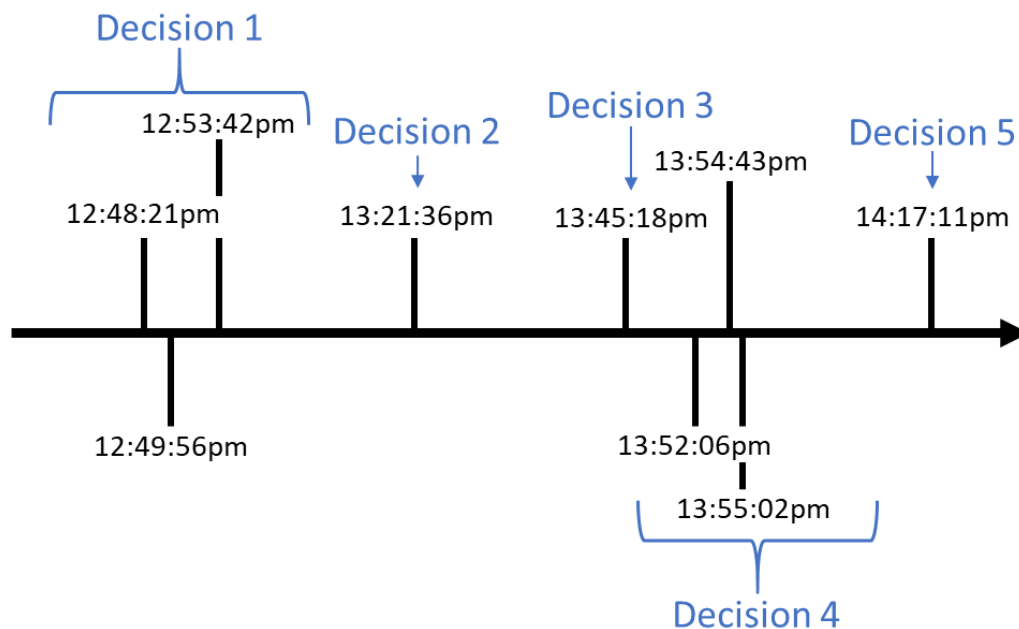


Figure 3 A timeline representing a sequence of urban space entry that may occur, with five different decision events. The time points represent an individual entering the urban space. An individual must enter within 5 minutes of the last individual that entered to be part of the same decision event. Individuals also need to be in the urban space for at least 1 minute, therefore, if the first individual in decision 1 exited the urban space before 13:49:21, then this would not be counted. Decision, 2, 3 and 5 would also be excluded in the analyses of groups,

as they are individual events. This schematic is an example and does not represent any data that was collected during the study period.

Social dominance and decision events

Dominance ranks of each baboon were provided (see Bracken et al., 2021; Fürtbauer et al., 2020) for details), between 0 and 1, with one indicating the highest rank and 0 being the lowest rank. I used these ranks to investigate whether decision events tended to be made up of low- or high-ranking baboons. To do this, ranks for individuals in an event were summed and then divided by the respective group size (i.e. mean rank of the group). This meant that decision events with groups made up of lower-ranking baboons would have a lower score, and conversely decision events involving higher-ranking baboons would have a higher score. Any differences in mean rank would disappear when large groups comprised of mixed social status entered the urban space.

Leadership and decision events

Potential leadership – where certain individuals lead the group into urban spaces - was investigated by testing the order of individuals entering the urban space for any decision event, assuming the first entry as a proxy for leadership (Hall, 1960; King et al., 2008; Leca et al., 2003). The number of occasions an individual was leading was compared to an expected value, where expected values were calculated as the sum of possible outcomes multiplied by the likelihood of each outcome will occur. In this case, the possible outcomes would be each collared baboon being a leader across the study period, and the likelihood of each baboon being a leader would be equal, as in this case the “expected” is that leadership is equally distributed. For example, if there were 130 group entry events, then the expected value for each baboon would be 10, as 13 baboons were sampled. The sexes of leaders were also investigated this way. The relationship between dominance rank of individuals who entered first and group size were also investigated, to see whether dominance rank influenced the number of followers.

Group composition for decision events

We created social networks during decision events and extracted certain network metrics to further investigate the associations of individuals when moving into the urban space. First a symmetrical matrix was made, describing the occasions when pairs of individuals were involved in a decision event (moving into the urban space together). Matrices were created for group sizes 1-6 (because there were too few decision events involving larger group sizes) and the simple ratio index was used to create an index of association. This matrix was then used to create a network map using the igraph package in R version 4.0.4 (1.2.6; Csardi & Nepusz, 2006), and different network metrics were extracted to investigate associations of individuals entering the urban space. Degree, strength, eigenvector centrality, betweenness and assortativity (Table 1) were extracted from the network. This was carried out on all three datasets created (i.e. “all day”, “daytime” and “evening hours”). I investigated correlations between the network metrics and dominance ranks of individuals, to reveal if more or less dominant individuals are frequently involved in decision events, and with whom.

Table 1 Definitions of the network metrics described in the methodology.

Network metric	Definition
Strength	The number of links to a node (Farine and Whitehead, 2015; Sosa et al., 2021)
Degree	The sum of links' weights in a weighted network. Degree and strength may be correlated, but this is not the case always (Sosa et al., 2021)
Eigenvector centrality	A measure of an individual's (node) influence within a network. An individual's eigenvector value can be linked to the degree strengths of the nodes connected to them as well as its own strength value (Farine & Whitehead, 2015). For example, a node can have a high degree score may have a low eigenvector score because their connections are with low scoring nodes
Betweenness	Betweenness is used to indicate which how much a node connects subgroups in a population (Sosa et al., 2021)
Assortativity	A measure to study homophily, with values ranging from -1 (complete dissortativity, nodes associate with those with very different characteristics) to 1 (complete assortativity). Characteristics can include age, social rank, sex, and personality. (Sosa et al., 2021)

Statistical tests

Statistical analyses were conducted in Rstudio version 1.4.1106, R version 4.0.4 (R Core Team, 2021) with α set at 0.05. Normality tests were used and where appropriate, nonparametric tests were used. To test whether there were more prominent leaders into the urban space than the expected values, chi-squared tests were used to test this. Chi-squared tests were used to determine which sex is more likely to lead group entries. Spearman's rho correlation coefficients were used on the rank sum data to determine if there is a correlation between the group sizes and overall dominance rank of the group. Spearman's rho was used to test for a correlation between group size, dominance and time spent inside the urban space. Various correlation tests were used on network metrics to determine a correlation between the metrics and dominance ranks of individuals in the network.

Results

Decisions to enter the urban space

A total of 88 individual and 117 group events to enter the urban space were recorded across 49 days, with varying numbers of individuals involved in a given group decision ranging between 2 -12 individuals (Figure 4b-d) and staying an average \pm standard error 2535 ± 98 seconds. The majority of these decision events fell in the early morning or evening when the baboons tended to be close to their frequently used sleeping site (Figure 4a), meaning that 73/113 (62%) of these events occurred in daytime hours only, partly supporting my first prediction that events would be earlier in the day. Because of the strong temporal component, I therefore present the results that follow for 'all day data', 'evening data' and 'daytime data', since the context of the decisions to move into town are likely to differ.

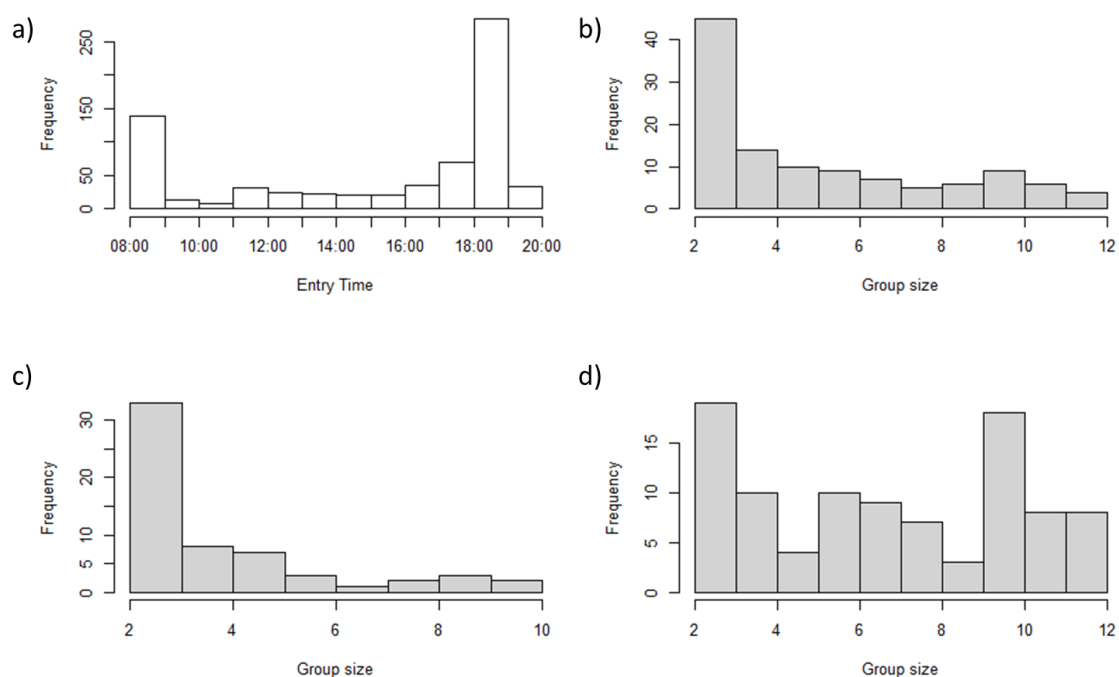


Figure 4 The hourly entry frequencies during the 08:00 – 20:00 hr daily observation periods 8:00am – 8:00pm daily (a). The frequency of different group sizes entering the urban space during the study period b) all recorded hours of the observation period c) the “daytime” dataset, consisting of the hours 8:00am – 6:00pm d) Evening hours dataset, consisting of the hours after 6:00pm to 8:00pm.

During daytime hours, the biggest group consisted of 10 individuals (maximum possible = 13 collared individuals). Most entries into the urban space in daytime hours (65.75%) involved

fewer than 5 individuals, with the median group size being 4, supporting my second prediction. I also find a significant negative correlation between the size of the group entering the urban space, and the time that the group spent in the urban space for the daytime dataset (Spearman's rho: $r_s(73) = -0.137$, $p < 0.001$), but no correlation was present for the "All day" dataset (Spearman's rho; $r_s(115) = -0.019$, $p = 0.781$), and evening only dataset (Spearman's rho: $r_s(42) = -0.0493$, $p = 0.307$) (figure 5a-c). Social dominance rank of individuals was negatively correlated with the mean time spent in the urban space (Pearson's correlation: $r(11) = -0.584$, $df = 11$, $CI = -0.859, -0.051$, $p = 0.036$, figure 5d), meaning lower ranked baboons spent more time in urban space.

Social dominance of groups and decision events

Dominance ranks scores for groups entering urban space did not change with their respective group size using, in the all-day data (Spearman's rho: $r_s(115) = 0.114$, $p = 0.104$), evening data (Spearman's rho: $r_s(42) = -0.015$, $p = 0.879$), or the daytime only data (Spearman's rho: $r_s(73) = 0.214$, $p = 0.161$) suggesting smaller or larger groups are not made-up of higher or lower ranked individuals. However, lower ranking individuals on average were more often involved in urban foraging groups of smaller sizes, than more dominant individuals (Figure 6b).

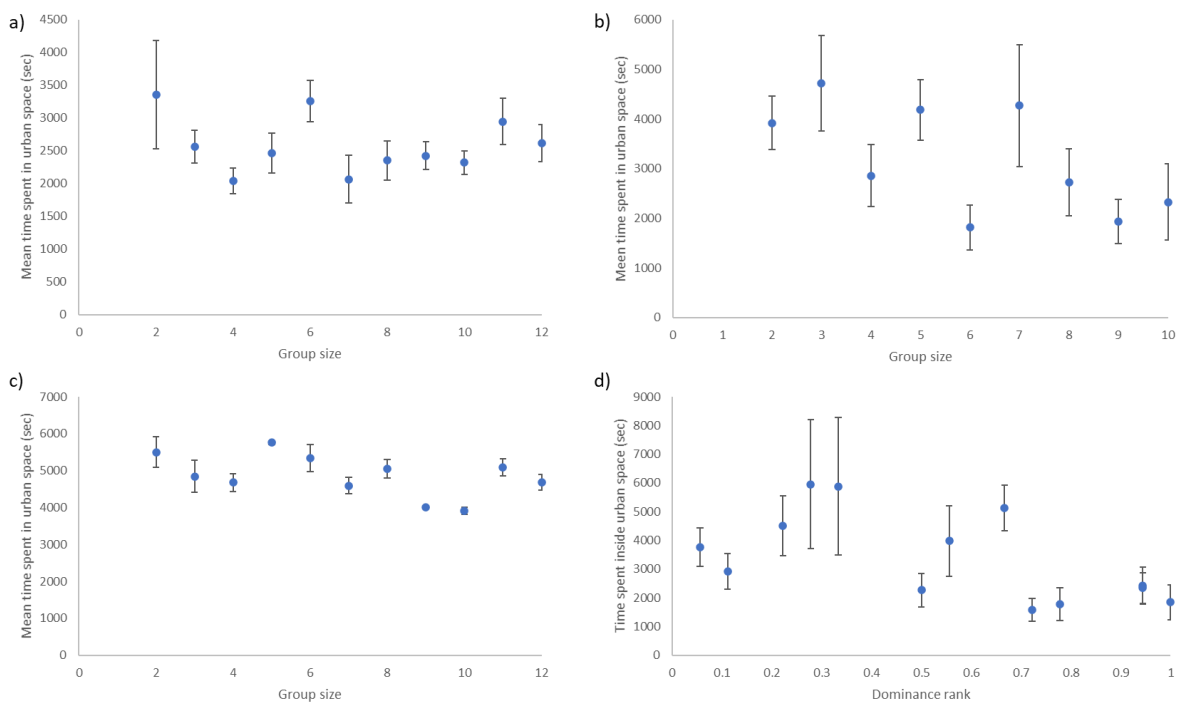


Figure 5 Correlations of findings of time spent in urban space with different factors. The correlation between group size and time spent in the urban space for the "all day" dataset (a), the "daytime dataset" (b) and evening only dataset (c). D) the correlation between the

dominance rank of individuals and time spent in the urban space after decision events for the daytime dataset. Error bars represent standard error.

Leadership

The identity of leaders when moving into the urban space was not significantly different from expected for the all day data ($\chi^2 = 143.229$, $df = 142$, $p = 0.454$), evening ($\chi^2 = 124.787$, $df = 129$, $p = 0.589$) or daytime only data ($\chi^2 = 137.8332$, $df = 116$, $p = 0.082$), contrary to my final prediction. The dominance rank of the 'leading' individual did not change with group size when using all data (Spearman's rho: $r_s = 0.06$, $p = 0.374$), or the evening data (spearman's rho: $r_s = -0.016$, $p = 0.897$), or daytime only data (spearman's rho: $r_s = 0.0904$, $p = 0.301$). For the daytime data and all day dataset, the sexes contributed to leadership as expected (all day: $\chi^2 = 2.371$, $df = 1$, $p = 0.124$; daytime: $\chi^2 = 0.059$, $df = 1$, $p = 0.808$), but not for the evening only data (evening: $\chi^2 = 7.901$, $df = 1$, $p = 0.005$).

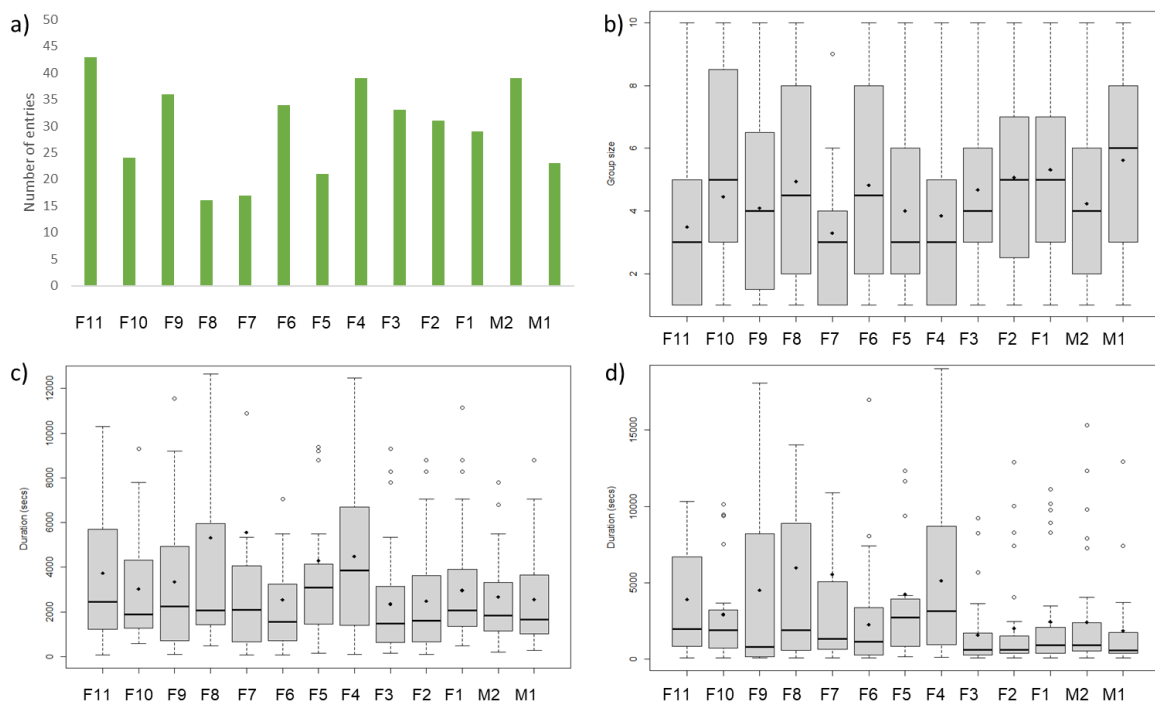


Figure 6 Decision data during daytime hours for each individual baboon. Dominance rank of an individual increases from left – right. a) the number of decision events each collared baboon was involved in. b) the mean group sizes that each baboon was involved in c) duration of the group decision events each baboon was involved in (group decision duration = the mean time that all individuals involved in the entry event spent in the urban space). d) the individual durations of baboons in the urban space. Boxplot black lines represent medians, black points represent means.

Group composition for decision events

Since groups moving into urban space tended to be smaller, were not often composed of groups of lower or higher-ranked baboons, but lower-ranked baboons spent more time in the urban space when they entered in a group, I used network level analysis to further investigate associations of baboons when moving into urban space (These networks are visually represented in figure 7, network metrics for all datasets in Appendix B). All day data for associations in urban space had higher mean degree and strength values: degree: all day = $11.538 \pm \text{SE } 0.627$, daytime = $11.333 \pm \text{SE } 0.257$, evening = $9.076923 \pm \text{SE } 1.282$; strength: daytime = $0.542 \pm \text{SE } 0.018$, all day = $0.555 \pm \text{SE } 0.024$, evening = $0.506 \pm \text{SE } 0.261$. Eigenvector centrality and strength for associations in the urban space was significantly correlated with dominance rank (Pearson's correlation: $r(11) = 0.587$, CI = 0.019, 0.868, $p = 0.045$) for the daytime dataset, but strength was not (Pearson's correlation: $r(11) = 0.501$, CI = -0.103, 0.835, $p = 0.097$). Strength and eigenvector centrality of individuals were not correlated with social rank for the 'all day' dataset (pearsons correlation: $r(11) = 0.374$, CI = -0.223, 0.767, $p = 0.208$; Spearman's rho: $rs(11) = 0.467$, $p = 0.110$), or the evening only dataset (pearsons correlation: $r(11) = 0.124$, ci = -0.458, 0.6318, $p = 0.686$; spearman's rho: $rs(11) = 0.214$, $p = 0.482$). Eigenvector centrality is significantly correlated with size of groups they have led for the daytime data (Spearman's rho: $rs(73) = 0.243$, $p = 0.005$), meaning that more central baboons are more likely to lead larger groups into the urban space. Eigenvector centrality of was also negatively correlated with mean time spent in the urban space (Pearson's correlation: $r(11) = -0.763$, CI = -0.925, -0.366, $p = 0.002$), but there was no correlation for the all day dataset (spearman's rho: $rs(11) = -0.286$, $p = 0.344$), or the evening only dataset (spearman's rho: $rs(11) = 0.044$, $p = 0.992$). Eigenvector centrality was positively correlated with the number of entries made for the daytime (pearsons correlation: $r(11) = 0.678$, CI = 0.227, 0.899, $p = 0.009$), evening (pearsons correlation: $r(11) = 0.731$, CI = 0.303, 0.914, $p = 0.019$) and all day (pearsons correlation: $r(11) = 0.871$, CI = 0.614, 0.961, $p < 0.001$). Assortativity values for the "all day", "daytime" and "evening" datasets were -0.069 and -0.051, and -0.047 respectively.

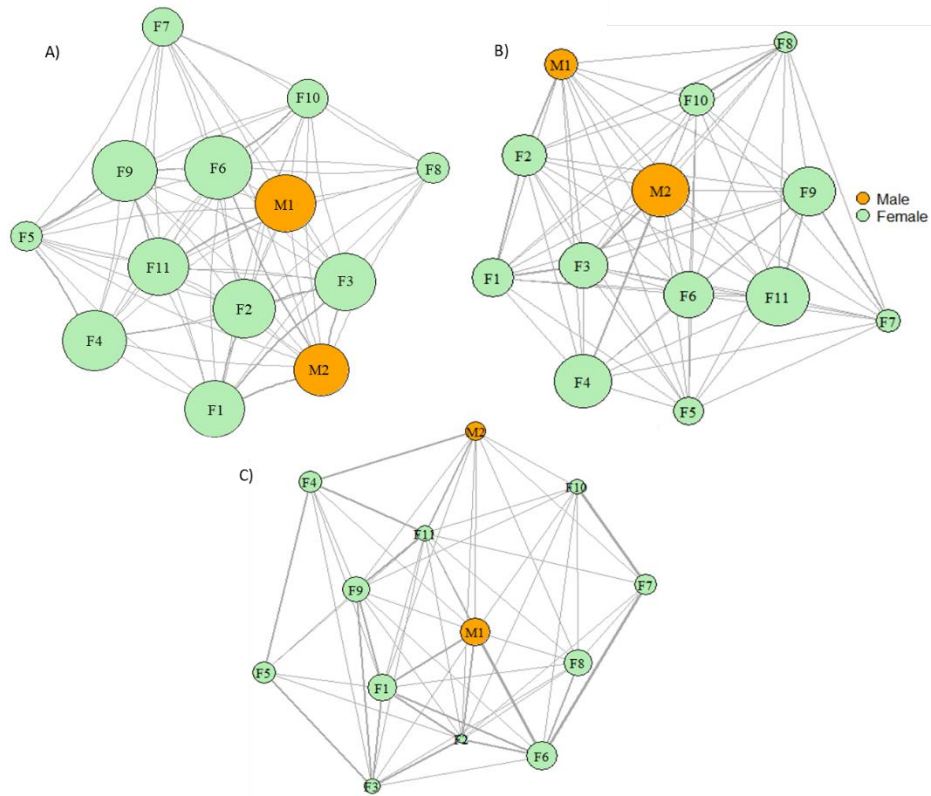


Figure 7 Social affiliation network diagram based on associations among individual whilst entering the urban space together (at different group sizes), for $N = 13$ baboons for a) all day, b) daytime hours and c) evening only hours. Edges/connections between individuals (nodes) represent the simple ratio index calculated from the number of events individuals were identified to be in the urban space. Colours represent sexes. The width of the edges represents the strength of their association when entering the urban space. The size of the node corresponds to their respective number of group entries into the urban space.

Discussion

By using GPS data to study the decision-making mechanisms of a group of adult chacma baboons (*Papio ursinus*) when using urban space, I find that the groups entering the urban space tended to be small, and composed of individuals of varying ranks, but lower ranking individuals were generally part of smaller groups. Moreover, higher-ranking individuals did tend to have higher importance in the urban association network and spent less time in the urban space after decisions to enter that space. These findings can suggest high behavioural flexibility and adaptation in response to current management strategies placed upon the troop. I discuss each of my main findings in turn.

I found baboon's entries into urban space were frequently in the early morning and evening, partly supporting my first prediction. Evening entries were likely associated with individuals going to their urban sleeping site, whilst early entries are as the troop comes down from their sleeping site at the edge of the urban space. The large number of individual entries earlier in the day too (08:00 – 09:00), is similar to findings of a study of a chacma baboon troop in Zimbabwe, where most urban and crop foraging events occurred earlier in the day (between 08:00am and 10:00am, Schweitzer et al., 2017). I find that the mean duration in the urban space after decision events to be considerably longer than the average of 4.8 minutes seen in this troop (Bracken et al., 2021), which is due to the conditions I have set for recursions to be considered a "decision event" for my analyses, whereas Bracken et al considered all recursions in their analysis.

The troop did not tend to enter the urban space together as a cohesive group. Instead, whilst group sizes varied, the sizes of groups entering the urban space were generally small, consisting mostly of four individuals, which supports my second prediction that urban foraging groups are smaller than natural groups (Priston et al., 2012; Schweitzer et al., 2017; Wallace & Hill, 2012; Warren, 2009). Being in a smaller group makes them more inconspicuous and therefore less likely to be detected in the urban space than larger groups (Strum, 1994). I expected the groups making the decisions to enter urban space to be composed of lower ranked baboons (Prediction 3). I did not find groups composed of all lower or higher ranked baboons, but lower ranking individuals had a lower mean group size for events they participated in, meaning that generally they were apart of smaller groups when entering the urban space more than higher ranking individuals. All of this indicates that sub-

groups entering the urban space can frequently change its compositions across all group sizes (high degree fission-fusion dynamics), suggesting that individuals may prioritise their own needs and self-interests.

My final prediction was that individuals higher up in the social dominance hierarchy would more likely be followed and lead into the urban space, I found there were not significant individual leaders identified more than chance if leadership was distributed equally across decision events and group sizes. A similar lack of relationship between initiator identity and number of followers have been reported in natural collective movements in baboons (Petit & Bon, 2010; Strandburg-Peshkin et al., 2015). There was not a significant relationship between the dominance rank of leading individuals and group size. This contrasts with literature studying collective movements of baboon species and other primates in natural environments, where more dominant individuals have more of a say and more likely to lead collective movements in chacma baboons (King et al., 2008, 2011; Sueur, 2011) and across baboon and primate species (Boinski & Garber, 2001). This finding could also suggest individuals are following their own self-interests over following the needs of dominants.

For the daytime entries, there was a correlation between baboon dominance rank and eigenvector centrality within the proximity network of urban entry. Hence, lower-ranking individuals were less “important” in the urban network and tended to not associate with other baboons in the urban space. Meaning that they were in smaller groups, or more alone than dominants. Individual eigenvector centrality in the urban entry network is also positively correlated with the group sizes they lead, so whilst dominance rank had no significant correlation with number of followers directly, higher ranking individuals were more central in the network and are more likely to have a larger following into the urban space, and conversely, lower-ranking individuals will have less followers into the urban space. The group’s urban assortativity score shows that there is no strong urban entry assortativity, or disassortativity (Sosa et al., 2021), related to their dominance rank, suggesting that subgroups frequently change and have different compositions.

In chacma baboon networks, alpha males that hold central positions in grooming and spatial networks usually have higher numbers of followers when on the (Kaplan et al., 2011; King et al., 2011). What is most interesting here is that the dominant alpha male of the focal troop is less central in the network for entries into urban space, with the beta male in the group having

the highest eigenvector centrality in the network and made more entries into the urban space than the alpha. This may be the adaptations to overcome management interventions implemented the group. Due to management regimes targeting the males of troops, particularly alphas (Fehlmann et al., 2017), the alpha's role in urban entry may have been altered, where they spend less time in the urban space and are involved in group entries less. Therefore, the second highest-ranking male has taken over in his place as most central in the urban entry association network, as they may be targeted less by field rangers than the alpha. Lower-ranking individuals of the Da Gama troop have been recorded entering the urban space more frequently than the core troop (Bracken et al., 2021). Although this is not the case in my study, where all baboons make many of entries into the urban space my analyses show that both dominance rank and eigenvector centrality are negatively correlated with time spent in the urban space after decision events. This could be an adaptive result to management practice on the troop, as proposed in Bracken et al (2021). Due to the high focus on the alpha with the core group, these lower-ranking females may have used the available opportunity to fission from the group and use the urban space separately. Low-ranking females avoid joining others at eating patches when foraging (King et al., 2009), are more likely to adopt innovative behaviours (Reader & Laland, 2001) and prioritise exploration over socialisation and relationships (Fehlmann et al., 2020). In addition, lower-ranking females less socially cohesive with alphas (Archie et al., 2014) and they are likely to split from a group when there is conflict of interest (King et al., 2008). This could be encouraging lower ranking individuals to act separate from the core group, whom are the primary target of current management strategies (Fehlman et al., 2017). In addition, as these less central and dominant individuals are separate from the core, they are less likely to be detected when in the urban space, which could be allowing them to spend more time in the urban space than dominants. Further study into individual's movements will help identify behavioural types of individuals and flexibility of these behaviours (Hertel et al., 2020), which may result in more flexible management strategies being developed based on individual-level information.

The Da Gama troop exhibits high fission-fusion dynamics as an adaptation of their environment, in which their urban space recursions are frequent and consists of different compositions of varying size groups. This can make management more difficult as there are more separate units in different locations at the same time to keep track of. High levels of

fission-fusion dynamics like this can sometimes cause a permanent fission of the troops (Sueur et al., 2011), these groups are called “splinter groups” (Strum, 2010). This would create more challenge for management because this will result in baboons utilising the urban space more and spending more time in these areas (Hoffman & O’Riain, 2012) as if the group splits in two permanently, there will be more ground that the groups will be covering, and there would not be enough capacity to manage them. Being able to limit the small groups and solitary individuals will prevent these individuals from entering these urban spaces as well as the core, will reduce time in urban spaces and in turn prevent group fission events and splinter group formation in the long term. This will also prevent negative impacts, such as severe injury or sometimes death to individuals (Beamish, 2009; Beamish & O’Riain, 2014).

Monitoring of baboons with use of field rangers has proven to be successful in reducing baboon urban space use, however, the baboons are making adaptive changes to leadership and smaller groups are being undetected. As all age-sex classes partake in urban foraging (Shweitzer et al., 2017), and now without adult males in many small groups, male-focused management may no longer be the most appropriate method of deterrence of baboon groups. Management should now consider finding ways to reduce the probability of group fission. As the likelihood of fission increases with group size (Conradt and Roper, 2005; Kerth et al., 2011, Sueur et al., 2011), management should now consider focusing on finding methods to restrict sizes of troops. This may improve group cohesiveness (Sueur et al., 2011) and reduce the probability of groups fissioning under conflicts of interest (King et al., 2008). This will ease strain on field rangers. Finding a way to achieve this however will take some time to figure out how to effectively do so, without impacting the troop. For example, the option of the contraception of females will reduce increasing numbers of a population but can negatively affect the behavioural synchrony of groups (King & Cowlshaw, 2009).

As mentioned previously, more study into individual behaviour patterns and flexibility will enable more effective management (Hertel et al., 2020), as different behavioural types and personalities may be revealed, like which individuals are more exploratory or risk prone (Merrick & Koprowski, 2017), or individuals which drive an increase or decrease of urban space use (King et al., 2018). For the time being, management should continue to focus on deterrence tools such as baboon-proofing of waste and fences (Kaplan et al., 2011), consistency is however needed for this to be fully effective. Understanding residents’

perspective of baboon-proofing practice will help management, as their actions are fundamental for the success of this method of management. In addition, investigation into people's views on different size and sex of baboons may help explain why low-ranking females access urban space for longer periods, the public may view males as more of a threat (Mormile & Hill, 2017), maybe as this species exhibits high sexual dimorphism where the males are nearly double the mass of females (Mitani et al., 1996).

Conclusions

With increasing spatial overlap between humans and wildlife, better understanding of the behavioural mechanisms of urban-residing species will result in effective management and a decrease in conflict. I used data acquired from urban foraging adult baboons of both sexes fitted with high resolution tracking collars to investigate the entries of individuals into the urban spaces and the dynamics of group movement into the urban space. Individuals can vary greatly in their use of urban areas, and individuals have different levels of importance in the urban network. Lower-ranking individuals spend more time in urban spaces when they enter it, than higher-ranking individuals. Higher-ranking individuals are more central in the urban groups. Individuals with higher eigenvector centrality scores tend to have higher number of followers into urban areas. The alpha male also is not as central in the network as the second highest-ranking male and spends less time in urban areas. These appear to be behavioural adaptations to current male-focused management practice on the troop (Bracken et al., 2021). These findings present evidence of high behavioural flexibility of individuals in the group and high-level fission-fusion dynamics. This underlines the importance of examining individual baboon movement and responses to human-landscapes and interactions. Further study is needed to provide more insight into individual movement, as this can discover important individuals which may be influencing other members to urban forage, or individuals more likely to explore risky environments. In addition, investigation into individual movement may reveal specific behavioural types and flexibility of these behaviours, which will help predict space use of individuals. This will assist management (Merrick and Koprowski, 2017) in producing effective and flexible management strategies.

Appendix A: Histograms of baboon data created when defining entry decisions

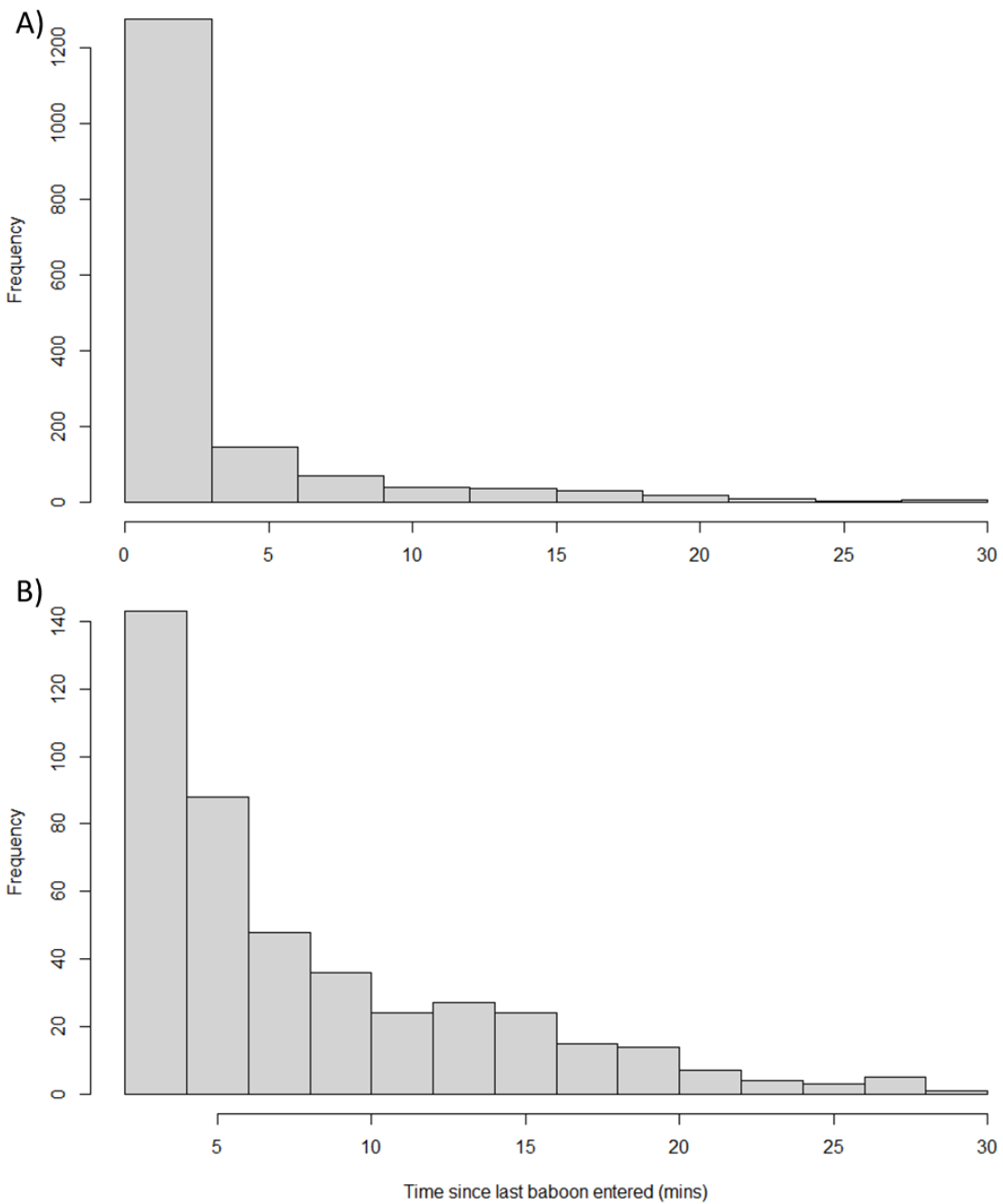


Figure 8 The frequencies of time intervals between baboons entering the urban space. B) has removed values below 2 minutes.

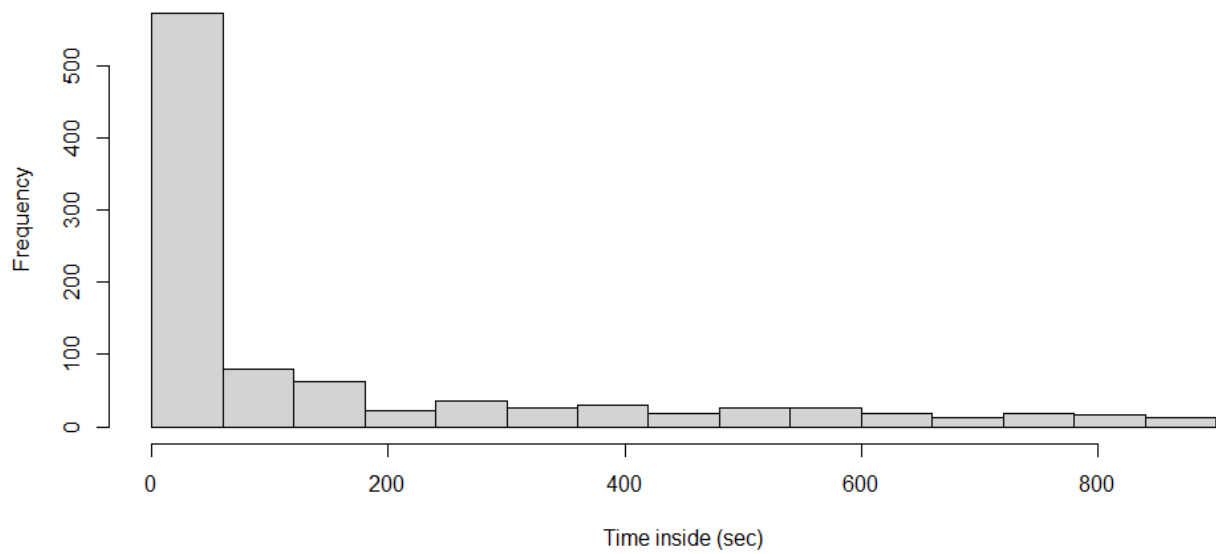


Figure 9 the frequencies that individuals spent inside the urban space.

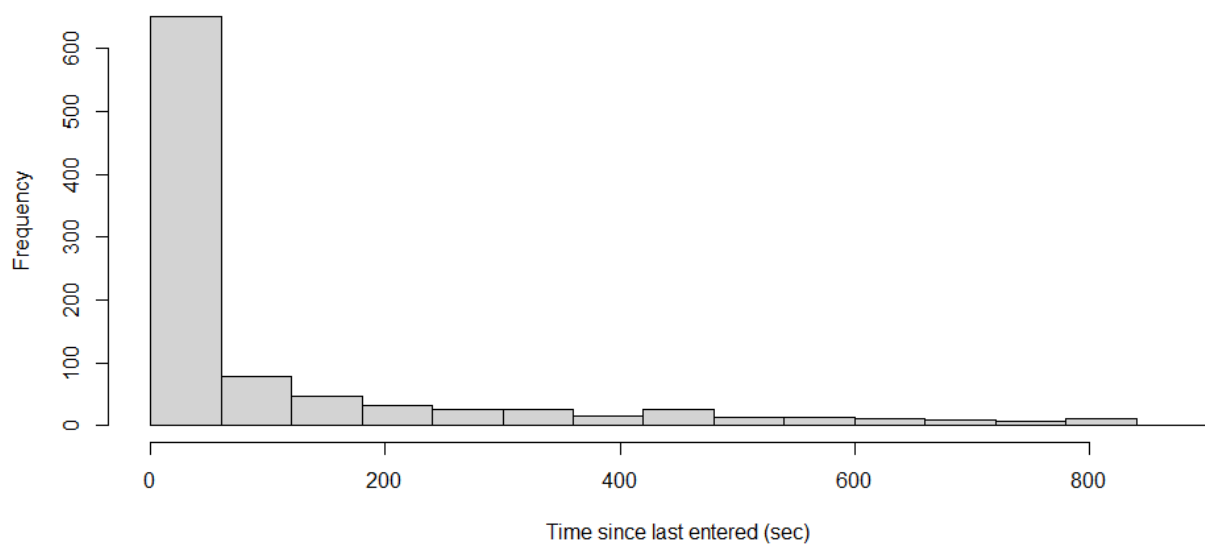


Figure 10 The frequencies of durations that individuals would enter the urban space after they last entered the urban space.

Appendix B : The network metrics of all datasets

Table 2 Network metrics of all baboons involved in this study, with all datasets included

ID	Dominance	Degree		Closeness		Strength		Eigenvector centrality		Day time	Evening	All data	Evening	All data	Day time	Evening	All data
		Day time	Evening	Day time	Evening	Day time	Evening	Day time	Evening								
Cindy	0.0555556	12	12	1.960349	1.557801	1.8625	0.510113	0.641931	0.536913	0.826074	0.984542	0.906415	2	14	2	14	2
Sunny	0.1111111	12	8	1.809426	1.251255	2.009875	0.552661	0.41045	0.497543	0.89	0.619131	0.810101	2	1	2	1	8
Azul	0.2222222	12	10	1.933049	1.244753	1.758639	0.517318	0.576814	0.568622	0.818044	0.96227	0.923824	5	5	4	3	1
Lola	0.2777778	10	9	1.943114	1.354783	1.911266	0.406723	0.405271	0.360421	0.67202	0.651677	0.611849	4	3	4	3	5
Don	0.3333333	9	6	1.518366	1.006905	2.271426	0.393078	0.39389	0.347486	0.642198	0.591546	0.569183	1	0	1	0	11
Trinity	0.5	12	9	1.7852	1.112529	1.684916	0.560161	0.592703	0.593502	0.942486	0.94913	0.96769	0	4	0	4	0
Nelly	0.5555556	11	7	1.718407	0.930298	2.117399	0.481991	0.398691	0.41931	0.79523	0.699514	0.701164	1	0	1	0	9
NN	0.6666667	11	8	1.740055	1.039826	1.759814	0.513769	0.447988	0.51477	0.865903	0.737154	0.858757	1	0	1	0	0
Kym	0.7222222	12	9	1.764808	1.219238	1.788553	0.566634	0.52691	0.559111	0.947408	0.90671	0.935771	4	0	4	0	0
Luna	0.7777778	11	11	1.615401	1.368336	1.666293	0.545471	0.615287	0.600135	0.900247	1	1	0	4	0	4	0
Hanson	0.9444444	11	10	1.578888	1.336182	1.617562	0.553366	0.591958	0.554149	0.923841	0.991819	0.939595	2	0	2	0	0
Sheb	0.9444444	12	9	1.624373	1.314744	1.655151	0.615622	0.443506	0.604175	1	0.690495	0.976455	0	6	0	6	0
Kangela	1	11	10	1.923165	1.474099	1.97616	0.456907	0.540688	0.506032	0.775992	0.92249	0.863287	1	8	1	8	2
Mean	0.9629629	11.33333	9.666667	1.708809	1.375009	1.749624	0.541965	0.525384	0.554785	0.899944	0.868268	0.926446	1	4.666667	1	4.666667	0.666667
SE	0.0904699	0.25705	0.445224	0.183114	0.051065	0.054753	0.017849	0.025647	0.023967	0.029429	0.044056	0.038888	0.455083	1.162563	0.455083	1.162563	1.100475

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