

Personalities are not associated with different reproductive tactics in male Cape ground squirrels, *Xerus inauris*

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Highlights

- Cape ground squirrels are a highly social species with low rates of aggression.
- Males have two discrete reproductive tactics; ‘natal’ and all-male ‘band’ groups.
- Males have docile personalities.
- Personalities are not associated with different reproductive tactics.
- Males became less docile with longer on-site tenure (years captured).

Abstract

Personality may influence social living and the maintenance of alternative reproductive tactics (ARTs). In some species, suppressing aggression may be important for facilitating social living, and different personalities may be linked with different types of social associations. Yet, few studies have examined personality in species with low levels of aggression. In Cape ground squirrels, males have two discrete ARTs. Males either live in family groups (‘natal’) or all-male groups (‘band’) and lack physical aggression and territoriality. We measured docility (during trapping and handling in 2014–2019, $N_{\text{males}} = 275$) and activity and exploration (during an open field test in 2015, $N_{\text{males}} = 34$) in adult males to determine whether personality contributes to the maintenance of ARTs. We found repeatability in docility (adjusted repeatability = 0.25–0.26) but not in activity or exploration, and docility was not associated with different ARTs. However, docility and ARTs were influenced by abiotic and biotic factors. Males were more docile after their first capture, and older males (longer on-site tenure) tended to be less docile. In years of higher rainfall, there were more band males, suggesting that ARTs may depend on ecological conditions.

Keywords: activity; alternative reproductive tactic; ART; docility; exploration; personality; sciurid

Personality has been found in many animals and may affect ecologically relevant traits associated with sociality (Webster & Ward, 2011). In group-living animals, behaviour may be influenced by environmental factors such as resource distribution and predation threat and social factors such as group size, relatedness, stability and the behaviours of other group members (Webster & Ward, 2011). Some of these behaviours may form personalities, which may interact with the physical and social environment to determine fitness and survival outcomes (Webster & Ward, 2011; Wolf & Krause, 2014). The effect that an individual's personality type has on the survival and reproductive outcomes may depend on the level of sociality of the species. For example, in an asocial species, bolder individuals may have higher fitness when food resources are scarce (Le Cœur et al., 2015), while in a social species, shyer individuals may secure favourable social positions, resulting in higher fitness compared to bolder individuals (Armitage & Van Vuren, 2003).

In species with alternative reproductive tactics (ARTs), where individuals of one sex adopt different strategies to achieve reproductive success, different tactics are often associated with differences in physiological, morphological and behavioural traits (Taborsky et al., 2008). For example, in Columbian ground squirrels, *Urocitellus columbianus*, males adopting a territorial reproductive tactic hold a territory, tend to be larger, older and more experienced than males adopting a satellite reproductive tactic, where males do not hold a territory (Balmer et al., 2019). Different ARTs may be maintained by several mechanisms including ecological changes that coincide with an individual's development, or flexible or plastic behavioural responses to environmental conditions (Taborsky et al., 2008). Sometimes, different reproductive tactics are associated with different personality types. In round gobies, *Neogobius melanostomus*, sneaker males are more active, explorative, bolder and less aggressive than guarder males (Synyshyn et al., 2021). Thus, personality may contribute to the maintenance of ARTs within a population. Likewise, sociality may influence the effects personality has on the maintenance of ARTs. For example, aggressive and active personalities are associated with different ARTs in the asocial round goby (Synyshyn et al., 2021). In contrast, personality traits do not influence tactic switching in the socially flexible striped mouse, *Rhabdomys pumilio*, whereby individuals may switch between solitary living and group living, with group living being associated with social breeding behaviours such as communal breeding, helpers at the nest or paternal care. Rather, tactic switching is attributed to changes in environmental conditions (Yuen et al., 2015). Thus, the mechanisms maintaining ARTs may differ in social versus asocial species.

Different personalities may also be associated with different social organizations (Webster & Ward, 2011), whereby organization is defined as features pertaining to group size and composition (Prox & Farine, 2020). For example, shy female eastern grey kangaroos, *Macropus giganteus*, forage in larger group sizes than bolder individuals (Best et al., 2015). In degus, *Octodon degus*, a social species that shares communal burrows during the night, explorative personalities are associated with social group composition. More explorative individuals share burrows with less explorative individuals (Chock et al., 2017).

Personality consequences on ARTs and social organization may also include aggression effects (Bergmüller & Taborsky, 2010). Species vary in the degree of aggression that they exert, and

given that sociality and aggression are different traits that are not necessarily linearly related (Wolf et al., 1999), some highly social species may exhibit high levels of aggression while other highly social species may have very low levels of aggression (Strier, 1994; van der Marel et al., 2020). As differences in aggressive tendencies may also affect reproductive tactics (Synyshyn et al., 2021) and social living (Schoepf & Schradin, 2012), in some species, suppressing aggression may be important for survival and fitness (Haigh et al., 2017; Strier, 1994) and thus may result in variation in aggressive traits. The costs and benefits of personality types depend on context and may vary with environmental conditions (Le Cœur et al., 2015; Santicchia et al., 2018). Hence, individuals living in different conditions may experience different consequences for the same personality type. For example, in Eurasian red squirrels, *Sciurus vulgaris*, the survival benefit of a bold personality type depends on habitat type (Santicchia et al., 2018). Therefore, examining personality across taxa that vary in the degree of social conditions and aggression increases our understanding of the relationship between personality and social living (e.g. Schoepf & Schradin, 2012).

The Cape ground squirrel is a socially living, burrowing species that inhabits open grasslands throughout southern Africa (LaFlèche & Waterman, 2020; Skurski & Waterman, 2005). Social groups dig large burrow clusters (burrow aggregations), which are sometimes shared with other species such as yellow mongooses, *Cynictis pencilata*, and meerkats, *Suricata suricatta* (Waterman & Roth, 2007). Females live in matrilineal family groups composed of related adult females and subadults of both sexes (Waterman, 1995). Sexually mature adult males exhibit either of two discrete male ARTs, which are associated with different social living situations. Upon maturity, males may live with their family group in their natal burrow cluster (hereafter, 'natal' males); natal groups on average consist of two adult females and three subadults of either sex (Waterman, 1995). Alternatively, males may leave their natal group and join other dispersed males in roving all-male bands of up to 19 individuals (hereafter, 'band' males; Waterman, 1995, 1997). These all-male bands have a fission–fusion social system with males forming ephemeral foraging sub-bands of two to eight individuals (Waterman, 1997). In some populations (such as the South African population that is the subject of this study), bands have no dominance hierarchy (Manjerovic & Waterman, 2015), while in other populations (Namibia), male bands have linear dominance hierarchies (Waterman, 1995).

The social grouping of male Cape ground squirrels is unique among rodents (Prox & Farine, 2020; van der Marel et al., 2020; Waterman, 1995) and most similar to the Barbary ground squirrel, *Atlantoxerus getulus* (van der Marel et al., 2020), as both species have all-male groups that do not exhibit within- or among-group aggression. Although male–male cooperation is found in many species (Díaz-Muñoz et al., 2014), male groups of most species are intolerant of other male groups and inherently aggressively compete with them (van der Marel et al., 2020), unlike Cape ground squirrels. Despite evidence of weak precopulatory selection in some populations of Cape ground squirrels (e.g. dominance, competitive searching for females; Waterman, 1995, 1998), most evidence suggests that male reproductive competition is largely via sperm competition (Manjerovic et al., 2008; Manjerovic & Waterman, 2015).

Personality has not been examined in Cape ground squirrels, so determining whether Cape ground squirrels have personality traits that may influence their social behaviours or social organization would contribute to our understanding of the maintenance of nonaggressive social living in this species. Furthermore, it remains unknown what drives and maintains the two ARTs in this species (Manjerovic & Waterman, 2015). So far, no differences in copulation frequencies, reproductive success (Manjerovic & Waterman, 2015), testosterone levels (Scantlebury, Waterman, & Bennett, 2008; Scantlebury, Waterman, Manjerovic, et al., 2008) or body mass (O'Brien et al., 2021; Scantlebury, Waterman, & Bennett, 2008) have been found between individuals showing different ARTs. However, individuals with different tactics differ in their body condition, ectoparasite loads and metabolic rates (Manjerovic & Waterman, 2015; O'Brien et al., 2021; Scantlebury, Waterman, & Bennett, 2008; Scantlebury, Waterman, Manjerovic, et al., 2008). Natal males spend more time feeding while band males spend more time in locomotion (Scantlebury, Waterman, & Bennett, 2008; Scantlebury, Waterman, Manjerovic, et al., 2008). Therefore, these ARTs represent two distinct behavioural phenotypes, which may form the basis of personality types.

Since personality traits have been found in other sciurid species (Boon et al., 2007; Clary et al., 2014; Dosmann et al., 2015; Montiglio et al., 2015; Petelle et al., 2013), and different personality types have been associated with different ARTs (Han & Jablonski, 2019; Synyshyn et al., 2021), we hypothesized that Cape ground squirrels may have personalities associated with different ARTs. Following the terminology and methodologies of Réale et al. (2007), we quantified behavioural expressions of docility during trapping and handling and activity and exploration during standardized open field behavioural assays to determine whether any of these behaviours were consistently repeatable within individuals after accounting for state-dependent variables such as weather and body condition. We then tested for any association between personality traits and reproductive tactics. We predicted that males of different tactics would have different personality types. Specifically, as band males have comparatively large range sizes compared to natal males (Manjerovic & Waterman, 2015; Waterman, 1995), we predicted that band males would be more active and more explorative than natal males. Also, as natal males remain in their family groups and participate in alloparental care (Waterman, 1995), we predicted that natal males would be more docile. Thus, we expected natal males to be more docile and less active and less explorative than band males. Additionally, we examined the effect of testosterone on active and explorative behaviours during an open field test. As increased mobility and mate searching in males has been associated with increased testosterone levels (Mills et al., 2009; Schradin & Yuen, 2011), we predicted that males with higher levels of testosterone would be more active and explorative.

Methods

Study Site

We conducted this study from 2014 to 2019 at S.A. Lombard nature reserve, a 4600 ha reserve 18 km northwest of Bloemhof, South Africa (27°35'S, 25°23'E), during the austral winter (May–August; mean \pm SD daily minimum temperature = 4.8 ± 4.8 °C, daily maximum temperature = 21.7 ± 4.8 °C, total winter precipitation = 19.8 ± 18.7 mm), which is cooler and drier than during the austral summer (November–February; mean \pm SD daily minimum temperature = 17.7 ± 3.6 °C, daily maximum temperature = 30.6 ± 5.1 °C, total summer precipitation = 304 ± 90.6 mm).

Our study site is a floodplain consisting mostly of dry *Cymbopogon–Themeda* veld and black soil turf veld, with some patches of bush and pan areas (Van Zyl, 1965). In years of high rainfall, food is abundant (O'Brien et al., 2021). Natural predators to Cape ground squirrels include mammals, reptiles and raptors, such as black-backed jackals, *Canis mesomelas*, Cape cobra, *Naja nivea*, and black-shouldered kites, *Elanus axillaris* (Unck et al., 2009).

Trapping and Body Measurements

During our study, we trapped 275 different males over 906 trapping occasions (Table 1). Throughout the field season, we conducted daily trapping rounds (2–4 rounds/day, ~70 traps/round), typically starting at 0800 hours and finishing at 1730 hours. Tomahawk live traps (15 × 15 × 50 cm, Tomahawk Live Trap co., Tomahawk, WI, U.S.A.) fitted with shade covers and baited with peanut butter and bird seed (Waterman, 1995) were checked every 1–2 h or less. Upon discovering a trapped animal, we (1) marked unfamiliar squirrels with a passive integrated transponder (PIT) tag (AVID Inc., Norco, CA, U.S.A.) for permanent identification, a dorsal freeze mark (Freeze Spray, CRC Industries Inc., U.S.A.; Rood & Nellis, 1980) and a black hair dye mark (Rodol D; Lowenstein and Sons Inc., New York, NY, U.S.A.) for identification from a distance, (2) scored docility as described below, (3) measured body mass to the nearest 5.0 g using a spring scale (Pesola AG, Baar, Switzerland), (4) measured spine length from the base of the skull to the base of the tail with a tape measure and (5) assessed reproductive condition. Adult males are scrotal year-round and are easily distinguished from subadults who are either nonscrotal or partly scrotal. We also (6) collected blood to measure plasma testosterone. All individuals were released in the area in which they were caught, by opening the handling bag at the site of capture and allowing the animal to move away.

Table 1. Number of trapping occasions and number of different adult males (unique tag identification) trapped and assessed for docility during 2014–2019 at S.A. Lombard Nature Reserve

| Year | Number of trapping occasions | Number of unique males |
|-----------|------------------------------|------------------------|
| 2014 | 57 | 25 |
| 2015 | 222 | 80 |
| 2016 | 81 | 73 |
| 2017 | 66 | 61 |
| 2018 | 213 | 119 |
| 2019 | 267 | 125 |
| 2014–2019 | 906 | 275 |

To compare our body condition results to previously published studies on Cape ground squirrels, we calculated body condition as the residuals of the ordinary least squares regression of log spine length and log body mass, whereby a positive residual value indicates better body condition (Schulte-Hostedde et al., 2005). However, even though calculating body condition as regression residuals was a standard method in earlier studies, the use of residuals to estimate condition is debated because input variables (e.g. body mass and spine length) have an error associated with them (Labocha & Hayes, 2012). Therefore, we also calculated body condition using principal component analysis (PCA), using the R package ‘psych’ (Revelle, 2022) as in Tranquillo et al. (2022). We calculated component scores on analyses using male body mass (g) and the spine length (mm) average for each male for all measurements taken that year. Body condition was then defined as the second component (PC2 loadings: 0.707 for body mass, –0.707 for spine length) as heavier males had a higher score than lighter males of the same spine length. As body condition estimates using both methods were highly correlated ($t_{1683} = 53.607$, $P < 0.001$), we used the PC2 body condition scores for all further analyses.

Docility Scoring

Docility is defined as an individual's reaction to trapping and handling, whereby docile individuals are generally quiet and easy to manipulate and do not struggle while being handled (Réale et al., 2000). Docility has been associated with aggression in several species, whereby more aggressive individuals struggle more during handling (Boon et al., 2007; Haigh et al., 2017; but see Blumstein et al., 2013).

We based our docility measurements on the methods of Réale et al. (2000). We assigned scores during four aspects of trapping and handling: approach, transfer, handling and release. Scoring was as follows: ‘approach’, which reflects the subject's response to the handler's approach to the trap: 0 = subject is quiet and still; 1 = subject starts alarm calling and hissing when the handler approaches within 1 m of the trap; 2 = subject reacts to the handler from a distance,

alarm calling, hissing and thrashing; 'transfer' from the trap to the handling bag: 0 = subject immediately enters the bag; 1 = subject resists but enters the bag after 30–60 s, and in some cases, only after the handler bangs on the trap; 2 = subject strongly resists bagging, so the handler must shake the trap or open the back and push the subject into the bag; handling: 0 = subject is quiet and still, no perceptible reaction; 1 = subject struggles, snorts and alarm-calls less than half the time during handling, but handling is manageable; 2 = subject struggles, snorts and alarm-calls more than half the time, making handling very difficult; upon 'release': 0 = the subject walks away; 1 = the subject runs away. Scores reflect the degree of reaction, such that high-scoring individuals were less docile and low-scoring individuals were more docile. Since different researchers took estimates on docility, we also included the handler identity as a random effect in subsequent models. Additionally, although docility behaviours were distinct and easy to qualify, we also assured similarity of docility measurements by training inexperienced researchers with an experienced researcher for several weeks and provided each researcher/trapping kit with a detailed written docility scoring protocol.

Open Field Test

We used a modified open field test to quantify two categories of behaviour: activity and exploration. Activity refers to an individual's general activity level, and exploration refers to their reaction to novel, but not risky, situations (Réale et al., 2007). We conducted open field tests on 34 individual males, three times each, during the austral winter (May–August) of 2015. All open field tests were performed on-site at the trap location immediately upon discovering a previously marked adult male in a trap. Individual identity was confirmed from the unique dye mark painted on the back of each individual. We could not standardize the length of time each subject waited in the trap before beginning the open field test. Our arena consisted of a 1 × 1 × 0.8 m plywood box, sealed with a polyurethane finish, with a divider separating the arena into two equal-sized compartments (Fig. 1). Subjects could move between compartments via a 10 cm diameter hole, which could be opened and closed by the handler from the outside with a sliding door. A novel object – rhinestone-covered red sunglasses – was placed at the end of the second compartment. The novel object was kept the same in all three trials to keep all test conditions constant. However, because using a novel object repeatedly is not a usual practice in novel object or neophobia tests, our open field test results cannot be interpreted as a measure of a reaction to a novel object beyond the first trial (see Discussion). The floor of the arena was marked with a 4 × 4 grid and the top was covered with a clear Plexiglas sheet, above which was mounted a tripod and camera (Sony HandiCam, Sony, Tokyo, Japan).

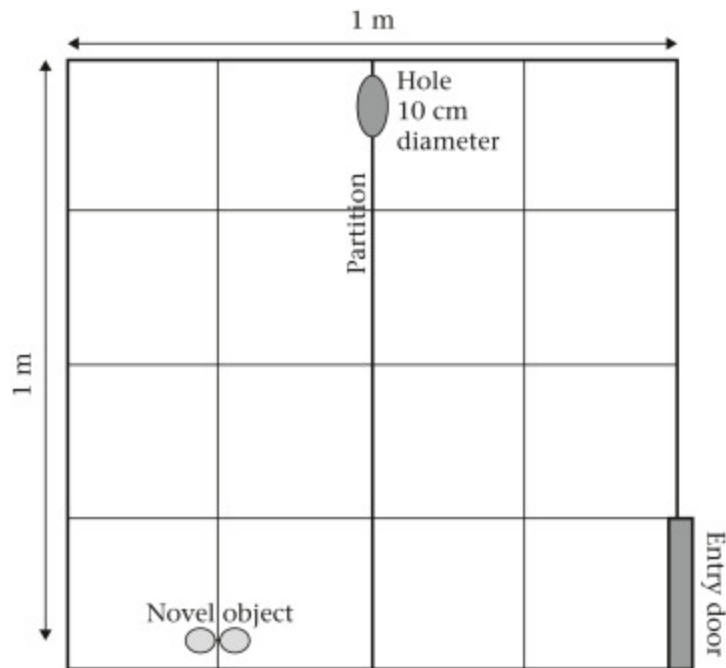


Figure 1. Diagram of the open field arena used in personality assays in 2015 on 34 male Cape ground squirrels. The arena measured $1 \times 1 \times 0.8$ m and was covered by a clear Plexiglas lid. In this diagram, compartment 1, where subjects entered at the start of the test, is on the right; compartment 2 is on the left.

Subjects were transferred from the trap directly into the first compartment via a door located at the bottom on the arena. The trap was placed flush against the open door, and the squirrel was coaxed into the arena without handling the animal. Once the squirrel entered the arena, the trap was pulled away and the door was closed and locked. In preliminary tests, upon first entering the arena, all subjects jumped and moved about, but this initial excitement subsided by 1 min. Therefore, subjects were left in the arena for a pretest habituation period of 1 min before the door to the second compartment was opened and the test began. The experimenter left the vicinity while the camera recorded the whole arena (both compartments) for 9 min. We then released subjects where they were trapped by lifting the Plexiglas lid and allowing animals to jump out. Next, we cleaned the arena and the sunglasses with a 50% vinegar and water solution (Shave & Waterman, 2017). Since weather affects behaviour in other ground squirrel species (Vispo & Bakken, 1993), we recorded cloud cover, wind speed and temperature with a Kestrel 3000 weather meter (Nielsen Kellerman, Boothwyn, PA, U.S.A.).

Some subjects did not enter the second compartment; however, all subjects were scored regardless. From the video footage, one researcher (S.V.) measured four behavioural variables: activity, jumps, squares crossed and latency to contact the novel object. Activity was measured as the total time in seconds spent in locomotion (i.e. limb movement resulting in displacement). Jumps, in which all four feet left the ground, were counted, since jumping has been found to correlate with locomotion in other squirrels (Aliperti et al., 2021; Boon et al., 2007). Exploration was quantified in two ways: as the number of grid squares entered, not counting re-entries, and as the latency in seconds for the subject to physically contact the novel object (Réale et al.,

2007; Yuen et al., 2015). Since the number of squares crossed was highly bimodal, with individuals either crossing most of the 16 total squares and others remaining near the door entrance, we analysed squares as a binary variable wherein test subjects crossed ≥ 9 squares or ≤ 8 squares. As latency to reach the novel object also had a bimodal distribution, with test subjects either reaching the sunglasses quickly, or not at all, we also analysed latency as a binary variable wherein the subject either reached the novel object (1), or did not reach the object (2).

Reproductive Tactic

We determined alternative reproductive tactic primarily by observing the males' sleeping arrangements and the composition of social groups at our study site. Band males sleep with other adult males in vacant burrows that are located away from or adjacent to female groups, while natal males sleep in their natal burrow cluster with their natal family group (Waterman, 1995). We used radiocollar transmitters (model number PD-2C, Holohil Systems Ltd, Carp, Ontario, Canada) to track males to their sleeping burrow in the mornings and late afternoons, when squirrels tend to be with their social groups in the vicinity of their burrow cluster (Unck et al., 2009; Waterman, 1995). We observed squirrels from observation towers and hides that were mounted atop vehicles at a distance of 50–100 m. Using 10 × 50 binoculars and 15–45 × 60 spotting scopes, we identified individuals from their dorsal dye marks (O'Brien et al., 2021; Scantlebury, Waterman, & Bennett, 2008). We also monitored female social groups at their burrow clusters, taking note of group composition at morning and afternoon emergence and males that continued to live with the female groups past adulthood. It is extremely rare for a male to revert to a natal reproductive tactic after dispersing and joining a band (J. M. Waterman, personal observation). Therefore, once we observed a male adopting the band-living tactic, we considered him to be a band male for the rest of his life.

Using the above methods, we determined the ART being adopted by the individual at the time of trapping and handling for 431 out of 906 docility observations. We therefore used a secondary alternative method based on the individuals' lifetime history of trapping locations as a proxy for home range to assign ART for an additional 82/906 docility measurements (Table 2). Band males move over a larger home range than natal males (~31 ha versus 11 ha; Manjerovic & Waterman, 2015) and sleep in different vacant burrows every night, while natal males return to the same burrow every night (Waterman, 1995). Therefore, males with a lengthy history of being trapped at various locations over a large area of the study site were assigned 'band' status, and young adult males trapped frequently and exclusively near their natal burrow were assigned 'natal' status. In total, 270 docility observations were conducted on band males and 243 on natal males. Docility measurements taken at times when there was insufficient information to support an ART assignment ($N = 393/906$) were excluded from further ART analyses.

Table 2. Methods used to assign alternative reproductive tactic (ART) at the time of capture for adult males trapped during 2014–2019 at S.A. Lombard Nature reserve

| ART assignment method | Reproductive tactic | |
|---|---|--|
| | Band | Natal |
| Observation of sleeping arrangement | Sleeping with other males ($N = 213$) | Sleeping with a female family group ($N = 218$) |
| Estimation from trapping location history | Frequent trapping at widespread locations, at least 500 m from their former natal burrow (when known), with few, if any, trapping incidents at the former natal burrow ($N = 57$) | Frequent trapping at their natal burrow, with few, if any, trapping incidents more than 500 m from their natal burrow ($N = 25$) |
| Total | 270 docility measurements on males adopting a band tactic | 243 docility measurements on males adopting a natal tactic |

ART was determined for 513 out of 906 docility measurements.

Testosterone

We took single measurements of circulating plasma testosterone for 29/34 males who underwent open field testing. We collected 1 ml of blood from the femoral vein using a sterile 26-gauge needle and a 1 ml syringe for hormone assays. Plasma was separated from whole blood by centrifugation at 6000 revolutions/min for 5 min (Spectrafuge mini, Labnet International, Edison, NJ, U.S.A.) and frozen at -20°C until processed. Plasma testosterone concentrations were determined using a commercially available coated tube assay kit (Coat-a-Count MG12191, IBL International GmbH, Hamburg, Germany) as in Scantlebury, Waterman, and Bennett (2008) and Scantlebury, Waterman, Manjerovic, et al. (2008). The assay was able to determine testosterone concentrations of 6–1200 ng/dl, and cross-reactivity of the Coat-a-Count testosterone antibody was 1.8% with 19-nortestosterone, 0.31% with dihydrotestosterone and $<0.01\%$ with other steroids tested. We validated the assay (procedure as in O'Brien et al., 2018, 2021) by testing for parallelism between serial dilutions of Cape ground squirrel plasma (obtained from an individual with high testosterone concentrations who was not used in further analyses) and the standard curve (data not shown). The curves were parallel and not significantly different from the reference preparation. The sensitivity of the assay (90% binding) was 5 ng/dl or 0.175 nmol/litre. The intra-assay coefficient of variation was 7.6%.

Statistical Analysis

All data manipulation and statistical analyses were done in R (R Core Team, 2021). We used R packages ‘tidyverse’ (Wickham et al., 2019) for code organization, ‘dplyr’ (Wickham et al., 2022) for data manipulation and ‘ggpubr’ for data visualization (Kassambara, 2020), and ‘MCMCglmm’ (Hadfield, 2010) and ‘coda’ (Plummer et al., 2006) for multivariate model analyses.

As multivariate models have been highlighted as an effective tool for investigating individual variation in behavioural response (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010), we used multivariate models to estimate within- and among-individual variation in behavioural responses measured during open field tests and during trapping and handling. To control for state-dependent behavioural plasticity, we included weather variables and physical and physiological measures as fixed effects in our models.

Repeatability of docility behaviours

We examined repeatability in docility behaviours using a Bayesian approach with Markov chain Monte Carlo multivariate GLMMs using the 'MCMCglmm' package (Hadfield, 2010), following methods described by Dingemanse and Dochtermann (2013). We fitted a model to investigate within- and among-individual variances and covariances for behavioural responses during all four components of docility assessment. Approach, transfer and handling were fitted as Poisson, and release was fitted as a categorical response. We fitted the following fixed effects: (1) capture, whether the individual was being trapped for the first time (first time = 1, all captures after the first = 0); (2) body condition; and (3) on-site tenure, the number of years since the adult was first captured. As Cape ground squirrels have been trapped annually at this field site since 2002, on-site tenure for all males is reasonably accurate. However, when interpreting on-site tenure as a proxy for age, for the males that were born on-site ($N = 90/275$), on-site tenure accurately reflects their age. For males that were born off-site and dispersed into our field site ($N = 185/275$), on-site tenure likely underestimates age. We also fitted (4) rainfall, the total precipitation from July of the previous year until June of the sampling year, which represents the amount of rainfall prior to the austral winter season and is associated with plant productivity (Van Zyl, 1965). Tenure, body condition and rainfall were z-centred (mean = 0, standard deviation = 1) to help with model fit and ease of interpretation (Houslay & Wilson, 2017).

We fitted three random effects: (1) tag, identity (ID) of the squirrel; (2) handler ID, because behavioural and physical measurements may be influenced by the human handler; (3) area, where the individual was captured, as areas vary in their degree of predation pressure and squirrels spend significantly less time vigilant in low-predator areas compared to high-predator areas (Unck et al., 2009).

To estimate the repeatability of each behavioural response independently, we set tag, area, handler ID and the R -matrix (residual covariance) to an 'idh' structure. We used noninformative inverse-Wishart priors throughout and ran all models for 4 000 000 iterations, with a burn-in of 5000 and thinning interval of 2000. Successive samples from the posterior distribution had low autocorrelation ($r < 0.01$). To confirm model convergence, we visually inspected posterior distribution trace and density plots (Hadfield, 2010) and calculated the autocorrelation between successive samples using the R package 'coda' (Plummer et al., 2006).

We calculated adjusted repeatability for approach, transfer and handling on the latent scale for Poisson error structure (log link) with additive overdispersion and calculated adjusted

repeatability for the categorical variable ‘release’ on the latent scale with binomial error structure (logit link) with additive overdispersion following Nakagawa and Schielzeth (2010). We calculated the point estimate and credible intervals for each repeatability estimate from the posterior modes and highest posterior density (HPD) intervals. We considered behavioural traits to be repeatable if posterior distributions were symmetrical and lower HPD intervals were >0.1 (as variance estimates were constrained between zero and one, with the HPD interval constrained to be positive).

Repeatability of open field test behaviours

We examined the repeatability of activity and exploration behaviours of 34 males using 102 trials of an open field test. As trial order and habituation to an experimental set-up may affect behavioural response (Mazzamuto et al., 2019; Montiglio et al., 2012; Santicchia et al., 2021), we examined the effect of trial number and intertrial interval on behaviour. However, as there was no intertrial interval for trial 1, we split our open field test analyses into two models: the ‘novelty’ model included the novel situation (trial 1) and trials 2 and 3; the ‘habituation’ model included only non-novel trials 2 and 3 and intertrial intervals.

We followed the same methods for determining repeatability as described above. In both novelty and habituation models, activity and jumps were fitted as Poisson, while squares and novel object latency were fitted as categorical responses. We fitted the following fixed effects: temperature, wind, cloud cover, testosterone level, body condition, trial number and intertrial interval (only ‘habituation’ model). Temperature, wind, cloud cover, testosterone level and body condition were z-centred. Tag was included as a random effect. We set tag and the *R*-matrix (residual covariance) to an ‘*idh*’ structure, used noninformative inverse-Wishart priors throughout and ran all models for 4 000 000 iterations, with a burn-in of 5000 and thinning interval of 2000. Model convergence was examined as described above. We calculated adjusted repeatability for activity and jumps on the latent scale for Poisson error structure (log link) with additive overdispersion and for the categorical variables squares and novel object on the latent scale with binomial error structure (logit link) with additive overdispersion. We calculated the point estimate and credible intervals for each repeatability estimate.

Effect of repeatable behaviours on reproductive tactic

As docility during transfer and handling were found to be repeatable, we fitted a multivariate GLMM to investigate among-individual variances and covariances for reproductive tactic, transfer and handling. Transfer and handling were fitted as Poisson, and reproductive tactic was fitted as categorical, whereby natal = 0 and band males = 1. We fitted the following fixed effects: capture (tested as a fixed effect for transfer and handling only), on-site tenure, rainfall and body condition (z-centred to improve model fit). Tag, area and handler ID were fitted as random effects. We estimated within- and among-individual covariance by fitting an unstructured ‘*us*’ *R*-matrix (within-individual variation) and an unstructured ‘*us*’ *G*-matrix (among-individual covariances) for tag. We used a noninformative Wishart prior and ran all models for 4 000 000 iterations, with a burn-in of 5000 and thinning interval of 2000. Successive

samples from the posterior distribution had low autocorrelation (the majority was $r < 0.02$, while all were $r < 0.05$). As variance components from model outputs are constrained to be positive in MCMCglmm, and 95% credible intervals that exclude zero, therefore, cannot be interpreted to indicate statistical significance, we standardized model covariances between response variables (handling, transfer, reproductive tactic) to a scale from -1 to 1 as described in Houslay and Wilson (2017). This analysis allowed us to obtain the correlation between these variables. Correlations were determined to be significant if the 95% credible interval of the correlation excluded zero.

Ethical Note

Animal handling and study protocols adhered to the ASAB/ABS guidelines (ASAB/ABS, 2022) concerning the use of animals in research and teaching and were approved by the ethics committee at the corresponding author's educational institution. Animal trapping was conducted by trained researchers and steps were taken to minimize captivity and handling time. Traps were provided with shade and checked every 1–2 h or less, and as our field season coincided with austral winter, animals did not suffer high temperatures in the traps, nor did they show signs of suffering from cold temperatures. Animals were handled using cone cloth bags that covered the animals' eyes and minimized handling and stress (Koprowski, 2002). As Cape ground squirrels have little ear pinnae, animals trapped for the first time were marked for identification using a small dorsal freeze mark (Freeze Spray, CRC Industries Inc., Horsham, PA, U.S.A.; Rood & Nellis, 1980) and a black hair dye mark (Rodol D; Lowenstein and Sons, Inc., New York, NY, U.S.A.) for identification at a distance and injected subcutaneously in the mid-lateral region of the back with a sterile PIT tag (AVID Inc.; 2.1×12 mm, 125 kHz, 0.1 g, $<0.0002\%$ of a female's body mass). Blood was drawn for testosterone analysis for 29/ 34 males who underwent open field testing the next time they were captured. All animals were released immediately after handling. To minimize captivity and handling time on days of open field testing, the 34 subjects were not handled by humans but were coaxed into the test arena directly from the trap. Open field tests lasted 10 min (1 min pretest habituation period + 9 min testing) and subjects were released directly from the arena at their site of capture upon test completion by removing the Plexiglas lid and allowing the animals to jump out.

Results

Repeatability of Docility Behaviours

From 2014 to 2019, we trapped, handled and scored docility 906 times for 275 adult male squirrels. On average, males were sampled 3.2 times each (range 2–24 times per individual). We found moderate repeatability ($R = 0.25$ and 0.26 ; Table 3) for ‘transfer’ and ‘handling’ (Table 3), which were significantly correlated (among-individual covariance = 0.49 , $CI = [0.13, 0.77]$; Fig. 2), indicating that males that were docile during transfer were also docile during handling. ‘Approach’ and ‘release’ were not repeatable (Table 3).

Table 3. Repeatability estimates from MCMCglmm models for trapping and open field test (OFT) behaviours

| Model | Behaviour | <i>R</i> | CI |
|----------------------|------------------|-------------|-------------------|
| M1 – Trapping | Approach | 0.00 | 0.00, 0.02 |
| | Transfer | 0.25 | 0.14, 0.36 |
| | Handling | 0.26 | 0.14, 0.37 |
| | Release | 0.06 | 0.00, 0.11 |
| M2 – OFT novelty | Activity | 0.32 | 0.00, 0.41 |
| | Squares (binary) | 0.38 | 0.00, 0.47 |
| | Jumps | 0.08 | 0.00, 0.18 |
| | Latency (binary) | 0.09 | 0.00, 0.21 |
| M3 – OFT habituation | Activity | 0.31 | 0.00, 0.42 |
| | Squares (binary) | 0.30 | 0.00, 0.41 |
| | Jumps | 0.07 | 0.00, 0.19 |
| | Latency (binary) | 0.07 | 0.00, 0.14 |

Significant results are shown in bold.

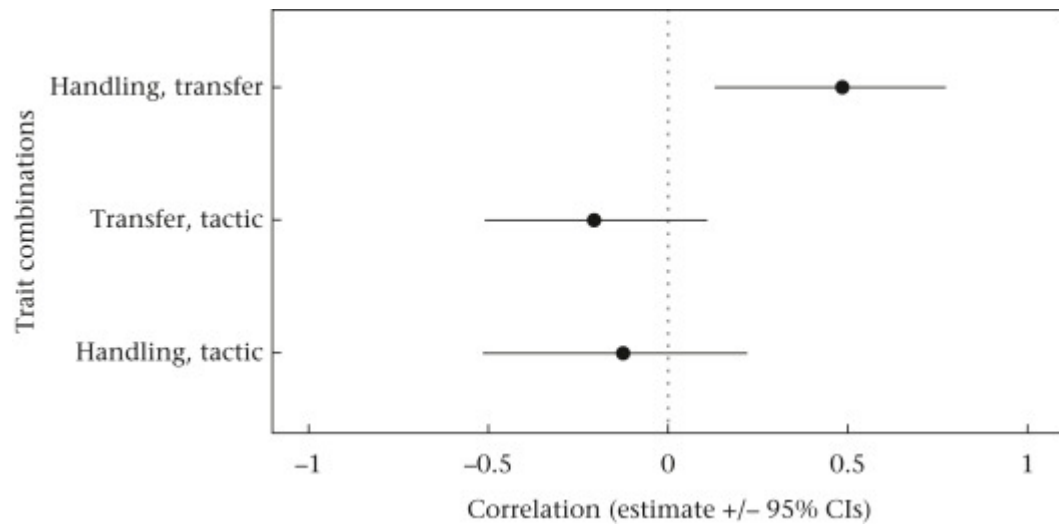


Figure 2. Correlations (estimate \pm 95% credible intervals) between dependent variables (handling, transfer, tactic) derived from a MCMCglmm model multivariate models for behaviours during trapping. Significant results are defined as credible intervals that do not overlap with 0.

Table 4. Estimated means (β) and 95% credible intervals (CI) for fixed factors included in MCMCglmm multivariate models for behaviours during trapping and open field tests

| Model | Covariate behaviour | Fixed factor | β | 95% CI | | P value |
|-------------------------------|---------------------|----------------|-------------|-------------|-------------|--------------|
| | | | | Lower | Upper | |
| Trapping (docility) | Approach | Capture | 0.46 | 0.22 | 0.70 | <0.001 |
| | Approach | Tenure | -0.28 | -0.40 | -0.15 | <0.001 |
| | Transfer | Capture | 0.58 | 0.22 | 0.95 | 0.001 |
| | Handling | Tenure | 0.20 | 0.02 | 0.39 | 0.04 |
| | Release | Tenure | -2.66 | -5.33 | -0.42 | <0.001 |
| Open field test (novelty) | Activity | Trial | -0.67 | -1.03 | -0.33 | 0.001 |
| | Jumps | Trial | -1.82 | -2.31 | -1.34 | <0.001 |
| | Latency (binary) | Trial | -75.23 | -143.65 | -12.82 | <0.001 |
| Open field test (habituation) | Squares (binary) | Trial | -89.75 | -194.14 | -1.70 | 0.02 |
| | Jumps | Trial | -0.91 | -1.92 | -0.05 | 0.05 |
| | Latency (binary) | Trial | -182.66 | -382.02 | -33.23 | <0.001 |

Individuals with low scores are more docile, and individuals with high scores are less docile. For conciseness, we only show significant results. Repeatable behaviours are shown in bold.

Capture number and on-site tenure (range 1–8 years) affected repeatable docility behaviours (Table 4). Males that had been captured more than once were more docile, and individuals that had longer tenure on-site (years captured) were less docile. Nonrepeatable docility behaviours were also affected by capture number and tenure on site. Males that were captured more than once were more docile during approach, and longer tenure males were more docile during approach and release (Table 2). We found no evidence that rainfall or body condition affected docility behaviours (see Appendix, Table A1, for statistics).

Repeatability of Open Field Test Behaviours

We performed 102 open field test trials on 34 male Cape ground squirrels. In 12 trials, individuals remained immobile (0 activity and jumps, remained on a single square and never reached the novel object). For a further 21 trials, individuals remained on a single square but were active (activity and jumps ≥ 1).

We performed repeatability analysis on 28 males (84 trials) where we had determined testosterone levels and body condition. No behaviours were repeatable in either the ‘novelty’ or ‘habituation’ model (Table 3). Activity and exploration decreased with trial number (Table 4), indicating that males tended to be less active and explorative after experiencing the test. We found no evidence that intertrial interval (mean \pm SE = 16.4 ± 0.9 days; range 2–43 days), daily temperature, wind speed, cloud cover, testosterone or body condition affected behaviour (see Appendix, Table A2 for further information).

Effect of Repeatable Behaviours on Reproductive Tactic

Of the 275 males that were trapped and scored for docility, we determined reproductive tactic, tenure and body condition at the time of capture for 107 males (506 observations). We found no evidence of among-individual covariance between docility and reproductive tactic (handling among-individual covariance = -0.12 , CI = $[-0.52, 0.22]$; transfer among-individual covariance = -0.21 , CI = $[-0.51, 0.12]$; Fig. 2). Furthermore, body condition did not covary with reproductive tactic ($\beta = -0.46$, 95% CI = $[-13.07, 11.27]$, pMCMC = 0.88). However, reproductive tactic covaried with on-site tenure ($\beta = 68.31$, 95% CI = $[29.24, 110.80]$, pMCMC = <0.0001); males with longer on-site tenure were more likely to be dispersed.

We also found strong evidence that rainfall affected tactic ($\beta = 16.22$, 95% CI = $[3.75, 29.640]$, pMCMC = <0.0001); in years of higher rainfall, there were more dispersed males. Of the 107 males in our analysis, 13 males were confirmed to have switched from a natal tactic to a band tactic within our study period. For all 13 of these males, annual rainfall was higher in the year of their dispersal compared to the previous year when they were natal (mean \pm SD difference in rainfall = 76 ± 24 mm). Furthermore, the proportion of males that were band males was higher in years with higher annual rainfall (2014: annual rainfall = 381 mm, proportion of band males = 0.33; 2015: 447 mm, 0.50; 2019: 454 mm, 0.74; 2018: 479 mm, 0.66; 2016: 541, 0.76; 2017: 552 mm, 0.64).

Discussion

Cape ground squirrels have docile personality traits, which is not surprising because personality traits have been found in many sciurid species, including tree squirrels (Boon et al., 2007; Mazzamuto et al., 2019; Santicchia et al., 2018, 2021) and ground squirrels (Clary et al., 2014; Dosmann et al., 2015; Piquet et al., 2018). However, we found no evidence of active or explorative personalities as found in other squirrel species (Clary et al., 2014; Mazzamuto et al., 2019). Furthermore, different docile personality types were not associated with different reproductive tactics. This finding is surprising because different personality types have been associated with different ARTs in other species (Han & Jablonski, 2019; Synyshyn et al., 2021) and because natal and band males differ in their behaviour (Scantlebury, Waterman, & Bennett, 2008; Scantlebury, Waterman, Manjerovic, et al., 2008) and home range sizes (Manjerovic & Waterman, 2015; Waterman, 1995). However, a lack of association between personality traits and reproductive tactics has also been found in a socially living European bitterling, *Rhodeus amarus* (Řežucha et al., 2012), and personality in the striped mouse, a socially flexible species, is not associated with social strategy and does not influence tactic switching (Yuen et al., 2015).

Docility

Understanding why docile personality traits are maintained in Cape ground squirrels depends on the ecological relevance of the Cape ground squirrels' reaction to trapping and handling. Docility, defined as an animal's response to human handling (Réale et al., 2009), may be associated with social aggression with conspecifics (Réale et al., 2009) or defensive aggression against predators and heterospecifics (Blumstein et al., 2013).

Both aggression and tolerance may influence grouping, with decreased aggression associated with group living in male African striped mice, *R.habdomys pumilio* (Schoepf & Schradin, 2012). Cape ground squirrels have low aggression levels compared to most ground squirrel species (van der Marel et al., 2020), they lack physical aggression and territoriality (Waterman, 1995, 1997) and males exhibit affiliative behaviours including allogrooming (Herzig-Straschil, 1978; Waterman, 1997). This high social tolerance in males has been documented in several primate species (Anderson, 2007; Kalbitzer et al., 2015; Strier, 1994) and another African ground squirrel, the Barbary ground squirrel (van der Marel et al., 2020; Waterman, 1997). In some species, selection acts on behaviours that limit social intolerance in potentially competitive situations (Hare et al., 2007), and our finding of docile personality traits suggest that docility may play an important role in the social lives of Cape ground squirrels.

We found that docility was also influenced by biotic factors. Males with longer on-site tenure were less docile. If on-site tenure (i.e. number of capture-years) is a proxy for age, then our finding is consistent with other studies showing that older individuals are more aggressive (Schoepf & Schradin, 2012) or less social (Hoset et al., 2011). For example, in the striped mouse, older individuals are more aggressive (Schoepf & Schradin, 2012), and in the root vole, *Microtus oeconomus*, older males have higher levels of asocial behaviours than younger males (Hoset et al., 2011). In these species, differences in aggression and sociality reflect differing needs as

individuals mature. In Cape ground squirrels, natal males provide alloparental care (Manjerovic & Waterman, 2015), and although we do not know whether docility is associated with alloparental care, perhaps changes in behavioural traits associated with age influence how much alloparental care is provided. Furthermore, the age at dispersal varies in male Cape ground squirrels (O'Brien et al., 2021). Given that dispersal may be associated with behavioural changes and/or personality traits (Cote et al., 2010) and personality influences social dynamics (Webster & Ward, 2011; Wolf & Krause, 2014), perhaps changes in docility influence the timing of dispersal in Cape ground squirrels.

Activity and Exploration

Activity and exploration were not repeatable traits in male Cape ground squirrels. Our findings contrast with studies of other small mammal species (Aliperti et al., 2021; Boon et al., 2008; Santicchia et al., 2021; Yuen et al., 2015), such as golden-mantled ground squirrels, *Callospermophilus lateralis*, for whom activity is a personality trait (Aliperti et al., 2021). However, we found that exploration was highly bimodal, with some individuals crossing all squares and reaching the novel object while others remained on a single square for the trial duration. A similar finding was reported for Barbary ground squirrels, in which many individuals did not enter the open field arena, preventing the researchers from properly estimating exploration time (Piquet et al., 2018). However, willingness to enter a novel space may be related to the shy–bold axis rather than exploration (Perals et al., 2017), and Piquet et al. (2018) found that willingness to enter the open field was repeatable. Also, our novel object remained the same in all three trials, which means that in trials 2 and 3, latency to reach the object was not a reaction to novelty. Indeed, males were quicker to reach the object in subsequent trials, which may be because of familiarization with the object. Therefore, further studies on Cape ground squirrels should modify the personality assay to include measures of boldness and/or reactions to novelty. For example, assays could score the latency to freely enter the arena, especially because Barbary ground squirrels are a closely related species with similarly low aggression and male grouping.

Furthermore, the lack of repeatability in exploration of squares may be due to the small arena size, which may have constrained exploration measurement, as the distinction between moderately and highly explorative individuals would be lost when the maximum number of squares was explored, and re-entries were not counted. However, a larger test array would be difficult to transport in the field, so a suitable alternative may be to take other exploration measures, such as the number of visits to each square (Aliperti et al., 2021), or use a different test array such as a hole-board (Martin & Réale, 2008). Additionally, increasing our sample size and considering other behaviours related to exploration such as sniffing (Boon et al., 2007), rearing (Ferrari et al., 2013) and time spent in contact with a novel object (Heyser & Chemero, 2012) should be considered for future studies.

The lack of repeatability in activity and exploration in Cape ground squirrels is also surprising because natal males spend more time feeding, while band males spend more time in locomotion and have higher resting metabolic rates (Scantlebury, Waterman, & Bennett, 2008;

Scantlebury, Waterman, Manjerovic, et al., 2008). However, feeding is associated with vigilance, a costly behaviour (Unck et al., 2009), so although time allocation to different activities varies between male tactics, our findings indicate that overall activity level did not vary between individuals of different tactics. Additionally, Cape ground squirrels in high-predation risk areas spend more time in high-cost vigilance behaviour than in low-cost vigilance/foraging behaviour compared with individuals in low-predation risk areas (Unck et al., 2009), suggesting that predation risk may influence activity levels in this species. Indeed, predation risk influences activity levels in captive chaffinch, *Fringilla coelebs* (Quinn & Cresswell, 2005), and predation is a proposed mechanism that may drive the maintenance of animal personality (Dingemanse & Réale, 2005).

Testosterone did not affect activity or exploration. Our findings contrast with studies on other rodents, such as bank voles, *Myodes glareolus*, where increased testosterone levels are associated with increased mate searching and mobility (Mills et al., 2009). Even though variation in testosterone levels has been linked to reproductive tactics in the striped mouse, *R.habdomys pumilio*, a facultatively social species (Schradin & Yuen, 2011), testosterone levels do not differ between male Cape ground squirrels adopting different reproductive tactics (Scantlebury, Waterman, & Bennett, 2008; Scantlebury, Waterman, Manjerovic, et al., 2008), nor are they associated with body mass (O'Brien et al., 2018). However, variation in testosterone levels in Cape ground squirrels may be related to other factors such as social interactions, as seen in degus (Soto-Gamboa et al., 2005). As male Cape ground squirrels exhibit no physical aggression towards conspecifics, testosterone levels may not be associated with aggression, although that remains to be tested. Indeed, in male North American red squirrels, *Tamiasciurus hudsonicus*, a species with a mating system similar to that of Cape ground squirrels, with promiscuous females (Boonstra et al., 2017), testosterone levels do not increase in response to a hormonal challenge (a proxy for competitive interactions).

Alternative Reproductive Tactics

As Cape ground squirrel ARTS are associated with different social living conditions (Waterman, 1995, 1997), we had expected an association between ARTs and docility. Personality traits have been linked to social conditions in some species (Best et al., 2015; Pike et al., 2008), such as in eastern grey kangaroos, *M.acropus giganteus*, where shy females are found in larger foraging groups (Best et al., 2015). However, personality may also affect social structure and cohesion, such that a mix of personality types within social groups may be favoured (Bergmüller & Taborsky, 2010; Webster & Ward, 2011; Wolf & Krause, 2014). For example, degus, socially living rodents, assort negatively by explorative phenotype when burrow sharing (Chock et al., 2017). Also, 'social niche partitioning', which results in different personalities and social roles within a social group, has been hypothesized to decrease social conflict (Bergmüller & Taborsky, 2010), demonstrating the potential value of mixed personality types in social groups. This personality variation is particularly interesting when it comes to male Cape ground squirrels because band males associate in ephemeral fission–fusion subgroups that arise daily and vary in size and composition (Waterman, 1995). It is unknown what drives band and sub-band group formation and composition in Cape ground squirrels, but perhaps different levels of docility

contribute to the persistence of band male grouping, such that one personality type for all band males is not beneficial. This hypothesis may explain why we did not find a particular docility phenotype associated with band males.

Within-group personality differences may also influence social functioning and interaction networks (Webster & Ward, 2011; Wolf & Krause, 2014). For example, in homing pigeons, *Columba livia*, collective movements are influenced more by bolder individuals than by shyer individuals, suggesting that 'leader' and 'follower' personality types influence collective movements (Sasaki et al., 2018). In guppies, *Poecilia reticulata*, groups of individuals with a mix of personality types feed more than groups of individuals with similar personalities, demonstrating a foraging benefit to mixed personality associations (Dyer et al., 2009). In Cape ground squirrels, older males on average attend more oestrus events than younger males, but younger males do not preferentially associate with older males (Waterman, 1997). However, if a mixture of personality types benefits band group functioning and dynamics, this mixture may explain why we did not find a discrete personality type associated with band males, compared to natal males. Consequently, further studies examining band and sub-band social structure and stability would allow for a greater understanding of how personality interacts with social networks and reproductive fitness.

Furthermore, although ground squirrel reproductive tactics were not associated with different personality types, dispersal and reproductive tactics may be related to external cues (Clobert et al., 2009). We found that increased rainfall was associated with dispersed males, and males dispersed in years where annual rainfall was higher. This finding is consistent with previous Cape ground squirrel studies showing that, in high rainfall years, rainfall is positively associated with body condition in band males but not in natal males (Manjerovic & Waterman, 2015), whereas in low rainfall years, natal males are in better body condition than band males (O'Brien et al., 2021), demonstrating that there is a trade-off between dispersal tactic and body condition. Altogether, these studies suggest that environmental conditions rather than personality influence the persistence of alternative reproductive tactics.

Study Limitations

Several factors limit the interpretation of our results. The repeatability of behavioural traits is influenced by the time intervals between measurements (Bell et al., 2009), and behavioural stability over time and contexts is important to consider when interpreting the influence of personality on life-history traits (Biro & Stamps, 2008). We measured docility across 6 years of study, which gives greater confidence in the stability of the repeatable behaviours (transfer and handling). However, individuals varied in the number of times they were sampled and were sampled across multiple years, which may have influenced repeatability estimates (Bell et al., 2009). Thus, future studies should consider standardizing the number of trials used from each individual or across years. Furthermore, as individuals may vary in behavioural plasticity (Dingemanse et al., 2010), and repeatability may vary with age (Bell et al., 2009; Petelle et al., 2013), considering standardizing samples across multiple individual demographic criteria may be prudent.

Studies involving personality traits should collect data from the same subjects in a real-life setting to determine the cross-context validity of behavioural assays or behaviours during trapping and handling (Carter et al., 2013). Additionally, social context may influence individual behaviour in social species, with individuals behaving differently in isolation when compared to a social situation (Webster & Ward, 2011). Thus, behavioural measures in our study that were collected from individuals in isolation may not be indicative of the individual's behaviour in a social setting. Future studies with this species should explore the relationship between behaviours exhibited in the wild and their proposed proxies observed during trapping and handling or in test arrays.

Conclusion

Personalities have been found in many species and may explain the maintenance of alternative reproductive tactics (Taborsky et al., 2008). Our results show that male Cape ground squirrels have docile personality types, although these personality types are not associated with different ARTs. However, as docility may influence the trade-offs associated with male sociality, further studies examining the relationships between personality, fitness and social groups may elucidate the role personality plays in the evolution of the social and mating system in this species. Furthermore, as socially tolerant species with male grouping are rare (Anderson, 2007; Kalbitzer et al., 2015; Strier, 1994; van der Marel et al., 2020), examining behavioural variation in Cape ground squirrels and other African ground squirrels (van der Marel et al., 2020) with low levels of aggression may help us understand the conditions surrounding the evolution and persistence of male grouping and sociality. As the study of animal behaviour has been biased in the past towards taking the perspective of aggression and conflict (Díaz-Muñoz et al., 2014), further studies on behavioural variation in nonaggressive species may lead to a greater understanding of the evolution of cooperation and social living.

Author Contributions

Conceptualization: J.M.W., M.H.W., S.B., S.V. Methodology: J.M.W., M.H.W., N.C.B. Investigation: N.C.B., R.J., S.V. Formal analysis: M.H.W. Data curation: M.H.W., S.B. Supervision: J.M.W. Funding acquisition: J.M.W. Visualization: M.H.W. Writing – original draft: M.H.W., S.B. Writing – review & editing: all authors.

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Data Availability

Data will be made available on request.

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Appendix.

Table A1. Estimated means (β) and 95% credible intervals (CI) for fixed factors included in MCMCglmm multivariate models for behaviours during trapping

| Model | Covariate behaviour | Fixed factor | β | 95% CI | | Empty Cell | <i>P</i> |
|---------------------|---------------------|-----------------------|--------------|--------------|-------------|------------|---------------|
| | | | | Lower | Upper | | |
| Trapping (docility) | Approach | Capture | 0.46 | 0.22 | 0.70 | | <0.001* |
| | Transfer | Capture | 0.58 | 0.22 | 0.95 | | 0.001* |
| | Handling | Capture | 0.14 | -0.31 | 0.54 | | 0.51 |
| | Release | Capture | 0.54 | -4.51 | 6.27 | | 0.83 |
| | Approach | Tenure | -0.28 | -0.40 | -0.15 | | <0.001* |
| | Transfer | Tenure | -0.08 | -0.29 | 0.12 | | 0.48 |
| | Handling | Tenure | 0.20 | 0.02 | 0.39 | | 0.04* |
| | Release | Tenure | -2.66 | -5.33 | -0.42 | | <0.001* |
| | Approach | Rainfall | -0.11 | -0.26 | 0.03 | | 0.14 |
| | Transfer | Rainfall | -0.13 | -0.32 | 0.08 | | 0.20 |
| | Handling | Rainfall | -0.07 | -0.25 | 0.12 | | 0.42 |
| | Release | Rainfall | 0.87 | -1.30 | 3.50 | | 0.37 |
| | Approach | Body condition | 0.00 | -0.10 | 0.10 | | 0.96 |
| | Transfer | Body condition | -0.07 | -0.24 | 0.09 | | 0.39 |
| | Handling | Body condition | 0.03 | -0.13 | 0.18 | | 0.69 |
| | Release | Body condition | -0.24 | -1.98 | 1.46 | | 0.75 |

Repeatable behaviours are shown in bold. Asterisks indicate significant results.

Table A2. Estimated means (β) and 95% credible intervals (CI) for fixed factors included in MCMCglmm multivariate models for behaviours during open field tests

| Model | Covariate behaviour | Fixed factor | β | 95% CI | | Empty Cell | <i>P</i> |
|---------------------------|---------------------|----------------|---------|---------|--------|------------|----------|
| | | | | Lower | Upper | | |
| Open field test (novelty) | Activity | Trial | -0.67 | -1.03 | -0.33 | | 0.001* |
| | Squares (binary) | Trial | -47.88 | -106.68 | 7.02 | | 0.06 |
| | Jumps | Trial | -1.82 | -2.31 | -1.34 | | <0.001* |
| | Latency (binary) | Trial | -75.23 | -143.65 | -12.82 | | <0.001* |
| | Activity | Temperature | -0.02 | -0.40 | 0.37 | | 0.93 |
| | Squares (binary) | Temperature | -46.25 | -131.56 | 48.04 | | 0.29 |
| | Jumps | Temperature | 0.21 | -0.25 | 0.70 | | 0.38 |
| | Latency (binary) | Temperature | -16.69 | -112.16 | 93.02 | | 0.75 |
| | Activity | Wind | 0.05 | -0.32 | 0.41 | | 0.79 |
| | Squares (binary) | Wind | -1.78 | -91.34 | 90.01 | | 0.98 |
| | Jumps | Wind | -0.25 | -0.76 | 0.18 | | 0.29 |
| | Latency (binary) | Wind | -30.71 | -130.24 | 75.73 | | 0.55 |
| | Activity | Clouds | 0.25 | -0.10 | 0.62 | | 0.17 |
| | Squares (binary) | Clouds | 58.14 | -22.37 | 141.26 | | 0.15 |
| | Jumps | Clouds | 0.27 | -0.16 | 0.68 | | 0.21 |
| | Latency (binary) | Clouds | 55.65 | -48.13 | 150.12 | | 0.24 |
| | Activity | Testosterone | -0.06 | -0.60 | 0.43 | | 0.81 |
| | Squares (binary) | Testosterone | 39.96 | -68.40 | 151.88 | | 0.42 |
| | Jumps | Testosterone | -0.30 | -0.80 | 0.24 | | 0.24 |
| | Latency (binary) | Testosterone | 54.92 | -41.74 | 166.22 | | 0.26 |
| | Activity | Body condition | -0.29 | -0.83 | 0.19 | | 0.23 |
| | Squares (binary) | Body condition | -11.21 | -123.96 | 100.43 | | 0.82 |
| | Jumps | Body condition | -0.47 | -1.06 | 0.03 | | 0.07 |
| | Latency (binary) | Body condition | -38.87 | -157.90 | 63.57 | | 0.46 |

| | | | | | | |
|--|------------------|---------------------|--------|---------|--------|------|
| Open field test (habituation) ^a | Activity | Intertrial interval | 0.05 | -0.47 | 0.57 | 0.84 |
| | Squares (binary) | Intertrial interval | -29.56 | -182.65 | 152.19 | 0.70 |
| | Jumps | Intertrial interval | 0.18 | -0.55 | 1.06 | 0.65 |
| | Latency (binary) | Intertrial interval | -11.63 | -253.84 | 231.94 | 0.93 |

None of the open field test behaviours were repeatable. Asterisks indicate significant results.

^aResults to the novelty model for the other six fixed factors were similar, so we report only the intertrial interval estimates here.