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Bridging animal personality with space use and resource use in a free-ranging population of an asocial ground squirrel

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Consistent individual differences in behaviour, or personality, likely influence patterns of space use and resource use in wild animals. However, studies on personality-dependent space use in natural ecosystems remain rare due to the difficulty of obtaining paired data sets on spatial dynamics and repeated personality measures from marked animals. We used repeated standardized assays (open field, mirror image stimulation, flight initiation distance and behaviour in trap) to perform the first characterization of personality in a free-ranging population of golden-mantled ground squirrels, *Callospermophilus lateralis*. We then used multilevel modelling to determine whether personality influenced 95% home range size, 50% core area size, movement speed or use of a preferred resource ('perches', vision-enhancing prominences such as rocks, which enhance survival) in nature. Data collected over 3 years showed that individual squirrels consistently differed in activity, sociability, boldness and aggressiveness (adjusted repeatability 0.16–0.44) and that activity was correlated with sociability (posterior mean correlation [95% credible interval] = 0.65 [0.39, 0.87]). We did not find an effect of personality on home range size, but bolder individuals maintained larger core areas than shyer individuals. More active and bolder individuals moved faster under natural conditions compared to their less active and shyer conspecifics. Individuals that scored higher for all four personality traits had more perches in both their home ranges and core areas compared to individuals with lower personality scores. Our results are indicative of personality-dependent space use and resource use in this study system. We hope our study will inspire future research that links animal personality with spatial ecology to inform wildlife management in natural ecosystems.
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Space use has important ties to many aspects of ecology, with implications for wildlife conservation and management. For example, the size and placement of an animal's home range influences access to resources and the speed and distance at which an animal moves may influence predator–prey interactions, competition, social networks or disease spread (Kurvers et al., 2014; Sih et al., 2012; Spiegel et al., 2015; Wolf & Weissing, 2012). Although spatial patterns are typically studied at the population or species level, individual differences in space use dynamics often account for a substantial amount of the variation exhibited at higher levels of biological organization (Börger et al., 2006; Merrick & Koprowski, 2017b; Spiegel et al., 2017), and thus may act as a link between process and pattern in ecology (Belisle, 2005). Individual variation in space use is well studied in relation to factors such as resource availability (Bowler & Benton, 2005; Lucherini & Lovari, 1996; Maher & Burger, 2011), physical traits (Armitage, 2009; Bakker & Van Vuren, 2004; Singleton & Garland, 2018) and social interactions among kin (Armitage et al., 2011; Bekoff, 1977; Hoogland, 2013); however, spatial variation due to individual differences in behaviour is still not well understood (Börger et al., 2006; Spiegel et al., 2017; Toscano et al., 2016; Wey et al., 2015).

A growing body of research suggests that variation in animal space use patterns may in part be explained by consistent individual differences in behaviour across time or contexts, a concept known as animal personality, behavioural types, temperament or coping styles (Gosling, 2001; Koolhaas et al., 1999; Réale et al.,

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2007; Sih, Bell, & Johnson, 2004). Indeed, individuals across many taxa exhibit limited plasticity in behavioural traits, such as boldness (risk-taking behaviour; Sih, Bell, Johnson, & Ziemba, 2004), aggressiveness (tendency to attack other individuals; Gosling, 2001) or sociability (reaction to the presence or absence of conspecifics; Réale et al., 2007), which may affect an animal's use of space through personality-driven movement and dispersal (Sih, Bell, Johnson, & Ziemba, 2004; Toscano et al., 2016; Wey et al., 2015). At times, two or more of these traits may be correlated ('behavioural syndromes'; Sih & Bell, 2008; Sih, Bell, Johnson, & Ziemba, 2004), affecting how an animal interacts with its environment and, ultimately, its fitness (Moiron et al., 2020; Sih et al., 2012; Smith & Blumstein, 2008; Wolf & Weissing, 2012). For example, risk-prone, bold individuals also tend to be more active and aggressive (Boon et al., 2008; Hertel et al., 2019; Réale et al., 2010; Sih, Bell, & Johnson, 2004). While this suite of behaviours likely results in greater acquisition of resources such as food and space, it also may increase the risk of mortality (Biro & Stamps, 2008; Blight et al., 2016; Réale et al., 2010).

Efforts to create a unifying framework for personality-dependent spatial ecology (Spiegel et al., 2017) have revealed links between individual differences in behaviour and space use across contexts. Space use, broadly defined here as the way in which individuals distribute themselves across a landscape (Wolf & Weissing, 2012), includes movement patterns (e.g. dispersal) and spatial organization (e.g. home range size and overlap). Studies assessing the relationship between personality and movement patterns have found that individuals that are less sociable may disperse during years of high density, whereas more sociable individuals remain in their natal home range (Cote & Clobert, 2007; Cote et al., 2010; Stamps, 2001). Furthermore, dispersing individuals tend to be more active and aggressive (Duckworth & Badyaev, 2007; Merrick & Koprowski, 2017a; Sih, Bell, & Johnson, 2004; Thorlacius et al., 2015), and individuals that are faster explorers (move more quickly, but with less attention to their environment) have been found to disperse farther (Clobert et al., 2009; Dingemanse et al., 2003; Réale et al., 2010). Studies assessing the relationship between personality and spatial organization have found that personality may play a significant role in shaping habitat preferences (Bonnot et al., 2015; Holtmann et al., 2017; Leclerc et al., 2016), which can in turn influence home range size and resource use (Minderman et al., 2010; Schirmer et al., 2020; Spiegel et al., 2015; van Overveld & Matthysen, 2010). As examples, more active North American red squirrels, *Tamiasciurus hudsonicus*, are more likely to travel farther and intrude on the territories of conspecifics (Boon et al., 2008), bolder individual bank voles, *Myodes glareolus*, occupy larger home ranges (Schirmer et al., 2019) and brown bears, *Ursus arctos*, exhibit consistent individual differences in habitat selection (Leclerc et al., 2016).

The potential influence of individual level behavioural differences on various spatial outcomes can be assessed using spatially explicit multilevel models that account for free-ranging movement of individuals in nature, personality of individuals in standardized assays and other variables that may confound the relationship between personality and space use (Börger et al., 2006; Dingemanse & Dochtermann, 2013; Fordham et al., 2014; Spiegel et al., 2017). These models are typically used in two types of studies that link personality with space use: (1) studies that assess personality-dependent space use by measuring a personality trait (e.g. boldness) and a spatial behaviour (e.g. dispersal or home range size), then correlating the two (e.g. Cote et al., 2010); (2) studies that measure spatial behaviour(s) on a group of individuals through space and time and evaluate repeatability of that behaviour (e.g. repeatability of home range size: Harrison et al., 2015; repeatability of habitat selection: Leclerc et al., 2016). While studies that examine the effects of behavioural type on space use and resource use in nature are becoming increasingly common, there is still a dearth of literature on this topic (Hertel et al., 2019; Leclerc et al., 2016; Singleton & Garland, 2018), probably due to the difficulty of obtaining paired data sets on spatial dynamics and repeated personality measures from marked animals (Leclerc et al., 2016; Schirmer et al., 2019; Wey et al., 2015).

We used standardized personality assays to characterize consistent individual differences in behaviour in order to determine whether these differences influence home range size, core area size, movement speed or use of a preferred resource ('perches', vision-enhancing prominences such as rocks, which enhance survival; Aliperti, 2020) in a population of free-ranging golden-mantled ground squirrels, *Callospermophilus lateralis*, an asocial and territorial species (Aliperti, 2020; Michener, 1983). Our overarching hypothesis was that interindividual differences in use of space and resources would be related to individual personality type. Given that boldness has been positively correlated with larger home range size in other prey species (e.g. Schirmer et al., 2019) and that territorial species are known to defend home ranges through aggression (Dugatkin, 2020), we predicted that boldness and aggressiveness would be positively related to home range and core area size in golden-mantled ground squirrels. Furthermore, we predicted consistent individual differences in sociability, and we anticipated that less sociable squirrels would tend to be more aggressive (a behavioural syndrome between asocial and aggressive personality types has been found in other studies; Godfrey et al., 2012; Réale et al., 2007). Following this expectation, we predicted that less sociable and more aggressive squirrels would have greater access to perches due to a presumed greater probability with which aggressive individuals may acquire and defend resources (Spiegel et al., 2015). Finally, we predicted that more active, bold and aggressive individuals would tend to move faster within their home ranges, following expectations for individuals that follow a 'fast life strategy' (Spiegel et al., 2017).

METHODS

Study System

We studied a population of golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, a high-elevation (2900 m) site located in the East River Valley, Gunnison County, Colorado, U.S.A. (38°57′N, 106°59′W), from 2016 to 2018. The 16 ha study area was delineated by the East River on the west, Copper Creek on the south and aspen (*Populus tremuloides*) forest on the north and east. Vegetation consisted of a mosaic of habitats, composed mostly of dry subalpine meadow, intermixed with wet meadow, stands of aspen, spruce (*Picea engelmannii*) and willow (*Salix* spp.). Golden-mantled ground squirrels generally prefer more open habitats and, in our study area, they strongly prefer dry meadow habitat, which provides both food (mostly forbs, such as dandelions, *Taraxacum officinale*) and enhanced visibility for detecting predators (Aliperti, 2020). Predators in our study area include red foxes, *Vulpes vulpes*, long-tailed weasels, *Mustela frenata*, and short-tailed weasels, *Mustela erminea* (Kneip et al., 2011).

Golden-mantled ground squirrels hibernate for up to 8 months of the year, from late August until the approximate time of snow melt, typically during May (Hostetler et al., 2012; Kneip et al., 2011). Squirrels breed shortly after emerging from hibernation, after which females gestate for approximately 28 days, then give birth underground to one litter of one to eight pups per year (mean = 4.8; Kneip et al., 2011; Wells & Van Vuren, 2017). Juveniles emerge from their natal burrow about 30 days after birth (Phillips, 1981), at which time they typically are weaned and forage independently (Wells et al.,

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2017). While most juveniles disperse (leave their natal home range permanently) during the summer of birth (Michener, 1983), some delay dispersal until the following summer and others remain philopatric (Jesmer et al., 2011). Early dispersal of golden-mantled ground squirrels relative to other species of ground-dwelling squirrels is presumed to be driven by their small body size (150–300 g), which facilitates rapid development (maturity is reached at 1 year) and decreases the opportunity for social bonds to form; hence, golden-mantled ground squirrels are considered to be asocial (Armitage, 1981; Michener, 1983). Adult golden-mantled ground squirrels are generally agonistic towards conspecifics (Ferron, 1985), and there is minimal spatial overlap among the core areas of adult home ranges, perhaps because those areas are defended as territories (Aliperti, 2020; Jesmer et al., 2011).

We conducted field work each year from June to late August during the summer active season. We conducted an annual census during early June in which all golden-mantled ground squirrels in the study area were captured and identified by using Tomahawk live-traps (Model 201, Hazelhurst, WI, U.S.A.). We trapped all pups within 2 days of their emergence from natal burrows, typically late June to mid-July. We used numbered eartags and unique dye marks on the fur (Nyanzol D dye, Greenville Colorants, Greenville, SC, U.S.A.) to identify all captured individuals, and we recorded sex, body mass and reproductive status at each capture; details of trapping procedures are provided by Wells and Van Vuren (2017). We retrapped squirrels as necessary within a given year to renew dye marks and conduct personality assays. We used binoculars to visually identify squirrels at a distance based on their dye marks and to determine spatial locations; golden-mantled ground squirrels are diurnal and clearly observable when above ground. Only a portion of the study area was in view at any one location, so we rotated randomly among different sections of the study area in search of squirrels. Once one or more squirrels were in view, we initiated an instantaneous scan sampling approach, in which we identified and recorded the location of all individuals at 1 min intervals until squirrels were no longer in view, usually less than 10 min. Squirrels disappeared by either entering a burrow or leaving the area. Locations were based on a map of the study area with 7×7 m gridded cells. We covered all sections at least twice daily, once during the morning and once during the afternoon, to ensure that observations captured possible heterogeneity in use of space by different squirrels at varying times of day. Because active squirrels were often more easily observed, we redirected sampling effort to focus on under-represented squirrels when appropriate. Squirrels in our study area frequently encounter humans and rarely reacted to our presence at the observation distances we used; locations of those that did react were excluded. We pooled spatial observations for each individual each year for analyses.

Squirrels in our study area often use 'perches', protruding features such as rocks or stumps that elevate a squirrel's point of view (Aliperti, 2020). Because access to perches was found to enhance survival in golden-mantled ground squirrels (Aliperti, 2020), we estimated the effect of consistent individual differences in behaviour on access to perches in dry meadow habitat, the only habitat that is preferred by golden-mantled ground squirrels (Aliperti, 2020). A perch was defined as a feature that extended above the maximum height of vegetation within a given grid square. We counted the number of perches in each grid square that supported dry meadow habitat up to 10 perches and, for grid squares containing more than 10 perches, we assigned them 11 perches each.

Spatial Outcomes

We registered squirrel locations into a spatial data base of our study area in ArcGIS v.10 (ESRI, 2018). We reduced spatial autocorrelation among locations of individual squirrels by including only the first observation when a squirrel was recorded in the same location more than once within a 10 min sampling bout (Aliperti, 2020); squirrels are able to cross a given grid square within a few seconds. To promote an accurate representation of space use, we filtered the resulting autocorrelation-corrected data set to include only individuals that were observed at least 35 times over at least 14 different calendar days within a given year. We delineated annual home ranges for each squirrel by defining 95% and 50% minimum convex polygons through package adehabitatHR (v.0.4.16; Calenge, 2006) in the R software (v.3.6.1; R Core Team, 2019). The 95% home range characterizes the area that an individual uses to carry out its day-to-day activities, while the 50% home range, also known as the core area, characterizes the region of concentrated activity within the home range (Powell & Mitchell, 2012; Samuel et al., 1985). We calculated the total number of perches in each squirrel's 95% home range and 50% core area by summing the number of perches across all dry meadow grids that fell within that individual's 95% home range and 50% core area boundaries.

Movement speed was quantified for each individual each year through R package adehabitatLT (v.0.3.24; Calenge, 2006). We divided all spatial observations (without filters pertaining to autocorrelation or sample size) into 10 min blocks of time known as 'bursts'. For each individual that was observed 3–10 times within a given burst, we divided the total distance moved by that individual (m) by the total amount of time (s) that passed between the first and final observations within that burst. Distance measurements were based on the centroids of grid squares; hence, if a squirrel moved from one grid square to anywhere within an adjacent grid square, the linear distance between the centroids of the two squares was recorded. We calculated the average movement speed across all bursts for those individuals that were observed for three or more bursts in a given year.

Personality Assays

We quantified personality in golden-mantled ground squirrels through four types of repeated, standardized behavioural assays (open field, mirror image stimulation, flight initiation distance and behaviour in trap), each performed at least twice per individual within a given year. The first assay was an open field (OF) test, a commonly used method to measure activity (tendency towards movement) and exploration (tendency towards investigation) in a novel environment (Boon et al., 2007; Cummins & Walsh, 1976; Martin & Réale, 2008; Mazzamuto et al., 2019; Montiglio et al., 2010). The second assay was a mirror image stimulation (MIS) test, which measures sociability or aggression (nonagonistic and agonistic behaviour towards conspecifics, respectively; Armitage & Van Vuren, 2003; Svendsen & Armitage, 1973). The OF and MIS assays took place in the same trial period, with the OF assay immediately preceding and thus serving as a habituation period prior to the MIS assay (Boon et al., 2007; Krause et al., 2015; Svendsen & Armitage, 1973). Both assays were performed during 2016 and 2017 in a portable arena, which consisted of a white rectangular box ($L \times W \times H = 92 \times 46 \times 56$ cm) fitted with a Plexiglas lid. There were four circular holes cut into the floorboard, each 5 cm in diameter and 12 mm deep (Appendix, Fig. A1).

The inclusion of floorboard holes is a suggested means to differentiate activity from exploration, behaviours that are typically correlated; activity pertains to movement, while 'head-dipping behaviour', in which the animal inserts its head into a hole, pertains to exploration (Martin & Réale, 2008). Individual golden-mantled ground squirrels were trapped, then released into a small, wooden 'acclimation box' ($L \times W \times H = 42 \times 13 \times 13$ cm), where

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the squirrel rested for 3 min before the OF assay began. The front edge of the acclimation box, up to but not including a lift-up sliding door, was inserted into an opening located on the side of the arena. The sliding door was raised and the squirrel was gently prodded into the arena, marking the beginning of the OF assay. Immediately following the OF assay, the MIS assay was initiated by removing a sliding wall at the back end of the arena, in turn revealing a mirror. The mirror was affixed to and covered most of the far wall of the arena such that the squirrel could see its reflection. A GoPro Hero camera that was mounted on a tripod above the arena recorded squirrel behaviour during all OF and MIS assays. OF and MIS assays were 4 min each (8 min total testing session), a duration that is considered appropriate for reducing physiological stress and habituation to novel conditions, and which is within the recommended range for squirrel species (Dosmann et al., 2015; Mazzamuto et al., 2019; Montiglio et al., 2010). All assays took place within the home range of the focal individual. The experimenter remained silent and out of the squirrel's view for the entirety of each assay. At the conclusion of each session, the squirrel was released at its point of capture and the arena was sprayed with 70% alcohol, then dried.

Squirrel behaviour recorded during OF and MIS assays was quantified with EthoVision tracking software (Noldus EthoVision XT 11.5, Noldus Observer, Noldus Information Technology, Wageningen, The Netherlands). We reviewed all videos to ensure that footage was recorded appropriately and that the focal individual was tracked accurately by the software program. For each OF assay, we quantified total distance moved, mean and maximum velocity attained and total time spent moving. We also divided the arena into zones: 'vestibule' to describe the front of the acclimation box, the location most immediate to the arena's entrance; 'near corner' to describe the corners closest to the entrance; 'centre' to describe the area of the arena that was most exposed, away from surrounding walls; and 'far end' to describe the area farthest from the arena entrance, where the mirror was revealed during the MIS assay. For each OF assay, we quantified the amount of time spent within each zone and the number of visits to each zone. For each MIS assay, we quantified total distance moved, as well as the time spent within and number of visits to the vestibule and far end zones. For each 4 min OF and MIS assay, we tracked the focal individual at 30 frames/s, for a total of 7200 sample points. All 282 recorded assays had missed sample rates (percentage of recorded time in which the squirrel could not be tracked) of $\leq$4.8%. We used EthoVision's interpolation feature to interpolate missing values for all assays with missed sample rates greater than 0%. Our final data set contained a mean of 7192 samples per assay, representing a missed sample rate of 0.1%.

In addition to using automated tracking software, we watched all recorded assays and manually quantified an ethogram of behaviours that we were not able to measure in EthoVision. The behaviours analysed for the OF assay included number of jumping events, number of climbing events, time spent sniffing and the duration and frequency with which a squirrel investigated floorboard holes. The behaviours manually analysed for the MIS assay included time spent looking towards versus away from the mirror and total time spent interacting with the mirror image. Interaction with the mirror took the form of either the forepaw or the nose touching the mirror surface, similar nose-to-nose and forepaw-to-body greets commonly observed under natural conditions and interpreted to be amicable social interactions, usually among littermate pups and their mother (Armitage, 1986; Ferron, 1985; Wells & Van Vuren, 2017). All behaviours were explicitly defined, and all observers were trained to identify the defined behaviours on video. To eliminate interobserver bias, we assigned a different set of behaviours to each observer, such that a given behaviour was quantified by the same observer for all recorded trials.

In addition to performing arena assays, we conducted standardized flight initiation distance (FID) and behaviour in trap (BIT) tests during 2017 and 2018. FID, the distance at which an animal flees from an approaching human (a perceived threat), is a common method used to quantify consistent individual differences in shyness; shyer individuals tend to have greater FID scores (flee from a farther distance) than individuals that are bolder (Blumstein, 2003; Ydenberg & Dill, 1986). We quantified FID after identifying a golden-mantled ground squirrel that was not alert or in distress; we spent several minutes observing the individual at a distance before performing the test. Following Petelle et al. (2013), the observer walked directly towards the focal squirrel at a consistent pace of approximately 0.5 m/s. Markers were placed to identify the location of the observer at the start of the test, the location of the observer when the squirrel first fled and the location of the squirrel before it fled. At the conclusion of each test, the observer determined the distance between the observer and the squirrel when the test began (start distance) and when the squirrel fled (FID). All distances were recorded as heel-to-toe footsteps and then converted to metres. Squirrels typically fled to a burrow less than 10 m from their starting location, then emerged and resumed normal activity within minutes of being tested.

We conducted BIT trials to quantify consistent individual differences in docility, which can be measured as an individual's tendency to remain calm when trapped (Petelle et al., 2013; Réale et al., 2000). At each trapping event, before an individual was handled, an observer sat quietly approximately 0.5 m from the trapped squirrel for 2 min and recorded binary (i.e. 0/1) scores that indicated whether that individual bit the trap, uttered an alarm call or chattered its teeth during the trial. For each trial, we subtracted the sum of all scored behaviours from the maximum potential score (following Réale et al., 2000); hence, personality scores ranged from 0 (less docile) to 3 (more docile). We conducted FID and BIT trials only if there were no signs of disturbance (i.e. predators, other humans or alarm calls by other squirrels) preceding the trial period; if an individual's behaviour could have been influenced by a disturbance unrelated to the assay itself, the trial was discarded. We took the negative value of the outcomes from FID and BIT trials to obtain FID scores that represented boldness and BIT scores that represented aggressiveness.

Statistical Analyses

Consistent individual differences in behaviour

For both the OF and MIS assays, we used principal component analysis (PCA) with varimax rotation to reduce the number of measured behavioural variables into a smaller number of synthetic variables that independently represent personality traits (Martin & Réale, 2008; Nawroth et al., 2017). Each PCA was performed on the correlation matrix of measured variables (separately for OF and MIS), which standardized data to mean 0 and standard deviation 1. Only variables that met the conditions of the Barlett test and the Kaiser–Mayer–Olkin criterion were retained for each PCA (Field et al., 2012). We identified which components to retain based on identifying the 'elbow', or point of curvature, of a scree plot (Cattell, 1966), and all retained components had an eigenvalue >1 (Wold et al., 1987).

We calculated the repeatability of individual behaviour scores (scores from retained principal components from the OF and MIS assays and scores from the FID and BIT assays) by running a series of repeatability models with the R package rptR (v.0.9.22; Stoffel et al., 2017). Animals are considered to exhibit personality for specific behavioural traits when the between-individual variation is

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consistently greater than the within-individual variation for those traits; hence, high repeatability values indicate personality when individuals behave consistently across time and when individuals consistently differ from one another (Leclerc et al., 2016). We ran a separate linear mixed effects model (LMM) with the behavioural scores from each personality assay set as the dependent variable and squirrel identity as a random effect; we confirmed that residuals met normality conditions for each model. We controlled for age class (adult or juvenile), year and trial number as fixed effects. Successive trials of a given individual for any one personality assay were separated by one or more days (following Minderman et al., 2010; Schirmer et al., 2019); hence, we included trial number to account for the passing of time between trials, which varied among individuals due to the unpredictability of recapturing free-ranging subjects (Aplin et al., 2014). Additionally, because start distance may significantly influence FID (Blumstein, 2003), we controlled for start distance as a fixed effect in our FID repeatability model. It is possible that personality may change over time, such that repeatability may vary as a function of age class (Petelle et al., 2013). Hence, we also ran all repeatability models separately for adults and juveniles. Age-specific repeatability models contained the same structure as other repeatability models, although age was removed as a fixed effect and year was not included in the FID repeatability model for adults because all adults that completed two or more FID assays were tested during 2017. Model outputs returned adjusted repeatability values (the proportion of behavioural variation explained by consistent individual differences in behaviour, after controlling for fixed effects) and the statistical significance of repeatability. Statistical significance ($P < 0.05$) was based on a likelihood ratio test (LRT), which compared the fit of each repeatability model with and without inclusion of individual as a random factor (Stoffel et al., 2017).

Retained principal components that contained significantly repeatable scores were labelled as the personality type most appropriately described by the behaviours within each component that contained the highest loadings. We used the means of only those behaviour scores that were significantly repeatable as quantitative, individual-based measurements of personality in subsequent spatial models. We investigated the potential for behavioural syndromes by fitting Bayesian bivariate mixed effects models using R package brms (Bürkner, 2017). We set each pairwise combination of personality types as dependent variables, and we included individuals as random effects. We controlled for age class and sex as fixed effects in all models and for start distance as an additional fixed effect in our FID (boldness) model. Model outputs returned the among-individual correlation among personality traits.

Personality-dependent use of space and resources

To assess the effects of personality on each spatial outcome variable (home range and core area sizes, number of perches, movement speed), we ran a series of LMMs and generalized linear mixed effects models (GLMMs) according to the error distribution and corresponding link function of the underlying data. Our sample size was limited because we could not perform all personality assays each year or record adequate spatial data for all squirrels; hence, we fitted separate models for the effects of each personality trait on each spatial outcome (following Schirmer et al., 2019).

We analysed the effects of personality on home range size (separately for the 95% home range and 50% core area) by fitting a log linear model with a Gaussian distribution. In addition to personality scores, we included age class, sex, an interaction between age class and sex, year and the total number of spatial observations used to delineate the home range as fixed effects; we included the interaction because males were expected to have larger home ranges than females, but only as adults. To assess the effects of personality on number of perches within the 95% home range and 50% core area, we modelled data with a Poisson error distribution and log link. We regressed the number of perches against personality score, age class, sex, year and home range size; we controlled for home range size (either 95% or 50% core area) under the assumption that larger home ranges likely contain more perches. To analyse the relationship between personality and movement speed, we fitted LMMs with a Gaussian distribution that assessed movement speed in relation to personality score, and we accounted for age class, sex, year and the total number of bursts used to calculate an individual's average speed as fixed effects. We scaled and centred all continuous predictor variables and accounted for individuals as random effects in all spatial outcome models except those analysing boldness; there were no individuals that experienced FID trials across years. We included an extra interaction term between age class and personality score in models analysing scores that were not significantly repeatable in both adults and juveniles. Following Zurr et al. (2009), we started with a full fixed effects structure for each model, then iteratively removed nonsignificant predictors and compared Akaike's information criterion corrected for small sample size (AICc) to choose the most parsimonious models that minimized prediction error. We used R packages lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2017) to fit all models.

Ethical Note

The golden-mantled ground squirrel is not threatened and is common throughout the East River Valley of Colorado. All procedures followed guidelines of the American Society of Mammalogists (Sikes & Animal Care and Use Committee of the American Society of Mammalogists, 2016), were permitted by Colorado Parks and Wildlife (Colorado Scientific Collecting Permit No. TR334) and were approved by the Institutional Animal Care and Use Committees of the University of California, Davis (Protocol No. 21422) and the Rocky Mountain Biological Laboratory (Protocol No. 21). To minimize stress to captured animals, traps were set only during morning and afternoon when temperatures were moderate, and traps were not set during rainy weather. Furthermore, traps were equipped with cloth covers to reduce the chance of thermal stress. Traps were checked every 30 min or less, and captured individuals were transferred to a cone-shaped cloth handling bag that gently restrained the squirrel while also blocking the squirrel's vision. Squirrels readily enter the bag, perhaps because it resembles an escape burrow; using a handling bag has been found to reduce physiological stress in squirrels (Koprowski, 2002). Captured individuals were weighed, eartagged and dye-marked by trained researchers in about 10 min, then released at the point of capture. Before entering the acclimation chamber of the arena, captured squirrels were set aside with a cloth draped over the trap. To minimize stress to reproductive females, those individuals were assayed first if more than one squirrel was trapped at a given time. The experimenter remained silent and out of the squirrel's view for the entirety of each arena assay, then sprayed the arena with 70% alcohol to remove potentially aggravating scents. All behavioural assays took place within the home range of the focal animal. Individuals were never assayed when a predator was within view or when a conspecific was alarm calling. Mortality rate as a result of trapping was 0.16%, with no additional injuries associated with trapping.

RESULTS

We tested spatial outcomes for 64–98 squirrel-year pairs, personality assays for 28–61 squirrel-year pairs and personality-dependent space use for 21–52 squirrel-year pairs (Table 1).

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Table 1
Sample sizes for spatial analyses, personality assays, and models of personality-dependent space use

		Individual-year pairs	Unique individuals
Spatial outcome	HR size	64	48 (29 adults, 35 juveniles)
	Perches	64	48 (29 adults, 35 juveniles)
	Speed	98	77 (37 adults, 59 juveniles)
Personality assays	Arena	42	36 (12 adults, 24 juveniles)
	FID	28	28 (10 adults, 18 juveniles)
	BIT	61	53 (14 adults, 41 juveniles)
Personality-dependent space use	HR size	36 (Arena), 21 (FID), 38 (BIT)	30 (Arena), 21 (FID), 31 (BIT)
	Perches	36 (Arena), 21 (FID), 38 (BIT)	30 (Arena), 21 (FID), 31 (BIT)
	Speed	38 (Arena), 28 (FID), 52 (BIT)	32 (Arena), 28 (FID), 44 (BIT)

HR = home range; FID = flight initiation distance; BIT = behaviour in trap.

Spatial Outcomes

Golden-mantled ground squirrels maintained 95% home range areas (mean ± SE) of 1.02 ± 0.15 ha (range 0.05–7.12 ha) and 50% core areas of 0.19 ± 0.04 ha (range 0.003–2.26 ha). Home ranges included a mean of 318 ± 33.1 perches (range 38–1503), and core areas included a mean of 94 ± 13.1 perches (range 0–572). There was a mean of 13.6 ± 1.42 movement bursts per individual per year (range 3–60 bursts). Mean movement speed across individuals was 0.04 ± 0.003 m/s, or 144.0 ± 10.80 m/h (range 0–0.12 m/s). Individuals exhibited wide variation within age and sex classes in all spatial outcome variables (Appendix, Figs A2, A3).

Consistent Individual Differences in Behaviour

We recorded a mean (±SE) of 3.46 ± 0.18 OF trials and 3.40 ± 0.17 MIS trials per individual in a given year, and five individuals were assayed in both 2016 and 2017. We retained two principal components from the OF assay data, which explained 69% of the total variance. The first principal component (OF1) explained 49% of the total variance and was characterized by behaviours related to movement, jumping and climbing, while the second principal component (OF2) explained 20% of the total variance and described a tendency to investigate floorboard holes (Table 2). We retained two principal components from the MIS assay data, which explained 66% of the total variance (39% explained by the first principal component, MIS1, and 27% by the second component, MIS2). MIS1 was characterized by a propensity to move towards and interact with the mirror image, while MIS2 described a tendency to look towards versus away from the mirror image. The first component, but not the second component, from each of the OF and MIS assays was significantly repeatable at the individual level (Table 2). Based on PCA loadings, OF1 is hereafter referred to as activity, and MIS1 is hereafter referred to as sociability.

We found no effect of age class or trial number on either activity or sociability scores, although golden-mantled ground squirrels were generally less active and less sociable during 2017 compared to 2016 (Table 3). Age-specific repeatability models showed repeatability for activity and sociability in adults (activity: $r \pm SE = 0.41 \pm 0.15$, $LRT = 10.00$, $P = 0.0008$; sociability: $r \pm SE = 0.24 \pm 0.13$, $LRT = 3.38$, $P = 0.033$) and in juveniles (activity: $r \pm SE = 0.25 \pm 0.13$, $LRT = 6.58$, $P = 0.005$; sociability: $r \pm SE = 0.22 \pm 0.13$, $LRT = 3.29$, $P = 0.035$).

Boldness and aggressiveness were also significantly repeatable (Table 3). We found no effect of age class, year or trial number on either boldness or aggressiveness scores (Table 3). However, start distance had a significant, positive effect on FID (when approached from a farther distance, squirrels fled sooner; $\beta \pm SE = 0.38 \pm 0.05$, $t = 7.34$, $P < 0.0001$). Boldness was repeatable in both adults ($r \pm SE = 0.44 \pm 0.16$, $LRT = 12.40$, $P = 0.0002$) and juveniles ($r \pm SE = 0.33 \pm 0.16$, $LRT = 3.63$, $P = 0.028$). Age-specific repeatability models revealed that aggressiveness was significantly repeatable in adults ($r \pm SE = 0.26 \pm 0.10$, $LRT = 13.60$, $P = 0.0001$), but not in juveniles ($r \pm SE = 0.10 \pm 0.08$, $LRT = 1.53$, $P = 0.108$). However, an unadjusted repeatability model showed borderline significant repeatability in juveniles ($r \pm SE = 0.13 \pm 0.08$, $LRT = 2.59$, $P = 0.053$); unadjusted repeatability, also known as the broad sense or agreement repeatability (Biro & Stamps, 2015; Nakagawa & Schielzeth, 2013), quantifies repeatability while accounting for individual as a random effect but does not control for any fixed effects.

We found a behavioural syndrome between activity and sociability in which these two behaviours were positively correlated at the individual level (posterior mean correlation [95% credible interval] = 0.65 [0.39, 0.87]; Fig. 1). However, we did not find evidence of a behavioural syndrome between any other pairs of personality traits ($cor_{activity\text{-}boldness} = 0.203$ [−0.272, 0.660], $cor_{activity\text{-}aggressiveness} = 0.132$ [-0.276, 0.528], $cor_{sociability\text{-}boldness} = 0.432$ [−0.021, 0.823], $cor_{sociability\text{-}aggressiveness} = -0.164$ [−0.580, 0.246], $cor_{boldness\text{-}aggressiveness} = -0.157$ [−0.560, 0.263]).

Personality-dependent Use of Space and Perches

Given the lack of adjusted repeatability for aggressiveness in juveniles, we included an interaction term between age class and individual personality score in all spatial models pertaining to aggressiveness. We did not find an effect of activity, sociability, boldness or aggressiveness on 95% home range size in golden-mantled ground squirrels (Table 4). In general, males had larger 95% home ranges than females, but only as adults (Appendix, Fig. A4). However, there was a significant effect of an interaction between aggressiveness and age class on 95% home range size, in that more aggressive juveniles (those with scaled aggressiveness scores of approximately 1 or greater) tended to have larger home ranges compared to other squirrels (Fig. 2a, Appendix, Fig. A4). We found no effect of activity, sociability or aggressiveness scores on the 50% core area (Table 4). However, bolder individuals maintained significantly larger 50% core areas (Table 4, Fig. 3a) than shyer individuals, and there was a significant, positive effect of an interaction between juveniles and aggressiveness on the 50% core area (Fig. 2b, Appendix, Fig. A4). We found no effect of year or of the total number of spatial observations on the 95% home range size or on the 50% core area; hence, year and total observations were removed from all 95% home range and 50% core area models during model selection.

After controlling for home range size, there were significant relationships between each individual-based personality score and the number of perches in that individual's 95% home range and 50% core area (Table 4). Squirrels that scored highly on activity, sociability, boldness and aggressiveness assays had significantly more perches in their 95% home ranges (Fig. 3b–e), as well as in their 50% core areas (Fig. 3f–i) compared to their less active, less sociable,

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Table 2
Standardized loadings (based on a correlation matrix) for behaviours included in principal component analyses of open field (components OF1 and OF2) and mirror image stimulation (components MIS1 and MIS2) assays in golden-mantled ground squirrels

Behaviour	Activity		Behaviour	Sociability	
	OF1	OF2		MIS1	MIS2
Mean velocity	**0.93**	0.30	Distance	**0.94**	0.17
Distance	**0.93**	0.30	Visits to far end	**0.91**	0.17
Jumping events	**0.93**	0.16	Time interacting with mirror	**0.82**	0.22
Visits to centre	**0.89**	0.34	Visits to vestibule	**0.63**	−0.06
Visits to vestibule	**0.89**	0.19	Time looking away from mirror	−0.12	**0.89**
Maximum velocity	**0.79**	0.23	Time looking towards mirror	−0.09	**−0.84**
Time moving	**0.76**	**0.49**	Time in far end	**0.48**	**0.56**
Climbing events	**0.75**	0.20	Time in vestibule	−0.31	**−0.49**
Visits to near corner	**0.74**	0.05			
Visits to far end	**0.63**	0.29			
Time sniffing	**0.56**	**0.44**			
Time in far end	−0.17	−0.15			
Time investigating holes	0.16	**0.96**			
Hole investigation events	0.12	**0.95**			
Time in centre	0.17	**0.42**			
% Total variance	49.0	20.0		39.0	27.0
% Repeatability	34.2	7.2		22.6	3.8
LRT ($df = 1$)	20.1	0.492		7.08	0.047
P value	<0.0001	0.241		0.004	0.414

Behaviours with loadings equal to or greater than 0.40 are noted in bold font. A likelihood ratio test (LRT) was used to test for statistical significance of repeatability.

Table 3
Results of linear mixed effects repeatability models showing consistent individual differences in behaviour

Behaviour	Repeatability	Age class	Trial number	Year
Activity	0.34 ± 0.10, LRT = 20.10, $P < 0.0001$	−0.37 ± 0.24, $t = -1.50$, $P = 0.139$	−0.08 ± 0.06, $t = -1.19$, $P = 0.238$	2017: −0.54 ± 0.20, $t = -2.69$, $P = 0.008$)
Sociability	0.23 ± 0.10, LRT = 7.08, $P = 0.004$	0.34 ± 0.22, $t = -1.54$, $P = 0.131$	−0.06 ± 0.07, $t = -0.82$, $P = 0.414$	2017: −0.39 ± 0.19, $t = -2.03$, $P = 0.045$
Boldness	0.36 ± 0.12, LRT = 16.90, $P < 0.0001$	0.04 ± 0.91, $t = 0.04$, $P = 0.967$	0.03 ± 0.14, $t = 0.26$, $P = 0.800$	2018: −0.55 ± 0.96, $t = -0.58$, $P = 0.570$
Aggressiveness	0.16 ± 0.07, LRT = 16.10, $P < 0.0001$	0.05 ± 0.15, $t = 0.31$, $P = 0.756$	0.02 ± 0.02, $t = 1.33$, $P = 0.186$	2018: −0.16 ± 0.13, $t = -1.28$, $P = 0.202$

All coefficients are presented ± SE. Results for age class reflect model coefficients for juveniles in reference to adults. Results for year are in reference to 2016 (for activity and sociability) and in reference to 2017 (for boldness and aggressiveness).

shyer and more docile counterparts. A significant interaction between aggressiveness and age class revealed that aggressive juveniles had more perches in their 95% home ranges compared to other squirrels (Fig. 2c, Appendix, Fig. A4), although this interaction was not significant in the 50% core area model and was removed during model selection. In general, squirrels had fewer perches in their 95% and 50% home ranges in 2018 than in 2017, and juveniles had more perches in their 95% home ranges and 50% core areas than adults (Appendix, Fig. A4).

Individuals that were more active and bolder moved faster per burst compared to squirrels that had lower activity and boldness scores (Table 4, Fig. 3j and k). However, we found no effect of sociability or aggressiveness on movement speed (Table 4), and an insignificant interaction between aggressiveness and age class was removed during model selection. Models analysing the effect of boldness and aggressiveness on movement speed revealed that males tended to move faster than females, and adults tended to move faster than juveniles (Appendix, Fig. A4).

DISCUSSION

We found that golden-mantled ground squirrels consistently differed in activity, sociability, boldness and aggressiveness. These behaviours represent four out of the five major categories of animal personality considered most relevant to ecological studies (Réale et al., 2007) and have been found to be repeatable in other species of ground-dwelling squirrels, such as yellow-bellied marmots, *Marmota flaviventer* (Armitage, 1986; Armitage & Van Vuren, 2003; Petelle et al., 2013), Siberian chipmunks, *Tamias sibiricus* (Boyer et al., 2010), eastern chipmunks, *Tamias striatus* (Montiglio et al., 2012), least chipmunks, *Tamias minimus* (Bohn et al., 2017), Belding's ground squirrels, *Urocitellus beldingi* (Dosmann et al., 2015), and Barbary ground squirrels, *Atlantoxerus getulus* (Piquet et al., 2018). However, we did not find significant repeatability in exploration, the fifth major behaviour category. Ground squirrel studies that report consistent individual differences in exploration often combine exploration with movement in a novel environment (e.g. 'activity-exploration'; Boyer et al., 2010) or quantify exploration speed instead of exploration tendency (e.g. Montiglio et al., 2012). We included movement speed as a variable in our calculation of activity, and we quantified exploration tendency as visits to floorboard holes in the arena, which might have facilitated the disentangling of activity and exploration behaviours (Martin & Réale, 2008). Overall, repeatability of among-individual variation in behaviours ranged from 16 to 44%, which is consistent with other personality studies (repeatability across taxa is roughly 35%; Bell et al., 2009).

Individual squirrels differed in space use and perch use in a nonrandom manner that was dependent on their personality type. While we found no effect of personality on home range size, bolder individuals maintained larger core areas than shyer individuals (Table 4, Fig. 3a). An association between boldness and home range size has been reported in free-ranging populations of other species, including bank voles (Schirmer et al., 2019) and sleepy lizards,

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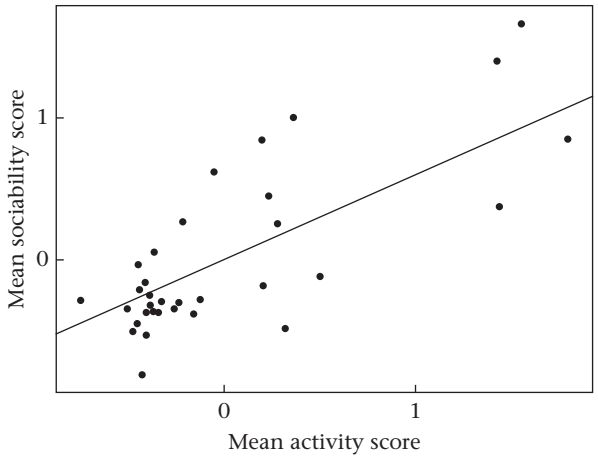

Figure 1. Results of a Bayesian bivariate model showing the relation between mean activity and sociability scores. Black dots represent posterior predictive values and the black line represents the slope of the correlation ($r = 0.65$).

Tiliqua rugosa (Spiegel et al., 2015). In the case of female bank voles, which are solitary and territorial, bolder individuals maintain larger core areas and larger overall home ranges, suggesting a potential link between boldness and territoriality (Schirmer et al., 2019). Hence, it is possible that boldness influenced core area size but not overall home range area because golden-mantled ground squirrels appear to defend only their core areas, and not their entire home ranges, as territories (Aliperti, 2020; Jesmer et al., 2011). We were surprised to find this link between apparent territoriality and boldness rather than aggressiveness, given known associations between aggressiveness and territorial defence in mammals (Morrell & Kokko, 2005; Siracusa et al., 2017; Wolff, 1993). However, an individual's home range would be considered a territory only if it were used exclusively by that individual, and it is possible that squirrels with higher aggressiveness scores more effectively excluded conspecifics from their home ranges, regardless of home range size. Additionally, a positive effect of boldness on core area size may relate to predation risk. Predation is a significant source of mortality for golden-mantled ground squirrels (Kneip et al., 2011), and bolder individuals are, by definition, more risk-prone (Réale et al., 2007; Sih, Bell, & Johnson, 2004); hence, it is possible that shyer individuals restrict movements to well-known, safer areas, while bolder individuals regularly venture out into riskier areas, thereby expanding their core area by using habitat patches that shyer individuals avoid (Schirmer et al., 2019). For example, bolder burrowing owls, *Athene cunicularia*, breed in territories closer to roads (Carrete & Tella, 2010), and bolder dunnocks, *Prunella modularis*, select habitat in areas with higher indices of human disturbance (Holtmann et al., 2017). In our study area, riskier habitat patches might include areas that are more densely vegetated; dense vegetation diminishes visibility of predators and is thus generally avoided (Aliperti, 2020).

Individuals with higher (more positive) scores for all four personality traits (activity, sociability, boldness, aggressiveness) had significantly more perches in both their home ranges and core areas compared to individuals with lower personality scores (Fig. 3b–i); perches are a preferred resource that likely decreases predation risk by elevating a squirrel's point of view over the surrounding vegetation (Aliperti, 2020). Hence, even though between-individual variation in personality was not significantly associated with home range size, personality appears to influence access to resources within those home ranges. It is not surprising that more active, bold and aggressive individuals tended to have greater access to perches, as these behavioural types, which are often correlated as 'proactive' or 'fast' behavioural syndromes (Réale et al., 2010; Sih et al., 2012; Spiegel et al., 2017), are typically thought to exhibit greater use of resources and space (Cote et al., 2010; Spiegel et al., 2017; Toscano et al., 2016; van Overveld & Matthysen, 2010). For example, bold individuals may range across larger distances, likely increasing the probability of encountering patchily distributed, preferred resources (Spiegel et al., 2017; Toscano et al., 2016). However, we were surprised that more sociable squirrels had greater access to perches than their less sociable counterparts, as asocial personality types are often considered to be more proactive (Réale et al., 2010; Sih, Bell, & Johnson, 2004) and therefore conceivably more effective at exploiting resources. We also found evidence of a behavioural syndrome between activity and sociability (Fig. 1). The explanation may lie in spatial overlap among squirrels: perhaps more sociable squirrels are more likely to actively search for conspecifics, increasing the probability with which they share overlapping home ranges and therefore resources such as perches. We did not find behavioural syndromes among any other pair of personality traits, perhaps due to our relatively small sample size of individuals that experienced repeated trials for each assay type; the Bayesian multivariate mixed effects models we employed are 'data hungry' (Dingemanse & Wright, 2020), leading to model uncertainty (wider credibility intervals) if sample size is small. Hence, behavioural syndromes often go undetected (Garamszegi et al., 2012), and there might be other significant behavioural correlations that we could not identify with certainty due to the structure of our data set.

In accordance with our expectation, individuals that were either more active in the arena or bolder during FID assays moved faster during bursts compared to their less active and shyer conspecifics (Table 4, Fig. 3j and k). The importance of activity revealed that this

Table 4
Results of linear and generalized linear mixed effects models showing personality-dependent space use

Fixed effects	Home range size		Number of perches		Movement speed
	95% HR	Core area	95% HR	Core area	
Activity	0.13 ± 0.16, $t = 0.82$, $P = 0.423$	0.29 ± 0.23, $t = 1.30$, $P = 0.202$	0.51 ± 0.08, $z = 6.52$, $P < 0.0001$	1.07 ± 0.16, $z = 6.56$, $P < 0.0001$	0.01 ± 0.002, $t = 2.40$, $P = 0.022$
Sociability	0.10 ± 0.17, $t = 0.60$, $P = 0.551$	0.27 ± 0.23, $t = 1.15$, $P = 0.259$	0.25 ± 0.04, $z = 5.67$, $P < 0.0001$	0.32 ± 0.08, $z = 3.86$, $P = 0.0001$	0.002 ± 0.002, $t = 0.83$, $P = 0.411$
Boldness	0.33 ± 0.27, $t = 1.22$, $P = 0.239$	0.98 ± 0.26, $t = 3.83$, $P = 0.001$	0.10 ± 0.02, $z = 5.85$, $P < 0.0001$	0.32 ± 0.05, $z = 6.74$, $P < 0.0001$	0.01 ± 0.003, $t = 4.26$, $P = 0.0003$
Aggressiveness	−0.26 ± 0.24, $t = -1.09$, $P = 0.289$	−0.38 ± 0.31, $t = -1.22$, $P = 0.245$	0.08 ± 0.03, $z = 2.73$, $P = 0.006$	0.41 ± 0.09, $z = 4.58$, $P < 0.0001$	0.001 ± 0.002, $t = 0.71$, $P = 0.489$
Aggressive juveniles	0.83 ± 0.37, $t = 2.25$, $P = 0.032$	1.31 ± 0.50, $t = 2.64$, $P = 0.013$	0.31 ± 0.12, $z = 2.47$, $P = 0.013$	–	–

All coefficients are presented ± SE. Results for an interaction between aggressiveness and age class is presented for juveniles (listed as aggressive juveniles) in reference to adults.

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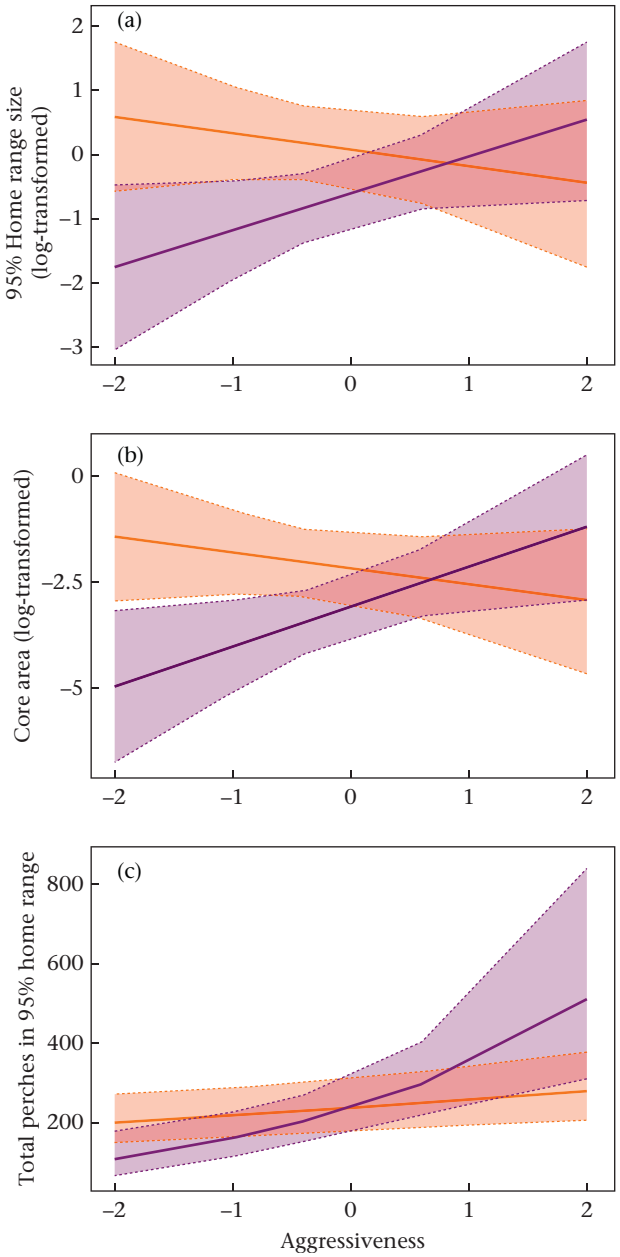

Figure 2. Effects of an interaction between age class and aggressiveness on (a) 95% home range size, (b) 50% core area and (c) total number of perches in the 95% home range. Represented are effects (predicted values) obtained from linear or generalized linear mixed effect models. Dotted areas represent 95% confidence intervals. Adults are depicted in orange and juveniles are depicted in purple.

behaviour, which was assayed in a controlled setting, accurately predicted a similar behaviour under natural conditions. Our results are consistent with theoretical groundwork that suggests more active or bold animals also tend to be superficial explorers (i.e. exhibit faster and straighter movement patterns; Réale et al., 2010), perhaps because animals with these behavioural types spend less time surveying their surroundings or have higher metabolic rates (Schirmer et al., 2019). However, most experimental studies that relate activity or boldness to space use do so within the context of dispersal (e.g. Fraser et al., 2001; Merrick & Koprowski, 2017b; Thorlacius et al., 2015). Whether golden-mantled ground squirrels that move faster would either be more likely to disperse or disperse farther would require further investigation. Nevertheless, it seems plausible that personality may influence the dispersal decision; golden-mantled ground squirrels usually disperse as juveniles, and we found consistent individual differences in activity and boldness, behaviours that were associated with faster movement speed, in juveniles as well as adults. This is in contrast to yellow-bellied marmots, which delay development of at least one personality trait (boldness) until their yearling year, perhaps because that trait is correlated with dispersal and that is the year during which individual marmots typically disperse (Petelle et al., 2013). We found that aggressive juveniles had larger home ranges and core areas, as well as more perches in their home range, compared to all other squirrels (Table 4, Fig. 2). Hence, it is possible that aggressiveness influenced the decision to disperse, and that the significant interaction between juveniles and aggressiveness reflected the point at which more aggressive juveniles started to leave their natal home range.

We recognize that our study design constrained the scale at which we were able to calculate movement speed, possibly biasing some results. For example, we were unable to track individual movement distances on a scale finer than that of a grid square. In addition, each movement burst was an opportunistic snapshot in time, and we acknowledge this can vary according to internal and external factors when studying a free-ranging population. We controlled for some of these factors (e.g. we controlled for risk level by not collecting data in the presence of predators or alarm calling), but could not control for all of them, such as internal state or potential social interactions that took place shortly before we saw the focal animal. Hence, we set a minimum threshold of bursts to decrease the probability with which any one burst would inaccurately portray a given individual's tendency towards movement.

It is well known that certain behavioural types are favoured in some environments over others, resulting in personality-dependent ecological trade-offs (Smith & Blumstein, 2008; Toscano et al., 2016). For example, bolder foragers presumably benefit within the context of competition, at the cost of shorter life spans within the context of predation (Sih et al., 2012). However, we found that bolder squirrels tended to have access to more perches, a resource associated with increased annual survival in a predation context (Aliperti, 2020), compared to shyer squirrels. Accordingly, a recent study found that risk-taking individuals have significantly longer life spans than shyer individuals when studied in the wild as opposed to a laboratory setting (Moiron et al., 2020). Hence, the personality of free-ranging animals may interact with environmental variables to differentially affect individual fitness, with potentially important consequences for population level processes. For instance, active individuals may also move faster and be more likely to disperse, but due to speed–accuracy trade-offs (Chittka et al., 2009), foraging efficiency (and thus dispersal success) may be lower in habitats with patchily distributed resources (Spiegel et al., 2017; Webber et al., 2020). Furthermore, variables such as landscape connectivity (or more complicating intrinsic factors, such as state dependence or cognition) may interact with personality to influence social interactions or diet preference, which may in turn bias studies on animal movement or habitat selection (Toscano et al., 2016; Wolf & Weissing, 2012). Hence, successful implementation of wildlife management programmes may depend on the explicit recognition and incorporation of personality in individual-based models of movement, habitat preference and population dynamics (Merrick & Koprowski, 2017b). From a conservation-based perspective, accounting for personality in wildlife management initiatives may be especially important when predicting wildlife responses to novel conditions, such as modification or destruction of habitat due to human-induced rapid environmental change ('HIREC'; Sih et al., 2011; Sih et al., 2012).

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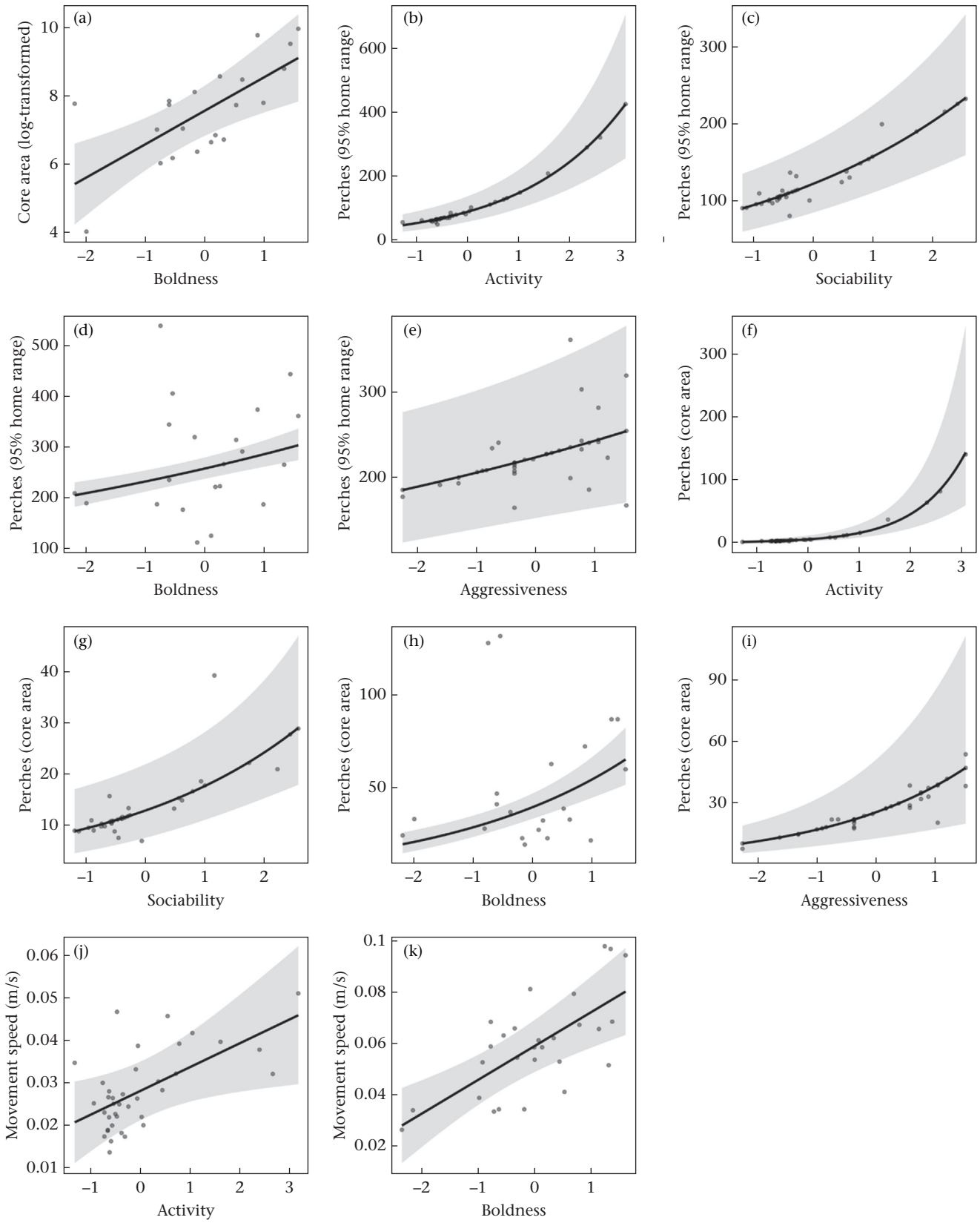

Figure 3. Effects of mean personality scores on the (a) 50% core area, number of perches in the (b–e) 95% home range and (f–i) 50% core area, and (j–k) mean movement speed in free-ranging golden-mantled ground squirrels. Represented are effects (predicted values) obtained from linear or generalized linear mixed effect models. Shaded areas represent 95% confidence intervals, and grey dots represent partial residuals from each model.

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Conclusion

Our results show personality-dependent space use and resource use in a free-ranging population of golden-mantled ground squirrels. Overall, we found that bolder individuals maintained larger core areas, more active and bold individuals moved faster, and more active, bold and aggressive individuals had greater access to fitness-enhancing perches in their home ranges. We also found that activity was correlated with sociability and that sociability was associated with access to perches in the home range, suggesting there is a potential benefit within an asocial species of being relatively more sociable. Given that individuals of differing personality types may occupy separate ecological niches (Schirmer et al., 2019) and that these ecological differences may scale-up to population or community level processes (Wolf & Weissing, 2012), we hope our results will inspire future research that links animal personality with spatial ecology in natural ecosystems.

Author Contributions

Conceptualization, methodology, software, investigation, formal analysis, writing – original draft, funding acquisition and project administration (Jaclyn Aliperti); software and formal analysis (Brittany Davis); resources (Nann Fangue, Anne Todgham); conceptualization, investigation, supervision, writing – review and editing, funding acquisition, project administration and resources (Dirk Van Vuren).

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Appendix

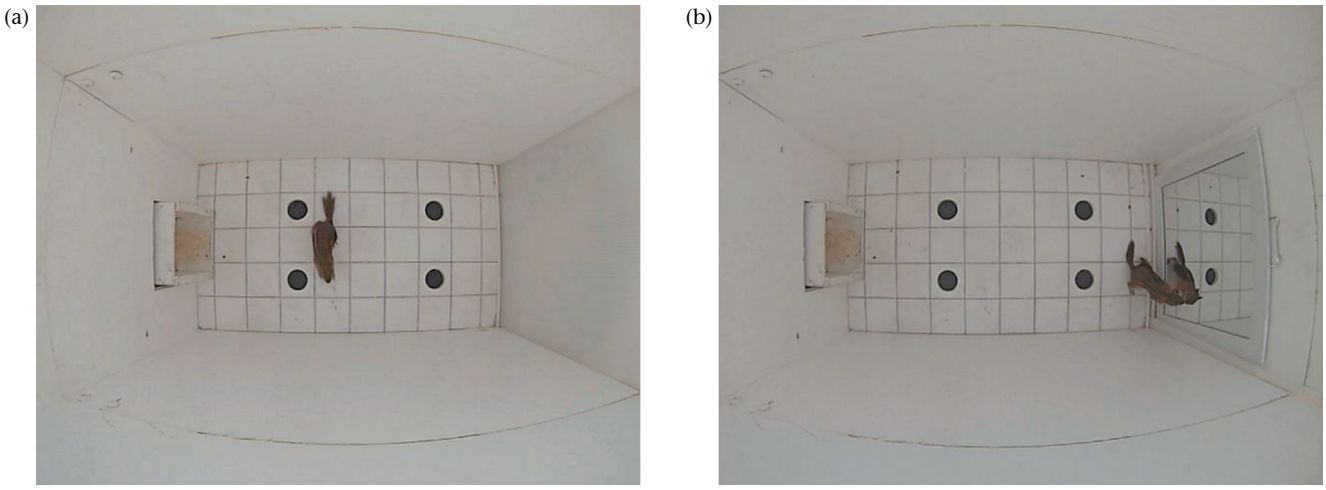

Figure A1. Images of a golden-mantled ground squirrel inside of the arena during (a) an open field and (b) mirror image stimulation trial. Each of four black circles is a hole that was cut into the floorboard and extended 12 mm downward towards the base of the arena, creating a shallow indentation. The squirrel entered the arena from the acclimation box, part of which is shown along the entrance wall, directly across from the mirror and to the left of the floorboard holes.

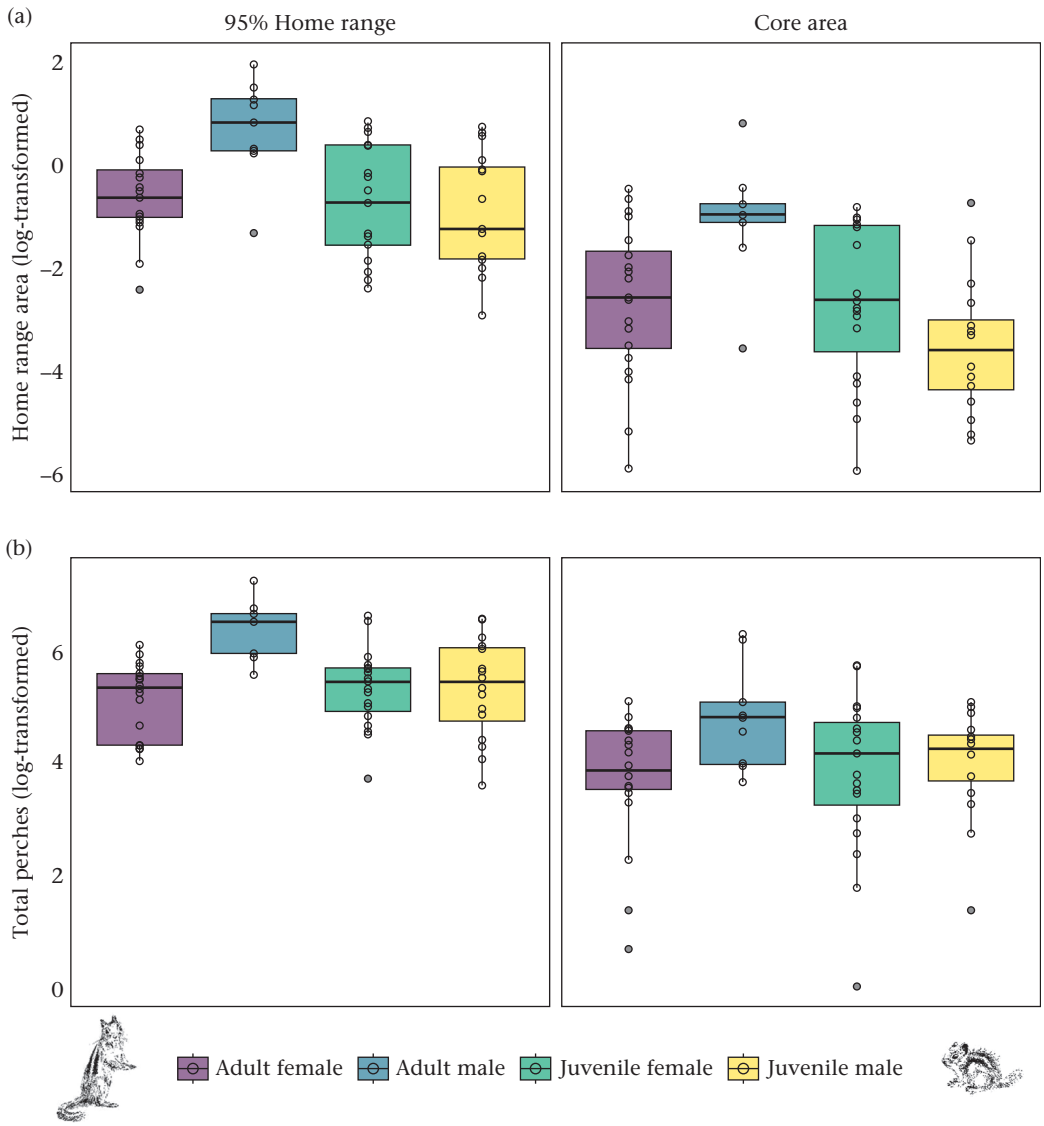

Figure A2. Adult and juvenile (a) home range area and (b) total number of perches (features, such as rocks or stumps, which protrude above the surrounding vegetation) in the 95% home range and 50% core area of golden-mantled ground squirrels. Box plots include the median as the centre line, interquartile range (IQR) as the box, values 1.5 times the IQR as the whiskers and values greater than 1.5 times the IQR as black points. Open circles denote individual data points. Data were log-transformed for visual representation.

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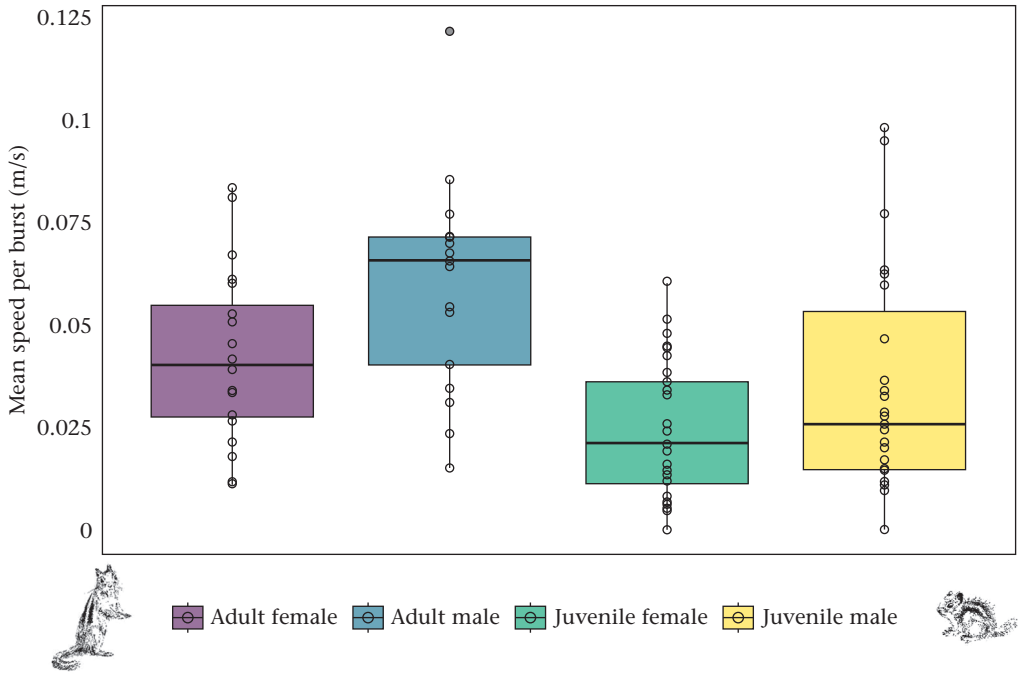

Figure A3. Mean movement speed per 10 min 'bursts' in free-ranging golden-mantled ground squirrels. Box plots include the median as the centre line, interquartile range (IQR) as the box, values 1.5 times the IQR as the whiskers and values greater than 1.5 times the IQR as black points. Open circles denote individual data points.

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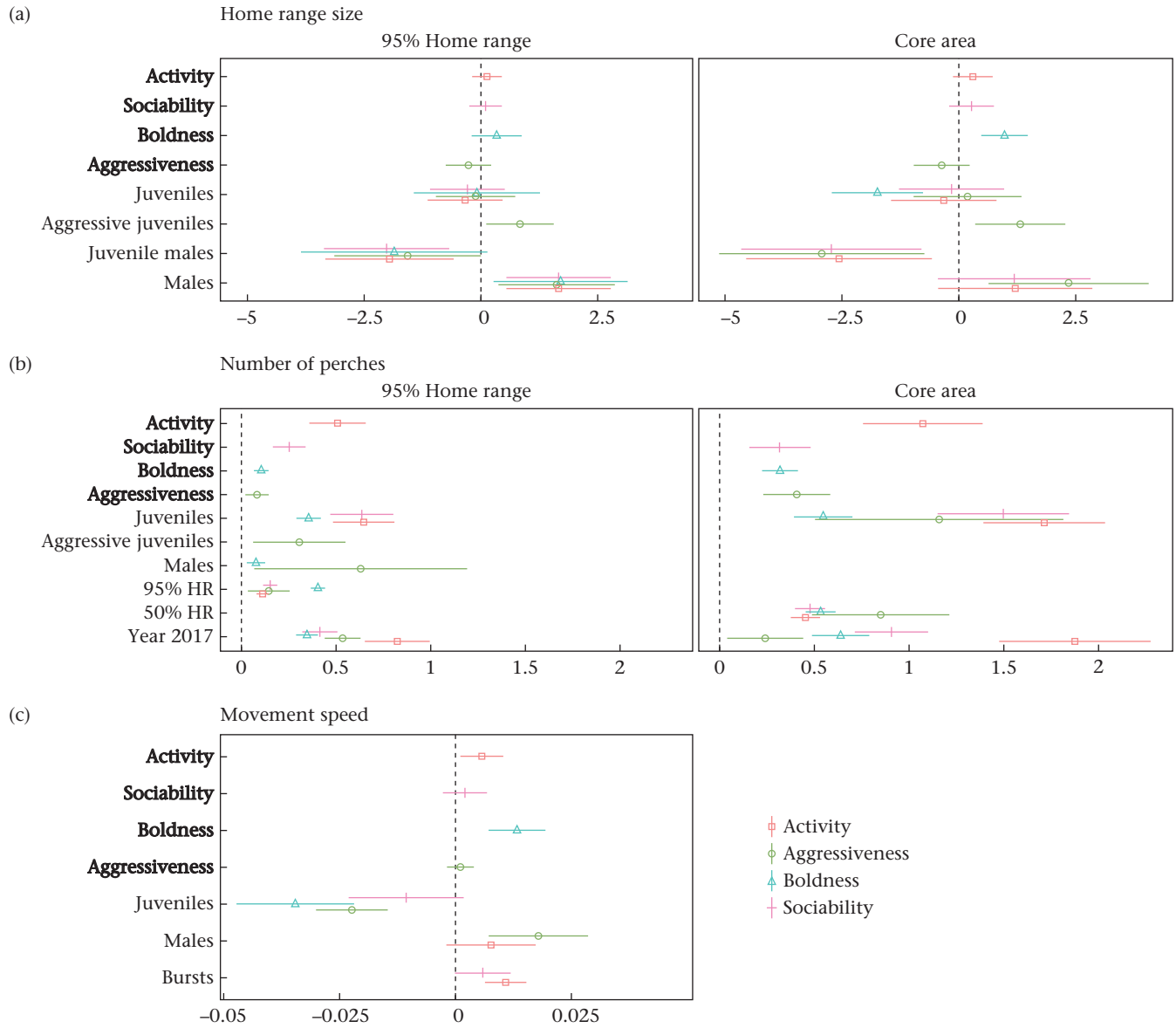

Figure A4. Plot of coefficients for fixed effects in each of five mixed effects models analysing the effect of personality on (a) home range size (95% home range on left, 50% core area on right), (b) number of perches in the home range (95% home range on left, 50% core area on right) and (c) mean movement speed. Shapes (unique to each model) represent mean point estimates and lines represent 95% confidence intervals. Personality scores included in each model are in bold font. Variables whose coefficients do not overlap with the dotted line in a given plot had a significant effect on that outcome. Model coefficients for juveniles are shown in reference to adults, and coefficients for males are shown in reference to females. Results for year in (b) are presented for year 2017 in reference to 2018. Results for an interaction between aggressiveness and age class are presented for juveniles (listed as aggressive juveniles) in reference to adults. All reference categories were fixed to their mean values.

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