Animal Behaviour 212 (2024) 13–30

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Linking animal personality and habitat restoration for a keystone species

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ARTICLE INFO

Article history:
Received 12 July 2023
Initial acceptance 1 September 2023
Final acceptance 31 January 2024
Available online 17 April 2024
MS. number: A23-00363R

Keywords:
animal personality
Dipodomys spectabilis
habitat restoration
keystone species
movement behaviour
shrub encroachment

Animal personality should be highly relevant to recovery of species following habitat restoration, but empirical evaluations remain scarce. In the Chihuahuan Desert of the southwestern United States and globally, grasslands are threatened with shrub encroachment, prompting landscape-scale restoration efforts to remove shrubs and improve habitat for grassland species. We examined the behavioural response of a keystone rodent of grasslands, banner-tailed kangaroo rats, *Dipodomys spectabilis*, to extensive shrub removal efforts in New Mexico, U.S.A. We captured individuals from replicated restoration and remnant grassland habitats and used standardized behavioural assays to determine whether *D. spectabilis* exhibits personality and whether it varies between restoration and remnant habitats. We also conducted a movement experiment using artificial shrubs to test whether personality mediates movement choices through shrub cover, which could be a mechanism contributing to the colonization dynamics of restoration sites. We found repeatable differences among individuals for multiple behaviours, including movements, providing evidence of personality. We also documented a syndrome in which bolder and more active individuals moved through movement trials quicker, indicating personality-dependent movement. *Dipodomys spectabilis* also exhibited personality-dependent movement through artificial shrub cover, suggesting the choice to move through shrublands may depend on personality. This result could have consequences for colonization dynamics of restoration sites if a subset of individuals is more likely to traverse low-quality shrublands and settle in habitats treated for shrub removal. Surprisingly, there was weak divergence in behavioural traits at the population level between restoration sites and remnant grasslands. This outcome could reflect personality-dependent colonization early in the restoration trajectory being eroded by subsequent gene flow and facilitation of alternative behavioural types. We hope our study will stimulate future research integrating animal personality with habitat restoration to benefit biodiversity in degraded ecosystems.

Animal personality, or consistent among-individual differences in behavioural traits, has important implications for understanding species' responses to changing environments (Brehm & Mortelliti, 2021; Sih et al., 2012; Wolf & Weissing, 2012). Indeed, growing evidence suggests anthropogenic disturbance can shift the distribution of personality types within a population (Brehm et al., 2019; Cosentino & Droney, 2016) or alter associations between personalities and ecological outcomes, ultimately affecting population and community dynamics (Boone et al., 2022; Brehm & Mortelliti, 2021). Habitat restoration often involves anthropogenic changes to the environment and may strongly influence, or be influenced by, animal personalities. However, integrating animal personality research into restoration ecology remains uncommon (Hale et al., 2020; Lindell, 2008). This divide requires attention because explicitly accounting for personality in target species may improve population recovery following restoration actions, ultimately influencing biodiversity targets (Haage et al., 2017; Hale et al., 2020).

Animal personality is relevant to habitat restoration in distinct ways. First, if an individual's willingness to move through a landscape matrix and colonize newly restored habitats is dependent on personality type (i.e. dispersal syndrome; Cote, Clobert et al., 2010), then accounting for such constraints could help forecast species re-establishment (Hale et al., 2020; Merrick & Koprowski, 2017). For example, highly mobile individuals can be more exploratory, bolder, aggressive or asocial than residents and more likely to settle in new areas (Cote, Fogarty et al., 2010; Dingemanse et al., 2003; Duckworth & Badyaev, 2007). These large-scale processes are

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https://doi.org/10.1016/j.anbehav.2024.03.003

difficult to quantify, but movement behaviour at fine scales (e.g. homing behaviour) can translate to movements at landscape scales, including how individuals respond to habitat structure (Schooley & Wiens, 2003, 2004). Second, personality type may influence an individual's ability to persist in habitats undergoing restoration. For instance, if restoration efforts create novel ecosystems (Coffman et al., 2014; Hobbs et al., 2009), then individuals that are more exploratory, bolder or active may be better able to survive because they can exploit novel resources or cope with novel stressors (Tuomainen & Candolin, 2011; Wong & Candolin, 2015). Such examples highlight the potential consequences of animal personality in habitat restoration, but such relationships are rarely investigated (Hale et al., 2020).

Grass-dominated drylands are threatened globally because of shrub encroachment and are often targets of habitat restoration programmes involving shrub removal (Archer & Predick, 2014; Ding & Eldridge, 2023). The Chihuahuan Desert of southwestern New Mexico, U.S.A. has experienced broad-scale grassland loss caused by the encroachment of two native shrubs, creosotebush, *Larrea tridentata*, and honey mesquite, *Prosopis glandulosa* (Grover & Musick, 1990; Peters et al., 2006), impacting ecosystem services and biodiversity (Whitford, 2002). Such state transitions have prompted land management agencies to initiate shrub removal programmes to reverse the process and restore encroached grasslands (Bestelmeyer et al., 2018, 2019). Notably, the U.S. Bureau of Land Management (BLM) in New Mexico has applied selective herbicides across vast areas to control encroaching shrubs and increase the cover of perennial grasses. Over 300 000 ha have been treated for shrub removal since 1982, with 74% of that area treated after 2005 (Bestelmeyer et al., 2019). Although herbicide treatments reduce shrub cover from ~15% to 5%, grass recovery and composition are highly variable, and restoration efforts create novel savannah-like states across broad spatial extents (Coffman et al., 2014). Nevertheless, shrub removal increases the occurrence and abundance of declining grassland species in the region (Coffman et al., 2014; Cosentino et al., 2013; McAllister et al., 2014), including a keystone rodent, the banner-tailed kangaroo rat, *Dipodomys spectabilis* (Cosentino et al., 2014).

Dipodomys spectabilis is a grassland specialist experiencing habitat loss and fragmentation caused by shrub encroachment, resulting in population declines across its range (Waser & Ayers, 2003). Their sensitivity to shrub cover may involve changes to predation risk or resource availability, and populations are locally extirpated when shrub cover exceeds 15–20% (Cosentino et al., 2014; Krogh et al., 2002). *Dipodomys spectabilis* is also considered a keystone species of grasslands because community organization is strongly shaped by their engineering (Davidson & Lightfoot, 2007; Guo, 1996; Schooley & Wiens, 2001) and nonengineering activities (Bowers & Brown, 1992; Bowers et al., 1987; Davidson & Lightfoot, 2006). Therefore, understanding constraints to their population recovery is essential for maintaining ecosystem structure and function in Chihuahuan Desert grasslands (Krogh et al., 2002; Longland & Dimitri, 2021; Mallen-Cooper et al., 2019).

Dipodomys spectabilis has responded positively to shrub removal efforts, with greater densities in treated habitats than in untreated shrublands (Cosentino et al., 2014). Moreover, the recovery of grassland lizards and ants on treated sites was positively related to *D. spectabilis* densities (Cosentino et al., 2013; McAllister et al., 2014). Thus, *D. spectabilis* can mediate biodiversity trajectories following shrub removal. However, substantial recolonization of restoration sites by *D. spectabilis* often takes ≥10 years even when shrub cover is reduced. This lagged response may reflect their limited dispersal abilities and insufficient connectivity to source populations (Cosentino et al., 2014). Younger treatments (i.e. <10 years following shrub removal) and untreated shrublands are occupied by *D. spectabilis* at low densities (Cosentino et al., 2014), however, suggesting individuals may vary in their ability to colonize or tolerate areas recently treated for shrub removal.

Here, we examined linkages between grassland restoration efforts and variation in *D. spectabilis* behaviour. We hypothesized that movement decisions through shrub cover are mediated by personality, which could be a mechanism contributing to early colonization of restoration sites. Also, disturbances from shrub removal may influence the development and expression of *D. spectabilis* behavioural traits (Sih et al., 2012; Wong & Candolin, 2015), and restoration efforts may favour individuals with specific personalities. To test these hypotheses, we captured individuals from replicated restoration and remnant grassland habitats across a broad region. We then used standardized assays to determine whether *D. spectabilis* exhibits personality and whether it varies between restoration and remnant grassland habitats. We also conducted an experiment to test whether movements through shrub cover depend on behavioural traits. We predicted that, if colonization of shrub removal sites is nonrandom and driven by personality-dependent dispersal (Cote, Clobert et al., 2010), then movement decisions through shrub cover will depend on personality, which will be spatially structured across habitats. In particular, sites under restoration are often surrounded by intact shrublands that could be perceived as risky to move through (Bouskila, 1995), resulting in bolder and more exploratory or aggressive individuals colonizing restoration sites (Cote, Clobert et al., 2010). Alternatively, novel savannah states created by partial shrub removal may lead to long-term persistence of individuals that are more exploratory, active or bold because they can cope with novel environmental conditions (Sih et al., 2012).

METHODS

Study Species

Dipodomys spectabilis is a large heteromyid rodent (often >120 g) endemic to the Chihuahuan Desert and is listed as near threatened by the IUCN Red List (IUCN, 2023). The species is a grassland specialist that occupies open habitat with sparse shrubs (Schroder, 1987; Waser & Ayers, 2003) where it forages primarily on seeds and other vegetation. It is a central place forager that constructs large, conspicuous mounds typically occupied by a single adult. Both sexes are territorial and defend mounds and seed caches from conspecifics (Randall, 1984; Schroder, 1979).

Study Region and Sampling Design

We conducted research at five sites in the Chihuahuan Desert of New Mexico, U.S.A. (Appendix, Fig. A1). Specifically, we sampled individuals from populations on three restoration sites treated for shrub removal and two unencroached, remnant grasslands. The restoration sites were treated for shrub removal by the BLM in 2009 and 2010 (i.e. 9–10 years prior to our sampling) to facilitate recovery of perennial grasses (Bestelmeyer et al., 2019; Cosentino et al., 2019). The slow colonization of *D. spectabilis* (Cosentino et al., 2014) required us to select sites ~10 years post treatment because densities on sites treated prior to 2009 were too low to acquire adequate sample sizes for statistical comparisons.

Shrub removal treatments primarily targeted creosotebush, the dominant shrub (Coffman et al., 2014), and consisted of a single aerial application of the herbicide tebuthiuron (0.56 kg/ha). The area of herbicide application typically ranges from 265 to 2317 ha (Cosentino et al., 2013). The two remnant grasslands were never treated for shrub removal. Distances between sites were >15 km. Remnant grasslands and restoration sites differed substantially in

habitat structure (Coffman et al., 2014). Shrubs were uncommon on remnant grasslands (Fig. 1a) and cover of perennial grasses was high (Coffman et al., 2014). In contrast, restoration sites (Fig. 1b) were savannah-like with some shrubs and patchy grass cover (Coffman et al., 2014; Cosentino et al., 2019).

Live Trapping

We trapped individuals from June to August 2019. We focused our trapping effort within a 9 ha area for all sites (Cosentino et al., 2019) where we located 15–20 mounds with fresh *D. spectabilis* activity (Schooley & Wiens, 2001). We placed two to three live traps (Model XLKGDT, H.B. Sherman Co., Tallahassee, FL, U.S.A.) baited with a millet-sunflower seed mix at the entrances of active mounds. Traps were set approximately 1 h before sunset and checked at regular intervals ($\leq$3 h) until five to seven individuals were captured or until 2 h before dawn. We closed all traps after sampling each night. We trapped at each site for 2–5 days or until $\geq$10 individuals were captured. Individuals were marked with uniquely numbered eartags (Model 1005-1, National Band and Tag Co., Newport, KY, U.S.A.) and weighed. We recorded the sex of individuals and determined age class based on body mass (juveniles: <90 g; adults: $\geq$90 g). Sites were revisited 7–17 days (mean = 10.5 days) after the first trapping session to administer repeated personality assays and movement trials.

Personality Assays

Before tagging and weighing individuals, we measured personality using established protocols for rodents, including heteromyids (Baker et al., 2016; Dochtermann et al., 2012; Dochtermann & Jenkins, 2007; Mazzamuto et al., 2019). Specifically, we used a hole-board assay, a mirror image simulation (MIS) assay and an emergence test. A hole-board assay is a modified open field test that consists of blind holes on the arena floor and measures an individual's response to a novel environment (i.e. exploration and activity; Martin & Réale, 2008; Walsh & Cummins, 1976). The MIS assay includes a mirror that simulates the presence of a conspecific and measures an individual's response to its reflection (i.e. sociality and aggression; Svendsen & Armitage, 1973). The MIS assay has been validated as an appropriate surrogate for intraspecific aggression in other heteromyids (i.e. *Dipodomys merriami*; Dochtermann et al., 2012). We therefore consider it a reliable measure of aggression in *D. spectabilis*. The emergence test measures the latency to enter an unfamiliar environment such as the personality arena and assesses risk taking and boldness (Carter et al., 2013). All assays were administered in a single arena in the following order: (1) hole-board emergence test, (2) hole-board assay, (3) MIS emergence test and (4) MIS assay. Full details on arena specifications are in the Appendix.

We carried captured individuals to a central location at each site (mean distance = 137 m; range 37–332 m) where we administered personality assays. We placed the focal individual in an entrance chamber to the arena for a 2 min resting period. We then raised a sliding panel, allowing the individual to voluntarily enter the arena (i.e. hole-board emergence test). If the individual did not enter after 5 min, we gently pushed it into the arena. This gentle pushing of individuals did not influence repeatability estimates for measured behaviours (Appendix, Table A1). We shut the sliding panel after individuals entered, then recorded behaviour from the hole-board assay for 5 min.

Following the hole-board assay, we captured the focal individual in the arena using a cloth net and placed it back into the entrance chamber for another 2 min resting period. We then removed a panel covering a mirror and placed a dish containing 10 g of white millet seed centred in front of the mirror (Dochtermann et al., 2012; Dochtermann & Jenkins, 2007). Millet seed was used to measure an individual's tolerance to a conspecific while foraging (Toscano et al., 2016). We also placed a rock (14 cm diameter) in the back right quadrant of the arena relative to the mirror, which provided refuge from the individual's reflection (Dochtermann et al., 2012; Dochtermann & Jenkins, 2007). Finally, we covered the blind holes on the arena floor using wood dowels. The focal individual was then allowed to enter the arena for a second time (MIS emergence) following procedures previously outlined. We recorded behaviour from the MIS assay for 5 min. We recorded all assays using an infrared video camcorder (Sony 4K Handycam FSR-AX53) attached to a tripod overlooking the arena.

Measured Behaviours

We used the event-recording software BORIS (Friard & Gamba, 2016) to score and quantify behaviours from videos (ethogram in the Appendix, Table A2). A single observer scored all videos to

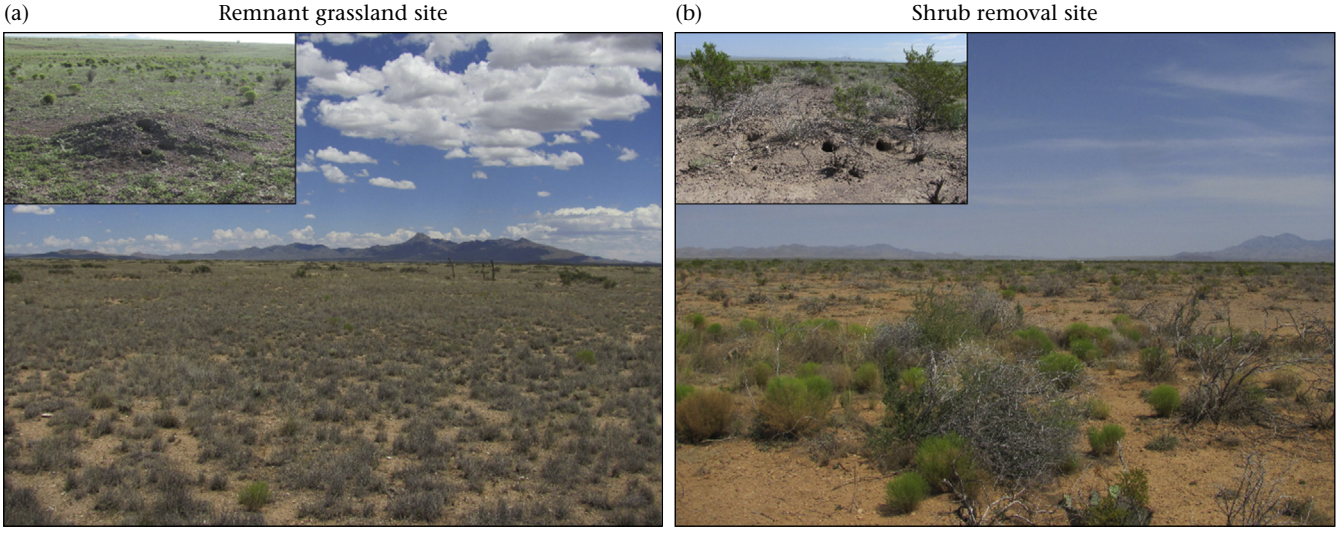

Figure 1. Habitat characteristics of (a) a remnant grassland site and (b) a shrub removal site in New Mexico, U.S.A. Inserts illustrate differences in microhabitat conditions around banner-tailed kangaroo rat mounds.

reduce bias. Intraobserver agreement was >98% across all measured variables for a subset of individuals ($N = 15$). For the hole-board assay, we recorded the proportion of time spent locomoting, still, sniffing, scanning and rearing and the frequency of jumps and head-dips. For the MIS assay, we recorded the proportion of time spent foraging/caching millet seeds in front of the mirror, in the front half of the arena, on top of the rock and while locomoting. We also recorded the frequency of direct mirror encounters and foraging/caching bouts. Finally, we measured the total mass of seed remaining.

We measured latency to enter the arena (s) for the hole-board and MIS emergence tests. However, emergence latencies were repeatable for the MIS test but not for the hole-board test (see Results). We suspect that individuals did not perceive the arena as risky during the hole-board test because most entered quickly with little variation in latencies (Appendix, Fig. A2). In contrast, MIS latencies varied considerably among individuals (Appendix, Fig. A2). Perceived risk may have been greater during the MIS emergence test because individuals were exposed to a stressful situation when recaptured following the hole-board assay, or they perceived their reflection in the mirror as a source of risk. Thus, we assumed emergence latencies reflected boldness and risk taking in *D. spectabilis* for the MIS test but not for the hole-board test.

Experimental Movement Trials

We conducted a movement experiment to understand links between personality and movement decisions in *D. spectabilis*, including whether the willingness to move through shrubs depended on behavioural traits. Specifically, we released each individual from a holding box and allowed it to move through either a treated or control area while returning to its home mound. The treated area consisted of eight artificial shrubs, and the control area had no shrubs. To mimic shrub cover, we used a combination of 5-gallon (18.93-litre) camouflage buckets (Leaktite, Leominster, MA, U.S.A., Model number 05GLCMO) attached with trimmings of live creosotebush (full details in the Appendix). Four artificial shrubs were placed in the cardinal directions around the holding box, and four were placed in between those. Artificial shrubs were placed 1.5 m from the holding box and formed a 9.4 m circular perimeter around the box (Appendix, Fig. A3). The artificial shrub treatment simulated a situation in which a dispersing *D. spectabilis* might encounter shrubs and make movement decisions. We recognize that the artificial shrubs represented novel obstructions, but we believe they simulated key structural elements of shrub cover, and thus should produce similar cues and behavioural effects in *D. spectabilis* (Hawlena et al., 2010; Kelt et al., 2005; Rosenzweig, 1973).

For the control, we delineated the same 9.4 m circular perimeter used for the shrub treatment but replaced the artificial shrubs with eight 10 × 5 cm wood dowels. The dowels were used as visual aids to record the time taken for an individual to exit the box and move through the perimeter. We also placed a single dowel at the base of each artificial shrub during the shrub treatment to ensure the dowels did not bias movement decisions.

We conducted trials by releasing individuals 6 m from the periphery of their home mound. We selected a release location with minimal natural vegetation and clear sightlines back to the mound. Individuals were assigned either the shrub or control treatment during the first trapping session and were given the alternative treatment during the second session. To ensure a balanced data set, we randomly assigned the first individual captured at each site to either the shrub treatment or the control treatment, then systematically alternated between treatment or control trials for subsequent individuals.

Following personality assays, we returned each individual to their home mound for the movement experiment in a wooden box designed to house small mammals (25.4 × 17.8 cm and 17.8 cm high; You & Me, https://younme-online.com/). We modified the box by attaching a movable door to the entrance and a wooden floor. Additionally, we attached a 10 m release cord for opening the door. We placed the holding box directly in the centre of the circular perimeter formed by either the artificial shrubs or the control dowels and oriented the box towards the home mound. We allowed 5 min for the animal to acclimate after being moved. Then, an observer located 10 m away pulled the release cord to open the door and allow the individual to move to its mound. A second observer located 15 m from the box recorded the trial using a night vision scope (Bestguarder Digital Night Vision Monocular, https://www.bestguarder.net/, Model WG-50). Both observers were positioned perpendicular to the release box and were not behind the box or between the box and the mound. We used videos to determine the latency (s) for individuals to exit the box and move through the treatment or control perimeter (i.e. movement latency). If an individual did not exit the box after 10 min, we ended the trial, released the individual back at their home mound and assigned the maximum latency of 10 min. We selected 10 min because of time constraints of administering personality assays and movement trials for multiple individuals during a night. We accounted for censored times in the analyses.

Statistical Analyses

We followed established guidelines for quantifying animal personality (Dingemanse & Dochtermann, 2013; Houslay & Wilson, 2017). Specifically, we conducted four analyses: (1) estimated the repeatability of measured behaviours and movement latencies; (2) estimated the covariance between repeatable behaviours (i.e. behavioural syndromes); (3) tested whether repeatable behaviours differed between habitat types; (4) assessed whether movement latencies through artificial shrubs depended on behavioural traits. All statistical analyses were conducted using R version 4.0.4 (R Core Team, 2021).

Although raw behavioural variables could have been used in our assessments (e.g. Brehm & Mortelliti, 2018), this approach would have made our analysis increasingly complex because of the number of measured behaviours. Thus, we selected a principal component analysis (PCA) to reduce the dimensionality of our data and identify orthogonal personality factors (Carter et al., 2013; Schirmer et al., 2019). Principal components were calculated separately for the hole-board and MIS assays using the correlation matrix (Appendix, Tables A3–A4). We ran parallel analyses to determine the number of components to extract, and we applied the Bartlett sphericity test to determine sampling adequacy of the correlation matrix (Budaev, 2010). We applied a single PCA on behaviour from each assay using the combined data from trials and habitats to facilitate comparisons and consistent interpretations (Cosentino & Droney, 2016). Principal components from separate PCAs for trials and habitats revealed similar results (Appendix, Table A5). We used the package 'psych' (Revelle, 2015) with a varimax rotation to conduct PCAs. All downstream analyses were performed on individual scores calculated from PC loadings. However, we used the raw repeated measures for movement (i.e. shrub and control) and emergence latencies in all analyses.

We used univariate linear mixed-effects models to quantify repeatability (Nakagawa & Schielzeth, 2010). We ran separate models for each PC axis and each emergence test (i.e. hole-board and MIS) and for movement latencies from the release experiment. We modelled PC scores with Gaussian errors using the package 'lme4' (Bates et al., 2015). We estimated repeatability,

confidence intervals and *P* values for PC scores using the package 'rptR' (Stoffel et al., 2017). Confidence intervals and *P* values were estimated using parametric bootstrapping with 1000 simulations. We assessed model fit by visually inspecting *Q*–*Q* plots and histograms of the residuals and by plotting fitted values against residual values. We log-transformed the PC scores from the first axis of the MIS assay to normalize residuals. We modelled emergence and movement latencies with censored Poisson errors with a log link function ('MCMCglmm' package; Hadfield, 2010) to account for censored times (i.e. emergence and movement latencies were censored at 5 min and 10 min, respectively). Repeatability for latencies was determined by extracting the mode of the posterior distribution generated by dividing the among-individual variance by the total variance for each MCMC sample. We calculated credible intervals around the mode using the 'HPDinterval' function with the 'coda' package (Plummer et al., 2006).

In all models, we fitted *D. spectabilis* identity (ID) as a random effect and included sex, average body mass and trial number as fixed effects. We also included wind speed as a fixed effect when modelling movement latency because exploratory analyses revealed a moderate correlation between variables. Wind speed was log-transformed, and wind speed and average mass were mean-centred. Although moonlight can influence rodent behaviour and activity (Prugh & Golden, 2014), we found no effect of lunar illumination on *D. spectabilis* repeatability scores (Appendix, Table A6). We therefore did not include the variable in our analyses to reduce model complexity. Because we included fixed effects, our repeatability estimates are considered 'adjusted repeatabilities' (Nakagawa & Schielzeth, 2010).

To identify correlations between repeatable behaviours, we applied Bayesian bivariate mixed-effects models using the 'MCMCglmm' package (Hadfield, 2010; Houslay & Wilson, 2017). We ran separate models using all pairwise combinations of repeatable behaviours ($N = 13$ pairs), including movement latency. We included movement latency in our analysis to understand the degree of variability that may exist in movements and how that variability covaries with other behavioural traits. We included the same random and fixed effects as outlined in the repeatability analysis, and the response variables were PC scores from personality assays and latencies from the MIS emergence test and movement trials. We rescaled all covariances between variables as correlations (Houslay & Wilson, 2017). Priors and diagnostics for Bayesian models are presented in the Appendix.

To determine whether behavioural traits differed between restoration and remnant habitats, we compared linear mixed-effects models with habitat type as a fixed effect to models excluding the variable using likelihood ratio tests (for PC scores) or deviance information criterion (DIC; for latencies). We fitted repeatable behaviours as the response variable and included *D. spectabilis* ID as a random effect and sex, average mass and trial number as fixed effects. We used maximum likelihood procedures to compare models and restricted maximum likelihood procedures to estimate parameters and standard errors (Zuur et al., 2007). We evaluated habitat differences for MIS emergence latency using DIC implemented in the package 'MCMCglmm'. We were unable to test whether behavioural syndromes also differed between contrasting habitats because our restricted data set for each habitat type caused model convergence issues, precluding us from estimating the covariance among traits for each habitat type separately.

To determine whether movement behaviour was affected by shrub cover or habitat type, we ran mixed-effects models with movement latency as the response variable and treatment (control versus shrub) and habitat type (remnant versus restoration) included as fixed effects. We also included two-way interactions between personality and shrub treatment to assess the hypothesis that personality type mediates movement patterns through shrub cover. We included ID as a random effect and sex, average mass, trial number and wind speed as fixed effects.

We extracted 90% confidence intervals (CI) or credible intervals (CRI) to evaluate uncertainty for our parameter estimates. We considered parameters to have statistical support if 90% intervals excluded zero. Similarly, we considered point estimates to have strong support when *P* values were <0.05 and moderate support when *P* values were ≥ 0.05 and <0.10. We selected these values because of the multidimensionality of factors influencing animal behaviour (Carere & Maestripieri, 2013; Sih et al., 2004) and our moderate sample size resulting from a regional field study. Additionally, this approach emphasizes inferences based on the effect size while acknowledging measurement uncertainty (Amrhein et al., 2019).

Ethical Note

All aspects of animal capture and handling adhered to guidelines provided by the American Society of Mammalogists and were permitted by New Mexico Department of Game and Fish (NMDGF Scientific Collecting Permit 3501) and covered under Protocol 16161 from the Institutional Animal Care and Use Committee of the University of Illinois Urban-Champaign. We used trapping methods designed to quickly survey and capture *D. spectabilis* while minimizing the risk of injury (Cross & Waser, 2000). Traps were checked within 3 h of setting. The mean time between capture and the start of personality assays was 61 min. The mean time to complete behavioural observations was 27 min. We also minimized stress to captured animals by conducting observations in the dark between 2000 and 0300 hours, not trapping during cold or rainy nights, using red LED headlamps while handling animals and remaining quiet and out of view during assays. We released individuals at the point of capture during movement trails to reduce the likelihood an individual was released outside of its home range. Once an individual completed both assays, we disinfected the arena with a diluted concentration of Lysol to reduce the transmission of disease and any scent from a conspecific. To minimize impacts on juvenile recruitment, we only used adults for behavioural observations. We only trapped mounds during this second session that had captures during the first session to prevent disturbance to nontagged individuals.

RESULTS

Captures

We captured and tagged 62 individuals, including 35 from restoration sites and 27 from remnant grasslands. Thirty-six individuals were male (restoration = 18, grassland = 18) and 26 were female (restoration = 17, grassland = 9). We recaptured 59 of the 62 (95%) tagged individuals for repeated assays. We recaptured all individuals from restoration sites and 24 (male = 16, female = 8) individuals from remnant grasslands. Our sampling effort yielded 238 video observations for the hole-board ($N = 119$) and MIS ($N = 119$) assays. We conducted repeated movement trials (i.e. control and shrub) for 57 of the 62 tagged individuals.

Principal Component Analysis

The Bartlett's sphericity test confirmed the correlation matrices were appropriate for the hole-board ($\chi^2_{21} = 293.76$, $P < 0.001$) and MIS ($\chi^2_{28} = 732.28$, $P < 0.001$) assays. Parallel analyses revealed the optimal number of components to extract from each assay was two.

Table 1
Principal component (PC) loadings for behaviours measured during a hole-board (HB1, HB2) and mirror image simulation assay (MIS1, MIS2) for banner-tailed kangaroo rats in New Mexico, U.S.A.

Behaviour	PC loadings		Behavioural trait	PC loadings	
	HB1	HB2		MIS1	MIS2
Still	−0.14	**−0.80**	Time mirror	0.00	**0.94**
Sniff	**0.81**	−0.06	Forage	**0.96**	−0.07
Scan	**−0.64**	−0.19	Front	**0.72**	**0.52**
Locomotion	0.29	**0.67**	Rock	−0.19	−0.32
Jump rate	**−0.64**	−0.02	Locomotion	**−0.43**	**0.51**
Head-dip rate	**0.61**	0.12	Mirror rate	−0.06	**0.91**
Rearing	−0.13	**0.69**	Seed mass	**−0.95**	0.00
			Forage rate	**0.91**	0.02
Eigenvalue	2.21	1.38		3.42	2.36
Proportion of variance explained	0.28	0.23		0.43	0.30

Loadings in bold represent behaviours that were heavily loaded (>0.40) on the PC axis. $N = 119$ observations from 62 individuals.

The first axis from the hole-board assay (HB PC1) explained 28% of behavioural variation, with positive loadings for head dipping and sniffing and negative loadings for jump rate and scanning (Table 1). HB PC1 scaled from 'explorative' individuals willing to explore the arena and blind holes to 'nonexplorative' individuals spending more time scanning and trying to jump out of the arena. Thus, we refer to HB PC1 as a cline of exploration tendency. The second axis from the hole-board assay (HB PC2) explained 23% of variation, with positive loadings for locomotion and rearing and a negative loading for remaining still (Table 1). HB PC2 varied from highly mobile individuals to sedentary individuals. We refer to this axis as activity.

For the MIS assay, the first axis (MIS PC1) explained 43% of behavioural variation, with positive loadings for duration foraging, forage rate, time in front and negative loadings for locomotion and mass of remaining seed (Table 1). MIS PC1 captured variation in an individual's willingness to forage in the presence of its reflection and varied from individuals who harvested all the millet seed to individuals that avoided foraging. Whether an individual chooses to forage in the presence of a conspecific (e.g. reflection) can be influenced by individual variation in sociability (Toscano et al., 2016). Thus, we refer to MIS PC1 as a sociability axis that ranges from social to asocial individuals. The second axis from the MIS assay (MIS PC2) explained 30% of behavioural variation, with positive loadings for time near mirror, mirror rate, locomotion and time in front and a negative loading for time on rock (Table 1). MIS PC2 varied from individuals engaging in agonistic behaviour towards their reflection (e.g. jumping at mirror) to complete avoidance. We refer to this axis as gradient of aggression.

Although we recognize there could be other interpretations of behavioural axes, we labelled personality types that were best described by the highest loadings of behaviours within each component. Moreover, our labelling is consistent with other studies measuring personality in rodents, including heteromyids (Baker et al., 2016; Dochtermann et al., 2012; Dochtermann & Jenkins, 2007; Mazzamuto et al., 2019).

Table 2
Adjusted repeatability estimates (R) with 90% confidence intervals (CI) or credible intervals (CRI) for banner-tailed kangaroo rats in New Mexico, U.S.A.

Behaviour	*R*	90% CI	*P*
Exploration (HB PC1)	0.565	0.414–0.710	<0.001
Activity (HB PC2)	0.368	0.180–0.571	0.003
Sociability (MIS PC1)	0.443	0.271–0.623	<0.001
Aggression (MIS PC2)	0.209	0.019–0.443	0.067
Behaviour	***R***	**90% CRI**	
Hole-board emergence	0.103	0.000–0.246	
Boldness (MIS emergence)	0.381	0.160–0.593	
Movement latency	0.470	0.273–0.669	

HB: hole-board assay; PC: principal component; MIS: mirror image simulation assay. Movement and emergence latencies were modelled with Bayesian mixed-effects models using censored Poisson errors (see Methods). $N = 119$ observations from 62 individuals.

Repeatability of Behaviour

All measured behaviours were repeatable over time with the exception of latency to emerge during the hole-board assay (Table 2, Appendix, Table A7). Adjusted repeatability for behavioural traits and movement ranged from 0.10 to 0.57. Exploration (HB PC1), sociability (MIS PC1) and movement latency had high repeatability estimates (Table 2). Activity (HB PC2), boldness (MIS emergence) and aggression (MIS PC2) had moderate repeatability (Table 2). Collectively, individuals differed consistently in behavioural traits and movements.

Behavioural Syndromes

Emergence latency was positively correlated with movement latency (Table 3), indicating that bolder individuals who quickly entered the MIS arena also moved quickly through movement trials (Fig. 2a). There was a negative correlation between activity and movement latency (Table 3), in which more active individuals moved through movement trials quicker (Fig. 2b). We acknowledge

Table 3
Estimated correlations between measured behaviours and movement latency for banner-tailed kangaroo rats in New Mexico, U.S.A.

Among-individual correlations	Estimate	90% CRI
Exploration (HB PC1)		
Sociability (MIS PC1)	−0.158	(−0.495, 0.178)
Aggression (MIS PC2)	0.336	(−0.182, 0.827)
Activity (HB PC2)		
Sociability (MIS PC1)	0.020	(−0.446, 0.453)
Aggression (MIS PC2)	0.198	(−0.432, 0.815)
Boldness (MIS latency)		
Sociability (MIS PC1)	−0.132	(−0.560, 0.323)
Aggression (MIS PC2)	−0.082	(−0.682, 0.608)
Exploration (HB PC1)	0.272	(−0.113, 0.669)
Activity (HB PC2)	−0.136	(−0.660, 0.332)
Movement latency		
Boldness (MIS latency)	0.568	(0.247,0.938)
Sociability (MIS PC1)	−0.199	(−0.591, 0.195)
Aggression (MIS PC2)	−0.196	(−0.827, 0.379)
Exploration (HB PC1)	0.301	(−0.024, 0.663)
Activity (HB PC2)	−0.418	(−0.813, −0.025)

CRI = credible interval; HB: hole-board assay; PC: principal component; MIS: mirror image simulation assay. $N = 119$ observations from 62 individuals.

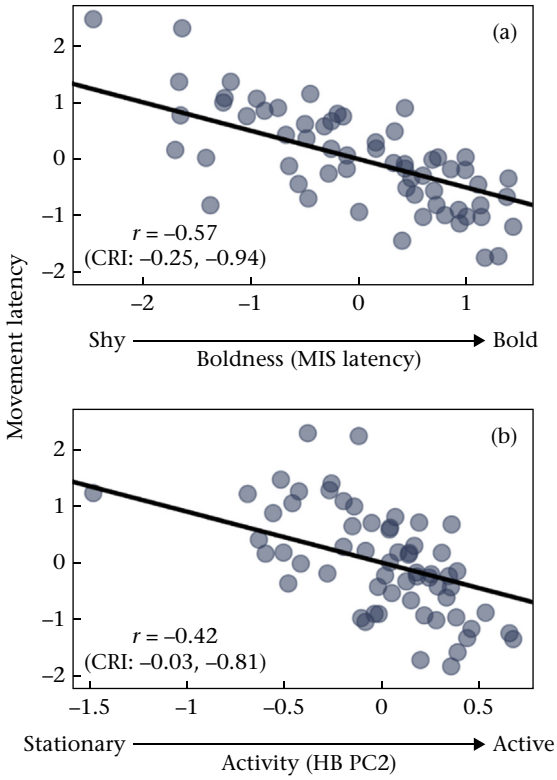

Figure 2. Relationship between (a) movement latency and boldness (mirror image simulation assay, MIS emergence latency) and (b) movement latency and activity (hole-board assay, principal component 2, HB PC2) for 62 banner-tailed kangaroo rats in New Mexico, U.S.A. Plotted values are the estimated posterior modes for individuals (i.e. individual random intercept) extracted from multivariate mixed-effects models. Boldness scores were multiplied by −1 for ease of interpretation. CRI = 90% credible interval.

the lack of precision in the point estimate between activity and movement latency, but we believe this uncertainty was driven by an outlier in our data set (Fig. 2b) and because activity had an interactive effect on movement treatment (see below). There was no clear evidence of covariation between other pairs of behaviours (Table 3).

Habitat Differences in Personality

Mean aggression scores differed between restoration and remnant habitats (Table 4). Individuals on remnant grasslands were more aggressive than those on restoration sites (Fig. 3). No other behaviours differed between habitats (Table 4).

Effects of Personality and Shrub Treatments on Movement Behaviour

Movement latencies did not differ between control and shrub treatment trials (Appendix, Fig. A2) or between habitats (Appendix, Fig. A2, Table A8). However, there were multiple interactions between personality and the shrub treatment (Appendix, Table A8). Exploration and shrub cover had an interactive effect in which nonexplorative individuals moved more quickly through the shrub treatment, but there was no relationship during the control trials (Fig. 4a). More active individuals also moved more quickly through shrub treatments (Fig. 4b) and did not respond strongly to the control. Finally, individuals with high sociability scores moved through the shrub treatment quicker, whereas their response to the control was marginal (Fig. 4c). Collectively, these findings suggest that an individual's decision to move through shrub cover depended on aspects of its personality.

DISCUSSION

Animal personality is relevant to applied ecology (Merrick & Koprowski, 2017; Wolf & Weissing, 2012), yet relationships between animal personality and habitat restoration remain understudied (Hale et al., 2020). We addressed this gap by quantifying the behavioural response of a keystone species to grassland restoration efforts in the Chihuahuan Desert. Our behavioural assays identified multiple personality traits in *D. spectabilis* including activity, aggression, boldness, exploration and sociability. Our movement experiment with artificial shrubs also indicated that animal personality can underlie movement behaviour in areas undergoing habitat restoration. Specifically, individuals that were more active, social and less exploratory moved through shrub treatments quicker and individuals that were bolder moved quicker regardless of treatment. However, we did not find behavioural divergence at the population level between restoration and remnant grassland habitats, potentially due to gene flow among habitats (Cosentino et al., 2015) or initial colonizers promoting establishment by other personality types (Wolf & Weissing, 2012). Our findings suggest extensive efforts to restore grasslands may not strongly select for *D. spectabilis* personalities, but certain individuals may be more willing to move through or tolerate areas with high shrub cover. We expand on these outcomes including implications for *D. spectabilis* recovery, and more broadly the role of animal personality in restoration ecology.

Table 4
Comparison of models testing whether banner-tailed kangaroo rat behaviour differed between restoration and remnant grassland habitats in New Mexico, U.S.A.

Response variable	Model	logLik	*L* ratio	*K*	β (SE)	*P*
Sociability (MIS PC1)	Nested	−152.16		6	–	–
	Grass-Treat	−151.95	0.416	7	0.133 (0.212)	0.519
Aggression (MIS PC2)	Nested	−161.04		6	–	–
	Grass-Treat	−159.50	3.082	7	−0.339 (0.197)	0.079
Exploration (HB PC1)	Nested	−151.89		6	–	–
	Grass-Treat	−151.60	0.571	7	−0.166 (0.227)	0.450
Activity (HB PC2)	Nested	−158.30		6	–	–
	Grass-Treat	−158.23	0.136	7	0.075 (0.213)	0.713
Response variable	**Model**	**Deviance**	**DIC**	***K***	**β (90% CRI)**	**pMCMC**
Boldness (MIS latency)	Nested	472.52	564.618	5	–	–
	Grass-Treat	473.00	564.818	6	−0.327 (−1.221,0.608)	0.537

logLik: log likelihood; *K*: number of parameters; MIS: mirror image simulation assay; PC: principal component; HB: hole-board assay; DIC: deviance information criterion; CRI: credible intervals. Remnant grasslands were used as the contrast. Models were compared by a log likelihood ratio test or deviance information criterion. 'Nested' is the model excluding habitat type. pMCMC is included in the standard output of MCMCglmm for fixed effects and is analogous to *P* values in maximum likelihood procedures.

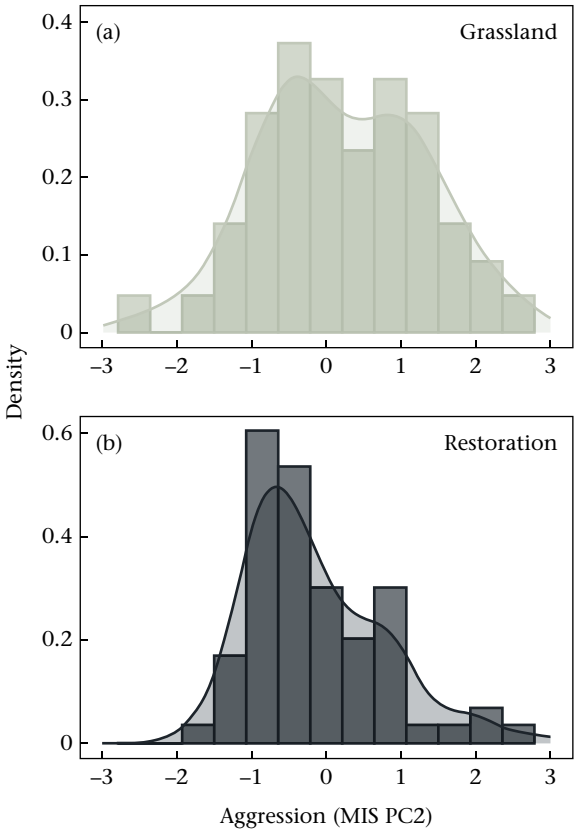

Figure 3. Frequency distributions of individual aggression scores for banner-tailed kangaroo rats from (a) remnant grasslands and (b) restoration sites in New Mexico, U.S.A. MIS: mirror image simulation assay; PC: principal component.

Movement Behaviour and Links to Personality

Movement latencies of *D. spectabilis* varied in a repeatable manner, with nearly half of the variation attributable to among-individual differences. This result adds to a growing number of studies documenting among-individual variation in movement behaviours in field settings (Michelangeli et al., 2022; Spiegel et al., 2017). Moreover, variation in movement decisions in *D. spectabilis* was correlated with personality. Specifically, bolder and more active individuals moved through movement trials quicker. Individual variation in movement and space use is linked to boldness and activity in other rodents. For example, boldness in bank voles, *Myodes glareolus*, and striped field mice, *Apodemus agrarius*, strongly influences home range size, core area size and movement distances (Schirmer et al., 2019, 2020). Likewise, individual differences in activity for American red squirrels, *Tamiasciurus hudsonicus*, affect home range size and whether females travel outside of their territories (Boon et al., 2008). Individuals of *D. spectabilis* vary greatly in the extent and intensity of their movements (Schroder, 1979; Steinwald et al., 2013), which may be driven in part by differences in boldness and activity.

Our movement experiment highlights the potential for personality-dependent colonization of restoration sites. In our study area, restoration sites are surrounded by shrublands, and movements through the shrub treatment in our experiment depended on repeatable behaviours, suggesting movement decisions through shrub-dominated areas are mediated by personality. For instance, activity levels in *D. spectabilis* influenced their willingness to move through the shrub treatment, with the most active individuals having the shortest latencies. This pattern is consistent with other documented associations between activity and dispersal. For example, active individuals of common lizards, *Lacerta vivipara*, are more likely to disperse from their current patch (Meylan et al., 2009), and dispersal latencies in male house mice, *Mus musculus*, decrease with increasing activity (Krackow, 2003). Our results also support links between individual variation in activity and departure decisions (Cote et al., 2022), and activity-dependent dispersal in *D. spectabilis* might be a behavioural mechanism facilitating movements through shrublands.

Sociability also influenced movements through artificial shrubs. Specifically, individuals considered more social and that spent more time foraging in the presence of their reflection exhibited shorter latencies for the shrub treatments. Our measure of sociability may also index risk taking in *D. spectabilis* because more social individuals tolerated the risk of a conspecific while foraging. Accordingly, sociability may influence the risk individuals are willing to take while moving within home ranges to find resources (Toscano et al., 2016). In turn, this may translate to greater tolerance of shrub cover by social individuals at fine scales and explain links between sociability and movement latency in *D. spectabilis*.

Nonexplorative individuals also moved quickest through the shrub trials. This result may seem counterintuitive and contradicts studies demonstrating that fast explorers are more likely to disperse relative to slow explorers (e.g. Dingemanse et al., 2003). However, inverse relationships between exploration and movement occur in

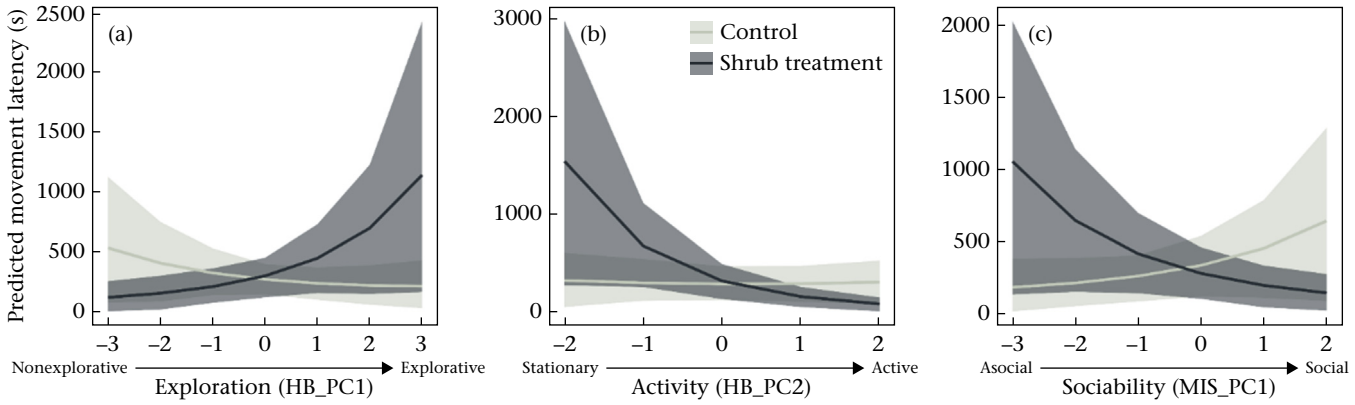

Figure 4. Interactive effects of shrub cover and (a) exploration, (b) activity and (c) sociability on predicted movement latencies of banner-tailed kangaroo rat in New Mexico, U.S.A. Control trials are depicted in light grey; shrub treatment trials are depicted in dark grey; shaded areas represent 90% credible intervals. HB: hole-board assay; PC: principal component; MIS: mirror image simulation assay.

other rodents. For example, exploration of an open field test by bank voles was negatively related to distance moved in the field (Schirmer et al., 2019). We suggest that nonexplorative individuals spent less time acquiring information during shrub trials (i.e. assessing whether shrubs are a risk) compared to explorative conspecifics, resulting in shorter latencies. If so, nonexplorative individuals may exhibit a greater probability of crossing through shrub cover.

These multiple interactive effects, combined with intraspecific variation in movement latencies, indicate that individuals differ in their sensitivity to shrub cover and, thus, the propensity to traverse shrubby areas may depend on personality. This result could be consequential for colonization potential of restoration sites and reinforcement of established populations (Clobert et al., 2004). For example, if our movement trials reflect broader-scale dispersal in *D. spectabilis*, then more active, social and nonexplorative individuals may be more likely to move through low-quality shrublands. Such constraints related to personality could then influence restoration dynamics because of the mediating effects that *D. spectabilis* has on biodiversity (Cosentino et al., 2013; McAllister et al., 2014).

One limitation of our study is that we did not measure long-range dispersal directly, but rather short-distance movement behaviour within an individual's territory. However, our aim was to assess whether movement tendency and shrub avoidance might depend on personality in this keystone species. Moreover, movement behaviour in animals during homing experiments can be similar to their natural movement behaviour in the wild, indicating that homing experiments can detect effects of landscape structure on animal movement (Volpe et al., 2014). Nevertheless, more research is necessary to reveal the full extent of how behavioural variation links to dispersal in *D. spectabilis* and whether that ultimately scales up to influence colonization dynamics of grassland restoration sites. Recent technological and statistical advances in automated tracking tools provide an exciting avenue for testing such hypotheses (Costa-Pereira et al., 2022).

Personality in Restoration and Remnant Populations

Dipodomys spectabilis behaviour consistently varied among individuals, but our results did not support our prediction that personality would differ between habitats. We offer two potential explanations for this outcome. First, evidence is accumulating that personality is underpinned by substantial heritable variation (Boulton et al., 2018; Dochtermann et al., 2014; van Oers & Sinn, 2013). A previous study quantified genetic structure and dispersal level gene flow between restoration and remnant populations of *D. spectabilis* and found no genetic divergence between restoration and remnant populations, indicating that founder effects during colonization of restoration sites are weak or absent (Cosentino et al., 2015). Extensive gene flow between restoration sites and surrounding remnant populations early in the restoration trajectory (Cosentino et al., 2015) may therefore minimize the degree of behavioural divergence at the population level.

Second, early colonizers may facilitate other personality types during the colonization process (Wolf & Weissing, 2012). For example, in western bluebirds, *Sialia mexicana*, nonaggressive individuals will only settle in habitats previously colonized by aggressive individuals (Duckworth, 2008). Accordingly, *D. spectabilis* personality in recently colonized populations on restoration sites may have differed from older populations on remnant grasslands early in the restoration trajectory, but those differences were attenuated by the time of our sampling because of facilitation (Clobert et al., 2009; Wolf & Weissing, 2012). Thus, detecting a behavioural response to habitat restoration may depend on temporal scales (Le Cœur et al., 2015; Phillips et al., 2006; Thomas et al., 2001), and understanding how animal personality changes along restoration trajectories deserves further consideration.

Although most behaviours were similar between habitats, individuals from remnant grasslands scored higher on the aggression axis than those from restoration sites. Aggressiveness in animals can increase with density and competitive pressure from conspecifics (Araya-Ajoy & Dingemanse, 2017; Dochtermann et al., 2012). *Dipodomys spectabilis* densities were two to six times greater on remnant grasslands than on restoration sites (C. J. Wagnon, personal observation), and a post hoc analysis revealed that aggression scores were related positively to *D. spectabilis* densities ($\beta = 0.046$, $SE = 0.024$, $P = 0.059$). Hence, greater densities on remnant grasslands may promote more aggressive behaviour in *D. spectabilis*, similar to other heteromyids (e.g. *D. merriami*: Dochtermann et al., 2012). Alternatively, more aggressive individuals in remnant grasslands may have displaced less aggressive individuals to surrounding shrublands and restored habitats (Cote, Clobert et al., 2010; Sih et al., 2012).

Conclusions

Our results show repeatable differences in *D. spectabilis* behavioural traits and movements, adding to the evidence of personality in animals (Carere & Maestripieri, 2013; Merrick & Koprowski, 2017). We also documented a syndrome in which bolder and more active individuals moved through movement trials quicker, indicating personality-dependent movement. Moreover, *D. spectabilis* exhibited personality-dependent movement through artificial shrub cover, suggesting that choices to move through shrublands may depend on personality type. However, we did not detect a strong behavioural response at the population level to habitat changes caused by shrub removal. Personality-dependent colonization soon after restoration might have been muted by gene flow and facilitation of alternative personality types. These contrasting outcomes at the individual and population levels emphasize the challenges of understanding links between animal personality and restoration trajectories of species (Hale et al., 2020; Hale & Swearer, 2017). We hope our study will stimulate research linking animal personality with habitat restoration in degraded ecosystems.

Author Contributions

Casey Wagnon: Data curation, Formal analysis, Writing—Original draft, reviewing & editing. **Bradley Cosentino**: Conceptualization, Funding acquisition, Resources, Writing—Original draft, reviewing & editing. **Robert Schooley**: Conceptualization, Funding acquisition, Project administration, Resources, Writing—Original draft, reviewing & editing.

Data Availability

The full data are available as supplementary material.

Declaration of Interest

None.

Acknowledgments

We thank H. Campos, B. Goncarvos, M. Suchewski and P. Murphy for field assistance. We also thank B. Bestelmeyer, L. Burkett, L. Lister and J. Anderson for facilitating research activities. We are especially grateful to K. and D. Stockton for giving permission to

access their ranch for research activities. We are grateful to J. Miller and T. Benson for comments on earlier versions of the manuscript. Shrub removal treatments were applied by the U.S. Bureau of Land Management–Las Cruces. This work was supported by the U.S. National Science Foundation to New Mexico State University for the Jornada Basin Long-Term Ecological Research Program (DEB 2025166) and by the Agroecosystem Management Program Grant (No. 2016-67019-25212) from the U.S. Department of Agriculture, National Institute of Food and Agriculture.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.03.003.

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Appendix

Additional Methods

Design of personality arena

We designed our arena following other studies measuring personality in rodents (e.g. Dochtermann et al., 2012; Martin & Réale, 2008). Specifically, we used a rectangular box (80×60 cm and 60 cm high) constructed from plywood and fitted with a Plexiglas top. An entrance chamber (16×12 cm and 12 cm high) was positioned on one of the longer sides of the arena. The arena floor consisted of four blind holes, each 5 cm in diameter and 5 cm deep, equidistant from the walls. The blind

holes provided animals the opportunity to explore. The wall opposite the entrance chamber had a sliding panel that covered a mirror (61 × 30.5 cm). The cover panel was in place for the hole-board assay but was removed for the mirror image simulation assay.

Artificial shrub assembly

We mimicked the presence of shrub cover during movement trials using artificial shrubs assembled in the field. Specifically, we used eight artificial shrubs, each consisting of two stacked buckets (1.5 m tall) secured with two branches of creosotebush inside of the top bucket and two inserted on opposite sides of the bottom bucket (Fig. A3). The two creosotebush branches placed inside the top bucket were each approximately 1.0–1.5 m long and 0.5–0.75 m wide. We attached the branches to the inside of the top bucket using black zip ties. Additionally, we secured two creosotebush branches each 0.5–0.75 m in length on opposite ends of the bottom bucket by inserting the branches into two, predrilled holes. The two holes were drilled 5 cm from the top of the bottom bucket.

Model priors and diagnostics

We applied these general modelling procedures for all analyses conducted with the 'MCMCglmm' package. We modelled PC scores with Gaussian errors and latencies with censored Poisson errors. The censored Poisson model takes data as two columns: the first column specifies the lowest possible value the data can take and the second column includes the largest value the data can take (Hadfield, 2010). However, only a single linear predictor is fitted for that distribution (associated with the uncensored but unobserved data; Hadfield, 2010). We used the default priors for all fixed effects and used an inverse-Wishart prior ($V = 1$, degree of belief (nu) = 0.002) for the residuals. We used uninformative parameter-expanded priors ($V = 1$, nu = 2, alpha.mu = 2, alpha.V = 625) for the random effect of ID. We ran models for 750 000 iterations with a burn-in of 50 000 and a thinning interval of 175. To assess model convergence and the proper mixing of chains, we visually inspected plots of traces and the posterior distributions (Hadfield, 2010; Houslay & Wilson, 2017). We used the function 'autocorr' to determine the absence of autocorrelation between posterior samples. Auto correlation was <0.05 and effective sample size was approximately 4000 for all estimates.

Table A1
Summary of coefficients (β), standard errors (SE) and *P* values for the fixed effect 'pushed' on repeatability (*R* with 90% confidence intervals, CIs) of banner-tailed kangaroo rat behavioural traits in New Mexico, U.S.A.

Response variable	*R*	90% CI	β (SE)	*P*
Exploration (HB PC1)	0.574	0.422–0.723	−0.303 (0.281)	0.285
Activity (HB PC2)	0.365	0.206–0.576	0.024 (0.318)	0.940
Sociability (MIS PC1)	0.443	0.272–0.624	0.028 (0.213)	0.900
Aggression (MIS PC2)	0.204	0.0167–0.428	−0.218 (0.232)	0.350

HB: hole-board assay; PC: principal component; MIS: mirror image simulation assay. We included the variable pushed as a binary predictor (i.e. individuals were pushed into the arena or entered freely). Whether an individual was pushed into the arena had no effect on repeatability values (see Table 2 in main text for comparisons).

Table A2
Ethogram and catalogue of behaviours used to describe banner-tailed kangaroo rat behaviour in a hole-board assay and a mirror image simulation (MIS) assay

Assay/behaviour variable	Type of measure	Description and interpretation
Hole-board assay		
Still	Duration	Proportion of time spent standing still, defined as when an individual is immobile (head and body) for ≥2 s. Individuals spending more time standing still would indicate low exploratory behaviour and activity[2,3,4,7,11,13]
Locomotion	Duration	Proportion of time spent ambulating, a direct measure of locomotion and activity. Individuals that spend more time moving would indicate high exploratory behaviour and activity[1,2,4,7,11,13]
Jump rate	Frequency	Number of jumps per unit time (s). Jump is defined as a complete bipedal vertical leap and is a direct measure of activity or anxiousness. Individuals that have a greater frequency of jumping would indicate increased activity or anxiousness[1,2,4,7]
Sniff	Duration	Proportion of time spent sniffing holes, walls or floors. Sniffing is a behaviour characterizing an axis of exploration. A greater proportion of time sniffing would indicate high exploratory behaviour[1,4,12,13,14]
Head-dip rate	Frequency	Number of times head is placed into false hole per unit time (s). A head dip is defined when both eyes disappear into a false hole. Head-dip rate is a common behaviour characterizing exploration. Increased head dipping would indicate high exploratory behaviour[1,4,5,7,11,13]
Rearing	Duration	Proportion of time spent standing on hindlegs. Rearing is defined when an individual remains in an upright position while standing on digits with forearms off the floor. Rearing is commonly assessed as correlating with activity and locomotion. A greater rearing rate would indicate higher activity[1,4,6,7,10,11,13]
Scan	Duration	Proportion of time spent moving the head or head and body while remaining in the same locale. Individuals spending more time scanning may indicate stress and anxiousness[1,4,7,11]
Mirror image assay		
Mirror rate	Frequency	Number of approaches to the mirror (i.e. direct contact with mirror) per unit time (s). A direct contact is defined as an individual oriented towards the mirror while engaging with their reflection. Individuals that are in contact with mirror more frequently would be considered more aggressive[1,2,4,7,13]
Rock	Duration	Proportion of time spent standing on the rock. Individuals that spent more time on the rock would presumably be using the rock as a refuge from the mirror and would be considered less aggressive or asocial[2,8]
Time mirror	Duration	Proportion of time spent near the mirror (within 5 cm and oriented towards the mirror). Individuals spending more time near the mirror would be considered more aggressive or social[1,2,4,7,8,13]
Locomotion	Duration	Proportion of time spent ambulating. Individuals that spend more time moving may indicate anxiousness towards mirror reflection[1,2,3,4,7,11,13]
Forage rate	Frequency	Number of foraging–caching bouts per unit time (s). Individuals with a greater forage rate would be considered more tolerant of conspecifics (i.e. social)[8,9]
Duration forage	Duration	Proportion of time spent foraging at seed tray. Individuals spending more time foraging would be considered more tolerant of a conspecifics[8,9]
Seed mass	–	Total weight of seed remaining. Individuals gathering a greater mass of seeds in front of the mirror would be considered more tolerant of conspecifics[9]
Duration front	Duration	Proportion of time spent in the front half of the arena closest to the mirror. Individuals spending more time in the front of the arena would be considered more tolerant of conspecifics[1,4,7,8,9,12]

We scored behaviours using the event recorder BORIS at 0.7× speed. Included are the behavioural variables for each assay, the type of measure (duration or frequency), a description and interpretation of each behaviour and a nonexhaustive list of references.

1 Archer (1973).
2 Baker et al. (2016).
3 Boon et al. (2007).
4 Boon et al. (2008).
5 Casarrubea et al. (2010).
6 Choleris et al. (2001).
7 Cooper et al. (2017).
8 Dochtermann et al. (2012).
9 Dochtermann and Jenkins (2007).
10 Malange et al. (2016).
11 Martin and Réale (2008).
12 Mazzamuto et al. (2019).
13 Réale et al. (2007).
14 Roth and Katz (1979).

Table A3
Correlation matrices of banner-tailed kangaroo rat behaviour measured during a hole-board assay in New Mexico, U.S.A.

Behaviour	Still	Sniff	Scan	Locomotion	Jump rate	Head-dip rate	Rearing
Still	1	−0.25	−0.01	−0.42	0.11	−0.15	−0.38
Sniff	−0.25	1	−0.43	−0.09	−0.45	0.31	−0.01
Scan	−0.01	−0.43	1	−0.48	0.08	−0.27	−0.05
Locomotion	−0.42	−0.09	−0.48	1	−0.21	0.18	0.08
Jump rate	0.11	−0.45	0.08	−0.21	1	−0.23	−0.01
Head-dip rate	−0.15	0.31	−0.27	0.18	−0.23	1	0.04
Rearing	−0.38	−0.01	−0.05	0.08	−0.01	0.04	1

We used the correlation matrices to calculate principal component scores from a principal component analysis (PCA). $N = 119$ observations from 62 individuals.

Table A4
Correlation matrices of banner-tailed kangaroo rat behaviour measured during a mirror image simulation (MIS) assay in New Mexico, U.S.A.

Behaviour	Time mirror	Duration forage	Front	Rock	Locomotion	Mirror rate	Seed	Forage rate
Time mirror	1	−0.08	0.47	−0.16	0.38	0.88	0.01	0.04
Duration forage	−0.08	1	0.64	−0.15	−0.38	−0.13	−0.92	0.85
Front	0.47	0.64	1	−0.25	−0.06	0.37	−0.63	0.59
Rock	−0.16	−0.15	−0.25	1	−0.1	−0.15	0.16	−0.09
Locomotion	0.38	−0.38	−0.06	−0.1	1	0.3	0.32	−0.31
Mirror rate	0.88	−0.13	0.37	−0.15	0.30	1	0.06	−0.03
Seed	0.01	−0.92	−0.63	0.16	0.32	0.06	1	−0.84
Forage rate	0.04	0.85	0.59	−0.09	−0.31	−0.03	−0.84	1

We used the correlation matrices to calculate principal component scores from a principal component analysis (PCA). $N = 119$ observations from 62 individuals.

Table A5
Principal component (PC) loadings, eigenvalues and variance explained from principal component analyses (PCAs) of banner-tailed kangaroo rat behaviour during a hole-board assay and a mirror simulation assay in New Mexico, U.S.A.

Data subset	Hole-board assay (HB)			Mirror image simulation assay (MIS)		
	Behavioural trait	PC loadings		Behavioural trait	PC loadings	
		HB1	HB2		MIS1	MIS2
Trial 1	Still	−0.22	**−0.70**	Time mirror	−0.19	**0.93**
	Sniff	**0.88**	0.07	Forage	**0.96**	−0.07
	Scan	**−0.51**	**−0.47**	Front	**0.73**	**0.49**
	Locomotion	0.19	**0.83**	Rock	−0.15	**−0.50**
	Jump rate	**−0.66**	−0.21	Locomotion	**−0.59**	0.27
	Head-dip rate	**0.80**	0.07	Mirror rate	−0.17	**0.91**
	Rearing	−0.01	**0.71**	Seed mass	**−0.95**	0.02
				Forage rate	**0.90**	0.03
	Eigenvalue	2.90	1.27	Eigenvalue	3.61	2.25
	Proportion of variance explained	0.31	0.28	Proportion of variance explained	0.45	0.28
Trial 2	Still	−0.09	**−0.89**	Time mirror	0.24	**0.93**
	Sniff	**−0.81**	0.05	Forage	**0.95**	−0.14
	Scan	**0.77**	−0.05	Front	**0.79**	**0.43**
	Locomotion	−0.22	**0.69**	Rock	−0.24	−0.04
	Jump rate	**0.57**	−0.08	Locomotion	−0.32	**0.59**
	Head-dip rate	−0.11	0.21	Mirror rate	0.09	**0.91**
	Rearing	0.42	**0.54**	Seed mass	**−0.94**	0.06
				Forage rate	**0.91**	−0.02
	Eigenvalue	1.82	1.62	Eigenvalue	3.51	2.21
	Proportion of variance explained	0.26	0.23	Proportion of variance explained	0.43	0.28
Grasslands	Still	−0.11	**−0.88**	Time mirror	0.22	**0.90**
	Sniff	**0.82**	−0.12	Forage	**0.96**	−0.06
	Scan	**−0.69**	−0.01	Front	**0.67**	**0.46**
	Locomotion	0.30	**0.76**	Rock	−0.11	**−0.57**
	Jump rate	**−0.61**	−0.11	Locomotion	−0.23	**0.70**
	Head-dip rate	**0.59**	0.14	Mirror rate	0.05	**0.84**
	Rearing	−0.19	**0.73**	Seed mass	**−0.96**	−0.02
				Forage rate	**0.93**	0.05
	Eigenvalue	2.21	1.72	Eigenvalue	3.49	2.31
	Proportion of variance explained	0.29	0.28	Proportion of variance explained	0.41	0.32
Restoration	Still	**−0.59**	0.11	Time mirror	−0.07	**0.97**
	Sniff	**0.83**	−0.07	Forage	**0.97**	−0.07
	Scan	−0.26	**0.81**	Front	**0.76**	**0.56**
	Locomotion	−0.04	**−0.91**	Rock	−0.27	0.00
	Jump rate	**−0.57**	0.14	Locomotion	**−0.57**	0.27
	Head-dip rate	**0.60**	−0.24	Mirror rate	−0.09	**0.95**
	Rearing	**0.43**	−0.17	Seed mass	**−0.95**	0.05
				Forage rate	**0.90**	−0.02
	Eigenvalue	2.27	1.32	Eigenvalue	3.64	2.25
	Proportion of variance explained	0.28	0.23	Proportion of variance explained	0.45	0.28

PCAs were conducted separately for trial and habitat type. Loadings in bold represent behaviours that were heavily loaded (>0.40) on the PC axis.

Table A6
Summary of coefficients (β), standard errors (SE) and *P* values for the fixed effect lunar illumination on repeatability (*R* and 90% confidence intervals (CI) or credible intervals (CRI)) of *D. spectabilis* behavioural traits and movement latency in New Mexico, U.S.A.

Response variable	*R*	90% CI	β (SE)	*P*
Exploration (HB PC1)	0.559	0.431–0.715	0.002 (0.032)	0.960
Activity (HB PC2)	0.369	0.190–0.554	0.022 (0.037)	0.552
Sociability (MIS PC1)	0.440	0.268–0.630	0.011 (0.034)	0.740
Aggression (MIS PC2)	0.205	0.029–0.439	0.111 (0.039)	0.005
Response variable	***R***	**90% CRI**	**β (90% CRI)**	**pMCMC**
Boldness (MIS latency)	0.378	0.172–0.590	0.024 (−0.166, 0.218)	0.788
Movement	0.492	0.306–0.676	0.118 (−0.028, 0.245)	0.100

HB: hole-board assay; PC: principal component; MIS: mirror image simulation assay. Lunar illumination was logit-transformed and had no effect on repeatability values (see Table 2 in main text for comparisons). Movement and emergence latencies were modelled with Bayesian mixed-effects models using censored Poisson errors.

Table A7
Results from mixed-effects models estimating sources of variation in banner-tailed kangaroo rat behaviour in New Mexico, U.S.A.

	β (90% CI)	σ^2 (90% CI)	*R* (90% CI)	*P*
Exploration (HB PC1)				
Fixed effects				
Intercept	−0.230 (−0.521, 0.061)			0.204
Sex (M)	0.492 (0.131, 0.852)			0.031
Visit (trial 2)	−0.122 (−0.316, 0.075)			0.309
Mass	−0.232 (−0.411, −0.052)			0.041
Random effects				
Among-individual		0.528 (0.32, 0.81)		
Within-individual		0.410 (0.28, 0.53)		
Repeatability			0.565 (0.414, 0.710)	<0.001
Activity (HB PC2)				
Fixed effects				
Intercept	0.381 (0.010, 0.663)			0.031
Sex (M)	−0.287 (−0.625, 0.051)			0.173
Visit (trial 2)	−0.439 (−0.672, −0.205)			0.003
Mass	−0.168 (−0.337, 0.001)			0.112
Random effects				
Among-individual		0.342 (0.148, 0.596)		
Within-individual		0.587 (0.408, 0.754)		
Repeatability			0.368 (0.180, 0.571)	0.003
Sociability (MIS PC1)				
Fixed effects				
Intercept	−0.084 (−0.356, 0.189)			0.621
Sex (M)	−0.369 (−0.704, −0.035)			0.078
Visit (trial 2)	−0.010 (−0.308, 0.116)			0.452
Mass	0.171 (0.003, 0.339)			0.104
Random effects				
Among-individual		0.385 (0.207, 0.618)		
Within-individual		0.483 (0.331, 0.622)		
Repeatability			0.443 (0.271, 0.623)	<0.001
Aggression (MIS PC2)				
Fixed effects				
Intercept	0.358 (0.087, 0.626)			0.035
Sex (M)	−0.113 (−0.430, 0.205)			0.567
Visit (trial 2)	−0.596 (−0.856, −0.336)			<0.001
Mass	−0.067 (−0.228, 0.094)			0.5
Random effects				
Among-individual		0.194 (0.015, 0.435)		
Within-individual		0.733 (0.509, 0.919)		
Repeatability			0.209 (0.019, 0.443)	0.067
	β (90% CRI)	**σ^2 (90% CRI)**	***R* (90% CRI)**	**pMCMC**
Hole-board emergence				
Fixed effects				
Intercept	2.330 (1.806, 2.790)			<0.001
Sex (M)	−0.216 (−0.813, 0.312)			0.514
Visit (trial 2)	−0.145 (−0.623, 0.394)			0.64
Mass	−0.138 (−0.420, 0.140)			0.419
Random effects				
Among-individual		0.303 (0.001, 0.738)		
Within-individual		2.571 (1.865, 3.343)		
Repeatability			0.103 (0.001, 0.246)	
Boldness (MIS emergence)				
Fixed effects				
Intercept	3.686 (2.896, 4.405)			<0.001

(*continued on next page*)

Table A7 (*continued*)

	β (90% CI)	σ^2 (90% CI)	*R* (90% CI)	*P*
Sex (M)	−0.439 (−1.318, 0.461)			0.43
Visit (trial 2)	−1.003 (−1.640, −0.390)			0.012
Mass	−0.471 (−0.909, 0.021)			0.091
Random effects				
Among-individual		2.330 (0.613, 3.965)		
Within-individual		3.685 (2.262, 4.946)		
Repeatability			0.381 (0.160, 0.593)	
Movement latency				
Fixed effects				
Intercept	4.314 (3.731, 4.880)			<0.001
Sex (M)	−0.167 (−0.877, 0.533)			0.703
Visit (trial 2)	−1.586 (−2.036, −1.134)			<0.001
Mass	0.014 (−0.334, 0.380)			0.954
Wind	−0.615 (−0.888, −0.354)			<0.001
Random effects				
Among-individual		1.707 (0.666, 2.711)		
Within-individual		1.861 (1.183, 2.519)		
Repeatability			0.470 (0.273, 0.669)	

HB: hole-board assay; PC: principal component; MIS: mirror image simulation assay. Estimates were derived separately for each behaviour. Individual identity was included as a random effect. We provide point estimates for each fixed (β) and random (σ^2) effect, as well as adjusted repeatabilities (*R*). We report 90% confidence intervals (CI) or credible intervals (CRI) for all parameters. $N = 119$ observations from 62 individuals. *Note*: Movement and emergence latencies were modelled with Bayesian mixed-effects models using censored Poisson errors (see Methods).

Table A8
Results from univariate mixed-effects models investigating two-way interactions between personality traits and shrub treatment for banner-tailed kangaroo rats in New Mexico, U.S.A.

Fixed effects	Exploration	Activity	Sociability	Aggression	Boldness
	β (90% CRI)	β (90% CRI)	β (90% CRI)	β (90% CRI)	β (90% CRI)
Intercept	4.229 (3.446, 4.984)	4.309 (3.570, 5.056)	4.368 (3.601, 5.227)	4.443 (3.660, 5.252)	3.620 (2.766, 4.415)
Sex (M)	−0.269 (−1.046, 0.405)	−0.183 (−0.870, 0.465)	−0.132 (−0.845, 0.659)	−0.161 (−0.900, 0.565)	0.025 (−0.672, 0.716)
Personality trait	−0.101 (−0.510, 0.281)	−0.025 (−0.369, 0.317)	0.247 (−0.195, 0.682)	−0.076 (−0.430, 0.269)	0.006 (0.003, 0.009)
Treatment (shrub)	0.054 (−0.395, 0.502)	0.051 (−0.400, 0.514)	−0.243 (−0.713, 0.210)	−0.040 (−0.495, 0.269)	0.194 (−0.375, 0.750)
Visit (trial 2)	−1.423 (−1.883, −0.927)	−1.721 (−2.243, −1.218)	−1.667 (−2.130, −1.203)	−1.814 (−2.343, −1.301)	−1.443 (−1.920, −0.981)
Mass	0.068 (−0.275, 0.416)	−0.047 (−0.355, 0.306)	−0.015 (−0.367, 0.335)	−0.013 (−0.388, 0.327)	0.084 (−0.222, 0.455)
Wind	−0.658 (−0.930, −0.378)	−0.625 (−0.892, −0.323)	−0.609 (−0.874, −0.326)	−0.576 (−0.848, −0.288)	−0.539 (−0.805, −0.252)
Habitat (restoration)	0.076 (−0.611, 0.803)	0.097 (−0.597, 0.796)	0.054 (−0.680, 0.804)	0.002 (−0.757, 0.717)	0.084 (−0.679, 0.738)
Interaction term	0.603 (0.095, 1.076)	−0.674 (−1.214, −0.150)	−0.662 (−1.185, −0.135)	−0.334 (−0.904, 0.222)	−0.002 (−0.007, 0.002)
Random effects	**σ^2 (90% CRI)**	**σ^2 (90% CRI)**	**σ^2 (90% CRI)**	**σ^2 (90% CRI)**	**σ^2 (90% CRI)**
Among-individual	1.564 (0.613, 2.613)	1.205 (0.000, 2.021)	1.886 (0.815, 2.900)	1.718 (0.680, 2.758)	1.460 (0.436, 2.433)
Residual within-individual	1.896 (1.177, 2.621)	2.104 (1.277, 2.911)	1.824 (1.167, 2.503)	1.968 (1.213, 2.657)	1.888 (1.167, 2.584)
Movement repeatability	***R* (90% CRI)**	***R* (90% CRI)**	***R* (90% CRI)**	***R* (90% CRI)**	***R* (90% CRI)**
	0.445 (0.222, 0.646)	0.356 (0.114, 0.617)	0.501 (0.329, 0.709)	0.458 (0.273, 0.673)	0.427 (0.198, 0.645)

The fixed effect 'personality trait' represents the behaviour labelled in each column, and the fixed effect 'interaction term' represents the two-way interaction between each personality trait and shrub treatment. We provide point estimates for each fixed (β) and random (σ^2) effect, as well as adjusted repeatability (*R*) for movement latency. We report 90% credible intervals (CRI) for all parameters. $N = 119$ observations from 62 individuals. Models supported a two-way interaction between exploration, activity and sociability and shrub treatment.

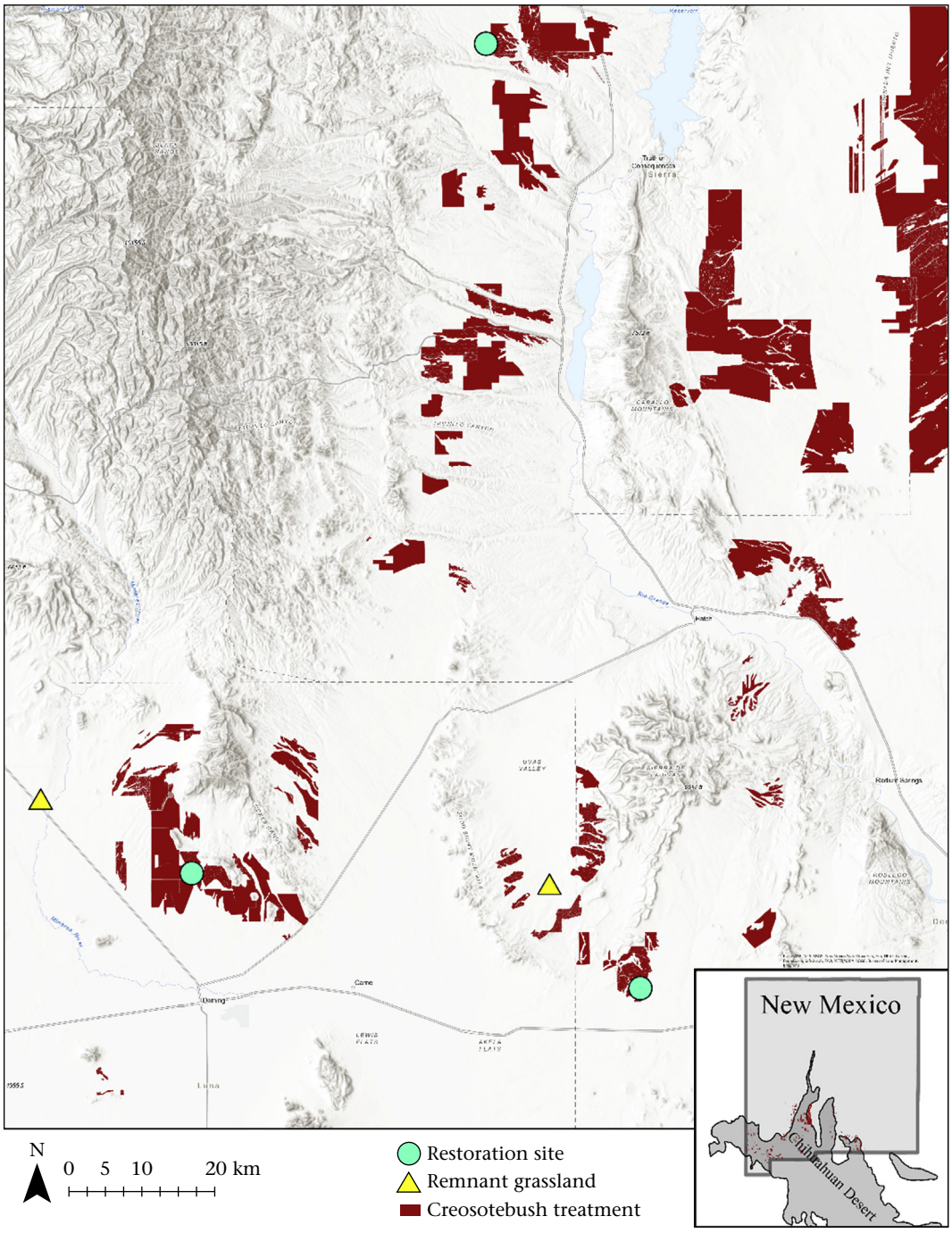

Figure A1. Map of study region in southwestern New Mexico, U.S.A. Circles represent restoration sites that were treated for shrub removal in 2009–2010. Triangles represent remnant, unencroached grasslands. Red polygons signify areas treated for creosotebush removal by the U.S. Bureau of Land Management since 1981.

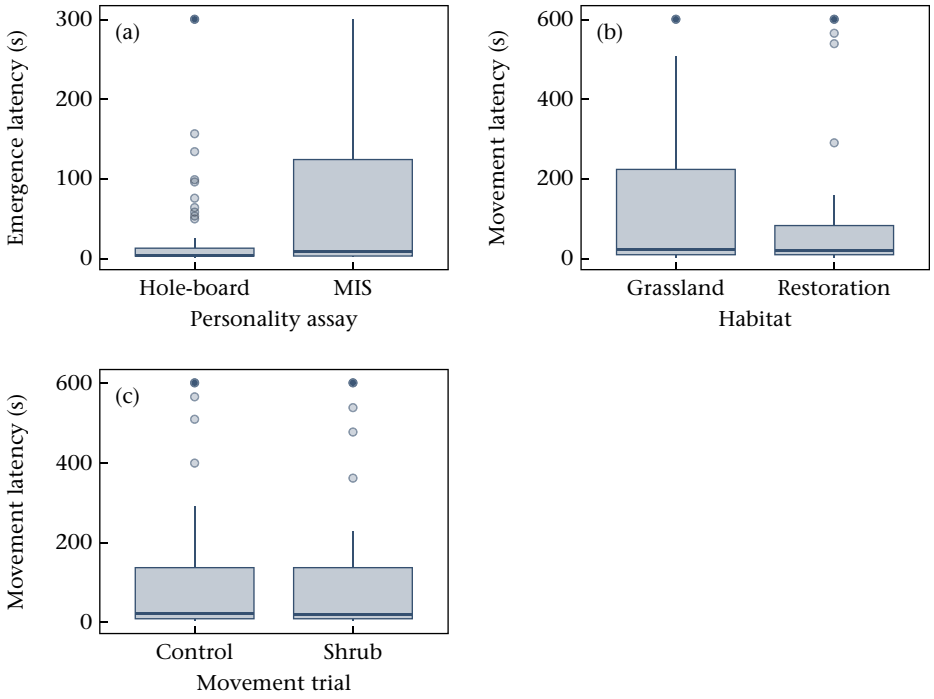

Figure A2. Box plots for (a) emergence latencies for the hole-board and mirror image simulation (MIS) assays, (b) movement latencies for restoration and remnant habitats and (c) movement latencies for control and shrub treatment trials. Measurements collected from 62 banner-tailed kangaroo rats in New Mexico, U.S.A. Box plots represent the median and 25th and 75th percentiles; whiskers represent the 10th and 90th percentiles; circles are outliers.

Figure A3. Artificial shrub treatment applied to banner-tailed kangaroo rat movement trials in New Mexico, U.S.A. Shrubs were spaced 1.5 m from the release box and formed a circular perimeter 3 m in diameter. Both the control (8 wood dowels; not shown) and the shrub treatment were placed 6 m from the home mound of an individual *D. spectabilis*.