



RESEARCH ARTICLE

Personality, spatiotemporal ecological variation and resident/explorer movement syndromes in the sleepy lizard

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Abstract

1. Individual variation in movement is profoundly important for fitness and offers key insights into the spatial and temporal dynamics of populations and communities. Nonetheless, individual variation in fine-scale movement behaviours is rarely examined even though animal tracking devices offer the long-term, high-resolution, repeatable data in natural conditions that are ideal for studying this variation. Furthermore, of the few studies that consider individual variation in movement, even fewer also consider the internal traits and environmental factors that drive movement behaviour which are necessary for contextualising individual differences in movement patterns.
2. In this study, we GPS tracked a free-ranging population of sleepy lizards *Tiliqua rugosa*, each Austral spring over 5 years to examine consistent among-individual variation in movement patterns, as well as how these differences were mediated by key internal and ecological factors.
3. We found that individuals consistently differed in a suite of weekly movement traits, and that these traits strongly covaried among-individuals, forming movement syndromes. Lizards fell on a primary movement continuum, from 'residents' that spent extended periods of time residing within smaller core areas of their home range, to 'explorers' that moved greater distances and explored vaster areas of the environment.
4. Importantly, we also found that these consistent differences in lizard movement were related to two ecologically important animal personality traits (boldness and aggression), their sex, key features of the environment (including food availability, and a key water resource), habitat type and seasonal variation (cool/moist vs. hot/drier) in environmental conditions.
5. Broadly, these movement specialisations likely reflect variation in life-history tactics including foraging and mating tactics that ultimately underlie key differences in space use. Such information can be used to connect phenotypic population structure to key ecological and evolutionary processes, for example social networks and disease-transmission pathways, further highlighting the value of examining individual variation in movement behaviour.

KEYWORDS

animal personality, animal telemetry, behavioural syndrome, behavioural type, GPS tracking, movement ecology, spatiotemporal variation

1 | INTRODUCTION

Individuals exhibit remarkable variation in their movement which is fundamentally important for ecology and evolution (Nathan et al., 2008; Shaw, 2020). Diverse movement patterns emerge in response to environmental and social conditions and likely reflect individual internal states and tactics for maximising fitness, as well as motion and navigation capacity (Hawkes, 2009; Nathan et al., 2008). Individuals that move differently may utilise different habitats, forage in alternative food patches, and have different social and ecological interactions. Hence, individual variation in movement underlies key differences in space use and shapes the distribution of phenotypes across a landscape with wide-ranging implications for predator-prey dynamics (DeCesare et al., 2014; Mumma et al., 2017), social networks (Kurvers et al., 2014) and parasite-disease transmission (Dougherty et al., 2018; Lloyd-Smith et al., 2005). Quantifying individual variation in movement can thus offer important insights into the spatial-temporal dynamics and ecological breadth of populations and communities (Bastille-Rousseau & Wittemyer, 2019; Spiegel et al., 2017).

Consistent individual variation in movement has primarily been studied in the context of broad-scale movement patterns or events such as dispersal (Cote et al., 2011; Michelangeli et al., 2017), foraging tactics (Abrahms et al., 2018; Cecere et al., 2020; Patrick et al., 2014) or the timing and frequency of migration (Bunnfeld et al., 2011; Eggeman et al., 2016; Lehnert et al., 2018). In contrast, individual variation in fine-scale or daily movement behaviours has until very recently been largely ignored (but see: Hertel et al., 2019, 2020; Shaw, 2020; Webber et al., 2020). This is somewhat surprising given that wildlife tracking devices offer ecologists the opportunity to collect long-term, high-resolution, repeatable data in natural settings which are ideal for studying individual variation in movement, but also variation in animal behaviours more generally (Hertel et al., 2020). Indeed, distinguishing between fine-scale movement patterns among individuals of the same species can be inherently difficult, particularly for species that are relatively sedentary (Abrahms et al., 2017; Nathan et al., 2008). Furthermore, heterogeneity in intra-individual movements, reflecting diverse states and needs (e.g. foraging versus escaping; Fryxell et al., 2008), adds to the challenge of comparison among individuals.

In a recent study, Abrahms et al. (2017) derived a suite of simple movement metrics from a variety of species trajectories and found movement syndromes—correlated movement metrics at the among-species level—that consistently recurred across disparate taxa and ecotypes (i.e. aerial, marine and terrestrial), from range-resident movement such as territoriality and central place foraging, to nomadism and migration (Abrahms et al., 2017). Conceptually, as long

as the data are detailed enough, a similar approach can be used at the within-population level whereby movement and spatial descriptors are derived from individual movement trajectories to detect among-individual (co)variation in fine-scale movement traits that provide insight into broader individual movement patterns (Hertel et al., 2020). Instead of classifying individuals into distinct movement modes (e.g. range resident vs. migratory) as is common in wildlife and movement ecology, this approach places individuals along a continuum(s) of movement behaviour.

Beyond differences in movement per se, individuals can also consistently differ in their average expression across a range of behavioural traits. Such persistent among-individual differences in mean-level behaviour (often termed animal personality; Réale et al., ; Sih et al., 2004) can emerge both due to differences in internal state (stress, sex) or environmental factors, but also due to inherent variation in genetic architecture or developmental history (Niemelä & Dingemanse, 2018; Royauté et al., 2020; Sih et al., 2015). Animal personality can influence important ecological processes including range expansion (Duckworth & Badyaev, 2007), predator-prey dynamics (McGhee et al., 2013) and responses to human-induced environmental change (Villegas-Ríos et al., 2018). Animal tracking data combined with environmental information have recently been highlighted as a useful tool for measuring animal personality in the wild (Hertel et al., 2020). This is because movement often underpins commonly assayed personality traits, such as activity and exploration (Hertel et al., 2019; Villegas-Rios et al., 2017), and also individual variation in habitat and resource selection (Bastille-Rousseau & Wittemyer, 2019; Leclerc et al., 2016; Webber et al., 2020). However, not all commonly assayed personality traits (e.g. aggression and boldness) are strongly dependent on movement, and connections between personality and movement are not always clear because studies have typically sampled these traits non-independently (Spiegel et al., 2017).

Because movement represents the outcome of behavioural decisions based on local ecological and social conditions as well as the individual's needs, it provides an essential link between personality, the environment and the spatial and social structure of a population. It is therefore essential to also consider the internal traits and environmental factors (e.g. proximity to resources) that affect the movement of individuals in order to contextualise individual movement tactics (Morales & Ellner, 2002; Nathan et al., 2008; Shaw, 2020). Furthermore, a key challenge is to disentangle individual variation in movement that arises as result of true identity effects (e.g. genes, personality) versus those that emerge as result of spatial heterogeneity (e.g. personality-dependent habitat choice; Hertel et al., 2020). Doing so at least requires tracking multiple individuals through extended periods of time (i.e. throughout their entire active season

and/or across multiple years) over large areas with spatial heterogeneity in order to evaluate the long-term consistency of individual movement. Such datasets are challenging to obtain, but necessary for discriminating between the role of environmental heterogeneity and internal factors in the emergence of individual variation in movement patterns (Spiegel et al., 2017).

In this study, we tracked free-ranging sleepy lizards *Tiliqua rugosa* over a 5-year period to investigate consistent, long-term individual differences in movement and how these differences are linked to internal and environmental factors. Specifically, we have a unique and comprehensive dataset in which multiple individuals were tracked for almost their entire 4-month long activity period across several years (for some individuals we have 5 years of tracking data). Using individual trajectories for every year, we derive six movement traits on a weekly basis and tested for (a) individual consistency in each movement trait and (b) the presence of movement syndromes. Regarding movement syndromes, among-individual covariation in movement traits may provide a statistical signature of broader movement patterns (sensu Abrahms et al., 2017; Hertel et al., 2020). Beyond describing consistency and syndromes, we also explored how individual movement was linked to both environmental (food and water resources, habitat quality) and internal (sex, size and personality) factors. While some prior studies have linked personality to individual variation in space use and movement (e.g. Harrison et al., 2015; Hertel et al., 2019; Leclerc et al., 2016), they have often derived these personality metrics non-independently from the individual's movement trajectory (Spiegel et al., 2017). In contrast, in this study we assayed two common personality traits (boldness and aggression) in designated tests, independently from our movement data. Finally, because ecological conditions at our study site become drier and more resource depleted as the lizard activity season progresses, we also examined population-level seasonal shifts in movement behaviour. Given previous evidence on personality and seasonally dependent space use in our system (Spiegel et al., 2015), we predicted that (a) lizards would exhibit consistent individual differences in movement traits and that these differences would remain across years, and that (b) these consistent individual differences in movement traits would covary to form movement syndromes that characterise lizard movement along a primary continuum ranging from residency behaviour (e.g. high site fidelity, area-restricted movement) to explorer behaviour (e.g. explorative movement with relatively low site fidelity). We also predicted that (c) individual movement would be linked to key differences in habitat use, sex and personality, (d) but that these effects would be dependent on season.

2 | MATERIALS AND METHODS

2.1 | Study system

The sleepy lizard is a common skink species to South Australia. They are large bodied (adults are 400–950 g, snout-vent length

25–35 cm), long lived (up to ~48 years) and slow moving (Dubas & Bull, 1991). They have been found to maintain relatively stable and consistent home ranges (HRs) over multiple years (our tracking covering up to 8 years; mean 95% HR area in hectares [95% CI]; females: 3.53 [3.07, 4.01] and males: 4.91 [4.42, 5.43]; E. Payne, O. Spiegel, D. L. Sinn, S. T. Leu, M. Gardner, S. S. Godfrey, C. Wohlfeil, & A. Siha, unpublished). We studied a population within a ~ 1.2km² field site near Bunday Bore Station (33.888240 S, 139.310718 E). Our field site has semi-arid Mediterranean climate and is primarily chenopod shrubland dominated by bluebush *Maireana sedifolia* and some black oak *Casuarina cristata*. Various annual plants, including the lizards' preferred food item, the invasive Ward's weed *Carrichtera annua* (Dubas & Bull, 1991), tend to grow around and under these shrubs. The field site has a seasonal dam that retains water and soil moisture for longer than other parts of the area. Lizards at this field site are primarily active from September (early spring) to December (early summer; Kerr & Bull, 2006). The beginning of the lizard's activity period is characterised by moderate temperatures and higher relative abundance of food and water. Early spring is also the breeding season in which lizards form monogamous pairs for up to 10 weeks before they mate (Bull, 1988; Leu et al., 2015). During this time males perform more scent marking and competition is higher, potentially leading to sex differences in movement behaviour early in the season (Leu et al., 2011, 2016). On the other hand, the late season is hotter and drier, and food and water resources become increasingly scarce and patchier in distribution.

2.2 | GPS data collection

Lizards at our field site have been monitored since 2006, but here we focus on data collected from 2013 to 2017. At the beginning of each activity period (September), adult lizards were searched for visually and caught by hand, identified individually by toe clipping, and radio transmitters and GPS units (Technosmart, Gypsy 4) were attached to the lizard's tail with surgical tape (Leukoplast tape BSN medical GmbH). This apparatus constituted ~5.2% of an average lizard's body weight and has never been observed to have adverse effects on lizard behaviour, movement or body condition (Godfrey et al., 2012, 2013; Leu et al., 2010). All devices were removed at the conclusion of each field season (late December). During the 2013–2014 collecting seasons, GPS units (horizontal accuracy \pm 6 m; Leu et al., 2010) took one GPS fix per 10 min all day, while in 2015 through 2017, GPS units took one fix per 2 min during the day. GPS data from 2013 and 2014 were filtered to remove points taken at night (i.e. we only considered GPS points taken between 06:00 and 20:00). GPS errors were removed according to fix accuracy (e.g. horizontal dilution greater than three), using an algorithm adapted from Bjørneraas et al. (2010), as well as via manual inspection of GPS tracks for clear errors. For analysis, we thinned all GPS data to follow a 20 min resolution to reduce autocorrelation between fixes and reduce the influence of any undetected GPS error on our movement metric calculations.

2.3 | Summary of the dataset and the movement metric calculations

From the movement trajectories, we calculated six movement metrics.

1. *Daily distance travelled*—Distance travelled (m) was calculated as the sum of Euclidean distances between all consecutive GPS locations within a day. It is a metric that is commonly used as an estimate of general activity with longer distances travelled indicating more active individuals (e.g. Harrison et al., 2019; Hertel et al., 2019).
2. *Max daily displacement*—Maximum daily displacement (m) was calculated as the maximum Euclidean displacement from the starting point in a daily trajectory to the furthest point within that daily trajectory. We are using the maximum displacement, rather than the mean, to identify daily exploratory movement, with the expectation that exploratory individuals have higher maximum values (e.g. Hertel et al., 2019; O'Farrell et al., 2019; Turchin, 1998).
3. *Straightness index*—Straightness index measures the degree to which a movement trajectory deviates from a straight line and thus offers insight into movement directionality or path tortuosity (Benhamou, 2004; Seidel et al., 2018). Straightness index was calculated following Spiegel et al. (2013) as the daily maximum displacement divided by the total daily distance travelled to reach that maximum displacement. Higher values indicate a directional and informed movement.
4. *Residence time*—Residence time is typically used to identify frequently used or revisited areas and offers insight into space use intensity, and more broadly, range residency (Barraquand & Benhamou, 2008). Residence time is measured as the amount of time an animal spends inside a circle of a given radius centred around each location without leaving that radius for greater than a specified cut-off time (i.e. duration of time within a given area Van Moorter et al., 2016). To calculate residence time, we adapted code from Abrahms et al. (2017), and followed procedures outlined in Van Moorter et al. (2016) and Bracis et al. (2018). Briefly, we first tested the sensitivity of our data to radii of different sizes (mean step length (SL), $2 \times$ SL, $4 \times$ SL) and cut-off times (1, 3 and 8 hr). Based on the sensitivity analysis (Appendix Table A3), and our understanding of the study system, we determined that a 67m radius ($4 \times$ SL) and a 3-hr cut-off time was appropriate for our calculations because (a) sleepy lizards are slow moving (i.e. on average move 16.5 m every 20 min) and thus large cut-off times would not capture revisits to given areas (i.e. lizards would rarely leave the radius), (b) we wanted to minimise the influence of GPS error and thus smaller radii were excluded and (c) we desired a cut-off time and radius that would maximise possible space use variation among individuals (see Table A3 for results of sensitivity analysis). In this study system, individuals with stronger site attachment are expected to have longer residence times.
5. *Home range size and home range use ratio*—As a proxy for home range size we calculated an individual's weekly 95% minimum

convex polygon (MCP). We then divided an individual's weekly 95% MCP by its total yearly (i.e. entire active season) 95% MCP to get an individual's weekly home range use ratio. We included this latter measurement to help disentangle activity that occurred outside of consistently used areas from area-restricted movement within an individual's weekly 95% MCP (Webber et al., 2020). Higher home range use ratio values suggest that an individual routinely explores a larger portion of its yearly HR.

These metrics are commonly used to represent a range of possible movement and spatial patterns that we predicted might vary among lizards. These primarily include resident or restricted area use behaviour (e.g. territoriality or central place foraging; Abrahms et al., 2017) to explorative movement with relatively low site fidelity (e.g. nomadic or explorer like behaviour; O'Farrell et al., 2019; Teitelbaum & Mueller, 2019). Our chosen metrics also span across spatial-temporal scales (Benhamou, 2014). For example, most of our metrics were calculated at the daily scale, but home range use ratio had to be measured at the weekly scale due to data requirements for calculating home range size. Thus, to enable comparison between all metrics, we averaged the daily scale metrics within weeks. To eliminate correlation between the number of weekly GPS points and the corresponding movement metric value, we only included weeks in our analysis with at least 120 GPS locations (which represents ~ 3.5 days of GPS data, Table A1 in Appendix). Overall, we obtained GPS data from 128 lizards and a total of 569,341 GPS fixes (after sub-sampling that data to 20 min intervals). From these data, we obtained on average 17 ± 11.6 (mean \pm SD; range 2–45) weekly replicates for each movement metric over an average of 2.35 ± 1.4 (range 1–5) years per lizard. Each weekly replicate contained on average 189.64 ± 30.00 GPS points (range 120–294; see Table A2 in Appendix).

2.4 | Measurement of internal factors

During each active season (year), lizards were relocated approximately every 2 weeks via radio telemetry and weighed to the nearest 1 g. Each lizard's sex was also checked once per season based on its morphology and via eversion of hemipenes in males. During the 2015–2017 active seasons, lizard aggression and boldness behaviour was assayed two to three times per year (see Table A4), with each trial occurring at least 2 weeks apart. Details of these assays have previously been published (e.g. Spiegel et al., 2015 and earlier references therein), so we only briefly describe them here. To assess a lizard's boldness, we measured a lizard's response to a preferred food item (a piece of banana) in the presence of a potential threat (a looming observer). A lizard's boldness was ranked based on their response, from quickly approaching the food item and the observer (high boldness rank), to showing very little response (intermediate boldness), to quickly fleeing from the observer into refuge (shy). Boldness was ranked on a 1–10 scale in 2015 and on a 1–7 scale in 2016–2017, but higher ranks always referred to bolder animals and thus ranks were

standardised within year (by subtracting the mean and dividing by the standard deviation). To assess a lizard's aggression, we ranked a lizard's response to a simulated capture attempt by an observer which involved the observer's hand coming to within ~10 cm of the lizard's head. Responses were ranked on a scale of 1–11, from fleeing the observer into refuge (passive = 1) to attempting to bite the observer (high aggression = 11). Both aggression and boldness have shown to be repeatable over an 8-year period ($r \pm SE = 0.43 \pm 0.05$ and $r = 0.27 \pm 0.04$ respectively), and are only weakly positively correlated suggesting independence between the traits (correlation coefficient $\pm 95\%$ CI = 0.15 [–0.07, 0.39]; Payne et al., 2021). In the present study, we used the average personality score for each individual within each year in our analysis (see Figure A1).

2.5 | Measurement of environmental variables

Animal movement clearly depends on the local environment. Thus, to test whether observed effects of the internal factors on movement remain while accounting for these external environmental effects, we also measured a range of ecological variables. Some of these were extracted from the movement trajectories, and consequently are not entirely independent of our movement currencies, while others are from the habitat surveys of our field site. Specifically, from the movement trajectories within each year, we calculated an individual's mean weekly distance from the dam (DamDist) and the number of unique visits to the dam (i.e. DamVisits). A unique visit to the dam involved a lizard entering and then leaving a 15 m radius around the dam. The dam is the only reliable water resource at our field site, and lizards are often observed in this area, but we also know that approximately only about 50% of our study population access the dam within a given year (data not presented here). We also calculated a lizard 95% weekly HR overlap with 'forested' habitat (ForestHR). Forested areas tend to contain denser vegetation and refuge for lizards and may be preferred by lizards seeking shelter. Forested habitats were defined by drawing polygons around forested regions based on satellite images from Google Earth. During 2015–2017, we also conducted habitat surveys of food quality in 123 quadrats distributed in a grid over the field site (similar methods in Spiegel et al., 2015). Within each quadrat, we surveyed a 40m radius around a central point, and ranked the availability of moist food (i.e. primarily Ward's weed) on a 1–5 scale. Since lizard HRs could include multiple quadrats, we averaged the quadrat food scores within a lizard's 95% HR, weighted by the usage of that quadrat (relative to usage of all quadrats within the focal lizard's 95% HR), within each week, (FoodQualityHR). Correlations between environmental variables are presented in Table A5.

2.6 | Statistical analysis

Analysis was conducted in R version 3.6.2 (R Core Team, 2021). We used the Bayesian package *BRMS* (Bürkner, 2017) an interface to

Stan (Stan Development Team 2015a, 2015b) for generalised linear mixed models. Daily distance travelled, daily max displacement and straightness index were modelled with a Gaussian error distribution. Residence time, home range use ratio and home range size were modelled with a gamma distribution and log-link function. We used relatively uninformative priors, 4 chains, and ran models for 5,000 iterations with a 1000 warm-up. Models were checked for adequate mixing via trace plots and posterior-predictive checks, and all models converged with low among-chain variability (Rhat = 1, see Bürkner, 2017). We report posterior means for all estimated parameters with 95% credibility intervals.

2.6.1 | Movement repeatability

We used univariate mixed-effects models to calculate individual repeatability of each movement metric using all available data (2013–2017). First, we calculated an unadjusted repeatability using a model with only lizard identity fitted as the individual random intercept. Second, we calculated an adjusted repeatability estimate using a model that controlled for year, week, sex, body size (i.e. within-year average SVL) and three ecological factors (DamDist, DamVisits and ForestHR) which were measured across all years. We also included a second-order polynomial term for week to take into account that environmental conditions should be more similar in weeks that are closer together in time. Lizard identity was also fitted as an individual random intercept in these models. The personality and food quality variables were not included because these were obtained in only 2015–2017. Hence, adjusted repeatability estimates represent the amount of total phenotypic variation explained by among-individual differences after controlling for our specified predictor effects (Nakagawa & Schielzeth, 2010). We estimated repeatability (R) for Gaussian distributed variables following the formula:

$$R = \frac{Va}{(Va + Vw)},$$

where Va is the among-individual variance, and Vw is the within-individual (or residual) variance. For gamma distributed response variables, repeatability was estimated following the formula recommended by Nakagawa et al., 2017:

$$R = \frac{Va}{Va + \ln\left(1 + \frac{1}{v}\right)},$$

Where Va is the among-individual variance, and v is the shape parameter of the gamma distribution.

2.6.2 | Movement syndromes

To explore whether movement metrics are correlated between individuals and identify movement syndromes, we extracted the

posterior mean pairwise among-individual random intercept correlations and covariances of all movement metrics from a multivariate mixed-effects model. This model contained all measured movement metrics as response variables. The fixed and random effects structure of this model is outlined below. We then extracted the among-individual covariance matrix from this multivariate model and performed an eigen decomposition analysis on the matrix. This procedure is similar to a principal component analysis (PCA), but instead of using the total phenotypic (co)variation as is common for PCA, we isolate the among-individual covariance matrix to identify major axes (i.e. eigenvectors or principal components) that explain the majority of among-individual variation in our measured traits (see Houslay et al., 2018 for further details on this procedure). This approach is also preferable to a PCA, because unlike a PCA, it considers the hierarchical structure (and repeated measures) of the data.

2.6.3 | Internal and environmental effects on movement

To determine the effect of internal and environmental factors on each movement metric we included the following predictors in our multivariate model: year, four lizard internal factors (sex, mass, aggression and boldness) and four ecological factors (DamDist, DamVisit, ForestHR and FoodQualityHR). We also included an aggression * boldness interaction term and DamDist * DamVisit interaction term; this latter interaction term accounts for the probability that lizards which occupy areas close to the dam will also more likely visit the dam. All continuous predictors and Gaussian distributed response variables were scaled (mean = 0, SD = 1) prior to analysis to facilitate model fitting. We also included season (early: weeks 1–7 vs. late: weeks 8–14) in our model, and its interaction with all predictor terms (except year, DamDist and any two-way interactions). Season was included as a factor due to evident seasonal differences at our study site and their effect on both lizard movement and behaviours. Lizard ID was included as a random intercept. We compared models with and without the interaction terms using the widely applicable information criterion (WAIC; a generalisation of AIC for model comparison within a Bayesian framework whereby models with smaller WAIC values are preferred, Vehtari et al., 2017) to remove any negligible interaction terms from the final model. Because aggression, boldness and FoodQualityHR were only assessed in a subset of years, we only included these terms to model the 2015 through 2017 data. However, we also modelled all available data (i.e. 2013–2017) absent these predictors for comparison.

3 | RESULTS

3.1 | Movement repeatability

Our results show clearly that individuals differed consistently in their movement. Adjusted repeatability for our movement metrics ranged

TABLE 1 Unadjusted and adjusted repeatability (R) estimates with 95% credible intervals

Movement metric	Unadjusted R	Adjusted R
Daily distance travelled	0.209 (0.16–0.27)	0.179 (0.13–0.24)
Max daily displacement	0.372 (0.30–0.45)	0.348 (0.28–0.42)
Residence time	0.405 (0.34–0.48)	0.404 (0.33–0.48)
Straightness index	0.072 (0.04–0.11)	0.040 (0.02–0.07)
Home range use ratio	0.549 (0.48–0.62)	0.639 (0.57–0.70)
Home range size	0.495 (0.42–0.57)	0.596 (0.53–0.67)

from 0.04 to 0.64 (Table 1). Most movement metrics had moderate to high repeatability ($R = 0.20$ – 0.64). Only one metric, straightness index, exhibited low repeatability ($R = 0.04$). Hence, for all but one of the movement metrics, the percentage of movement variation explained by consistent among-individual differences was comparable to typical personality metrics (Bell et al., 2009).

3.2 | Movement syndromes

Adjusted repeatability, correlation and covariance estimates from our subset multivariate model (Table A6) were qualitatively similar to estimates from the top multivariate model of the full dataset (Table A7). We only present the results from the former here. We detected pairwise correlations and covariances between most of our movement metrics.

Results from our eigen decomposition analysis found two eigenvectors that jointly explained 89% of the among-individual variation in movement (see Figure 1). Eigenvector 1 explained 72% (credible interval: 65%–78%) with daily distance travelled, daily max displacement, home range use ratio, straightness index and home range size loading significantly in the same direction, and residence time loading heavily in the other direction. Thus, this first eigenvector corroborates strongly with the pairwise movement correlations and covariances. These results provide strong evidence that sleepy lizard movements fall on a primary movement continuum, ranging from individuals that are generally more active, have larger HRs and explore larger areas of their HR (henceforth 'explorers'), to individuals that restrict their movement to core areas of their HR (henceforth 'residents'; Figure 1). Furthermore, eigenvector 2 explained 17% (12%–23%) with residence time and home range use ratio loading heavily in one direction, and daily distance travelled, daily max displacement and home range size in the other. This second axis appears to characterise small HR residency. Lizards that have smaller HRs can cover a larger proportion of their HR without leaving central areas (i.e. thus accruing large residence times) or travelling large distances.

3.3 | Internal and environmental effects on movement

All movement metrics depended on internal and ecological factors, the effects of which varied between seasons (Table A8). However,

FIGURE 1 Posterior mean trait loading weights of movement metrics onto two eigenvectors of the between-individual covariance matrix. Horizontal lines represent 95% CI, with loadings considered nominally significant if their CIs do not overlap with zero (red vertical dashed line)

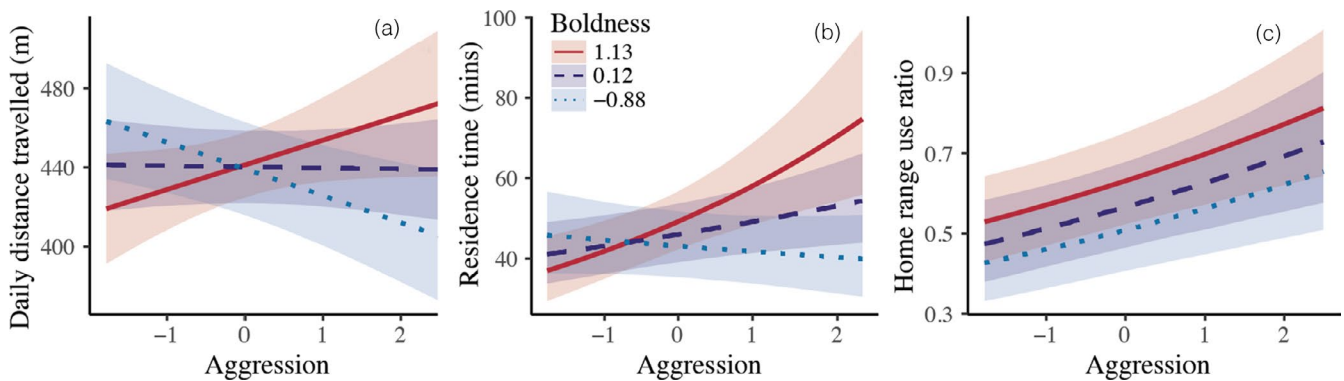
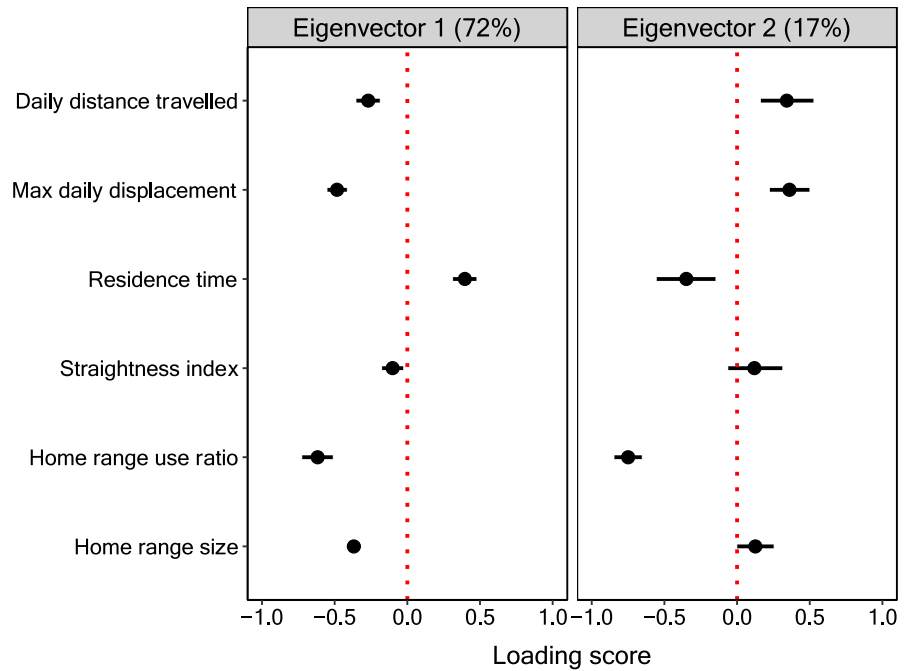


FIGURE 2 Model predictions for the effect of lizard aggression and boldness on (a) distance travelled, (b) residence time and (c) home range use ratio. The figures show the effect of aggression for low, medium and high values of boldness. Shading represents 95% credible intervals

given the strong among-individual covariance between movement metrics we only report the results for daily distance travelled (a proxy for activity), residence time (a proxy for space-use intensity), home range use ratio and home range size (proxy for home range utility and exploration). These metrics were chosen as representatives for the primary movement axes identified by our eigen decomposition analysis—but results for the remaining movement metrics can be found in the Supporting Information (see Table A9). Furthermore, since predictor effects were qualitatively similar between the subset dataset (2015–2017; for which personality and full environmental data were available; Table A9) and the full dataset (2013–2017; Table A10), we only report here the main results of the subset model because it contained the full set of predictors. Below, we show effect sizes (coefficient mean estimate \pm SE) that are reported on a standardised scale and are therefore unitless.

3.3.1 | Personality

We found evidence of personality-dependent movement (Table A9). Boldness and aggression had a positive interaction on daily distance travelled [0.06 ± 0.03] and residence time [0.09 ± 0.04]. Lizards that were shyer (low boldness) tended to travel greater distances if they were also unaggressive, whereas lizards that were bold tended to travel greater distances if they were also highly aggressive (Figure 2a). Bold, aggressive lizards also had considerably higher residence times than all other behavioural combinations, suggesting that these lizards exhibited greater space-use intensity (Figure 2b). Bolder lizards had a higher weekly home range use ratio than shyer lizards [0.11 ± 0.04], and aggressive lizards had a higher weekly home range use ratio than non-aggressive lizards [0.11 ± 0.03 ; Figure 2c]. This suggests that bolder, and more aggressive lizards consistently

covered a larger proportion of their 95% yearly HR per week. There were no clear effects of personality on home range size (Table A8).

3.3.2 | Sex and mass

Males and females differed considerably in their movement (Table A9). Males travelled greater daily distances [0.59 ± 0.09] and had lower residence times [-0.41 ± 0.11] compared to females. However, the effect of sex on these movement metrics was weaker later in the active season (Figure A1a,b). Males had larger home ranges than females [0.25 ± 0.09] (Figure A1c), but there was no clear effect of sex on home range use ratio. Finally, there was a marginal negative effect of mass on home range size [-0.05 ± 0.02], suggesting that larger lizards have smaller home ranges than smaller lizards (Figure A2b). Larger lizards also had higher residence times than smaller lizards in the early season, but not in the late season [mass * season interaction: 0.12 ± 0.04 ; Figure A1a]. Lizard mass had no other clear effects on movement (Table A9).

3.3.3 | Dam usage

We found a positive interaction between the average weekly distance a lizard spent from the dam and the number of weekly dam visits on home range use ratio [0.20 ± 0.06] and home range size [0.32 ± 0.04], but a negative interaction on residence time [-0.25 ± 0.07] (Figure 3 top row). Lizards that spent farther average daily distances from the dam, but still visited the dam regularly, used a greater proportion of their HR per week and had lower residence times than lizards that also spent farther average daily distances from the dam, but rarely visited the dam (Figure 3b,c). On the other hand, the smaller the distance between a lizard's average location and the dam, the weaker the relationship between dam usage and movement—presumably because in such circumstances large movements are not required in order to visit the dam (Table A9). However, lizards that visited the dam more regularly travelled greater daily distances [0.12 ± 0.02] regardless of their average weekly distance from the dam, suggesting that lizards that visit the dam more regularly are also generally more active (Figure 3a).

3.3.4 | Home range overlap with good food quality habitat

Lizards with 95% HRs that overlapped more with good food quality habitat travelled smaller daily distances [-0.09 ± 0.03] and had higher residence times [0.09 ± 0.03] than lizards whose 95% HRs overlapped less with good food quality habitat (Figure 3d,e). This suggests that lizards that occupy areas with better food resources tend to be overall less active and explorative, and instead use core areas of the landscape more intensely. Interestingly, we found no effect of FoodQualityHR on home range use ratio, but we did find

a negative effect on home range size [-0.07 ± 0.02]. This indicates that lizards with smaller HRs tend to occupy areas with better food resources (Figure 3f).

3.3.5 | Home range overlap with forested habitat

In contrast to FoodQualityHR, we found that lizards with 95% HRs that overlapped more with forested habitat travelled greater daily distances [0.31 ± 0.03] and had lower residence times [-0.30 ± 0.02]. We also found that lizards with larger home range use ratios [0.43 ± 0.03] and home range sizes [0.38 ± 0.02] tended to have 95% HRs that overlapped more with forested areas (Figure 3, bottom row). This suggests that lizards that use forested habitats more regularly tend to also be more active and explore greater areas of the landscape. We also found a positive interaction of season and ForestHR on daily distance travelled [0.07 ± 0.04] and home range use ratio [0.09 ± 0.03] indicating that the relationship between forested habitat and these movement traits becomes weaker later in the active season (Table A9).

4 | DISCUSSION

Individual variation in fine-scale or daily movement behaviour is pivotal for ecological and spatial dynamics, but such variation has largely been overlooked in movement and wildlife ecology (Hertel et al., 2020; Shaw, 2020). Accordingly, we GPS tracked free-ranging sleepy lizards over five activity seasons (years) and found that individuals consistently differed in a collection of interrelated movement metrics that could also be used to differentiate broader movement patterns at a within-population level. Our multivariate analysis revealed that sleepy lizards exhibit a central movement syndrome—that is, among-individual covariation in movement metrics—whereby lizard movement could be primarily characterised as falling along an ‘explorer–resident’ movement gradient. Specifically, along a gradient, ‘explorers’ move greater distances, explore vaster areas of the environment and have larger home ranges, while ‘residents’ spend extended periods of time residing within smaller core areas of their home range. A second movement syndrome was also found describing small home range residency, but this syndrome explained a much smaller proportion of among-individual variation (17%) relative to the explorer–resident movement gradient (72%). Importantly, we also show that consistent individual differences in lizard movement were influenced by two ecologically important personality traits (boldness and aggression), their sex, and key features of the environment including food availability, a key water resource and habitat type.

4.1 | Movement repeatability

Our findings add to a growing number of studies that have provided valuable insights into consistent individual differences in

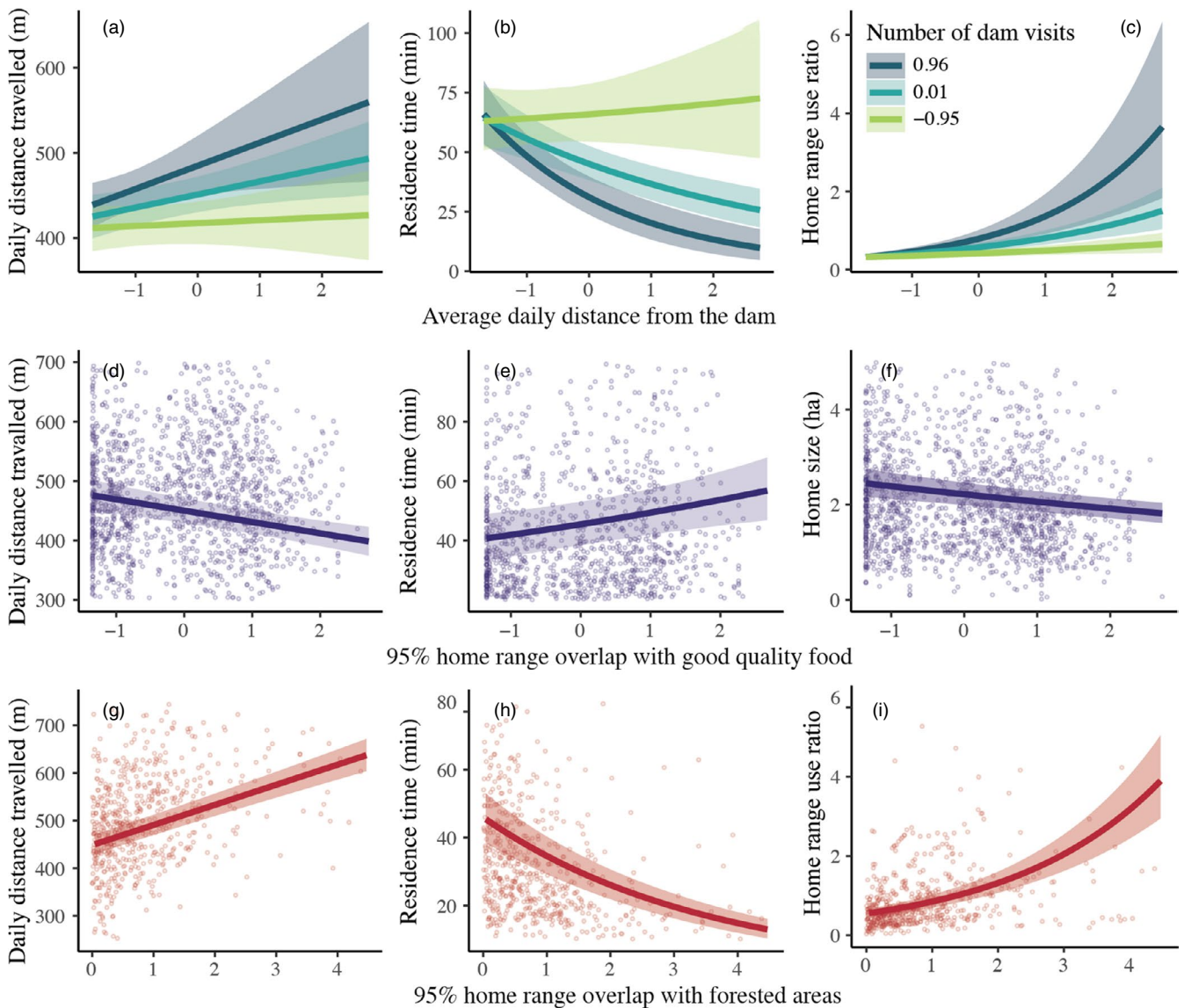


FIGURE 3 Model averaged predicted effects of environmental features on movement. Top: the interaction between the number of dam visits made by a lizard per week and the average weekly distance a lizard spent from the dam on (a) daily distance travelled, (b) residence time and (c) home range use ratio. Middle: the effect of an individual's 95% home range overlap with good food quality habitat on (d) daily distance travelled; (e) residence time and (f) home range size. Bottom: the effect of an individual's 95% home range overall with forested habitat on (g) daily distance travelled, (h) residence time and (i) home range use ratio. Shading represents 95% credible intervals. Open circles represent observed data used in the models, not just points matching counterfactual conditions of model predictions. Horizontal axes are on a standardised scale. Number of dam visits is also on a standardised scale

movement-related behaviours within natural conditions including general movement descriptors (e.g. diel activity and exploration: Harrison et al., 2019; Hertel et al., 2019), spatial descriptors (e.g. first passage time: Webber et al., 2020), foraging tactics (e.g. Patrick et al., 2017; Webber et al., 2020), habitat selection (e.g. Bastille-Rousseau & Wittemyer, 2019; Leclerc et al., 2016), dispersal propensity (e.g. Cote et al., 2011; Michelangeli et al., 2017) and migration tactics (e.g. Eggeman et al., 2016; Lehnert et al., 2018). Given that long-term repeatability estimates offer insight into the upper limit of standing genetic variation (Dochtermann et al., 2015; Edelsparre et al., 2014), and that movement behaviours likely have a genetic basis (e.g. Gervais

et al., 2020), our results are consistent with the possibility that individual differences in movement are heritable and have evolutionary potential. However, while our repeatability estimates were derived from models that controlled for some environmental factors and independent assays of personality (additional steps not often taken by studies of this kind), we are unable to fully tease apart whether our observed movement repeatability arises from true identity effects (e.g. genes, physiology) or from individual repeatability in environmental conditions experienced (e.g. personality-dependent habitat choice)—as this would likely require an experimental approach (Hertel et al., 2020; Niemelä & Dingemanse, 2017).

4.2 | Seasonal and habitat effects on movement and space use

As predicted, lizard movement was linked to ecological factors and important features of the environment including food availability, a key water resource and habitat type. Notably, lizards with 'resident' movement characteristics had smaller home ranges, lower residence times and travelled smaller daily distances, and yet their home ranges overlapped more heavily with good food quality habitat. These results suggest that resident lizards occupy core areas with better food resources thus limiting their need to move large distances to find food. This is indicative of an exploitation foraging tactic whereby resident lizards utilise core areas more thoroughly with stronger tendency to stay longer within patches of already discovered or predictable resources (Mehlhorn et al., 2015; Patrick et al., 2017; Spiegel et al., 2015; Webber et al., 2020). Indeed, smaller home ranges are expected to emerge in more favourable conditions (Bjørneraas et al., 2012; Van Moorter et al., 2016), and sleepy lizards are known to prefer areas with better food and maintain core areas that exclude same-sex individuals (i.e. are territorial; Kerr & Bull, 2006; Spiegel et al., 2015). Thus, resident lizards might be controlling and/or guarding these good food quality areas from other conspecifics, potentially due to superior competitive abilities (Spiegel et al., 2018); however, we have not explicitly observed this behaviour.

On the other hand, lizards with 'explorer' movement characteristics had home ranges that overlapped less with good food sites, but more with forested regions. In contrast to 'residents', 'explorers' seem to be adopting an exploration foraging tactic (Mehlhorn et al., 2015; O'Farrell et al., 2019; Patrick et al., 2017). By moving larger distances and exploring vaster areas of the landscape, explorers are more likely to find and acquire new resources and information about the environment. Such a tactic may be especially advantageous for finding patchily distributed resources like water in arid environments or responding to resource fluctuations (e.g. personality-dependent plasticity; Spiegel et al., 2017; Webber et al., 2020). Indeed, we did find that lizards which were generally more active were more likely to visit the dam. Dam usage has also previously been linked to improved body condition in sleepy lizards during the late season when environmental conditions are harsher (Leu & Bull, 2016). We know that not all lizards visit the dam, despite the dam being the only reliable water source at our study site, suggesting that lizards which adopt a 'resident' strategy may never actually find or visit the dam. However, we are unable to fully disentangle the effect of movement on the number of dam visits because our dam usage metrics were not estimated independently from the movement tracks. Nevertheless, this provides a possible example of an interesting life trade-off between resource exploitation and information acquisition in this study system that merits further exploration (Spiegel & Crofoot, 2016).

Many of the observed external effects on movement began to diminish later in the active season suggesting behavioural responses to the changing environment. For instance, males generally travelled

more distance and made greater weekly displacements than females (see Table A8), but these differences were considerably lower later in the season. Sex differences in sleepy lizard movement have been reported previously (Leu et al., 2011, 2016; Spiegel et al., 2018; Taggart et al., 2018) and are likely due to stronger intra-sexual competition in males relative to females whereby males need to move more to mark the boundaries of their territory and repel other males (Leu et al., 2016; Spiegel et al., 2018). The sleepy lizard breeding season primarily occurs in the early season. Thus, sex differences in movement might begin to decrease later in the season due to a reduced necessity for males to attract females and/or fight-off other males. Furthermore, the effects of food and habitat type on movement became less prominent later in the active season. This seasonal variation is perhaps not all that surprising given that the late season is typically hotter, and food resources begin to deteriorate reducing heterogeneity in food patch availability. Consequently, previously high-quality food sites may no longer be as profitable, and lizards may overall have to travel more distance to find food. Nevertheless, it should also be noted that our identified movement syndromes emerged regardless of season, indicating that consistent individual differences in movement are maintained throughout the entire season.

4.3 | Personality-dependent movement

By combining behavioural assays with GPS tracking data, our study also provides a robust example of personality-dependent movement. We assayed lizard boldness and aggression separate of their movement trajectories, as opposed to defining their personality from the movement trajectories. Interestingly, aggression and boldness are not correlated in our study system, suggesting that these traits have independent functional roles. Being highly aggressive, for instance, may arise in lizards that have a competitive advantage and engage in more agonistic interactions (thus obtaining social feedback), whereas high levels of boldness might only emerge in lizards that have a knowledge of reliable foraging sites or are consistently motivated by hunger. Variation in either of these factors can lead to the emergence of mismatched personalities and possible interactive effects on movement patterns. Indeed, we found that (a) lizards that are either bold and aggressive, or shy and unaggressive, travelled greater distances than lizards with mismatched behavioural traits; (b) lizards that were both bold and highly aggressive had the highest space use intensity relative to all other behavioural type combinations; and (c) bold and aggressive lizards used a larger proportion of their yearly 95% HR per week.

The fact that bold, aggressive animals move more fits general, ecological intuition and previous studies (Spiegel et al., 2017). In contrast, the fact that bolder, aggressive lizards also have higher space use intensity seems counter-intuitive. The explanation might lie in the effects of personality on HR size, HR use and sociality that were described in previous studies, and the positive effect of aggression on home range use ratio found in the present study.

High home range use ratio is expected to emerge when individuals regularly move outside of central areas of their HR, thus it appears that aggressive lizards use the peripheral regions of their HR more regularly than unaggressive lizards. This also supports past findings that aggressive lizards use core areas of their HR less intensely than unaggressive lizards (Spiegel et al., 2015). Social encounters between individuals, particularly male–male interactions, often occur at the peripheral regions of an individual's HR (i.e. where the boundaries of two HR's overlap; Spiegel et al., 2018). Aggressive lizards are also known to be less responsive to conspecific density (Godfrey et al., 2012; Spiegel et al., 2015) and engage in more agonistic interactions (Godfrey et al., 2012) than unaggressive lizards. Given these findings, it appears that the observed differences in movement and space use between aggressive and unaggressive individuals is an outcome of how they respond to the presence and activity of conspecifics (i.e. their willingness to confront or avoid potentially hostile interactions).

While we did not find clear effects of lizard personality on HR size in our study, previous work on a longer term home range study in our system (~8 years), found that aggressive lizards tend to have larger HRs than unaggressive lizards, and bolder lizards smaller HRs than shy lizards (O. Spiegel, D. L. Sinn, E. Payne, M. Michelangeli, J. R. Klein, J. Kirkpatrick, M. Harbusch, & A. Sih, unpublished, E. Payne, O. Spiegel, D. L. Sinn, S. T. Leu, M. Gardner, S. S. Godfrey, C. Wohlfeil, & A. Siha, unpublished). When bold lizards are also highly aggressive then they may also move larger distances and cover larger portions of their HR per week in order to patrol greater areas of their HR (e.g. the peripheries) and deter same-sex intruders (Spiegel et al., 2015). Such movement patterns could accrue high residence times if bold, aggressive individuals also continuously return to key sites after leaving (e.g. sites with good food) and/or settle at sites for long periods of time before moving long distances and settling again. In contrast, shy, unaggressive lizards, moved large daily distances, but did not accrue high residence times or use a high proportion of their HR per week. These lizards appear to be strictly moving within core regions of their HR and infrequently visiting the peripheries of their HR where they are more likely to come into contact with neighbours and potential agonistic interactions (Spiegel et al., 2018). Lizards with mismatched behavioural traits generally moved less than lizards with matched behavioural traits, but other observed space use patterns for these lizards were likely dependent on the size of their HR (i.e. how far they have to move to cover their HR) and their level of aggression (i.e. the extent to which they use the peripheries of their HR).

We did not directly test the relationship between personality and environmental variables in our study. However, in a food supplement experiment, Spiegel et al (unpublished) found that bold lizards were faster to discover and feed from artificial food patches, while aggressive lizards exhibited less discrimination between high- and low-quality food patches and greater general exploration suggesting personality-dependent search tactics that align with our findings of personality-dependent movement. Together with the present study,

these results begin to paint a picture of how personality and movement interact to shape differential foraging tactics that lead to key differences in habitat and space use. Importantly, these differences in habitat and space use likely in turn mediate conspecific interaction rates (Schirmer et al., 2020), and thus social networks (Aplin et al., 2013), that affect parasite transmission (Sih et al., 2018) and potentially feedback to affect and/or maintain individual variation in movement behaviour and personality (Schirmer et al., 2020; Sih et al., 2015). While beyond the scope of the current study, the next step is to disentangle this complex web to reveal the causal pathways that ultimately give rise to these individual specialisations.

5 | CONCLUSIONS

Animal movements are clearly affected by a wide range of factors such as sensory, memory and navigational capacities, many of which we did not consider in this study (Nathan et al., 2008; Spiegel et al., 2017). Nevertheless, by quantifying individual differences in a collection of simple movement descriptors in combination with independent behavioural assays, we demonstrate that individuals consistently differ from each other and also exhibit movement syndromes along a resident–explorer continuum, which underlie personality-dependent spatial patterns and habitat use. It is likely that these movement specialisations reflect individual variation in life-history tactics including foraging and mating strategies. For example, lizards which explore greater areas of the landscape (i.e. explorers) will likely interact with a higher number of individuals (including potential mates) and discover new resource patches, whereas residents might monopolise smaller, but more profitable areas of the landscape that are favoured by reproductive partners. Such information can ultimately be used to connect phenotypic population structure to key ecological and evolutionary outcomes (e.g. social networks, disease-transmission pathways), further highlighting the importance of analysing individual variation in behaviour and movement collectively. We encourage future research to adopt a similar analytical framework as outlined in this study to identify potentially generalisable movement patterns within a wide range of species.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

M.M., E.P., O.S. and A.S. were responsible for conceiving the idea for the manuscript; E.P., O.S., D.L.S., S.T.L., M.G.G. and A.S. collected the data; M.M. and E.P. conducted the data analysis; M.M. drafted the first version of the manuscript. All authors contributed to editing and crafting the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data are available at Dryad data repository: personality, spatiotemporal ecological variation and resident/explorer movement syndromes in the sleepy lizard, Dryad Digital Repository <https://doi.org/10.25338/B8RW6J> (Michelangeli, 2021).

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