Marwell Wildlife

UNIVERSITY OF Southampton

# PERSONALITY-DEPENDENT DISPERSAL IN THE SAND LIZARD, *LACERTA AGILIS*; IMPLICATIONS FOR REINTRODUCTION SUCCESS

A technical report prepared from an MRes Wildlife Conservation project, Marwell Wildlife & University of Southampton

**Emily Jordan**

Marwell Wildlife & University of Southampton

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# Abstract

Severe biodiversity loss threatens ecosystem stability and human quality of life, resulting in the need for urgent conservation interventions. Reintroductions are utilised to aid species recovery but remain high cost with uncertain success rates, necessitating evidenced-based planning. Dispersal is a key factor influencing the outcome of reintroductions and is known to be influenced by personality. Research has found evidence of dispersal syndromes and personality-dependent dispersal in natal scenarios, though limited studies have investigated the effects of personality on post-release dispersal. This study used behavioural assays to determine repeatable behaviour in a locally rare lizard, the sand lizard, *Lacerta agilis*. Immediate dispersal propensity was measured using a mock release set-up in a captive novel environment. Lizards were found to demonstrate repeatable exploratory and active behaviours indicative of exploration and activity personality types. Juvenile sand lizards demonstrated higher dispersal tendencies and more flexible behaviour than mature individuals, suggesting an ontogenetic component of behavioural variation. Principle component analysis gave evidence for the presence of an activity-exploration dispersal syndrome, and exploration and activity were found to be effective predictors of dispersal tendency. Knowledge of individual variation in behaviour can be used to predict response at release and inform reintroduction strategy, such as preferred age of release and soft-release trials. However, conclusions are limited by uncertainty surrounding the pertinence of results derived from captive assays to natural behaviour and true reintroduction scenarios. Further research throughout the reintroduction process is intended to validate the applicability of responses during the mock release to wild release responses, and whether immediate dispersal predicts long-term dispersal patterns.

**Key words:** *Individual variation; dispersal; reintroduction; animal personality; wildlife conservation; behavioural ecology*

**Target journal:** Applied Animal Behaviour Science

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# 1. Introduction

## 1.1 Wildlife Conservation in the 21st Century

Unprecedented rates of biodiversity loss are driving an urgent need to halt species declines, as anthropogenic activity contributes heavily to pressures such as pollution, climate change and habitat loss (Cardinale *et al* 2012; Newbold *et al* 2015; Venter *et al* 2016). Reductions are prolific across taxa, with a minimum of 40% of global bird populations in decline, 20% of mammal and reptile species at risk of extinction, and a predicted loss of around 75% of insect biomass across Europe since 1989 (Cox and Temple 2009; Hoffman *et al* 2011; Hallman *et al* 2017; Birdlife International 2018). These losses in biodiversity have a measurable detrimental effect on the ecological functions that underpin ecosystem services vital for human quality of life (Bennett *et al* 2015; Lefchek *et al* 2015; Sandifer *et al* 2015).

Conservationists have developed a range of approaches to counter the expanse of varying threats, across diverse species and contexts (Rands *et al* 2010). Research aims to provision evidence-based management decisions and influence policy-makers that can execute actions, such as the designation of protected areas, placing restrictions on resource exploitation, and developing sustainable energy initiatives (Johnson *et al* 2017; Jucker *et al* 2018). Large scale restoration efforts are used to reverse damage to degraded marine and terrestrial habitats, whilst targeted species conservation focuses on individual species requirements and countering specific threats such as poaching (Wei *et al* 2015; Barichievy *et al* 2017; Brancalion *et al* 2018; Condie *et al* 2018). Where threats have resulted in the eradication of species from an area, or rendered them extinct in the wild, conservation reintroductions are often the most viable option to promote recovery (Bremner-Harrison *et al* 2004; Fitzgerald *et al* 2015).

## 1.2 Reintroduction as a conservation tool

Conservation translocation refers to a group of tools where individuals of a species are deliberately relocated with the purpose of providing a benefit to conservation. This incorporates reintroduction, involving the intentional release of a species into an area it formerly inhabited, from either captivity or a successful in-situ population (IUCN/SSC

2013; Muths *et al* 2014). Breeding populations of rare species are often managed ex-situ in order to boost numbers prior to release and enhance genetic diversity (Beck *et al* 1994; Gilbert *et al* 2017; Brichieri-Colombi *et al* 2018). Aiding species recovery, and the restoration of the ecological functions they provide, are key outcomes cited for reintroductions (Seddon 2015; Hale and Koprowski 2018). However, the true conservation value of reintroductions has been widely debated (Canessa *et al* 2014; Ewen *et al* 2014; Haskins 2015).

Reintroduction projects are often high risk, high cost, and success is arguable (Armstrong and Seddon 2008; Moehrenschlager *et al* 2013; Berger-Tal & Saltz 2014; Muths *et al* 2014). Level of success is itself difficult to accurately determine due to inconsistencies in the definition of success, as well as a lack of adequate monitoring post-release and minimal reporting of failed programmes (Robert *et al* 2015; Seddon 2015; Shier 2015). Of the reintroductions published in the 'Global Perspectives' series between 2008-2018, 60% of authors identified their projects as highly successful or successful (Soorae 2008; 2010; 2011; 2013; 2016; 2018). This is similar to the 65% reported in a survey of North American translocations between 2000 to 2013, and 61% success rate of Australian macropod translocations during 1969-2006 (Clayton et al 2014; Brichieri-Colombi and Moehrenschlager 2016). However, this may not be an accurate reflection of global reintroduction success as the criteria used to measure success remains inconsistent across projects, and there is likely publication bias towards reporting successful results. An analysis investigating herpetofauna reintroductions in New Zealand concluded publication bias resulted in overestimation of success rates by over 40% (Miller *et al* 2014), whilst a review of plant survival following reintroduction found survey assessments reported a 33% survival rate, in contrast to the 78% reported in the literature (Godefroid *et al* 2011).

Additionally, there has been criticism that reintroduction programmes display taxonomic bias and are not always targeted at threatened species (Seddon et al 2014; Harding et al 2016). Species selected for reintroduction may not be globally or regionally rare, and 50% of reintroductions reported by the Reintroduction Specialist Group are of birds and mammals, despite these taxa representing only 18% and 8% of total known species respectively (Soorae 2008; 2010; 2011; 2013; 2016; 2018; Seddon et al 2014; Brichieri-Colombi and Moehrenschlager 2016).

Despite challenges, there have been several notable conservation successes. Reintroductions have re-established self-sustaining populations of species previously extinct in the wild, such as the Arabian Oryx, Prezwalski's horse and black-footed ferret, and resulted in the down-listing of several threatened species (Treydte *et al* 2001; Slotta-Bachmayr *et al* 2004; Harding *et al* 2007; Jachowski and Lockhart 2009; Xia *et al* 2014). Advances in reintroduction biology hold potential to benefit conservation, and the increasing popularity of reintroductions as a conservation tool in combination with the uncertainty of success, necessitates emphasizing the importance of research, rigorous planning, assessments and an adaptive management approach (Seddon *et al* 2012; Moehrenschlager *et al* 2013; Canessa *et al* 2014). Research into factors affecting the outcomes of reintroductions is therefore key to inform decision-making, and thus increase the validity and success of the approach (Ewen *et al* 2014).

### 1.2.1 Factors affecting reintroduction success

Failure to identify and mitigate against threats that led to initial extirpation is a prominent cause of reintroduction failure (Cochran-Biederman *et al* 2015). Continued high rates of predation from introduced predators have resulted in high post-release mortality leading to the failure of several projects reintroducing Australian mammals (Fischer and Lindenmayer 2000; Moseby *et al* 2011; Clayton *et al* 2014; Peters *et al* 2015; Hardman *et al* 2016). Post-release survival rates are also dependent on the release site containing appropriate habitat capable of supporting a viable population (Germano and Bishop 2009; Moorhouse *et al* 2009; McCoy *et al* 2014). A reintroduction of brown treecreepers, *Climacteris picumnus*, was deemed unsuccessful in part due to the release site providing limited foraging and refuge, resulting in extensive dispersal of released individuals in search of more favourable habitat (Bennett *et al* 2012; 2013).

Reintroductions are often more successful when individuals are wild-caught as opposed to captive-bred (Fischer and Lindenmayer 2000; Jule *et al* 2008). This is attributed to individuals becoming adapted to captivity, resulting in insufficiencies in natural behaviours such as predator avoidance and foraging (Dutra *et al* 2016). Efforts to improve success of captive releases have developed pre-release training and enrichment designed to help individuals re-learn wild behaviours such as hunting (Seddon *et al* 2007; Reading *et al*

2013; Clayton *et al* 2014). Stress associated with introduction to a novel environment can also detrimentally impact an individual's ability to perform natural behaviours to avoid threats and acquire resources, reducing rates of survival post-release (Dickens *et al* 2010; Villaseñor *et al* 2013). The stress response of the translocation process can also cue increased dispersal behaviour (Richardson 2015). Dispersal beyond the release site is counted as a loss to the population and dispersing individuals experience greater risk of mortality outside of appropriate habitat (Germano and Bishop 2009; Parlato and Armstrong 2013; McCoy *et al* 2014).

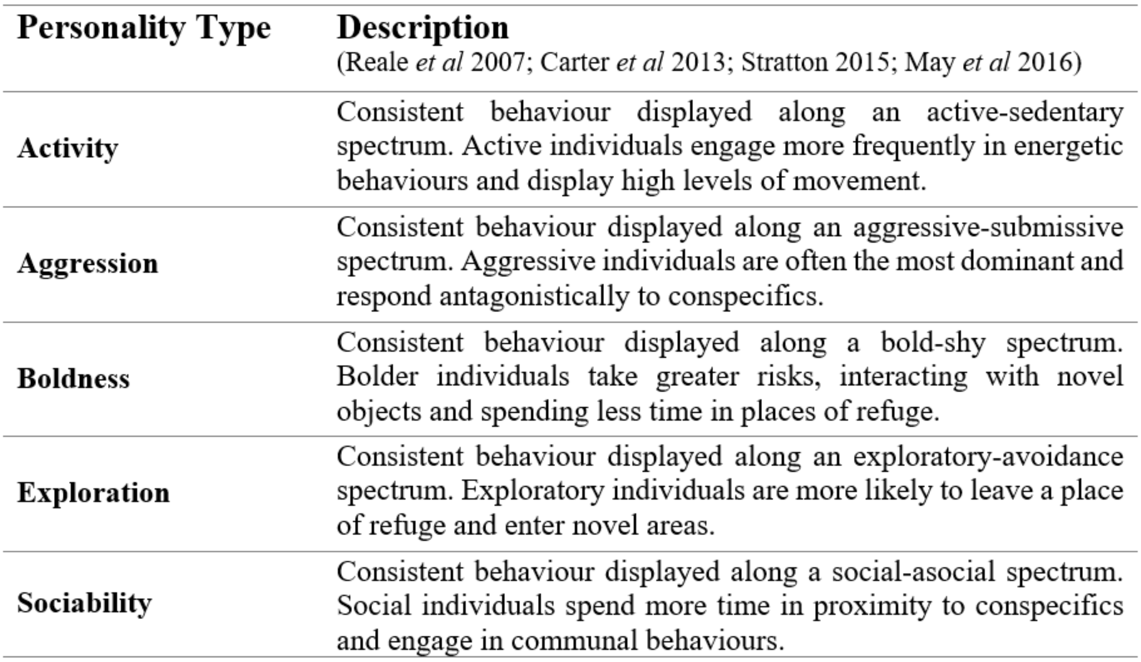
Knowledge of a species' life history strategy can predict its suitability for reintroduction and highlight the optimal developmental stage for release. A modelling approach demonstrated variation in survival rates and population size of the southern corroboree frog, *Pseudophryne corroboree,* dependent upon age of release (Canessa et al 2014; Fitzgerald et al 2015). Recent research has highlighted the importance of considering variation at the individual level, as certain individuals may be better suited to reintroductions due to physical and behavioural trait differences (May *et al* 2016; Lapiedra *et al* 2017). To be successful, an individual must acclimatize to a novel situation to an extent that they are capable of displaying the natural range of behaviours necessary to survive and reproduce in their new environment (Watters and Meehan 2007; Houde *et al* 2015). Factors affecting this ability may include physical condition, resilience to stress associated with the release procedure, plasticity, and consistent behavioural differences or 'animal personality' (McDougall *et al* 2006; Wolf and Weissing 2012).

## 1.3 Animal Personality

Behavioural research has increasingly reinforced the concept of individuals within species displaying distinct behavioural types, or personalities (Watters & Powell 2012). Animal personality can be defined as consistent between-individual differences in behaviours, whereby an individual acts in a repeatable manner across environmental contexts (Dall *et al* 2004; Rodríguez-Prieto *et al* 2011). This intraspecific variation is ecologically and evolutionarily significant, with greater diversity within a population resulting in higher adaptability to environmental change (Wolf & Weissing 2012; Cordero-Rivera 2017). Personality research commonly recognizes five core behavioural types, Table 1.

Personality types have been shown to be heritable and can be state-dependent, whereby factors such as body-size, condition, sex and age influence the expression of personality (Dingemanse *et al* 2002; Dochtermann *et al* 2015; Sih *et al* 2015; Kelleher *et al* 2017).

**Table 1.** Glossary of core personality types



| **Personality Type** | **Description**<br>(Reale *et al* 2007; Carter *et al* 2013; Stratton 2015; May *et al* 2016) |
|---|---|
| **Activity** | Consistent behaviour displayed along an active-sedentary spectrum. Active individuals engage more frequently in energetic behaviours and display high levels of movement. |
| **Aggression** | Consistent behaviour displayed along an aggressive-submissive spectrum. Aggressive individuals are often the most dominant and respond antagonistically to conspecifics. |
| **Boldness** | Consistent behaviour displayed along a bold-shy spectrum. Bolder individuals take greater risks, interacting with novel objects and spending less time in places of refuge. |
| **Exploration** | Consistent behaviour displayed along an exploratory-avoidance spectrum. Exploratory individuals are more likely to leave a place of refuge and enter novel areas. |
| **Sociability** | Consistent behaviour displayed along a social-asocial spectrum. Social individuals spend more time in proximity to conspecifics and engage in communal behaviours. |

The influence of personality on an individual's behaviour across contexts holds significant implications for individual fitness (Wolf and Weissing 2012; Kelleher *et al* 2018). Therefore, animal personality is an important factor to consider in reintroductions, holding repercussions for the ability of an individual to survive post-release, establish, and reproduce successfully (Merrick and Koprowski 2017). Higher survival rates were observed in bold Tasmanian devils, *Sarcophilus harrissii*, than shy individuals following translocation (Sinn *et al* 2014). However, in Swift foxes, *Vulpes velox*, bold individuals experienced higher mortality due to greater risk-taking behaviour when encountering novel threats such as road traffic (Bremner-Harrison *et al* 2004; Bremner-Harrison *et al* 2013). The effect of personality on post-release survival can be context-dependent. Exploration personality in the European mink, *Mustela lutreola*, was found to be both positively and negatively correlated with survival, depending on the time of release and release location (Haage *et al* 2013; Haage *et al* 2017). Understanding which temperaments are related to individual success post-release may aid the selection of appropriate candidates for reintroduction (Silva and Azevedo 2013; May *et al* 2016).

Individuals capable of surviving the translocation process may yet disperse from the intended release site, with implications for reintroduction success. Several studies have found behavioural traits that constitute an animal's personality are effective predictors of dispersal tendency, suggesting the presence of a behavioural syndrome linking consistent between-individual differences in behaviour with dispersal (Cote *et al* 2010a; 2010b).

## 1.4 Dispersal

Dispersal is an event whereby gene flow occurs over space, incorporating movements away from natal or release sites, between breeding sites, and the colonization of new areas (Hawkes 2009; Michelangeli *et al* 2017). Dispersal can be split into three stages, departure, the transience or exploration phase, and settlement, Figure 1 (Clobert 2012). Multiple environmental, social, and developmental cues can initiate dispersal behaviour, such as increasing population density and environmental disturbance (Massot *et al* 2002; Cote and Clobert 2012). Movement to an unknown site invariably holds consequences for fitness, incurring energetic costs, increased predation risks and the possibility of encountering less favourable conditions. However, dispersal also functions to reduce inbreeding, and offers the potential to settle novel areas with more favourable conditions (Ryberg *et al* 2004; Clobert *et al* 2009; Matthysen 2012). Dispersal is a key life history trait to consider in conservation, as it influences both $N$, $N_e$ and genetic diversity, thus effecting the resilience of a population to stochasticity (Anthony and Blumstein 2000).

Dividing dispersal into stages enables advances in our understanding of its underlying processes and mechanisms (Travis *et al* 2012). Reintroductions are often most concerned with the departure stage, as emigration from the release site results in the individual no longer contributing demographically or genetically to the intended population, thus a loss through dispersal may be considered equivalent to a mortality (Parlato and Armstrong 2013; Knox and Monks 2014; Richardson *et al* 2015). The reintroduction site is likely to have been selected as an optimal habitat, outside of which there may be greater risk of genuine mortality and settling in an unsuitable area where a population is unlikely to be established (Villaseñor *et al* 2013; Richardson *et al* 2015). The risks associated with dispersal are dependent on the size of appropriate habitat that constitutes the release site, and the nature of the surrounding area. If a site is larger than the dispersal distance a species is capable of, losses through dispersal are low risk, whilst dispersal may be desirable for species recovery where the surrounding area is viable for colonisation (Anthony and Blumstein 2000; Richardson *et al* 2015). The ability of individuals to disperse between sites can also contribute to population resilience, as dispersal is an important reaction to disturbance and unfavourable conditions. However, this is dependent on favourable conditions being accessible (Anthony and Blumstein 2000; Clobert *et al* 2009)

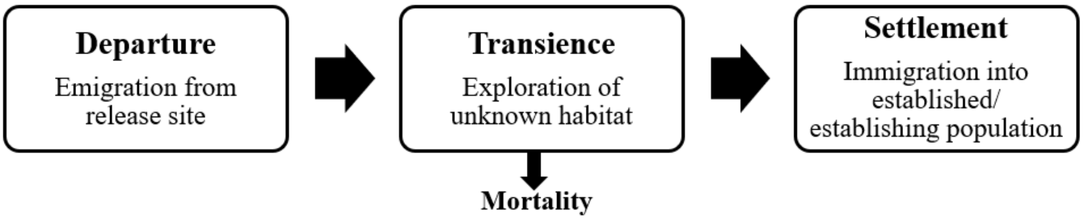


**Figure 1.** The three stages of dispersal regarding reintroductions.

### 1.4.1 Dispersal syndrome

Research has identified individual differences in physiology, morphology and behaviour, abiotic conditions at the release site, and biotic interactions as key factors mediating dispersal (Meylan *et al* 2002; Aragón *et al* 2006; Hawkes 2009; Knox *et al* 2017). Correlation between phenotypic traits and dispersal behaviour may be indicative of a dispersal syndrome, defined as the 'covariation of traits associated with dispersal' (Clobert 2012; Legrand *et al* 2016).

The presence of a dispersal syndrome suggests that individuals with a greater propensity to disperse display a suite of traits characteristic of 'dispersers' (Quinn *et al* 2011; Debeffe *et al* 2014). Dispersal syndromes have been identified in a wide range of taxa and have likely developed under multiple selection pressures (Stevens *et al* 2014). Dispersal is frequently male or female-biased, with one sex having a higher tendency to disperse (Legrand *et al* 2015; Denoël *et al* 2018). Morphology often correlates with locomotor ability and hence is often a predictor of an individual's capacity to disperse. Increased dispersal propensity has been linked to larger wings in butterflies, foot size in European land snails and body size in great crested newts, *Triturus cristatus* (Dahirel *et al* 2015; Legrand *et al* 2015; Denoël *et al* 2018).

Consistent behavioural traits can also correlate with dispersal tendency. Bolder individuals with higher activity budgets were found to be dispersers in roe deer, *Capreolus capreolus*, whilst more exploratory land snails dispersed further than snails that displayed avoidance behaviours (Debeffe *et al* 2014; Dahirel *et al* 2015).  In the invasive mosquitofish, asocial individuals were found to be primary dispersers, suggesting animals at the forefront of colonisations display a specific set of behavioural traits (Cote *et al* 2010b; 2017). Populations exhibiting a dispersal syndrome are likely to also demonstrate state-dependent dispersal. If dispersal responses are significantly affected by personality type, the population could be said to display personality-dependent dispersal.

### 1.4.2 Personality-dependent Dispersal Behaviour

Knowledge of an animal's personality may be used as a predictor as to how they will react in a given scenario, and intraspecific variation in dispersal behaviour has been linked to temperament in birds, mammals and reptiles (Cote & Clobert 2007; Cooper *et al* 2017; Richardson *et al* 2017). Studies investigating personality-dependent dispersal have found links between dispersal behaviour and all the 'Big five' personality types, aggression, exploration, boldness, sociability and activity (Cote *et al* 2010a; Cooper *et al* 2017; Michelangeli *et al* 2017).

Aggressive personality in delicate skinks, *Lampropholis delicata*, and *Silia* bluebird species, is an effective predictor of both distance and speed of dispersal (Duckworth and Badyaev 2007; Michelangeli *et al* 2017).  More exploratory great tits, *Parus major*, display greater dispersal tendencies which has been shown to have a basis in genetic variation (Dingemanse *et al* 2003; Korsten *et al* 2013). This relationship between exploration and dispersal has been observed in several species, including cane toads, *Rhinella marina*, and common lizards, *Zootoca viviparous*, which have further demonstrated increased dispersal associated with higher activity scores (Aragón *et al* 2006; Meylan *et al* 2009; Cote and Clobert 2012; Gruber *et al* 2017). Dispersal in common lizards has also been found to be affected by sociability in interaction with population density. Social individuals display a higher propensity to disperse when population is at a low density relative to asocial individuals and vice versa (Aragón *et al* 2006; Cote and Clobert 2007; 2012).

However most of this evidence stems from research into natal dispersal; limited research has been conducted into the effects of personality on dispersal post-release. The sole study found in an extensive literature search reported that reintroduced hihi, *Notiomystis cincta*, demonstrate variation in dispersal distances post-release, dependent on whether individuals distress-called during handling (Richardson *et al* 2017). Whilst natal studies provide valuable insights into personality-dependent dispersal, caution should be taken in using their results to predict outcomes in reintroduction scenarios (Richardson and Ewen 2016). Chronic stress associated with translocation into a novel environment can affect natural dispersal tendencies, with translocated individuals tending to disperse further than in a natural scenario (Dickens *et al* 2010; Richardson 2015).

Understanding the impacts of these factors on dispersal tendency can inform translocation strategy with links to reintroduction success (Canessa *et al* 2014; Fizgerald *et al* 2015). Methods have been trialled to increase fidelity to release sites, including the use of soft-release pens, food supplementation and conspecific cues (Hardman & Moro 2006; Bradley *et* al 2011; Ebrahimi & Bull 2012; Ebrahimi & Bull 2014; Knox et al 2017).

This study aims to investigate the presence of animal personality, dispersal syndrome and personality-dependent dispersal behaviour in a locally rare lizard, the sand lizard, to inform release strategy.

## 1.5 The Sand Lizard

The sand lizard, *Lacerta agilis*, is a small-bodied oviparous lizard distributed across Europe and Asia. Although not classified as globally threatened, loss of its favoured dune and heathland habitats have led to significant declines in Britain with current populations remaining fragmented (Agasyan *et al* 2010). They are currently protected under Schedule 5 of the Wildlife and Countryside Act, and Appendix II of the Berne Convention (Inns 2009; Edgar *et al* 2010). Due to risk of extirpation, captive-breeding and reintroduction programmes were initiated as part of species action plans and Marwell Wildlife has contributed 1892 release individuals over the past 25 years (Moulton & Corbett 1999; Edgar & Bird 2006; Woodfine *et al* 2017). Some of these reintroductions have resulted in established populations, however sand lizards in the UK remain a cryptic and understudied species and the populations’ status, behaviour and habitat selection tendencies are largely unknown (Woodfine *et al* 2017).

Studies on sand lizard dispersal tendency and mobility have revealed variation across populations, sex and age (Olsson *et al* 1996; Berglind 2005; Fearnley 2009; Blanke & Fearnley 2015). A study by Ryberg *et al* (2004) found that juveniles dispersed shorter distances when amongst a higher density of siblings, despite expectations of further dispersal to avoid inbreeding. This may be explained by the tendency of juveniles to aggregate, and the communal behaviours of sand lizards (Moulton & Corbett 1999).

There has been sparse research into personality in sand lizards, with behavioural observations limited by the elusive nature of the species. Current findings suggest that behaviours may vary with age (Fearnley 2009). Studying the captive population at Marwell zoo, Govier (2017) found that adult sand lizards exhibited consistent differences in behaviour, namely in terms of aggression.

Assessing dispersal propensity and the presence of personality types in a captive-breeding population of sand lizards will enable novel insights into sand lizard behaviour and the relationship between personality and post-release dispersal, with implications for reintroduction success.

# 2. Aims and objectives

This project intended to investigate the role of individual variation and dispersal behaviour on reintroduction success to inform the release strategy of captive-bred sand lizards, *Lacerta agilis*. The study generated five key **aims** with corresponding *objectives* and *null hypotheses ($H_0$)* where applicable:

1. **Determine whether sand lizards display consistent behavioural differences indicative of activity, exploration and sociability animal personality types.**

   *a) Conduct behavioural assays scoring active, exploratory and social behaviour.*

   *b) Analyse results of behavioural assays in a repeatability model to establish whether individuals display exploration, activity and sociability personality types.*

   - *$H_0$: There are no consistent between-individual differences in behavioural scores of exploration, activity or sociability.*

2. **Investigate individual variation in immediate dispersal tendency.**

   *a) Trial a mock release set up using a captive novel environment as a measure for immediate dispersal tendency.*

   *b) Conduct a repeatability analysis to examine individual variation in dispersal behaviour.*

   - *$H_0$: There are no consistent between-individual differences in immediate dispersal tendency.*

3. **Analyse the effects of sex and age on behavioural traits.**

   *a) Run linear mixed models and likelihood ratio tests with sex and age as explanatory variables.*

   - *$H_0$: Age has no effect on scores of exploration, activity, sociability or dispersal tendency.*
   - *$H_0$: Sex has no effect on scores of exploration, activity, sociability or dispersal tendency.*

b) *Evaluate the effect of age on the repeatability of behaviours.*

- *$H_0$: Repeatability does not differ across ages.*

4. **Evaluate the evidence for a dispersal syndrome and personality-dependent dispersal behaviour in sand lizards.**
   a) *Run correlations and a principal components analysis between behavioural trait scores of exploration, activity, sociability and dispersal tendency.*
   - *$H_0$: There is no correlation between behavioural trait scores.*

   b) *Run linear mixed models and likelihood ratio tests to determine whether personality types are significant predictors of dispersal behaviour.*
   - *$H_0$: Personality has no effect on dispersal tendency.*

5. **Discuss implications for reintroduction success and the potential to inform release strategy.**
   a) *Utilise previous research to infer the impact of results on reintroduction outcomes and suggest suitable release strategies.*

# 3. Methodology

## 3.1 Study Population, Management and Husbandry

32 sand lizards across two age categories were randomly selected from a captive-breeding facility at Marwell Zoo, Winchester. Numbers emerging from hibernation were monitored throughout March and April, and individuals were deemed to have reached a suitable body condition for handling by early May. Subjects were then captured, photographed and numbered for individual identification (Appendix A). The two-year old (sub-adult) cohort consisted of 8 males and 8 females, whilst the cohort of 16 one-year old juveniles were unable to be accurately sexed.

Each sample population was housed in separate semi-natural outdoor vivaria set on south facing slopes, with vegetation managed to match natural lowland heath habitat. These were set in a fenced off area with minimal human disturbance and covered by elevated netting to prevent access to potential avian predators. The lizards were fed a diet of gut-loaded black micro-crickets, *Gryllus bimaculatus*, supplemented with 'Nutrabol' nutrient powder 3 times a week, in addition to having the opportunity to catch natural prey that entered the vivaria. Water was sprayed over the vivarium on dry days as an analogue for rainfall, to maintain a drinking source with minimal intervention. Slates were provided for additional shelter and basking.

## 3.2 Data Collection

### 3.2.1 Morphometrics

Measurements of snout-vent length (SVL) were taken alongside the initial capture in order to minimise disturbance. SVL was measured from the tip of the snout to the cloaca using digital callipers. These measurements were included in analyses to account for the effect of body size on behaviour.

### 3.2.2 Behavioural Assays

Assays were conducted to determine whether sand lizards demonstrated personality types, and whether these types had an impact upon their initial dispersal behaviour, detailed below. Each assay was repeated 3 times per individual to test for consistency. A minimum of 1 week was left between repeats in order to minimise impact on the animals and promote reliability and independence of data. Longer breaks between assays would have been preferred but were shortened due to time constraints. Initial dispersal, activity and exploration assays were combined in the same test vivarium to minimise handling and reduce stress and carried out on separate days to sociability assays to further reduce stress and carryover effects (Diaz-Uriarte 2002; Bell 2013). The surface substrate of vivaria was raked between assays to minimise the likelihood of movements being influenced by odour trails, due to the use of olfactory sense during exploration (Blanke and Fearnley 2015).

Observations were recorded by the same observer throughout data collection to prevent inter-observer effects (Martin and Bateson 2007). Intra-observer effects were minimised by carefully defining parameters for when an individual had left the release square (initial dispersal assay), moved between grid squares (activity and exploration assay), or changed zones (sociability assay). An individual was considered to have left a square or zone once both the head and neck had passed its boundary. The observer moved slowly and remained 1 m from assay setups to avoid influencing subjects. The time of day at which an assay commenced was recorded, and repeats were scheduled to incorporate variation.

#### *3.2.2.1 Initial Dispersal*

Dispersal assays were performed in a discrete 267 cm x 55 cm vivarium, representing a novel environment, Figure 2. A video camera was set to record on a tripod overlooking a 50 cm x 50 cm ‘release square’ marked by four pegs and raised string. Each lizard was numbered vocally to enable individual identification, then placed by hand at the centre of the release square. This parallels the conditions of handling and release that individuals will be subject to when reintroduced. Video recording was continued until the individual had left the square, or 20 minutes had elapsed. The time taken for an individual to leave the release square, or whether it remains in the square, was recorded as a measure of initial dispersal propensity. This protocol is analogous to that used at the wild release site in order to obtain comparable data for a wider study (Gardner, R. pers. comm.).

### *3.2.2.2 Activity and Exploration*

Activity and exploration were measured over an observation period of 20 minutes, following the dispersal assay. The 267 cm x 55 cm vivarium was marked into 45 equal grid squares, replicated on data collection sheets, Figure 2. The movements of the focal lizard were drawn over this grid and the number of transitions between grid squares were used to score activity, whilst the total number of grid squares entered was used as a measure of exploration. Small heather stands were provided as refuge for avoidance and welfare purposes. Open field tests in novel environments are commonly used to score active and exploratory behaviours (Ibáñez *et al* 2009; Carter *et al* 2013; Perals *et al* 2017; Newar and Careau 2018).

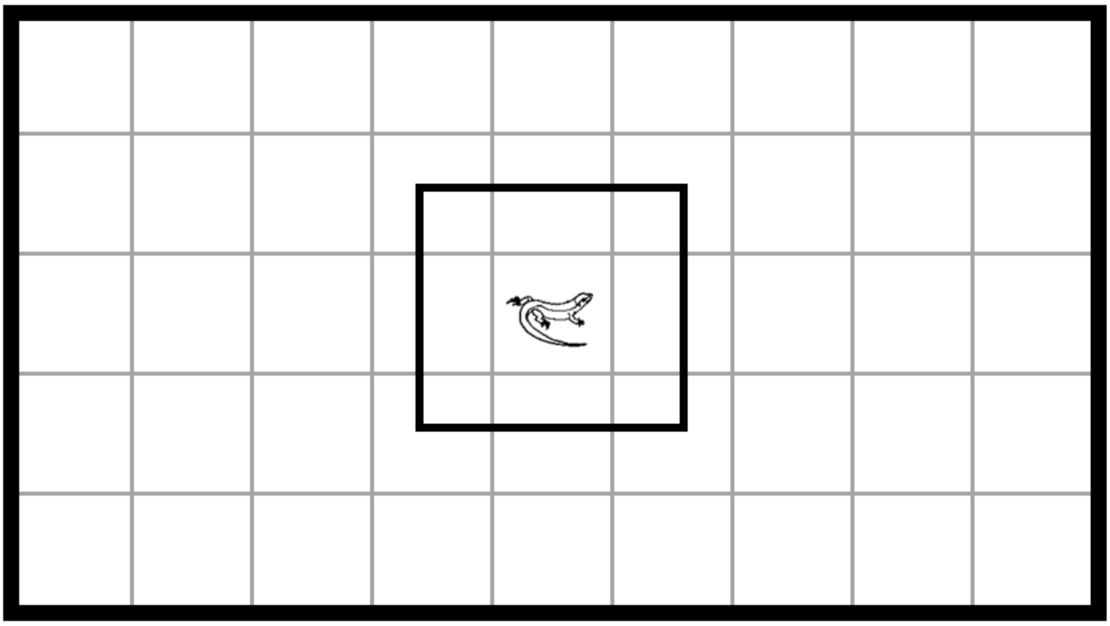


**Figure 2.** Diagrammatical representation of the 267 cm x 55 cm vivarium used for the dispersal, activity and exploration assays, split into 45 equal-size grid squares. The central square represents the 50 cm x 50 cm release square.

### *3.2.2.3 Sociability*

A separate 90 cm x 90 cm vivarium was split into three zones of equal size, with the edge zones running adjacent to a transparent barrier, Figure 3. Non-focal conspecifics were placed behind the barrier adjacent to the designated social zone, whilst the opposite side was designated the asocial zone and the zone between these considered neutral. Conspecifics were from the same age category as the focal individual, and only females were selected from the 2-year old cohort to prevent aggressive behaviour during the assay. Identical pieces of 15 cm x 25 cm slate were placed in the social and asocial zones, supported at one end to create cover and a southward facing slope for shelter or basking. This encouraged subjects to select a favourable site in either the social or asocial zone. Subjects were given a 10-minute acclimation period prior to data collection. The amount of time spent basking in the social zone was recorded over 20 minutes and used as a score of sociability. This methodology has previously been used to measure social behaviour in delicate skinks (Michelangeli *et al* 2017). The side used as the social zone was alternated each new assay day to eliminate confounding effects due to possible directional preference.

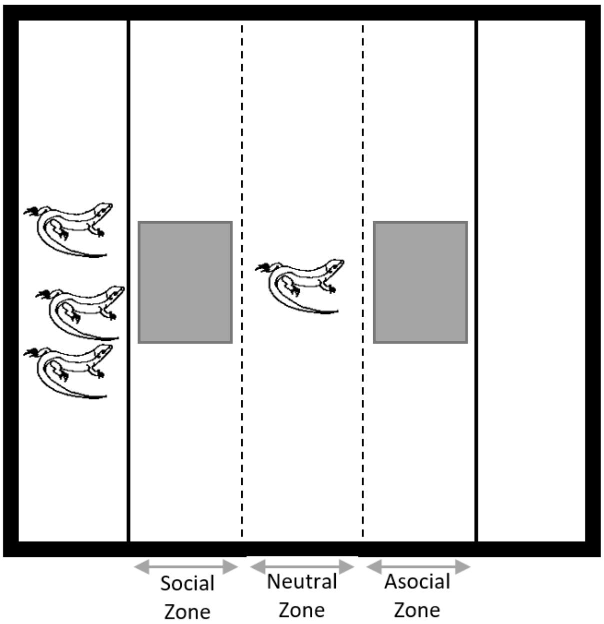


**Figure 3.** Diagrammatical representation of the 90 cm x 90 cm vivarium set up for the sociability assay. The grey squares represent 15 cm x 25 cm slate provided for shelter or basking. Non-focal conspecifics were placed behind perspex adjacent to the social zone. The focal individual was placed at the centre of the neutral zone prior to the 10-minute acclimation period.

### 3.2.3 Environmental Variables

Temperature and UV incidence have been found to impact sand lizard activity levels and were therefore recorded for inclusion in analysis as potential confounding factors (Blanke and Fearnley 2015). Environmental data was taken from Otterbourne weather station. Time of day was also recorded and sorted into categories ‘Early’ (9:01-11:30), ‘Mid’ (11:31-14:00), and ‘Late’ (14:01-16:30) to account for temporal variation in daily activity (Blanke and Fearnley 2015; Govier 2017).

## 3.3 Data Analysis

All statistical analyses were performed using R software, version 3.4.4 (R Core Team 2017). Statistical significance was assigned at $\alpha = 0.05$.

### 3.3.1 Effect of age and sex on behavioural traits

The significance of age and sex effects on behavioural trait scores were tested for using Linear Mixed Models (LMMs) performed using the ‘lmer’ function in package ‘lme4’ (Bates *et al* 2015). Temperature, UV, time of day and SVL were included as fixed effects to account for potential confounding influences. Sex and age were inputted as fixed effects whilst individual was included as a random effect. The model was reduced through stepwise removal of potential confounding factors, to ascertain which factors had no significant effect on the response variable. Separate models were utilised for each behavioural trait and retained for the calculation of repeatability. The significance of age and sex effects upon each behavioural trait was determined using likelihood ratio tests comparing a full model containing the effect under investigation against a model with that effect removed. All models used a Gaussian distribution, with dispersal scores log-transformed to meet the assumption of normality. Sociability scores displayed non-normal distribution but were unable to be fitted to any statistical families using transformation, preventing use of a General Linear Mixed Model. The unusual distribution of this response was considered when interpreting results. Residual plots of models were examined to confirm assumptions of normality and homogeneity of variance were met.

### 3.3.2 Repeatability of behaviours

The repeatability of behavioural traits was calculated with the function ‘rpt’ in package ‘rptR’ (Schielzeth and Nakagawa 2013) using the models retained from LMM analysis. Repeatability is a measure of consistent between-individual differences and a function of within-individual and between-individual variance (Nakagawa and Schielzeth 2010). For each model bootstrapping and permutation were set at 1000 runs to calculate 95% confidence intervals and significance respectively. UV was included as a confounding factor in models for exploration, activity and dispersal, therefore the repeatability values obtained for these measures are termed ‘adjusted repeatability’ (Nakagawa and Schielzeth 2010). Repeatability values were calculated for the whole sample population and for each age cohort separately.

### 3.3.3 Dispersal syndromes and personality-dependent dispersal

Behavioural trait data were analysed using Spearman’s rank correlation and Principal Component Analysis (PCA) to test for the occurrence of behavioural syndromes. The non-parametric Spearman’s rank correlation was chosen to account for the log-transformation on dispersal and the non-normal distribution of sociability. Analyses tested for the correlation of dispersal against activity, exploration and sociability, and correlations between activity, exploration and sociability. As some behavioural traits were correlated, a PCA was performed to obtain orthogonal principal components capable of highlighting multiple trait relationships linked in a behavioural syndrome. Principal components to be retained were determined through the examination of a scree plot and conducting parallel analysis using the package ‘paran’ (Dinno 2012). Only traits with a loading greater than 0.4 were considered to contribute to a principal component, following Lantová *et al* (2011). As exploration and activity had significant loadings, LMMs were run to test for an effect of exploratory or active personality types on dispersal. UV was included as a fixed factor in both models and significance was determined using a likelihood ratio test, as above.

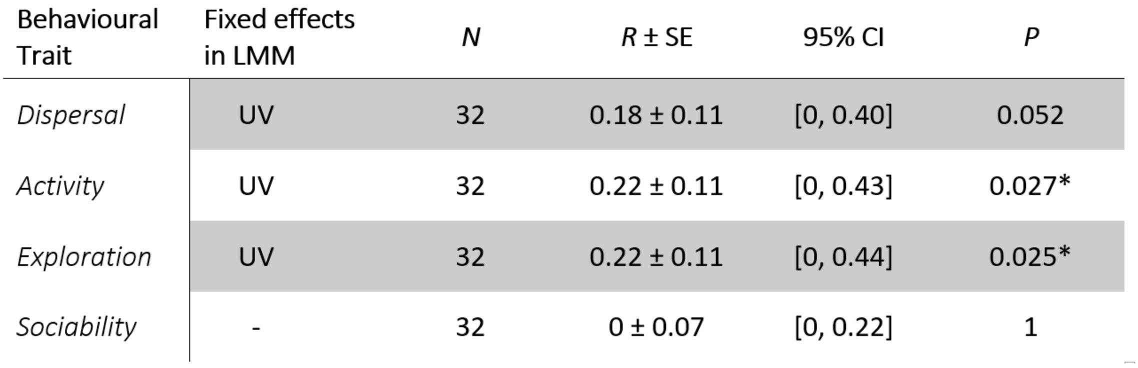
# 4. Results

Following stepwise removal of factors from LMMs, only UV was included in the final models for dispersal, exploration and activity as a significant confounding factor. None of the confounding factors examined were found to influence sociability scores.

## 4.1 Consistent behavioural differences between individuals

Exploration and activity scores demonstrated significant repeatability, Table 2. Dispersal times and sociability scores were not significantly repeatable.

**Table 2. Repeatability of behavioural traits.**



| Behavioural Trait | Fixed effects in LMM | *N* | *R* ± SE | 95% CI | *P* |
|---|---|---|---|---|---|
| *Dispersal* | UV | 32 | 0.18 ± 0.11 | [0, 0.40] | 0.052 |
| *Activity* | UV | 32 | 0.22 ± 0.11 | [0, 0.43] | 0.027* |
| *Exploration* | UV | 32 | 0.22 ± 0.11 | [0, 0.44] | 0.025* |
| *Sociability* | - | 32 | 0 ± 0.07 | [0, 0.22] | 1 |

### 4.1.1 Repeatability across ontogeny

The one-year old cohort did not demonstrate repeatable dispersal times, activity, exploration, or sociability, Table 3. The two-year old cohort displayed significantly repeatable dispersal times, activity and exploration, but not sociability.

**Table 3. Repeatability of behavioural traits for one-year and two-year old cohorts.**

| Behavioural Trait | Age | Fixed effects in LMM | *N* | *R* ± SE | 95% CI | *P* |
|---|---|---|---|---|---|---|
| *Dispersal* | 1 | UV | 16 | 0.19 ± 0.15 | [0, 0.53] | 0.101 |
| | 2 | UV | 16 | 0.18 ± 0.11 | [0, 0.41] | 0.048* |
| *Activity* | 1 | UV | 16 | 0.01 ± 0.11 | [0, 0.37] | 0.454 |
| | 2 | UV | 16 | 0.22 ± 0.11 | [0, 0.45] | 0.02* |
| *Exploration* | 1 | UV | 16 | 0 ± 0 | [0] | 1 |
| | 2 | UV | 16 | 0.23 ± 0.12 | [0.02 ,0.47] | 0.015* |
| *Sociability* | 1 | - | 16 | 0 ± 0.1 | [0, 0.36] | 1 |
| | 2 | - | 16 | 0.15 ± 0.15 | [0, 0.5] | 0.157 |

## 4.2 Age and sex effects

Effects of age and sex on behavioural traits are displayed in Table 4. Dispersal time was influenced by age, with one-year old individuals dispersing faster than two-year old individuals ($\chi^2_1 = 16.11$, $p < 0.001$, Figure 4a). There was no effect of age on activity ($\chi^2_1 = 1.99$, $p = 0.158$, Figure 4b), exploration ($\chi^2_1 = 2.99$, $p = 0.083$, Figure 4c) and sociability scores ($\chi^2_1 = 0.28$, $p = 0.599$, Figure 4d). Sex was found to influence all four behavioural traits, with males showing significantly higher activity ($\chi^2_1 = 6.25$, $p = 0.012$, Figure 5b) and exploration ($\chi^2_1 = 4.1$, $p = 0.043$, Figure 5c) scores, and dispersing from the release square faster than females ($\chi^2_1 = 7.11$, $p = 0.008$, Figure 5a), whilst females demonstrated higher sociability ($\chi^2_1 = 6.88$, $p = 0.009$, Figure 5d).

**Table 4. Summary of age and sex effects on behavioural traits. A ✓ indicates a significant effect.**

| Behavioural Trait | Age | Sex |
|---|---|---|
| *Dispersal* | ✓ $p < 0.001$ | ✓ $p = 0.008$ |
| *Activity* | $p = 0.158$ | ✓ $p = 0.012$ |
| *Exploration* | $p = 0.083$ | ✓ $p = 0.043$ |
| *Sociability* | $p = 0.599$ | ✓ $p = 0.009$ |

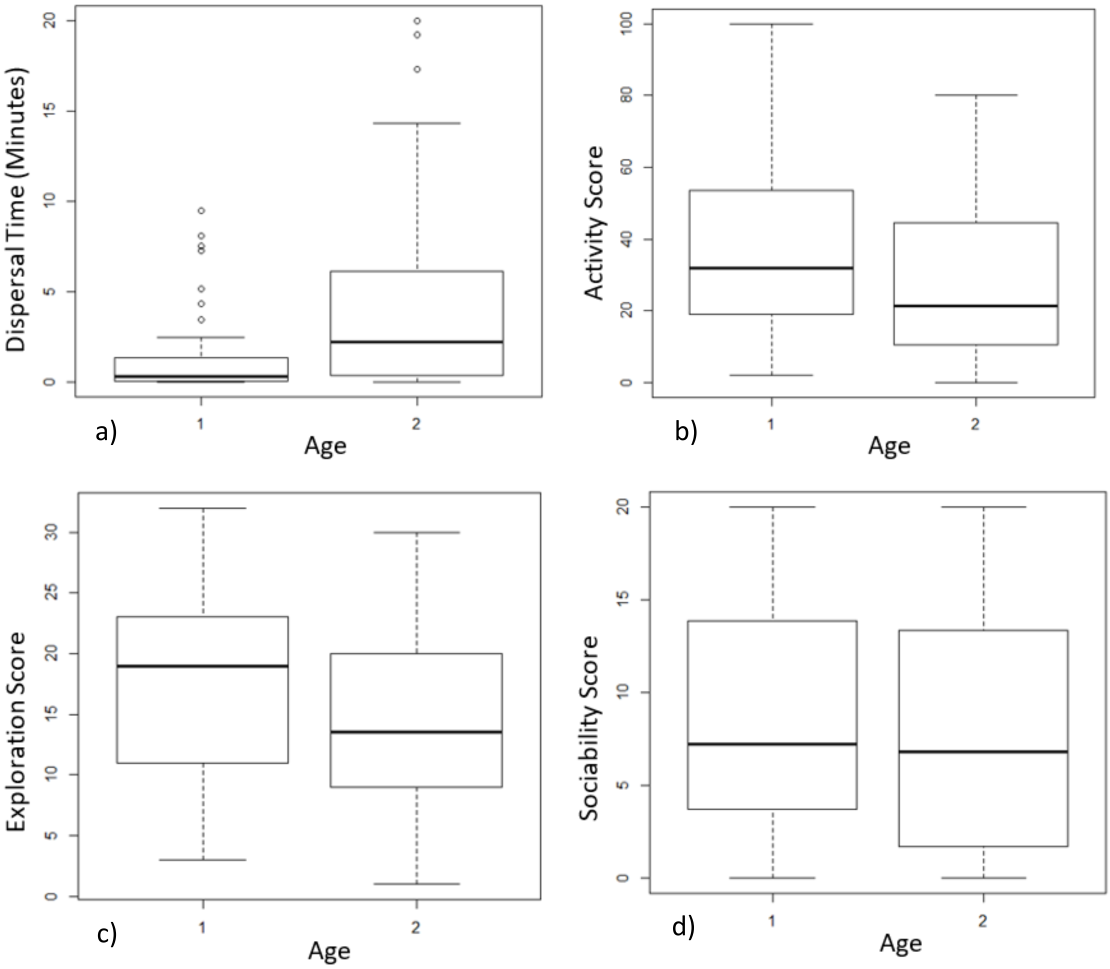


**Figure 4.** Boxplots presenting the mean, quartiles, and range of a) dispersal time, b) activity score, c) exploration score and d) sociability score for the one-year old cohort (1) and two-year old cohort (2).

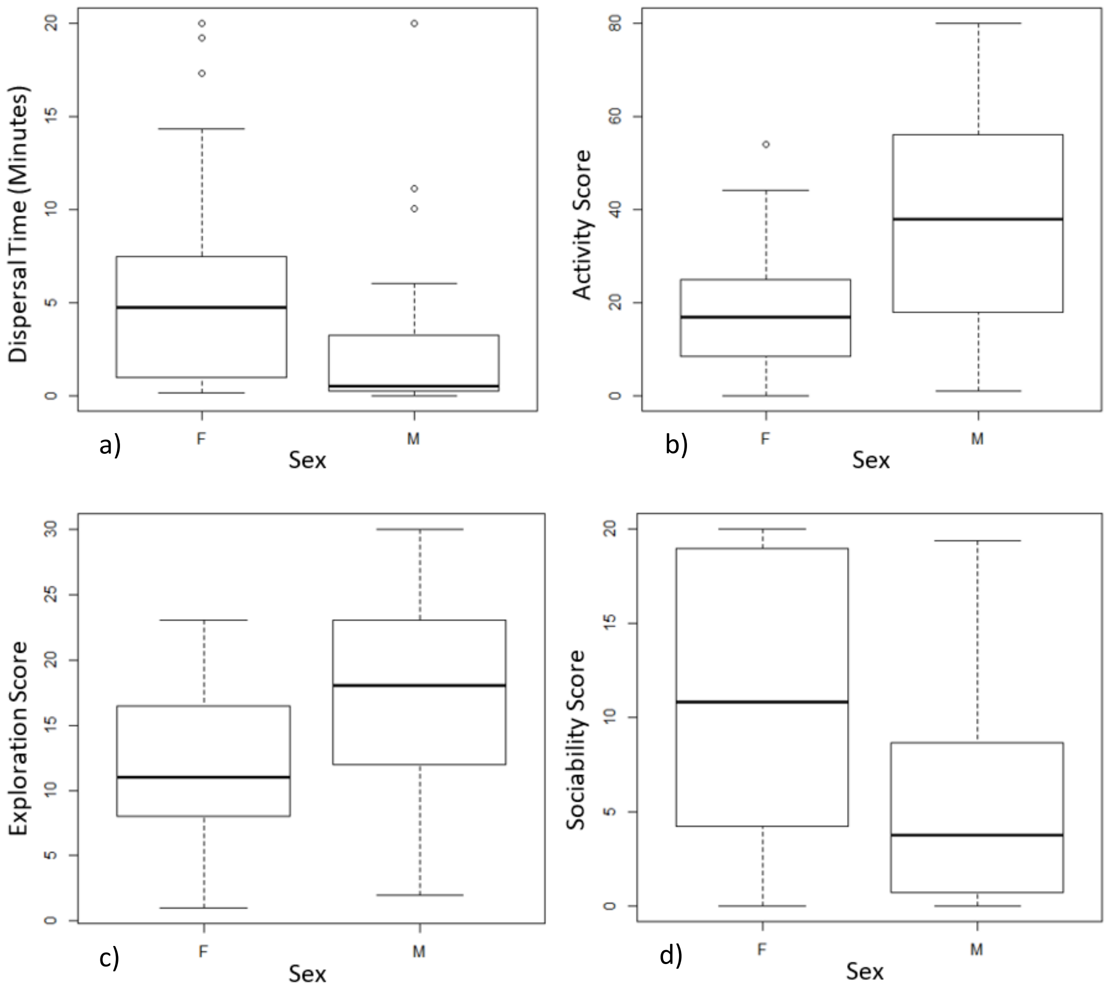
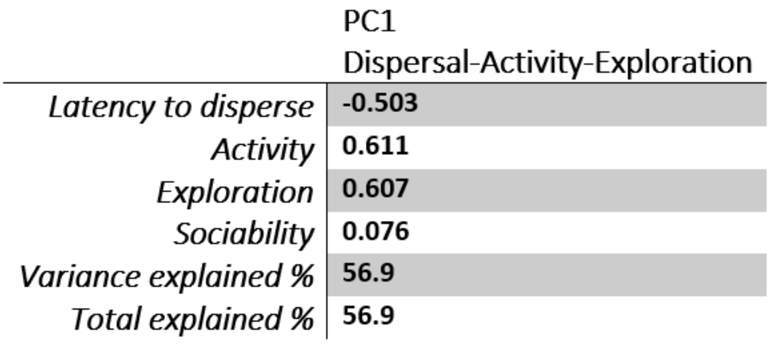


**Figure 5.** Boxplots presenting the mean, quartiles, and range of a) dispersal time, b) activity score, c) exploration score and d) sociability score for females (F) and males (M).

## 4.3 Dispersal syndrome

Dispersal correlated positively with exploration ($r_s = -0.534$, $p < 0.001$ ) and activity ($r_s = -0.562$, $p < 0.001$), but not sociability ($r_s = -0.106$, $p = 0.304$). Individuals with higher exploration and activity scores demonstrated a higher propensity for initial dispersal. Exploration and activity also correlated ($r_s = 0.872$, $p < 0.001$). Sociability did not correlate with either activity ($r_s = 0.036$, $p = 0.729$) or exploration ($r_s = 0.067$, $p = 0.515$). Following PCA, a scree plot (Appendix B) and parallel analysis argued for the retention of one principal component which accounted for 56.7% of the variance. Component loadings of dispersal, activity and exploration contributed to PC1, Table 5. Faster dispersal times present lower dispersal scores yet relate to greater immediate dispersal tendency, thus dispersal time is referred to here as ‘Latency to disperse’ to clarify the relationship of dispersal tendency to behavioural trait scores. Latency to disperse demonstrated a negative relationship with activity and exploration, Figure 6. Inversely, immediate dispersal tendency demonstrates a positive relationship with activity and exploration.

**Table 5. Principal component loadings for PC1**



| | PC1 Dispersal-Activity-Exploration |
|---|---|
| *Latency to disperse* | **-0.503** |
| *Activity* | **0.611** |
| *Exploration* | **0.607** |
| *Sociability* | **0.076** |
| *Variance explained %* | **56.9** |
| *Total explained %* | **56.9** |

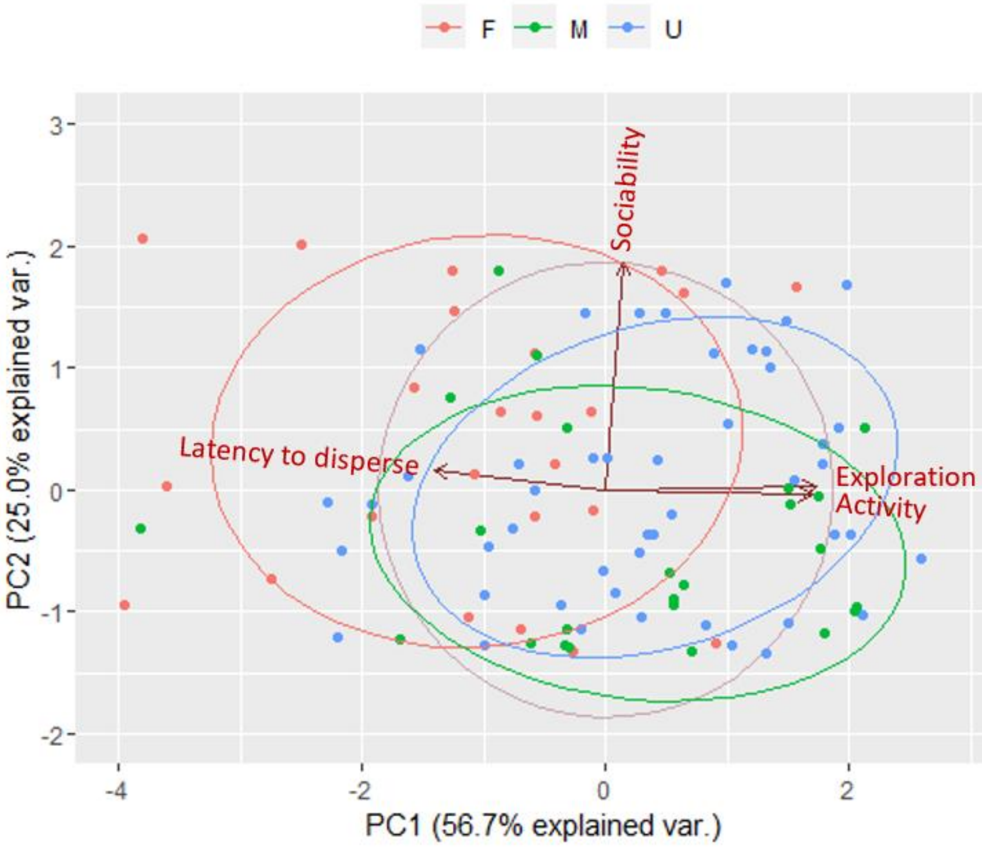


**Figure 6.** Behavioural trait scores and dispersal times on the first two axes of the PCA. As lower dispersal times relate to higher dispersal propensity the label 'Latency to disperse' is used to clarify the relationship between traits. Orange circles represent two-year old females (F), green circles two-year old males (M) and blue circles unsexed one-year olds (U), each with 95% confidence ellipses. Shown with correlation circle.

# 5. Discussion

Reintroduction outcomes can be affected by individual personality types and post-release dispersal. The presence of animal personality has been exhibited in numerous taxa, yet research into the effect of consistent behavioural differences on post-release dispersal remains limited (Richardson 2015; Weiss 2018). This study investigated individual variation in behavioural traits and immediate dispersal propensity in a captive population of sand lizards. Results provide evidence for exploratory and active personality types in captive-bred sand lizards, and the presence of a dispersal syndrome and personality-dependent dispersal. This study also demonstrated that repeatability can vary across age groups and behavioural trait scores can vary with age and sex.

## 5.1 Consistent behavioural differences in sand lizards

Significant repeatability of exploration and activity behavioural scores in captive sand lizards were observed, indicative of sand lizards displaying exploration-avoidance and active-sedentary personality types. Consistency in activity and exploratory behaviour has also been found in various species of birds, mammals, reptiles, amphibians and invertebrates, suggesting that these are common personality types found across taxa (Dingemanse *et al* 2002; Aragón *et al* 2006; Lantova *et al* 2011; Cote and Clobert 2012; David *et al* 2012; Kanda *et al* 2012; Herde and Eccard 2013; Dahirel *et al* 2015; Richardson 2015; Gruber *et al* 2017).

The presence of activity and exploration personality types in sand lizards holds implications for fitness and reintroduction success. Exploratory behaviour has been linked to an increased risk of predation and individuals with high exploration scores may have a greater chance of being predated upon (Jones and Godin 2010; Haage *et al* 2013). However, these individuals may also encounter more mating opportunities and novel resources (Haage *et al* 2013; Bosco *et al* 2017). The relationship between post-release fitness and personality is often complex, involving trade-offs and differing across contexts (Haage *et al* 2017). More active individuals can exhibit greater resource acquisition through increased foraging and prospecting but will likely also increase predation risk and energy expenditure (Sih *et al* 2015; Kelleher *et al* 2018).

Sociability scores were not consistent amongst individuals, suggesting that sand lizards demonstrate flexible social behaviour. This would imply that individuals are not inherently social or asocial and are unlikely to be affected by conspecifics during release. However, it is possible that the method used is inadequate to measure social behaviour in reptiles. Sand lizards are often in physical contact during social basking, possibly as a heat sharing mechanism, but focal lizards were physically separated from conspecifics (Blanke and Fearnley 2015). The study that developed this assay also failed to detect repeatable sociability behaviours in its study species, the delicate skink (Michelangeli *et al* 2017). The unusual distribution of sociability data further encourages caution, and additional study would be required to confidently claim that sand lizards do not exhibit social personalities.

Individuals did not show repeatable immediate dispersal tendency contrary to evidence for consistent dispersal behaviour in lizard species (Clobert 2012; Michelangeli *et al* 2017). However, repeatability was approaching significance ($p = 0.052$). The sand lizard population showed between-individual variation in dispersal tendency, yet this study could not confidently state that dispersal tendency is consistent within individuals. A larger sample size would provide confidence to state whether dispersal propensity is a repeatable trait in sand lizards.

Behavioural repeatability scores appeared low, even when significant, which is a common finding in personality studies (Cote *et al* 2010a). Meta-analysis of personality research found that repeatability results averaged around 0.37 and were lower in assay conditions and vertebrates than field experiments and invertebrates (Bell *et al* 2009). As repeatability is more commonly found when observing behavioural traits in more natural scenarios, it is possible that repeatability results in this study are underestimated. It is worth considering that unconsidered or unmeasurable confounding variables potentially impacted the results of assays. Behaviour can be state dependent, and not all possible states were measured due to practical constraints (Dochtermann *et al* 2015; Sih *et al* 2015; Kelleher *et al* 2017). For instance, hunger is known to effect behavioural response, but due to the semi-natural environment lizards were housed in between assays, feeding patterns could not be ascertained (Brodin 2009).

### 5.1.1 Behavioural repeatability across ontogeny

Due to the short-term nature of the project, a direct comparison of the state of the same individuals at different ages was unable to be made. However, it was possible to determine whether there were differences in repeatability between the juvenile and sub-adult cohorts, which provides information about the development of personality in sand lizards. Analysed separately, the 2-year old cohort showed significantly repeatable exploration, activity and dispersal tendency, whereas the 1-year old cohort did not. This is in concurrence with several studies that have found evidence of consistent behavioural differences in adults but not juveniles of the same species (Sinn *et al* 2008; Gyuris *et al* 2012; Urszán *et al* 2015; Favati *et al* 2016; Stanley *et al* 2017). These findings infer that behavioural traits could become fixed with age, suggesting behavioural flexibility declines over the course of development (Debeffe *et al* 2015; Stamps and Krishnan 2017; Zablocki-Thomas *et al* 2018).

Differences in repeatability across ontogeny may be rooted in the effect of new experiences, environments and changes in physiology, particularly at key developmental stages (Stanley *et al* 2017; Kelleher *et al* 2018; Zablocki-Thomas *et al* 2018). Hormonal and morphological changes associated with sexual maturation have the potential to cause changes in behavioural traits and thus personality (Stamps and Groothuis 2010; Bosco *et al* 2017; Zablocki-Thomas *et al* 2018). The 2-year old sand lizards in this study produced viable offspring, whilst this ability has not been observed in any 1-year old cohort. This implies that individuals sexually mature following their second hibernation and may concurrently develop more fixed behaviours. These differences in behavioural consistency likely have an adaptive component (Stamps and Groothuis 2010). Selection pressures vary with age, with sexual selection playing a significant role following maturation (Bosco *et al* 2017; Stanley *et al* 2017). Whilst younger individuals main pressure is to survive to reproductive age, there is increased pressure on mature individuals to reproduce (Stamps and Groothuis 2010; Bajer *et al* 2015). Juveniles may experience greater survival rates if they show flexible responses to new environments and experiences, whilst stabilisation of behaviour may result in mature individuals displaying patterns most effective to achieve reproductive success, possibly as a trade-off between reproduction and survival (Stanley *et al* 2017). Moreover, prolonged time in captivity can cause declines in behavioural flexibility (Mason *et al* 2013).

Consistent sociability was not observed in either age cohort. This could imply that social behaviour shows constant levels of variance across these life stages, with no development of social personality. Captive conditions can constrain social environments, disrupting the development of social behaviours (Mason *et al* 2013). However, aforementioned methodological constraints may have influenced results.

## 5.2 Factors influencing behavioural trait variation

UV influenced dispersal, activity and exploratory behaviour, concurrent with previous research that demonstrates UV incidence influences sand lizard behaviour and activity levels (Blanke and Fearnley 2015; Govier 2017). Size had no impact on behaviour scores contrary to studies that suggest body size can affect personality, with active and exploratory individuals often larger (Kelleher *et al* 2017; Niemelä and Dingemanse 2018; Zablocki-Thomas *et al* 2018). Temperature and time of day did not affect behaviour despite research suggesting that temperature and temporal factors influence daily activity (Blanke and Fearnley 2015; Govier 2017).

### 5.2.1 Effect of age and sex on behavioural traits

#### *5.2.1.1 Age*

The one-year old cohort demonstrated a greater propensity towards immediate dispersal than the two-year old cohort, aligning with observations that dispersal occurs predominantly in juvenile sand lizards (Blanke and Fearnley 2015). Natal dispersal often functions to reduce kin competition and prevent inbreeding, and it is possible the associated drive has been retained in these captive juveniles as they have been unable to disperse (Cote and Clobert 2012; Matthysen 2012). Conversely, the 2-year cohort reached sexual maturity and bred following prolonged experience in a confined environment, which may have reduced their tendency to disperse due to habituation and a loss of adaptive benefits (Clobert 2012; David *et al* 2012). Additionally, dispersers may be selected against due to lower fitness in a captive environment (Mason *et al* 2013; McCowan *et al* 2014). Age has previously been shown as a factor effecting mean behavioural scores, and experience can affect behavioural responses (Stamps and Groothuis 2010). Selection pressures on ages differ, potentially resulting in alternate behavioural strategies being optimal at different ontogenetic stages (Brodin 2009; Wilson and Krause 2012; Bajer *et al* 2015).

There was no difference in exploration, activity and social scores between ages. Natural history records imply greater social interaction between younger individuals, with juvenile sand lizards aggregating to bask (Blanke and Fearnley 2015). Greater exploratory behaviour has also been recorded for juveniles across taxa (Bajer *et al* 2015; Stanley *et al* 2017). These patterns may have not been observed in this study as the behaviour of captive-bred individuals can differ from wild counterparts, due to alternate pressures of a constrained environment (Mason *et al* 2013; McCowan *et al* 2014). However, exploratory behaviour may appear level across ages where exploration is important at multiple stages, despite different pressures, such as mate finding in mature cohorts and food acquisition in juvenile cohorts (Stanley *et al* 2017). Moreover, the stability of traits across development can be attributed a lack of flexibility in genetic mechanisms controlling behaviour (Brodin 2009; Dochtermann *et al* 2015; Kelleher *et al* 2018).

#### *5.2.1.2 Sex*

Males demonstrated greater dispersal tendency, exploration and activity scores than females, whilst females displayed greater average social behaviour. These differences may be in part due to ecological variation and sexual selection placing different pressures on males and females (Bosco *et al* 2017; Zablocki-Thomas *et al* 2018). Male-biased dispersal has been recorded in multiple lizard species and male sand lizards in a Swedish population were found to disperse further than females (Massot *et al* 2003; Johansson *et al* 2008; Ujvari *et al* 2008; Calsbeek *et al* 2014) This could be attributed to male sand lizards occupying larger home ranges (Olsson 1986; 1988; Olsson *et al* 1996). Sex-specific differences in behaviour can be related to a species mating system (Wey *et al* 2017). In polygamous species such as sand lizards, males that demonstrate greater activity and exploration likely have higher reproductive success due to increased mating opportunities (Olsson 1986; Haage *et al* 2013; Bosco *et al* 2017; Kelleher *et al* 2018). Although results provided no evidence of social personality in individuals, females demonstrated a higher mean tendency towards social interaction. Differences in social interactions have been observed between sexes in sand lizards. Female lizards are frequently found basking together whilst male-male interactions are often aggressive, especially during the breeding season (Blanke and Fearnley 2015).

## 5.3 Dispersal syndrome in sand lizards

PCA results provide evidence for an activity-exploration-dispersal syndrome, suggesting the presence of an active-exploratory disperser type. Significant correlations were found between dispersal and exploration, dispersal and activity and exploration and activity, further supporting the presence of a dispersal syndrome. Activity and exploration have been found to correlate with dispersal across various taxa (Debeffe *et al* 2014; Dahriel *et al* 2015; Cote *et al* 2017; Merrick and Koprowski 2017). Dispersal usually requires movement into novel environments, therefore it is logical to hypothesize that exploratory individuals have a higher propensity for dispersal (Anthony and Blumstein 2000; Dingemanse *et al* 2003). Dispersal itself has been used as a measure of exploration in the Iberian wall lizard (Rodríguez-Prieto *et al* 2011). In addition, a positive genetic correlation between exploration and dispersal has been discovered in the great tit, suggesting that dispersal and exploratory behaviour can be genetically coupled (Korsten *et al* 2013). As an active process, it is further reasonable to conclude that individuals at the sedentary end of the activity spectrum exhibit lower dispersal propensity (Cote *et al* 2010b; Debeffe *et al* 2014). The presence of a syndrome in sand lizards implies that there is selection for trait covariance, and that evolutionary pressures acting on one trait will likely act on other traits in the syndrome (Duckworth 2012; McEvoy *et al* 2015; Richardson 2015). However, it is advisable to be cautious when making inferences from syndromes as hidden variation may influence results (Ronce and Clobert 2012). Potentially confounding variables may have been overlooked or unfeasible to measure as discussed in section 5.1.

The positive correlation between exploration and activity could be attributed to these personality types being scored in a concurrent assay. Issues surrounding the independence of activity and exploration, measured using active behaviours or in simultaneous assays, have been highlighted in previous studies (Ibáñez *et al* 2009; Kanda *et al* 2012). Nevertheless, open field tests using a novel environment have been used to measure activity and exploration in numerous personality studies and are considered reliable indicators of these traits (Ibáñez *et al* 2009; Carter *et al* 2013; Perals *et al* 2017; Newar and Careau 2018). Whilst it could be argued that measuring both exploration and activity in the same assay could compromise independence, exploration is an inherently active trait and the two may not be functionally discrete (Cote *et al* 2010b). However, the assay used in this study distinguished activity as the overall movement observed, in contrast to defining exploration as the tendency to move into novel areas. Therefore, theoretically an individual could obtain a high activity score despite a low exploration score by being active in just a small section of the vivarium, and this was observed in some individuals.

No relationship was found between social behaviour and dispersal, suggesting that dispersers show similar variation in social behaviour to individuals with low dispersal propensity. This is concurrent with dispersal syndrome research in the delicate skink, however the study cautioned that a competitive environment may have impacted results (Michelangeli *et al* 2017). In contrast, social behaviour has been found to have a key role in dispersal decisions in the common lizard (Cote *et al* 2007). The uncertainty of sociability results, due to issues with method and data distribution discussed in section 5.1, advocates caution in concluding that there is no relationship between social behaviour and dispersal in sand lizards.

## 5.4 Personality-dependent dispersal

Exploration and activity were found to significantly effect dispersal tendency, suggesting the presence of personality-dependent dispersal in sand lizards. These results support growing evidence that suggests individual dispersal behaviour can be affected by personality. Dispersing individuals have been found to display more active personality types in the common lizard, (Aragón *et al* 2006; Meylan *et al* 2009) and more exploratory personality types in the great tit, house mouse, common lizard and cane toad (Dingemanse *et al* 2003; Krackow 2003; Cote and Clobert 2012; Gruber *et al* 2017).

The presence of personality-dependent dispersal implies that variation in personality types in a population creates variation in dispersal propensity amongst individuals. During each stage of dispersal individuals are subject to specific selection pressures, and different phenotypes are likely to arise which result in some individuals being better adapted, or more inclined, towards dispersal (Cote *et al* 2010a; Clobert 2012). It is possible that more exploratory and active individuals have higher fitness in dispersal scenarios and are better able to colonise new areas, resulting in the adaptation of a strategy linking these traits (Cote *et al* 2010a; Cote and Clobert 2012). This coupling has the potential to affect the structure of the population and spatial dynamics. If a non-random subset of a population emigrates following release, the remaining individuals will exhibit reduced variation in both dispersal and personality phenotypes, potentially reducing the behavioural diversity of the reintroduced population (Cote *et al* 2010a; Ronce and Clobert 2012).

## 5.5 Implications for reintroduction success

Sand lizards displayed consistent behavioural differences in exploratory and active behaviour, suggesting the population demonstrates variation along exploration-avoidance and active-sedentary personality spectrums. The presence of animal personality can impact demographic structure, maintain genetic diversity and influence the success of reintroductions (Merrick and Koprowski 2017). Variation in personality type implies that individuals will respond differently to the pressures of the translocation process, and knowledge of an individual's personality could be used to predict their response (Canessa *et al* 2014; Fitzgerald *et al* 2015). Using these predictions to select appropriate individuals for release has been recommended as a strategy to improve reintroduction success (Cote *et al* 2010a; Silva and Azevedo 2013; May *et al* 2016). For example, selectively releasing Tasmanian devils as they are predicted to have a higher survival rate following release (Sinn *et al* 2014). However, this would reduce behavioural variation in the reintroduced population, likely reducing adaptive potential and population resilience to environmental stochasticity (Cote *et al* 2010a; Richardson 2015). An alternate argument advocates for ensuring individuals with a variety of personality types are released in order to maximise the adaptive potential of the population (Powell and Gartner 2011; Stratton 2015; Cordero-Rivera 2017).

The propensity of younger individuals towards faster immediate dispersal could have some implication for the preferred age of release. Older individuals may be more likely to remain at the release site and contribute to the establishing population. However, there is a need to balance the potential benefits of delayed release with the cost of increasing time in captivity, which may lead to animals becoming adapted to the captive environment whilst incurring greater husbandry costs (Canessa *et al* 2014; Blanke and Fearnley 2015; Dutra *et al* 2016). Additionally, the 1-year old cohort showed greater variance in behaviour than the

2-year old cohort. If younger individuals display more flexible behavioural responses it could be inferred that they would be better suited to survive in a novel environment, as this implies they could respond quickly to environmental change (Nussey *et al* 2007; Carter *et al* 2012).

The presence of a dispersal syndrome and personality-dependent behaviour enables predictions to be made about the dispersal tendencies of individuals (Cote *et al* 2010a; Ronce and Clobert 2012). Results from this study would suggest that individuals with higher exploration and activity scores will show faster immediate dispersal following release. Previous studies would suggest that exploratory behaviour is an effective predictor of post-release dispersal, but caution that short-term dispersal patterns do not necessarily predict long-term dispersal (Dingemanse *et al* 2003; Richardson 2015). Further research is required to validate whether mock-release results successfully predict responses at wild release, and if the immediate dispersal metric is applicable to long-term dispersal patterns.

Soft-release strategies have been trialled to reduce post-release dispersal, in which animals are held in an acclimatisation pen at the reintroduction site prior to release. (Hardman and Moro 2006; Knox and Monks 2014). This strategy has produced mixed results in lizard species, resulting in reduced dispersal in jewelled geckos, *Naultinus gemmeus*, but increased dispersal in the pygmy bluetongue lizard, *Tiliqua adelaidensis*, attributed to the stress caused by confinement (Ebrahimi and Bull 2013; Knox and Monks 2014; Knox *et al* 2017). Soft-releases could be trialled as a tool to reduce post-release dispersal in sand lizards.

The context surrounding a reintroduction project may influence whether dispersal is considered advantageous, for instance increased dispersal could assist the colonisation of large sites (Richardson *et al* 2015). An integrated landscape approach, considering the site's structure and connectivity to surrounding areas, has the potential to aid the establishment of a network of metapopulations. Enabling movement between populations would promote gene flow and local resilience of species, resulting in more sustainable reintroduction outputs over the long-term (Anthony and Blumstein 2000; Clobert *et al* 2009; Richardson *et al* 2015). Scale should therefore be considered when planning reintroductions.

# 6. Limitations

Results are limited to the captive population studied and may have reduced applicability to natural systems. Furthermore, assays conducted focussed on precise behaviours measured in artificial circumstances and elements of behaviour observed were likely influenced by a stress-response from handling (Dickens *et al* 2010; Roche *et al* 2016). Acclimation times were implemented to enable individuals to resume normal behaviour before recording commenced and prevent stress effects confounding behaviours. Yet individuals likely demonstrate variation in stress response and there is uncertainty around the time needed for individuals to recover from handling (Carere and van Oers 2004; Roche *et al* 2016). Comparing measures to behavioural observations could validate the applicability of behavioural assays to daily behaviours of lizards in their semi-natural environment. However behavioural observations are limited where species are cryptic and are subject to multiple confounding factors (Martin and Bateson 2007; Carter *et al* 2013; Woodfine *et al* 2017).

Personality research is a relatively new field and there are common inconsistencies and obstacles that can add complexity to the interpretation of results (Carter *et al* 2013; Roche *et al* 2016). Methodology across studies are not standardised and often require modification to be practical or ecologically relevant to the study species (Dall and Griffith 2014; Weiss 2018). Additionally, there are discrepancies in labelling traits known as the 'jingle-jangle' fallacy which further confounds comparisons of results between studies (Roche *et al* 2016; Perals *et al* 2017). There can be uncertainty surrounding what is truly being measured in an assay, and whether it is appropriate to measure the behaviour or personality type in question (Carter *et al* 2013; Perals *et al* 2017). This can be clarified by conducting multiple assays intended to measure the same trait, and test correlations between them in a principal component analysis (Haage *et al* 2013; 2017). The dispersal assay measured the immediate tendency of an individual as the time to disperse from a release square, and the applicability of this metric to further aspects of dispersal behaviour is uncertain. Further research proposed to address this is detailed in section 7.

Statistical power was restricted by a small sample size, owing to the number of captive individuals available. Practical limitations are common in ecological studies, but future research would ideally incorporate larger sample sizes to increase the certainty of results and conviction of their associated implications (Nakagawa 2004; Taborsky 2010). There was substantial delay in commencing data collection due to poor weather conditions which restricted the amount of data gathered. In addition, repeats were pushed closer together than preferred, potentially reducing the independence of data. Short-term repeatability is more common than long-term repeatability, therefore shorter intervals between assays are more likely to give significantly repeatable results (Herde and Eccard 2013). Individuals could have become habituated across repeats, resulting in ‘novel’ environments becoming familiar and affecting responses (Ellenberg *et al* 2009; Rodríguez-Prieto *et al* 2011). Future study could incorporate measures of habituation in data collection and analyses.

Sociability scores displayed an unusual distribution which was unable to be transformed to fit a known family. A decision was made to include the response in analysis. As no significant results were found regarding the repeatability of sociability or its relationship with dispersal, there was no dilemma of possible false positives. The distribution was considered when discussing results and caution around inferences advised.

# 7. Further Study

Further data to be collected during the reintroduction process will be used to assess the predictive power of captive assays to individual responses at release. Immediate dispersal behaviour will be recorded during wild release using the methodology of this study, thus enabling comparison to the response shown in a captive novel environment. It is intended that focal individuals of appropriate weight will be radio-tagged and tracked using radio telemetry following release. Movement patterns will be monitored beyond the immediate release response, to determine whether this initial response is an effective predictor of long-term dispersal patterns. Results from this research can be used to determine whether a mock release trial in captivity can be used to predict an individual's response to release in the wild, and whether this is applicable to long-term movement patterns in addition to immediate dispersal. Post-release monitoring of focal individuals could also be used to assess the effect of personality on post-release survival and the movement ecology of tagged lizards. If variation in animal personality is found to relate to survival and movement patterns, this would provide a further predictive dimension to the outcome of sand lizard reintroductions.

Uncertainty around the personality type being measured is a common limitation of personality assays, as discussed in section 6 (Carter *et al* 2013). Confidence could be improved by comparing assays to behavioural observations, such as tongue-flicking for exploration, and alternate assays, as in Haage *et al* (2013; 2017). Multiple measures are taken from a combination of assays and analysed in a PCA. This determines which measures contribute to each principal component that can be attributed to personality types, minimising the risk of a jingle-jangle fallacy (Perals *et al* 2017). An alternate sociability assay could be conducted following Cote and Clobert (2007), which found evidence of repeatable social behaviour in the common lizard.

Further research could investigate additional variables that were beyond the scope of this project. Animals vary in their ability to cope with stressors dependent on their personality, and variation in individual stress coping responses has been found to effect dispersal and the outcome of translocations (Meylan et al 2002; Carere and van Oers 2004; Dickens *et al* 2010; Ebrahimi and Bull 2013). Stress can be monitored by recording hormone fluctuations and breath rate during handling. Analysis of behavioural responses in relation to indicators of stress could reveal the impact of stress on release responses and reintroduction outcomes (Meylan *et al* 2002; Carere and van Oers 2004). Locomotor ability may correlate with dispersal (Dahirel *et al* 2015; Legrand *et al* 2015; Denoël *et al* 2018). Locomotor performance in sand lizards has previously been assessed by Govier (2017) by inducing running in a 'racetrack'. The possible role of locomotor ability in a dispersal syndrome can then be tested for using PCA and correlations between locomotor performance, exploration, activity and dispersal (Newar and Careau 2018). Relatedness is another factor cited to effect dispersal and social behaviours. Closely-related individuals may show greater tolerance towards each other or greater drive to disperse from relations to avoid inbreeding (Cote *et al* 2010a; Cote and Clobert 2012). Inclusions of clutch identity in analysis could provide more robust sociability results and highlight any effects of relatedness on social behaviour and dispersal.

Future studies could take a genetic approach to personality-dependent dispersal, investigating the heritability of traits and exploring evolutionary causes and consequences. Techniques from quantitative genetics such as reaction norms can be adapted to behavioural research to examine these research questions (Wheat 2012; Roche *et al* 2016). Controlled breeding conditions would allow greater certainty of clutch origins, which would enable robust conclusions about heritability. Enhanced understanding of the evolutionary aspects of state-dependent behaviours will likewise improve knowledge of their ecological consequences, which can inform conservation (Duckworth 2012; Wolf and Weissing 2012).

# 8. Conclusion

This study reviewed the influence of individual variation in behaviour and dispersal tendency on reintroduction outcomes and examined the evidence for correlative and causative relationships between personality and dispersal. Assays were conducted to investigate the presence of personality, dispersal syndromes and personality-dependent dispersal behaviour in the sand lizard, *Lacerta agilis*.

Sand lizards demonstrated consistent behavioural differences between individuals indicative of exploration and activity personality types which may have implications for individual fitness and reintroduction success. Repeatability of exploration and activity was significant in the 2-year old cohort but not across 1-year olds, suggesting a developmental component of personality by which behaviours become more fixed over time. Age effected dispersal behaviour, whilst sex influenced all behavioural traits responses, likely due to ecological differentiation and variation in selection pressures. These results may hold implications for preferred age at release. This study found evidence for the presence of an activity-exploration-dispersal syndrome and personality-dependent dispersal behaviour in sand lizards, indicating the potential to predict individual responses to reintroduction. Individual variation should be considered in reintroduction planning and techniques such as soft-releases can be trialled to manage immediate dispersal.

Research was limited by time constraints, a small sample size and uncertainty surrounding the applicability of results to reintroduction scenarios, restricting the confidence of conclusions. Additional study has been outlined that will enable a comprehensive evaluation of the predictive power of captive assay data to release responses. Continued monitoring of sand lizards post-release will further inform management to improve the establishment of populations and long-term sustainability.

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# Appendices

## Appendix A. Individual Identification

ID sheets were compiled for focal sand lizards to enable individual identification. Individuals were identified visually using dorsal patterning and colouration, Figure 7.

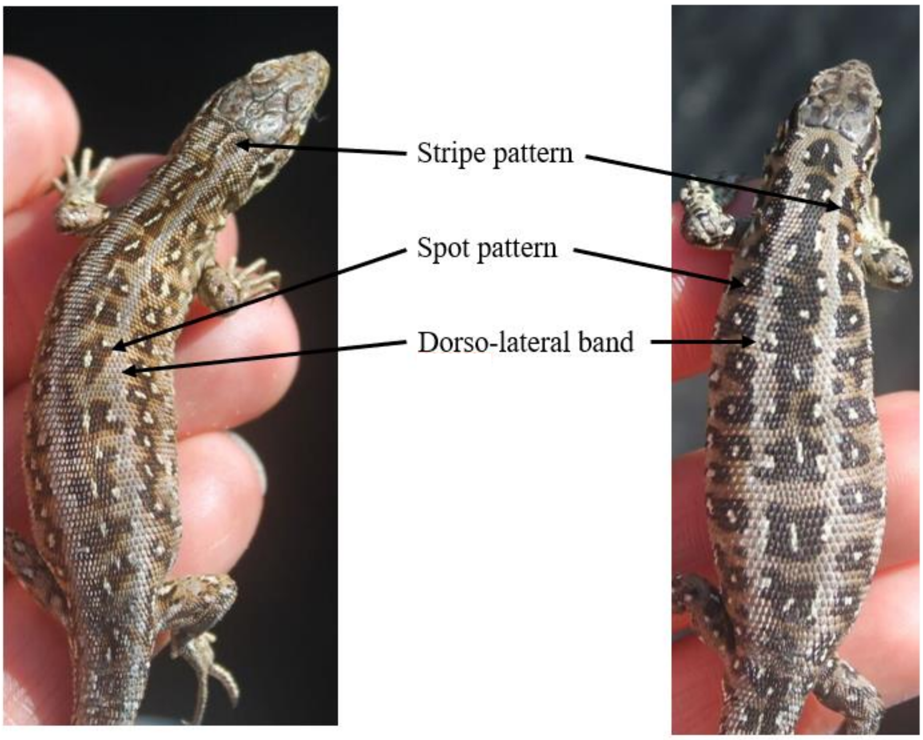

**Figure 7.** Individual identification photographs of two-year old female sand lizards; individual 17 (left) and individual 19 (right), for comparison. Individuals can be distinguished by examining the shape, size and colour of stripes, spot patterns and dorso-lateral bands.

# Appendix B. Scree plot

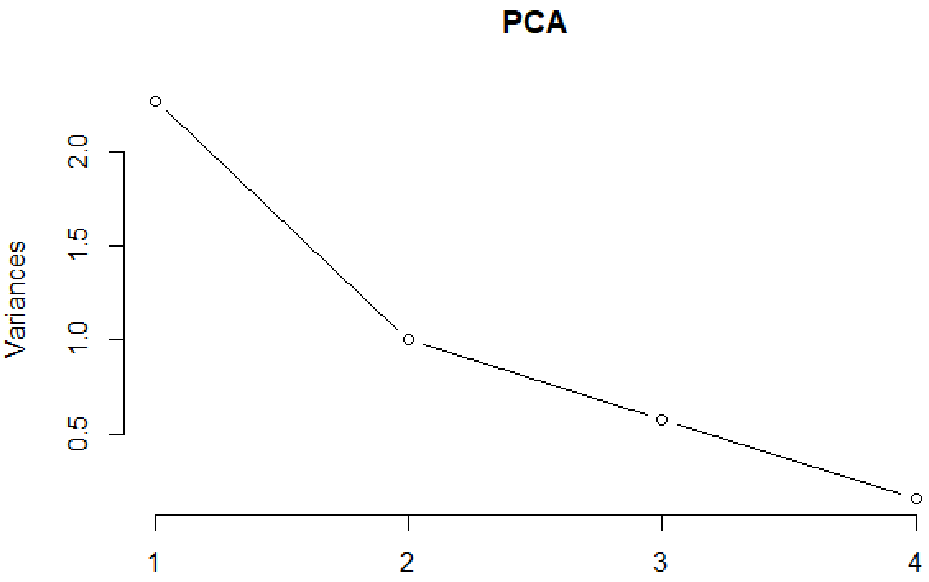

**Figure 9.** Scree plot of principal component analysis showing the variance of principal components. PC1 was retained and explained 56.7% of the variance.