

## RESEARCH ARTICLE

# Behaviour, body mass and sex: How intraspecific variation influences seed dispersal by a scatter-hoarding rodent

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**Abstract**

1. Intraspecific variation plays a pivotal role in shaping ecological dynamics. As the dispersal of seeds of most woody plants is mediated by animals, individual variation within the animal dispersers holds considerable implications for plant population and ecology.
2. We explored how individual traits (such as sex, body mass and exploration levels) of yellow-necked mice (*Apodemus flavicollis*) impact the dispersal of common oak (*Quercus robur*) acorns. Over 3 years, we collected data on seed fate and the specific mice responsible for their dispersal.
3. The relationship between individual traits and seed dispersal was not static, but influenced by yearly environmental conditions. Heavier individuals tended to carry seeds farther, yet contrary to our expectations, sex had no effect on the distance of seed dispersal. Moreover, the exploration rate showed an inconsistent association with seed consumption and dispersal distance, while it positively impacted the distance of dispersal from the nearest tree.
4. *Synthesis.* Our findings suggest a more nuanced role of individual traits in seed dispersal than often assumed, with noticeable annual variation significantly influencing these impacts. Consequently, it appears there is no single, universally beneficial individual type to ensure maximal benefits to plants. Rather, the traits conferring advantages in seed dispersal are dynamic, subject to change over time in response to environmental context.

**KEYWORDS**

animal personalities, behavioural ecology, conditional mutualism, functional ecology, individual variation, scatter-hoarding, seed dispersal, synzoochory

## 1 | INTRODUCTION

Intraspecific variation, a vital driver of ecological dynamics (Des Roches et al., 2018), has the potential to influence species interactions (Wolf & Weissing, 2012), community composition (Hausch et al., 2018) and ecosystem functioning (Bonaldo & Bellwood, 2008).

Intraspecific variation frequently manifests as ecologically significant differences in the morphology, physiology or behaviour of animals (Bolnick et al., 2003; Sih, Bell, & Johnson, 2004), stemming from factors such as sexual dimorphism (Shine, 1989), ontogenetic shift (Nakazawa, 2015) or personality traits (Sih, Bell, & Johnson, 2004). As a result, different individuals may assume quantitatively or

qualitatively different roles in interspecific interactions (McConkey & O'Farrill, 2015; Moran et al., 2022; Poisot et al., 2015). Moreover, if these roles are shaped by environmental context, they can undergo shifts over time in response to labile ecological conditions. Despite the importance of intraspecific variation, only a modest, albeit increasing, proportion of research studies collect and analyse ecological data at the individual level, as opposed to merely focusing on species averages (e.g. Eastcott et al., 2020; Jonsdottir et al., 2023; Khalil et al., 2019).

Seed dispersal is a critical ecological interaction that could be particularly affected by intraspecific variation (Schupp et al., 2019; Todd et al., 2022; Tsuji et al., 2020; Zvolak, 2018). Since seed dispersal is the primary means for plant movement, factors influencing this process can have direct effects on plant fitness, species distribution, community composition and patterns of biodiversity (Snell et al., 2019). By incorporating realistic variation in seed dispersal, as opposed to relying solely on mean estimates, the predicted risk of extinction, range shifts and biodiversity loss for plants maybe significantly modified (Snell et al., 2019).

Most woody plants depend on animals for seed dispersal (Herrera, 2002). Therefore, for these plants, intraspecific variation among animal seed dispersers truly matters (Zvolak, 2018). The influence of animal traits on seed dispersal is complex, as individuals within the same species can differ in multiple ways (Zvolak, 2018). Males and females, for example, may exhibit distinct seed dispersal patterns due to variations in morphology and behaviour (Clarke & Kramer, 1994; Karubian et al., 2012). Sex can affect roaming patterns and home range size (Cutrer et al., 2006), which in turn impact seed dispersal distance (Oleksy et al., 2015). Seed dispersal patterns are further influenced by a granivore's ontogenetic shift, resulting in within-individual variation over time (Nakazawa, 2015). Larger individuals can handle a greater range of seed sizes (Herrel et al., 2004; Larsen & Burns, 2012; Muñoz & Bonal, 2008) and consume more seeds (Herrel et al., 2004), leading to increased quantities of dispersed seeds (Correa et al., 2015; Eisenhauer et al., 2010; Larsen & Burns, 2012, but see Tulipani & Lipcius, 2014). Finally, recent studies have highlighted the critical impact of individual behavioural types on seed dispersal (Boone et al., 2022; Brehm & Mortelliti, 2021, 2022; Brehm et al., 2019; Dochtermann & Jenkins, 2007; Feldman et al., 2019), which have largely been ignored until recently. For instance, bolder and fast-exploring individuals are thought to be more inclined to cache seeds in riskier environment (Zvolak & Sih, 2020). In turn, proactive, fast-exploring animals with high energy demands (Careau et al., 2009) are expected to harvest more seeds than reactive, slow-exploring individuals (Zvolak & Sih, 2020). Consequently, certain individuals can play particularly important roles in seed dispersal and cannot be replaced by others (Sih et al., 2012).

Synzoochory, or seed dispersal facilitated by seed-caching animals, presents an excellent system to examine the impact of individual traits on interspecific interactions (Gómez et al., 2019; Lichti et al., 2017). Synzoochory is both common and ecologically significant. Seed-caching animals, also known as scatter-hoarders, disperse at least 1339 species of plants, including numerous dominant trees

(Gómez et al., 2019). These animals play a dual role as both seed dispersers and consumers. Whether they act as mutualistic seed dispersers or antagonistic seed predators hinges on individual foraging decisions (Pesendorfer et al., 2018; Schupp & Fuentes, 1995; Zvolak & Crone, 2012). Given that individual foraging strategies are influenced by the animals' traits (Bolnick et al., 2003), it might be feasible to use these traits to identify functional groups within species. While the concept of intraspecific functional variability is well-established in plant ecology (e.g., Albert et al., 2010; Doudová & Douda, 2020; He et al., 2021; Spasojevic et al., 2016), it appears less explored in animal ecology. However, using on a single value of a trait to characterize animal species can hide substantial functional diversity (Wood et al., 2017). By examining the differences in individual traits, we can better understand their impact on animal performance and key ecological processes, such as seed dispersal.

In this study, we investigated the influence of individual traits of yellow-necked mice (*Apodemus flavicollis*) on the dispersal of common oak (*Quercus robur*) acorns. We examined individual variation related to sex, body mass and exploration levels of rodents. Our study spanned 3 years, allowing us to investigate temporal fluctuations in this variability, which has received limited attention so far. Our first hypothesis (*H1*) posited that larger individuals would cache fewer seeds compared with their smaller counterparts, as their decision to consume seeds instead of caching may be driven by higher energy requirements (Lichti et al., 2017). Additionally, we hypothesized (*H2*) that larger individuals will carry seeds farther because the relative cost of seed transport decreases with increasing body mass (Muñoz & Bonal, 2008). Considering sex differences, we anticipated that male mice would cache seeds more frequently than female mice (*H3*), possibly due to superior spatial memory that enables them to retrieve a larger proportion of stored seeds (Zhang et al., 2016). Furthermore, we predicted that males would transport seeds farther than females (*H4*), given their considerably larger home ranges (Stradiotto et al., 2009). Finally, we proposed that more exploratory individuals, as assessed in open-field tests, would be more likely to consume rather than cache seeds (*H5*), transport them over greater distances (*H6*) and deposit them farther from trees (*H7*). Proactive, exploratory individuals may be less inclined to cache than reactive individuals, as they prioritize current rather than future reproduction (Wolf et al., 2007), and are hypothesized to invest less in spatial memory than slow-exploring individuals (Sih & Del Giudice, 2012). Moreover, they are also more likely to traverse greater distances and venture into risky environments (Fraser et al., 2001; Holtmann et al., 2017; Zvolak & Sih, 2020).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and small mammal trapping

We conducted this study in Puszcza Zielonka Landscape Park (52.6 N, 16.9 E), located in Greater Poland Voivodeship in Poland. We performed the experiment at six existing plots within a managed

forest, dominated by common oak (*Quercus robur*), European beech (*Fagus sylvatica*) and common hornbeam (*Carpinus betulus*). Key distinctions between this managed forest and more natural (protected) forests are a less diverse age structure of stands and a lower volume of coarse woody debris (Celebias, personal observation). At each plot, we established a trapping grid consisting of 100 live 'dziekanówka' traps (10×10 arrangement; size 16.5×8×9.5 cm, produced by PPUH A. Marcinkiewicz, Rajgród, Poland) with 10m spacing. We baited traps with oat flakes and sunflower seeds and checked twice per day. We conducted five 4-day long trapping sessions at 3-week intervals from June to September in 2020, 2021 and 2022, totalling 36,000 trap nights. We checked traps twice a day, at 8 AM and 6 PM. During each session, we assessed the sex and weight of each trapped animal. We double-marked all individuals with unique ear tags and passive integrated transponder (PIT) tags. The handling of animals not involved in the behavioural tests was typically completed in under 1 min, after which they were released at their point of capture.

### 2.1.1 | Animal personality test

We tested each captured individual for behavioural type using two tests: an open-field test to measure activity and exploration in a new environment (Bednarz & Zwolak, 2022; Montiglio et al., 2012) and a handling bag test to assess docility and struggle rate (Taylor et al., 2014). Each time we started with the handling bag test. We released the individual from the live trap into a clean, linen bag, and we recorded the struggle rate for 1 min. After the handling bag test was completed, we proceeded with the open-field test, releasing the individual into a 35×50×3 cm plexiglass arena. The arena was divided into four sections by two 2-cm high perpendicular partitions. We used the number of times each individual crossed the bars during the test as an exploration score. We rated the exploration score for 2 min, starting when the mouse made its first step. Between tests, the arena was thoroughly cleaned with paper towels and 70% ethanol. We recorded both experiments with hand-held digital cameras. The tests were conducted only after the morning trapping session, and afterwards, individuals were released at their point of capture. The Local Ethical Committee in Poznań approved all experimental procedures (Approvals No. 24/2018 and 19/2020).

### 2.1.2 | Seed tracking

To link seed fate to the decision-making of animals with known traits, we conducted seed-tracking experiments at the same sites that were used for small mammal trapping. To avoid the confounding effect of fluctuations in natural acorn availability, these experiments were performed from June to mid-September, before the natural acorn fall (October–November), using commercially purchased acorns. Like the small mammal trapping, the experiments

were conducted at three site pairs, over five 4-day sessions with 3-week intervals. Seed tracking was performed simultaneously for each pair of sites, immediately following their respective trapping sessions.

At each plot, we displayed acorns at four seed depots, each at least 30m apart. At each depot, we placed five acorns marked with a red plastic tag (20×40mm) attached to the acorn with a thin steel wire (length 100mm,  $\varnothing$  0.2mm).

We placed the acorns in the loop of a PIT-tag reader's antenna, with a Reconyx™ camera trap set up above them. The acorns were individually numbered and always placed in the same order on the Petri dish, allowing us to link the fate of an acorn (from the camera trap image) to the mouse (data from the PIT-tag reader). We set up the experiment at 8 PM and checked the following morning, starting at 8 AM.

We conducted time-constrained searches (20 min per station). For each found acorn, we recorded its distance from the seed depot, the distance from the nearest tree (beginning in September 2020), and the tree's diameter and species. Following (Zhang et al., 2008) we categorized acorns as left untouched at the station (IS—in situ), consumed at the seed station (EIS—eaten in situ), moved from the station and consumed (EAR—eaten after removal), removed from the station and cached (CAR—cached after removal), removed from the station and left on the forest floor (RS—removed and left on surface) and missing (M). Acorns were considered consumed when over 70% of the cotyledon was consumed, as less damaged seeds are still capable of germination (Giertych & Suszka, 2011; Perea et al., 2011).

Then, by comparing the timestamps on the images from the camera trap and the data from the PIT-tag readers, we linked individual mice to dispersed acorns. The unmarked mice were recorded by the camera trap, but not by the PIT-tag readers.

### 2.1.3 | Statistics

We evaluated the impact of individual traits of yellow-necked mouse on common oak seed dispersal among 3 years. The scale of inference was among individuals in the population in relation to the seed fate of the presented seeds (Table A1).

We conducted the analysis in R (R Core Team, 2018). Adjusted repeatability and associated 95% confidence intervals were calculated using the 'rptR' package (Stoffel et al., 2017) to determine which behavioural variables could be considered personality traits. We used the Poisson error family, performing 1000 parametric bootstrap and 100 permutations. The individual number of an ear tag was included as a random intercept and mice's body mass and sex were fixed effects. We also included individuals with a single test, as excluding such individuals can reduce rather than improve power in random regressions (Martin et al., 2011).

Then, we investigated the within-individual variability that occurs between repeated behavioural observations. For each individual, we calculated the mean best linear unbiased predictor (BLUP) with 'glmmTMB' package (Brooks et al., 2017). Due to the poor fit

and low repeatability of the handling bag struggle rate models, we used only the exploration rate in the open-field test as a personality trait in further analysis.

To assess the impact of mice's individual traits on exploration rate (represented by the number of crosses in an open-field test), we used generalized linear model (GLMMs) with negative binomial error terms and zero inflation, implemented via the 'glmmTMB' package (Brooks et al., 2017). We tested the impact of year, mice's body mass, sex, and number of open-field tests with site and individual (i.e. PIT-tag number) as random intercepts.

To analyse the effects of a mouse's sex and body mass on seed fate, we constructed two binomial mixed models. In one model, the response variable was the proportion of removed seeds that were cached, and in the other model, it was the proportion of removed seeds that were consumed. Body mass, sex, year of study and exploration rate were included as fixed effects, with seed depot, site and individual included as random intercepts. The initial GLMM models included all possible two-way interactions between the year and other explanatory variables. These interactions were retained in the final models only if they were statistically significant.

The impact of the yellow-necked mouse's exploration rate, sex, body mass and year of study on the distance of seed dispersal and the dispersal distance from the nearest tree, was tested using Gaussian-family GLMMs implemented via 'glmmTMB' package (Brooks et al., 2017), with square-rooted dispersal distance as the response variable and station, site and individual as random intercepts. These analyses included only seeds that were successfully dispersed, that is, removed and either cached or left uneaten on ground surface. In the initial GLMM models, we included two-way interactions between the year and other explanatory variables (retained when significant).

We tested for the statistical significance of fixed factors with Wald type II chi-square tests ('Anova' function from the 'car' package, Fox & Weisberg, 2019). Next, to understand the temporal patterns of our data, we used the 'relevel' function to alter the reference levels of our factors to the years 2020, 2021 and 2022. By examining the estimates and *p*-values from the 'summary' output, we assessed whether the effects in these years significantly differ from zero.

### 3 | RESULTS

We captured a total of 1247 yellow-necked mice (552 females and 695 males). We subjected 943 of these individuals to open-field tests with an average of 2.0 tests per individual (range: 1–11). The exploration rate during the open-field tests was not affected by sex ( $\beta \pm \text{SE}$ :  $-0.029 \pm 0.040$ ,  $p = 0.464$ ), but increased with mouse's body mass ( $\beta \pm \text{SE}$ :  $0.065 \pm 0.020$ ,  $p = 0.001$ ). Moreover, the exploration rate varied across the years of the study ( $\chi^2 = 14.483$ ,  $\text{df} = 2$ ,  $p < 0.001$ ) and was decreasing over repeated tests ( $\beta \pm \text{SE}$ :  $-0.04 \pm 0.011$ ,  $p < 0.001$ ). The adjusted repeatability of exploration was 0.57 on

the link scale (95% CI: 0.52–0.62,  $p < 0.001$ ) and 0.48 on the original scale (95% CI: 0.43–0.53,  $p < 0.001$ ).

### 3.1 | Impact of individual traits on seed dispersal

Over the 3 years of the study, we recorded 196 marked and behaviourally tested individuals dispersing 1451 experimental seeds (446 seeds in 2020, 372 in 2021 and 503 in 2022). Of the total number of seeds offered in the experiment, 10.1% of seeds were left intact in the seed depots, 26.7% were consumed (1.9% in seed depots and 98.1% after dispersal), 22.2% were cached after dispersal, 7.1% were dispersed and left on the ground surface, and 33.9% were not found. We were less likely to find seeds dispersed by heavier individuals ( $\beta \pm \text{SE}$ :  $0.04 \pm 0.018$ ,  $p = 0.011$ ), and the effect of sex differed by year. In 2020, seeds dispersed by females were found less often than male-dispersed ones ( $\beta \pm \text{SE}$ :  $-0.13 \pm 0.06$ ,  $p = 0.025$ ). Conversely, in 2021, seeds dispersed by males were less commonly found than female-dispersed seeds ( $\beta \pm \text{SE}$ :  $0.23 \pm 0.09$ ,  $p = 0.009$ ), while in 2022, there was no difference in seed dispersal between the sexes ( $\beta \pm \text{SE}$ :  $-0.06 \pm 0.06$ ,  $p = 0.341$ ).

#### 3.1.1 | Seed consumption

The impact of exploration rate, mouse's sex and body mass on the probability of seed consumption varied over time (significant interactions with year in Table 1a; estimates and standard errors are provided in Table A2). The exploration rate had a negative association with the probability of seed consumption in 2021 ( $p = 0.004$ ), while the relationships in the other years were non-significant (2020:  $p = 0.407$ ; 2022:  $p = 0.263$ ) (Figure 1a). Body mass had a positive relationship with the probability of seed consumption in 2020 ( $p = 0.047$ ) and non-significant effects in the other years (2021:  $p = 0.188$ ; 2022:  $p = 0.123$ ). Finally, females had a higher probability of seed consumption than males in 2020 ( $p = 0.019$ ), but the difference was no longer significant in 2021 ( $p = 0.253$ ) and 2022 ( $p = 0.371$ ).

#### 3.1.2 | Seed caching

The impact of exploration rate, sex and body mass on seed caching also varied across years (Table 1b; Table A3). The impact of body mass was negative in 2020 ( $p = 0.031$ ), but positive in 2021 ( $p = 0.015$ ) and 2022 ( $p < 0.001$ ) (Figure 1b). The impact of exploration rate was positive in 2021 ( $p < 0.001$ ; Figure 1c) and non-significant in other years (2020:  $p = 0.342$ ; 2022:  $p = 0.086$ ). Moreover, the probability of seed caching was higher for males than females in 2020 ( $p = 0.002$ ), but the opposite was true in the following years, with a marginally non-significant effect in 2021 ( $p = 0.052$ ), and significant in 2022 ( $p = 0.002$ ) (Figure 1d).

**TABLE 1** Summary of model output examining the relationship between (a) the probability of seed consumption, (b) caching, (c) distance of dispersal and (d) distance from the nearest tree by yellow-necked mice (*Apodemus flavicollis*) and the following variables: exploration in an open-field test, year (2020, 2021 and 2022), sex and body mass.

Category	Effects	$\chi^2$	df	p
(a) Consumption	Exploration rate	2.046	1	0.153
	Year	24.027	2	<0.001
	Sex	0.192	1	0.661
	Body mass	0.115	1	0.735
	Exploration rate:Year	8.154	2	<b>0.017</b>
	Sex:Year	7.451	2	<b>0.024</b>
	Body mass:Year	7.930	2	<b>0.019</b>
(b) Caching	Exploration rate	5.357	1	<b>0.021</b>
	Year	25.912	2	<0.001
	Sex	2.190	1	0.335
	Body mass	0.393	1	0.531
	Exploration rate:Year	23.02	2	<0.001
	Sex:Year	26.259	2	<0.001
	Body mass:Year	2.319	2	<0.001
(c) Distance of dispersal	Exploration rate	0.536	1	0.464
	Year	38.75	2	<0.001
	Sex	0.680	1	0.411
	Body mass	2.936	1	0.087
	Body mass:Year	14.988	2	<0.001
(d) Distance from the nearest tree	Exploration rate	6.505	1	<b>0.011</b>
	Year	14.112	2	<b>0.001</b>
	Sex	0.759	1	0.384
	Body mass	5.971	1	<b>0.015</b>
	Body mass:Year	6.127	2	<b>0.047</b>

Bold values denote statistical significance at the  $p < 0.05$  level.

### 3.1.3 | Distance of dispersal

On average, dispersed seeds were transported 6.2m from the depots (range: 0.1–49.7 m). The distance of dispersal was not affected by the mice's sex or their exploration rate (Table 1c; Table A4). The effect of body mass on the distance of seed dispersal, however, varied annually (body mass $\times$ year interaction in Table 1c; Figure 1e). A positive correlation between body mass and seed dispersal distance was observed in 2022 ( $p < 0.001$ ), whereas no significant association was found in 2020 ( $p = 0.462$ ) and 2021 ( $p = 0.452$ ).

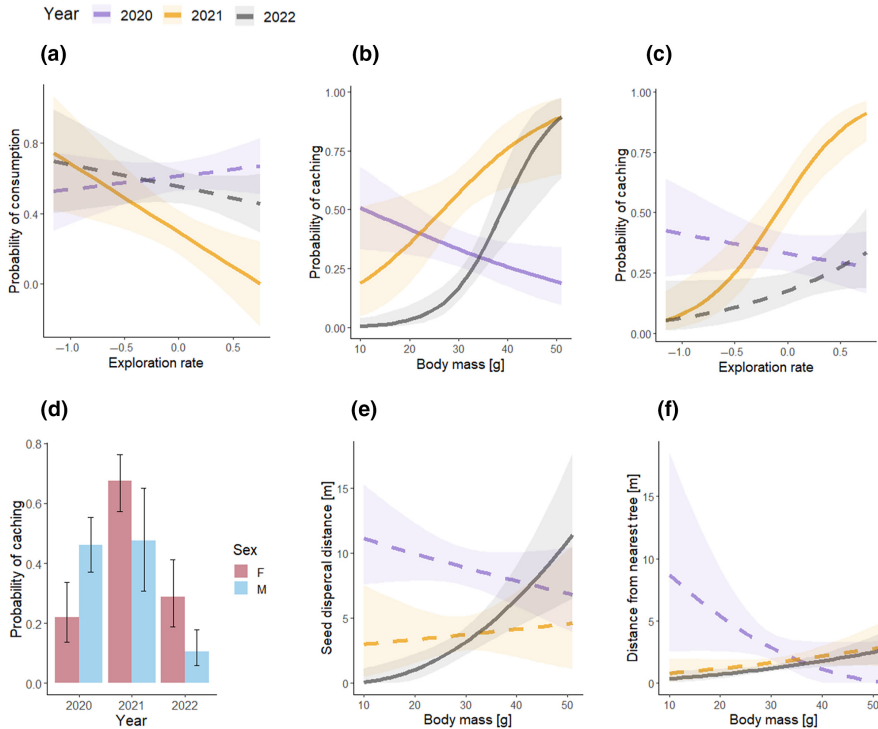
### 3.1.4 | Distance from the nearest tree

The distance of dispersal from the nearest tree was not influenced by the sex of the mice. However, individuals with a higher exploration rate dispersed seeds farther away from the trees (Table 1d). Furthermore, the body mass of the mice had varying effect on the distance from the nearest tree across different years (body mass $\times$ year interaction in Table 1d; Table A5; Figure 1e). Heavier mice transported seeds further in 2022 ( $p = 0.006$ ), but no effect was found in the other years (2020:  $p = 0.064$ ; 2021:  $p = 0.114$ ).

## 4 | DISCUSSION

Our study reveals that the relationship between individual traits and seed dispersal is not static but varies from year to year. This implies that environmental conditions may have a more decisive role than expected in determining which individual traits of mice aid or hinder tree regeneration. Such findings emphasize the value of multi-year studies when investigating seed dispersal dynamics. Furthermore, they suggest that the effects of individual traits on seed dispersal may be more multifaceted than previously assumed.

Seed-granivore interactions are highly context-dependent (Celebias & Bogdziewicz, 2023; Lichti et al., 2017; Ostoja et al., 2013). Several factors, such as the quality of the patch (Caccia et al., 2006), population size of granivores (Janova et al., 2016; Zwolak et al., 2021) and the availability of alternative food sources (Van Baalen et al., 2001), shape the decisions granivores make regarding encountered seeds. These factors exemplify the variability of the species-level influence of scatter-hoarders under different environmental conditions (i.e., considered by averaging out intra-specific variation among animal seed dispersers: Zwolak, 2018). Additionally, our data imply that the influence of scatter-hoarders' individual traits is equally contingent on ecological context.



**FIGURE 1** Impact of different traits of yellow-necked mice on probability of consumption (a), probability of caching (b–d), distance of dispersal from the seed depot (e) and the distance of dispersal from the nearest tree (f). Lines denote estimates from generalized linear mixed models (solid line for significant relationship and dashed line for non-significant relationship), shading corresponds to 95% CI, and colours indicate relationships in years 2020–2022.

**TABLE 2** Summary of tested predictions and results.

	Prediction	Is prediction supported?	Result
H1	Larger individuals cache fewer seeds compared with smaller individuals	Partially	The impact of body mass on caching behaviour varied annually, ranging from positive to negative
H2	Larger individuals carry seeds farther	Partially	The impact of body mass on seed dispersal distance varied annually, ranging from positive to non-significant
H3	Males cache seeds more frequently than females	Partially	The impact of sex on the probability of seed caching varied among years
H4	Males transport seeds farther than females	No	Sex had no effect on seed dispersal distance
H5	More exploratory individuals are more likely to consume acorns rather than cache them compared with less exploratory individuals	No	In various years of the study, the impact of the exploration rate on acorn consumption was either negative or non-significant, while its impact on acorn caching was either positive or non-significant
H6	More exploratory individuals transport acorns over greater distances than less exploratory individuals	No	Exploration rate had no effect on seed dispersal distance
H7	More exploratory individuals deposit acorns farther from trees than less exploratory individuals	Yes	Distance of dispersed acorn from the nearest tree was greater for more exploratory individuals

The predicted decrease in the probability of seed caching with body mass (H1; Table 2) only occurred in 2020, with the opposite trend in 2021 and 2022. Perhaps seed-handling challenges are more significant than the energetic requirements we initially focused on. Caching behaviour often involves carrying seeds over longer distances (Steele et al., 1996), a task possibly more challenging for smaller and more manageable for larger individuals (Muñoz & Bonal, 2008). This notion is supported by the finding that heavier individuals tend to carry seeds farther, a pattern observed in 2022, and providing partial support for our second hypothesis (H2; Table 2). Alternatively, fluctuations in the availability of alternative food sources could alter the body

mass-dependent trade-offs involved in caching rather than consuming seeds.

The results for hypothesis H3 (regarding a higher seed caching propensity in males compared with females) were inconsistent, with males caching more in 1 year, but not others. Hypothesis H4, which predicted that sex would influence seed dispersal distance, found no support; differences in the spatial behaviour of male and female yellow-necked mice are well-established (Bogdziewicz et al., 2016; Stradiotto et al., 2009), but they did not translate to seed dispersal distances in our study. While the effects of sex were less clear-cut than expected, future studies should also consider reproductive state, as the sexual cycle may influence the foraging behaviour

of both females and males (Ruivo et al., 2017; Scridel et al., 2023; Zwolak, 2018).

Moreover, the exploration rate had a negative or non-significant association with the probability of seed consumption and the distance of seed dispersal, contradicting hypotheses H5 and H6. This outcome complicates the intuitive idea that higher exploration correlates with increased energy gain and expenditure (Careau et al., 2008), but lines up with the nuanced views offered by more detailed models of this relationship (refer to figure 2 in Careau & Garland, 2012). In contrast, our hypothesis regarding the impact of exploration rate on the distance of dispersal from the nearest tree (H7) was confirmed. This aligns with established theories linking proactive personality traits and risk-prone behaviour (Koolhaas et al., 1999; Sih, Bell, Johnson, & Ziemba, 2004). Such behaviour can have important consequences for plant recruitment because seeds deposited farther away from adult plants often escape distance and density-dependent mortality, and thus can be more likely to germinate (Bell et al., 2006; Comita et al., 2014; but see Bogdziewicz et al., 2020).

Our results also diverge from previous studies by Brehm et al. (2019) and Brehm and Mortelliti (2022). In these studies, scatter-hoarding rodents with more proactive personalities (bolder, less timid, more active) displayed higher seed consumption rates and fewer cached seeds, suggesting a more antagonistic relationship with plants compared with their reactive counterparts. Yet, our study unveils a remarkable level of temporal context-dependence in these interactions. Consequently, it is challenging to assign mutualistic or antagonistic roles to individuals with specific traits in our study system since their interactions with seeds display dynamic, annual fluctuations.

Though mechanisms behind the context-dependency are unclear, we suggest potential explanations for annual variation. Environmental factors like weather (Wróbel & Bogdziewicz, 2015) and food availability (Fletcher et al., 2010) can impact the energy levels and foraging behaviour of mice, potentially interacting with individual traits to affect seed dispersal behaviour. Although we controlled for tree nut abundance by conducting our experiments before seed fall (and therefore removed probably the biggest driver of context-dependence in masting systems: Pesendorfer et al., 2016; Zwolak et al., 2016), the availability of other food sources could fluctuate annually. For example, in years with ample food, the effect of body mass on seed dispersal may be less pronounced, as both large and small individuals have sufficient resources to meet their energy requirements. Changes in food availability can also impact the relative importance of seed dispersal as a foraging strategy, and the trade-off between seed dispersal and other behaviours, such as mating or avoiding predators, may differ between mice with different individual traits.

Changes in population density, sex ratios and age structure can alter the behaviours and movements of individual mice, including those with specific traits (Schoepf et al., 2015). High population density might increase competition for resources and intensify the influence of traits like body mass or exploration levels on seed

dispersal behaviours, as individuals with specific trait combinations differentiate their foraging strategies to reduce competition (Araújo et al., 2011; Manlick et al., 2021; Noble et al., 2019). However, despite considerable variation in mouse abundance, it did not appear to drive the context dependence in our results (see supplementary analysis in Appendix S2: Impact of mouse abundance on seed fate). Predation risk can also affect traits' influence (Merz et al., 2023; Toscano et al., 2016). For instance, in years with higher predation risk, the influence of traits related to risk-taking behaviours, such as exploration levels, might be more critical for seed dispersal, as individuals that balance exploration with predation avoidance could disperse seeds more effectively. Given these potential variations, data collection over several years is crucial. Long-term studies tend to reveal more variability, and single-year studies may overestimate effects or miss context dependency (Chamberlein et al., 2014).

Future research should focus on identifying the mechanisms responsible for the varying effects of individual traits on seed dispersal. Examining the influence of environmental and ecological factors on this process will be crucial. Fluctuations in food availability and changes in predation risk appear particularly promising in this context. Moreover, investigations into the long-term effects of these fluctuations on plant recruitment could offer valuable insights. The interplay between individual traits and external factors emphasizes the importance of incorporating both individual variation and environmental context when studying seed dispersal.

In conclusion, our study underscores that seed dispersal research must account for year-to-year variations, which are likely tied to environmental shifts. Importantly, in the real-world rather than experimental scenarios, outcome variability might be even greater due to our control of the acorn crop. Our observations hint at a complexity in the role of individual traits in seed dispersal that exceeds initial assumptions, with these traits' impacts undergoing significant shifts with each passing year. Hence, there is not a single, consistent individual type that confers maximal benefits to plants; instead, this optimal type changes over time. By deepening our understanding of the complex interactions between individual traits and environmental factors that drive the yearly variations, we can gain a more comprehensive perspective on seed dispersal.

#### AUTHOR CONTRIBUTIONS

R.Z. designed the study. P.C., A.W. and M.Z. collected the trapping data and prepared the data for analysis. P.C. collected the seed data. P.C. and R.Z. analysed the data and wrote the manuscript. All authors contributed substantially to the revision and editing of the manuscript.

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### CONFLICT OF INTEREST STATEMENT

The authors declare that they do not have any conflict of interest with respect to this manuscript.

### DATA AVAILABILITY STATEMENT

The data are available from Knowledge Network for Biocomplexity <https://doi.org/10.5063/F11V5CFN> (Celebias et al., 2024).

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### REFERENCES

- Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., & Lavorel, S. (2010). Intraspecific functional variability: Extent, structure and sources of variation. *Journal of Ecology*, 98(3), 604–613. <https://doi.org/10.1111/j.1365-2745.2010.01651.x>
- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, 14(9), 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Bednarz, P. A., & Zwolak, R. (2022). Body mass and sex, but not breeding condition and season, influence open-field exploration in the yellow-necked mouse. *Ecology and Evolution*, 12(3), e8771. <https://doi.org/10.1002/ece3.8771>
- Bell, T., Freckleton, R. P., & Lewis, O. T. (2006). Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, 9(5), 569–574. <https://doi.org/10.1111/j.1461-0248.2006.00905.x>
- Bogdziewicz, M., Crone, E. E., & Zwolak, R. (2020). Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. *Journal of Ecology*, 108(3), 1009–1018. <https://doi.org/10.1111/1365-2745.13307>
- Bogdziewicz, M., Zwolak, R., Redosh, L., Rychlik, L., & Crone, E. E. (2016). Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology and Evolution*, 6(23), 8423–8430. <https://doi.org/10.1002/ece3.2513>
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulseley, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, 161(1), 1–28. <https://doi.org/10.1086/343878>
- Bonaldo, R. M., & Bellwood, D. R. (2008). Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the great barrier reef, Australia. *Marine Ecology Progress Series*, 360(May), 237–244. <https://doi.org/10.3354/meps07413>
- Boone, S. R., Brehm, A. M., & Mortelliti, A. (2022). Seed predation and dispersal by small mammals in a landscape of fear: Effects of personality, predation risk and land-use change. *Oikos*, 2022(2), e08232. <https://doi.org/10.1111/oik.08232>
- Brehm, A. M., & Mortelliti, A. (2021). Land-use change alters associations between personality and microhabitat selection. *Ecological Applications*, 31(8), e02443. <https://doi.org/10.1002/eap.2443>
- Brehm, A. M., & Mortelliti, A. (2022). Small mammal personalities generate context dependence in the seed dispersal mutualism. *Proceedings of the National Academy of Sciences of the United States of America*, 119(15), e2113870119. <https://doi.org/10.1073/pnas.2113870119>
- Brehm, A. M., Mortelliti, A., Maynard, G. A., & Zydlewski, J. (2019). Land-use change and the ecological consequences of personality in small mammals. *Ecology Letters*, 22(9), 1387–1395. <https://doi.org/10.1111/ele.13324>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. <https://doi.org/10.32614/RJ-2017-066>
- Caccia, F. D., Chaneton, E. J., & Kitzberger, T. (2006). Trophic and non-trophic pathways mediate apparent competition through Post-dispersal seed predation in a Patagonian mixed forest. *Oikos*, 113(3), 469–480. <https://doi.org/10.1111/j.2006.0030-1299.14390.x>
- Careau, V., Bininda-Emonds, O. R. P., Thomas, D. W., Réale, D., & Humphries, M. M. (2009). Exploration strategies map along fast-slow metabolic and life-history continua in muroid rodents. *Functional Ecology*, 23(1), 150–156. <https://doi.org/10.1111/j.1365-2435.2008.01468.x>
- Careau, V., & Garland, T., Jr. (2012). Performance, personality, and energetics: Correlation, causation, and mechanism. *Physiological and Biochemical Zoology*, 85(6), 543–571. <https://doi.org/10.1086/666970>
- Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117(5), 641–653. <https://doi.org/10.1111/j.0030-1299.2008.16513.x>
- Celebias, P., & Bogdziewicz, M. (2023). Consequences of intraspecific variation in seed size: Does the presence of small seeds reduce predation on large ones? *European Journal of Forest Research*, 142(1), 107–115. <https://doi.org/10.1007/s10342-022-01508-x>
- Celebias, P., Wróbel, A., Zduniak, M., Steele, M., Bogdziewicz, M., & Zwolak, R. (2024). *Behavior, body mass, and sex: How intraspecific variation influences seed dispersal by a scatterhoarding rodent*. Knowledge Network for Biocomplexity. <https://doi.org/10.5063/F11V5CFN>
- Chamberlain, S. A., Bronstein, J. L., & Rudes, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17(7), 881–890. <https://doi.org/10.1111/ele.12279>
- Clarke, M. F., & Kramer, D. L. (1994). Scatter-hoarding by a larder-hoarding rodent: Intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. *Animal Behaviour*, 48(2), 299–308. <https://doi.org/10.1006/anbe.1994.1243>
- Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., & Zhu, Y. (2014). Testing predictions of the Janzen–Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, 102(4), 845–856. <https://doi.org/10.1111/1365-2745.12232>
- Correa, S., Bibiana, J. K., Araújo, J. M. F., Penha, J. M., da Cunha, C. N., Stevenson, P. R., & Anderson, J. T. (2015). Overfishing disrupts an ancient mutualism between frugivorous fishes and plants in neotropical wetlands. *Biological Conservation*, 191(November), 159–167. <https://doi.org/10.1016/j.biocon.2015.06.019>
- Cutrer, A. P., Antinuchi, D. C., Mora, M. S., & Vassallo, A. I. (2006). Home-range and activity patterns of the south American subterranean rodent *Ctenomys talarum*. *Journal of Mammalogy*, 87(6), 1183–1191. <https://doi.org/10.1644/05-MAMM-A-386R1.1>



- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2(1), 57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- Dochtermann, N. A., & Jenkins, S. H. (2007). Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): A test of competing hypotheses. *Proceedings of the Royal Society B: Biological Sciences*, 274(1623), 2343–2349. <https://doi.org/10.1098/rspb.2007.0622>
- Doudová, J., & Douda, J. (2020). Along with intraspecific functional trait variation, individual performance is key to resolving community assembly processes. *Functional Ecology*, 34(11), 2362–2374. <https://doi.org/10.1111/1365-2435.13646>
- Eastcott, E., Kern, J. M., Morris-Drake, A., & Radford, A. N. (2020). Intrapopulation variation in the behavioral responses of dwarf mongooses to anthropogenic noise. *Behavioral Ecology*, 31(3), 680–691. <https://doi.org/10.1093/beheco/araa011>
- Eisenhauer, N., Butenschön, O., Radsick, S., & Scheu, S. (2010). Earthworms as seedling predators: Importance of seeds and seedlings for earthworm nutrition. *Soil Biology and Biochemistry*, 42(8), 1245–1252. <https://doi.org/10.1016/j.soilbio.2010.04.012>
- Feldman, M., Ferrandiz-Rovira, M., Espelta, J. M., & Muñoz, A. (2019). Evidence of high individual variability in seed management by scatter-hoarding rodents: Does 'personality' matter? *Animal Behaviour*, 150, 167–174. <https://doi.org/10.1016/j.anbehav.2019.02.009>
- Fletcher, Q. E., Boutin, S., Lane, J. E., LaMontagne, J. M., McAdam, A. G., Krebs, C. J., & Humphries, M. M. (2010). The functional response of a hoarding seed predator to mast seeding. *Ecology*, 91(9), 2673–2683. <https://doi.org/10.1890/09-1816.1>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *The American Naturalist*, 158(2), 124–135. <https://doi.org/10.1086/321307>
- Giertych, M. J., & Suszka, J. (2011). Consequences of cutting off distal ends of cotyledons of *Quercus robur* acorns before sowing. *Annals of Forest Science*, 68(2), 433–442. <https://doi.org/10.1007/s13595-011-0038-6>
- Gómez, J. M., Schupp, E. W., & Jordano, P. (2019). Synzoochory: The ecological and evolutionary relevance of a dual interaction. *Biological Reviews*, 94(3), 874–902. <https://doi.org/10.1111/brv.12481>
- Hausch, S., Vamosí, S. M., & Fox, J. W. (2018). Effects of intraspecific phenotypic variation on species coexistence. *Ecology*, 99(6), 1453–1462. <https://doi.org/10.1002/ecy.2346>
- He, D., Biswas, S. R., Xu, M. S., Yang, T. H., You, W. H., & Yan, E. R. (2021). The importance of intraspecific trait variability in promoting functional niche dimensionality. *Ecography*, 44(3), 380–390. <https://doi.org/10.1111/ecog.05254>
- Herrel, A., Vanhooydonck, B., Duncan, R. J., & Irschick, J. (2004). Frugivory in polychrotid lizards: Effects of body size. *Oecologia*, 140(1), 160–168. <https://doi.org/10.1007/s00442-004-1558-7>
- Herrera, C. M. (2002). Seed dispersal by vertebrates. In Herrera, C. M., & O. Pellmyr (Eds.), *Plant animal interactions: An evolutionary approach* (pp. 185–208). John Wiley & Sons.
- Holtmann, B., Santos, E. S., Lara, C. E., & Nakagawa, S. (2017). Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. *Proceedings of the Royal Society B: Biological Sciences*, 284(1864), 20170943. <https://doi.org/10.1016/j.scitotenv.2016.03.165>
- Janova, E., Heroldova, M., & Cepelka, L. (2016). Rodent food quality and its relation to crops and other environmental and population parameters in an agricultural landscape. *Science of the Total Environment*, 562(August), 164–169. <https://doi.org/10.1016/j.scitotenv.2016.03.165>
- Jonsdóttir, I. S., Halbritter, A. H., Christiansen, C. T., Althuisen, I. H., Haugum, S. V., Henn, J. J., Björnsdóttir, K., Maitner, B. S., Malhi, Y., Michaletz, S. T., Roos, R. E., Klanderud, K., Lee, H., Enquist, B. J., & Vandvik, V. (2023). Intraspecific trait variability is a key feature underlying high Arctic plant community resistance to climate warming. *Ecological Monographs*, 93(1), e1555. <https://doi.org/10.1002/ecm.1555>
- Karubian, J., Durães, R., Storey, J. L., & Smith, T. B. (2012). Mating behavior drives seed dispersal by the long-wattled umbrellabird *Cephalopterus penduliger*. *Biotropica*, 44(5), 689–698. <https://doi.org/10.1111/j.1744-7429.2012.00859.x>
- Khalil, M. I., Gibson, D. J., & Baer, S. G. (2019). Functional response of subordinate species to intraspecific trait variability within dominant species. *Journal of Ecology*, 107(5), 2040–2053. <https://doi.org/10.1111/1365-2745.13249>
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, 23(7), 925–935. [https://doi.org/10.1016/S0149-7634\(99\)00026-3](https://doi.org/10.1016/S0149-7634(99)00026-3)
- Larsen, H., & Burns, K. C. (2012). Seed dispersal effectiveness increases with body size in New Zealand alpine scree Weta (*Deinacrida connectens*). *Austral Ecology*, 37(7), 800–806. <https://doi.org/10.1111/j.1442-9993.2011.02340.x>
- Lichti, N. I., Steele, M. A., & Swihart, R. K. (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews*, 92(1), 474–504. <https://doi.org/10.1111/brv.12240>
- Manlick, P. J., Maldonado, K., & Newsome, S. D. (2021). Competition shapes individual foraging and survival in a desert rodent ensemble. *Journal of Animal Ecology*, 90(12), 2806–2818. <https://doi.org/10.1111/1365-2656.13583>
- Martin, J. G. A., Nussey, D. H., Wilson, A. J., & Réale, D. (2011). Measuring individual differences in reaction norms in field and experimental studies: A power analysis of random regression models. *Methods in Ecology and Evolution*, 2(4), 362–374. <https://doi.org/10.1111/j.2041-210X.2010.00084.x>
- McConkey, K. R., & O'Farrill, G. (2015). Cryptic function loss in animal populations. *Trends in Ecology & Evolution*, 30(4), 182–189. <https://doi.org/10.1016/j.tree.2015.01.006>
- Merz, M. R., Boone, S. R., & Mortelliti, A. (2023). Predation risk and personality influence seed predation and dispersal by a scatter-hoarding small mammal. *Ecosphere*, 14(1), e4377. <https://doi.org/10.1002/ecs2.4377>
- Montiglio, P.-O., Garant, D., Pelletier, F., & Réale, D. (2012). Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 84(4), 1071–1079. <https://doi.org/10.1016/j.anbehav.2012.08.010>
- Moran, N. P., Caspers, B. A., Chakarov, N., Ernst, U. R., Fricke, C., Kurtz, J., Lillie, N. D., Lo, L. K., Müller, C., Takola, R. R. E., Trimmer, P. C., van Benthem, K. J., Winternitz, J., & Wittmann, M. J. (2022). Shifts between cooperation and antagonism driven by individual variation: A systematic synthesis review. *Oikos*, 2022(1). <https://doi.org/10.1111/oik.08201>
- Muñoz, A., & Bonal, R. (2008). Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour*, 76(3), 709–715. <https://doi.org/10.1016/j.anbehav.2008.03.017>
- Nakazawa, T. (2015). Ontogenetic niche shifts matter in community ecology: A review and future perspectives. *Population Ecology*, 57(2), 347–354. <https://doi.org/10.1007/s10144-014-0448-z>
- Noble, J. D., Collins, S. L., Hallmark, A. J., Maldonado, K., Wolf, B. O., & Newsome, S. D. (2019). Foraging strategies of individual silky pocket mice over a boom–bust cycle in a stochastic dryland ecosystem. *Oecologia*, 190, 569–578. <https://doi.org/10.1007/s00442-019-04432-x>

- Oleksy, R., Racey, P. A., & Jones, G. (2015). High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. *Global Ecology and Conservation*, 3(January), 678–692. <https://doi.org/10.1016/j.gecco.2015.02.012>
- Ostoja, S. M., Schupp, E. W., & Klinger, R. (2013). Seed harvesting by a generalist consumer is context-dependent: Interactive effects across multiple spatial scales. *Oikos*, 122(4), 563–574. <https://doi.org/10.1111/j.1600-0706.2012.19969.x>
- Perea, R., San Miguel, A., & Gil, L. (2011). Leftovers in seed dispersal: Ecological implications of partial seed consumption for oak regeneration. *Journal of Ecology*, 99(1), 194–201. <https://doi.org/10.1111/j.1365-2745.2010.01749.x>
- Pesendorfer, M. B., Baker, C. M., Stringer, M., McDonald-Madden, E., Bode, M., McEachern, A. K., Morrison, S. A., & Sillett, T. S. (2018). Oak habitat recovery on California's largest islands: Scenarios for the role of corvid seed dispersal. *Journal of Applied Ecology*, 55(3), 1185–1194. <https://doi.org/10.1111/1365-2664.13041>
- Pesendorfer, M. B., Sillett, T. S., Morrison, S. A., & Kamil, A. C. (2016). Context-dependent seed dispersal by a scatter-hoarding corvid. *Journal of Animal Ecology*, 85(3), 798–805. <https://doi.org/10.1111/1365-2656.12501>
- Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ruivo, L. V., Stone, A. I., & Fienup, M. (2017). Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (*Saimiri collinsi*) in an Amazonian rainforest. *American Journal of Primatology*, 79(6), e22657. <https://doi.org/10.1002/ajp.22657>
- Schoepf, I., Schmohl, G., König, B., Pillay, N., & Schradin, C. (2015). Manipulation of population density and food availability affects home range sizes of African striped mouse females. *Animal Behaviour*, 99(January), 53–60. <https://doi.org/10.1016/j.anbehav.2014.10.002>
- Schupp, E. W., & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Écoscience*, 2(3), 267–275. <https://doi.org/10.1080/11956860.1995.11682293>
- Schupp, E. W., Zvolak, R., Jones, L. R., Snell, R. S., Beckman, N. G., Aslan, C., Cavazos, B. R., Effiom, E., Fricke, E. C., Montaña-Centellas, F., Poulsen, J., Razafindratsima, O. H., Sandor, M. E., & Shea, K. (2019). Intrinsic and extrinsic drivers of intraspecific variation in seed dispersal are diverse and pervasive. *AoB Plants*, 11(6), plz067. <https://doi.org/10.1093/aobpla/plz067>
- Scridel, D., Serra, L., Pirrello, S., Basso, M., Franzoi, A., Cardillo, A., Mengoni, C., Ramazzotti, F., Verza, E., Imperio, S., & Cecere, J. G. (2023). Sex-mediated changes in foraging behaviour according to breeding stage in a monomorphic seabird adapted to rural habitats. *Animal Behaviour*, 198, 181–193. <https://doi.org/10.1016/j.anbehav.2023.01.008>
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The Quarterly Review of Biology*, 64(4), 419–461. <https://doi.org/10.1086/416458>
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, 79(3), 241–277. <https://doi.org/10.1086/422893>
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278–289. <https://doi.org/10.1111/j.1461-0248.2011.01731.x>
- Sih, A., & Del Giudice, M. (2012). Linking Behavioural syndromes and cognition: A Behavioural ecology perspective. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 367(1603), 2762–2772. <https://doi.org/10.1098/rstb.2012.0216>
- Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., Lichti, N. I., Lustenhouwer, N., Schreiber, S. J., Strickland, C., Sullivan, L. L., Cavazos, B. R., Giladi, I., Hastings, A., Holbrook, K. M., Jongejans, E., Kogan, O., Montaña-Centellas, F., Rudolph, J., ... Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, 11(4), plz016. <https://doi.org/10.1093/aobpla/plz016>
- Spasojevic, M. J., Turner, B. L., & Myers, J. A. (2016). When does intraspecific trait variation contribute to functional beta-diversity? *Journal of Ecology*, 104(2), 487–496. <https://doi.org/10.1111/1365-2745.12518>
- Steele, M. A., Hadj-Chikh, L. Z., & Hazeltine, J. (1996). Caching and feeding decisions by *Sciurus carolinensis*: Responses to weevil-infested acorns. *Journal of Mammalogy*, 77(2), 305–314. <https://doi.org/10.2307/1382802>
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Stradiotto, A., Cagnacci, F., Delahay, R., Tioli, S., Nieder, L., & Rizzoli, A. (2009). Spatial organization of the yellow-necked mouse: Effects of density and resource availability. *Journal of Mammalogy*, 90(3), 704–714. <https://doi.org/10.1644/08-MAMM-A-120R1.1>
- Taylor, R. W., Boutin, S., Humphries, M. M., & McAdam, A. G. (2014). Selection on female behaviour fluctuates with offspring environment. *Journal of Evolutionary Biology*, 27(11), 2308–2321. <https://doi.org/10.1111/jeb.12495>
- Todd, C. M., Westcott, D. A., Martin, J. M., Rose, K., McKeown, A., Hall, J., & Welbergen, J. A. (2022). Body-size dependent foraging strategies in the Christmas Island flying-fox: Implications for seed and pollen dispersal within a threatened island ecosystem. *Movement Ecology*, 10(1), 1–15. <https://doi.org/10.1186/s40462-022-00315-8>
- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. *Oecologia*, 182, 55–69. <https://doi.org/10.1007/s00442-016-3648-8>
- Tsuji, Y., Campos-Arceiz, A., Prasad, S., Kitamura, S., & McConkey, K. R. (2020). Intraspecific differences in seed dispersal caused by differences in social rank and mediated by food availability. *Scientific Reports*, 10(1), 1532. <https://doi.org/10.1038/s41598-020-58381-0>
- Tulipani, D. C., & Lipcius, R. N. (2014). Evidence of eelgrass (*Zostera marina*) seed dispersal by northern diamondback terrapin (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay. *PLoS One*, 9(7), e103346. <https://doi.org/10.1371/journal.pone.0103346>
- Van Baalen, M., Krivan, V., van Rijn, P. C. J., & Sabelis, M. W. (2001). Alternative food, switching predators, and the persistence of predator-prey systems. *The American Naturalist*, 157(5), 512–524. <https://doi.org/10.1086/319933>
- Wolf, M., Sander van Doorn, G., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144), 581–584. <https://doi.org/10.1038/nature05835>
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>
- Wood, C. M., McKinney, S. T., & Loftin, C. S. (2017). Intraspecific functional diversity of common species enhances community stability. *Ecology and Evolution*, 7(5), 1553–1560. <https://doi.org/10.1002/ece3.2721>

- Wróbel, A., & Bogdziewicz, M. (2015). It is raining mice and voles: Which weather conditions influence the activity of *Apodemus flavicollis* and *Myodes glareolus*? *European Journal of Wildlife Research*, 61, 475–478. <https://doi.org/10.1007/s10344-014-0892-2>
- Zhang, D., Li, J., Wang, Z., & Yi, X. (2016). Visual landmark-directed scatter-hoarding of Siberian chipmunks *Tamias sibiricus*. *Integrative Zoology*, 11(3), 175–181. <https://doi.org/10.1111/1749-4877.12171>
- Zhang, H., Chen, Y., & Zhang, Z. (2008). Differences of dispersal fitness of large and small acorns of Liaodong oak (*Quercus liaotungensis*) before and after seed caching by small rodents in a warm temperate forest, China. *Forest Ecology and Management*, 255(3), 1243–1250. <https://doi.org/10.1016/j.foreco.2007.10.028>
- Zwolak, R. (2018). How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews*, 93(2), 897–913. <https://doi.org/10.1111/brv.12377>
- Zwolak, R., Bogdziewicz, M., Wróbel, A., & Crone, E. (2016). Advantages of masting in European beech: Timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia*, 180, 749–758. <https://doi.org/10.1007/s00442-015-3511-3>
- Zwolak, R., Clement, D., Sih, A., & Schreiber, S. J. (2021). Mast seeding promotes evolution of scatter-hoarding. *Philosophical Transactions of the Royal Society B*, 376(1839), 20200375. <https://doi.org/10.1098/rstb.2020.0375>
- Zwolak, R., & Crone, E. E. (2012). Quantifying the outcome of plant-granivore interactions. *Oikos*, 121(1), 20–27. <https://doi.org/10.1111/j.1600-0706.2011.19849.x>
- Zwolak, R., & Sih, A. (2020). Animal personalities and seed dispersal: A conceptual review. *Functional Ecology*, 34(7), 1294–1310. <https://doi.org/10.1111/1365-2435.13583>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Scale of inference and summaries of models output.

**Appendix S2.** Impact of mouse abundance on seed fate.

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