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**Analiza dynamiki oddziaływań pomiędzy drzewami
i konsumentami ich nasion: od globalnych wzorców do
zmienności w obrębie gatunku**

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PhD Thesis

**Exploring the dynamics of interactions between trees and
granivores: from global patterns to intraspecific variation**

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1. List of original publications

My doctoral dissertation consists of three publications listed below:

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2. Streszczenie

Interakcje między roślinami a zwierzętami zjadającymi nasiona różnią się w swoim natężeniu, od słabych do silnych, oraz we wpływie jaki mają oddziałujące na siebie organizmy, od negatywnego do pozytywnego. Aby w pełni zrozumieć te zależności, potrzebujemy zarówno globalnej syntezy licznych istniejących już wyników badań, jak i nowych eksperymentów, które pozwolą na opisanie pomijanych dotąd aspektów oddziaływań między roślinami a konsumentami nasion. Moja rozprawa doktorska ma na celu sprostanie obu tym wyzwaniom. Składa się ona z trzech części: (i) meta-analizy hipotezy wysycenia konsumentów nasion, (ii) eksperymentu badającego wpływ wielkości nasion na sposób żerowania gryzoni, (iii) eksperymentu badającego wpływ zmienności wewnątrzgatunkowej gryzoni na roznoszenie nasion. W pierwszej części mojej rozprawy przeprowadziłam meta-analizę 48 opublikowanych badań, które spełniały kryterium zawierania co najmniej 4 lat danych dotyczących produkcji nasion oraz wielkości ich konsumpcji przez zwierzęta. Hipoteza wysycenia konsumentów nasion jest jednym z powszechnie przyjętych wyjaśnień ewolucyjnych korzyści lat nasiennych. Według niej, okresowe występowanie masowego opadu nasion powstało, aby zmniejszyć proporcję nasion niszczonych przez konsumentów. W latach niskiego opadu nasion, populacja konsumentów nasion zmniejsza się w związku z niewystarczającą ilością pożywienia, natomiast w latach nasiennych konsumenci nasion zasypywani są większą ilością nasion, niż są w stanie zjeść, co sprawia, że więcej nasion przeżywa. W swoich badaniach potwierdziłam zarówno efekt zagłodzenia, jak i wysycenia drapieżników, jednak efekt wysycenia był widoczny tylko dla zwierząt bezkręgowych. Co więcej, efekt wysycenia drapieżników w ostatnich latach staje się coraz słabszy, co może mieć związek z globalnymi zmianami antropogenicznymi. W drugiej części mojej rozprawy zbadalam wpływ wielkości nasion dębu szypułkowego (*Quercus robur*) na ich roznoszenie przez gryzonia. Znaczna zmienność wielkości nasion w obrębie jednego osobnika związana jest z modułową budową drzew. Każdy osobnik posiada wiele kopii tego samego organu, np. nasion, które mogą wykazywać znaczącą zmienność. Wielu konsumentów nasion przejawia preferencje względem nasion o konkretnym rozmiarze, dlatego przewidywałam, że między dużymi i małymi nasionami powstają interakcje pośrednie, które mogą wpływać na przeżywalność nasion. Odkryłam, że interakcje między

żołędziami o różnych rozmiarach zmieniały się z roku na rok: w pierwszym, ale nie w drugim roku badania, obecność małych żołędzi chroniła duże przed usunięciem. W trzeciej części mojej rozprawy doktorskiej zbadalam wpływ zmienności wewnątrzgatunkowej myszarki leśnej (*Apodemus flavicollis*) na roznoszenie nasion dębu szypułkowego (*Quercus robur*). Wykazałam, że zwierzęta o większej skłonności do eksplorowania nowego środowiska mają tendencję do wynoszenia nasion dalej od drzew. Jednak inne efekty indywidualnych cech myszarki leśnej znacznie różniły się między latami, co wskazuje, że ich wpływ na interakcje z roślinami zmienia się, gdy warunki ekologiczne ulegają wahaniom. Podsumowując, wyniki moich badań podkreślają znaczenie prowadzenia wieloletnich badań w celu wykrycia zależności od kontekstu interakcji między gatunkami i długoterminowych trendów w zjawiskach ekologicznych.

Słowa kluczowe: interakcje między roślinami a konsumentami nasion, hipoteza wysycenia drapieżników, roznoszenie nasion, zmienność wewnątrzgatunkowa, osobowość zwierząt

3. Abstract

The relationship between plants and granivores varies in magnitude - from weak to strong – and in sign – from negative to positive. To make sense of this variation, we need global syntheses of numerous existing studies, and field studies that focus on overlooked sources of complexity in plant-granivore interactions. My thesis aimed to address both of these goals. The thesis consists of three parts: (i) a meta-analysis of the predator-satiation hypothesis, (ii) a study on the impact of variation in seed size on foraging decisions of rodents, (iii) a study on the effects of intraspecific variation in granivore traits on the patterns of seed dispersal. In the first part of my thesis, I revisited predator-satiation hypothesis in a meta-analysis based on 48 studies that gathered at least 4 years of data on seed production and seed predation. The predator-satiation hypothesis is one of the most widely known hypothesis explaining evolutionary advantages of mast seeding. It states that intermittent, abundant crops evolved to reduce seed losses by starving granivores between mast events and overwhelming them with seeds during mast years. I found evidence of both starvation between mast years and satiation during mast years. However, the effectiveness of predator satiation varied between predator types; there was evidence for satiation of invertebrates, but not vertebrates. Moreover, satiation became less effective over recent decades, probably due to global anthropogenic changes. In the second part of my thesis, I investigated the impact of acorn size on their removal and dispersal by granivores. Because trees have modular construction, copies of the same organ, such as seeds, may exhibit considerable variation. Since most granivores display preferences towards seeds of particular size, indirect interactions can arise between larger and smaller seed, which further impacts seed survival and seedling establishment. I found that interactions among different sized acorns varied from year to year: in the first, but not the second year of the study, the presence of small acorns protected large ones from removal. In the third part of my thesis, I investigated the impact of individual traits of yellow-necked mice on the dispersal of common oak acorns. I found that more explorative individuals tend to disperse seeds further from other trees. However, other effects of individual traits varied substantially among years, indicating that their impact on interactions with plants changes when ecological conditions fluctuate. Overall, my results underscore

the importance of conducting multi-year studies to detect context-dependent interactions between species and long-term trends in ecological phenomena.

Key words: plant-granivore interactions , predator satiation hypothesis, seed dispersal, intraspecific variation, animal personality

4. Introduction

The interactions between plants and animals constitute one of the most significant relationships between species. The origin of this relationship can be traced back to Devonian period, ~425 million years ago, when the first vascular plants emerged (Del-Claro and Torezan-Silingardi 2021). Less than 100 million years later, nearly all types of feeding strategies used by animals to consume plants had developed (Slansky and Rodriguez 1987; Conrad C. Labandeira 2002; Del-Claro and Torezan-Silingardi 2021). Given the extensive shared history and coevolutionary development between these two biological kingdoms, it is expected that their interaction serves as a cornerstone for both biodiversity (Bascompte and Jordano 2007) and ecosystem functioning (Loreau 2010).

Different features of plant-animal interaction underpin the structure and stability of ecological system (Wootton and Emmerson 2005; Okuyama and Holland 2008). The evolution of both plants and animals has been shaped by selective pressures, created both by environmental factors and the species they interact with (Rodríguez-Castañeda 2013; Valdés and Ehrlén 2021). According to Abrahamson (1989) we distinguish three main types of interactions between plants and animals:

- **Antagonistic** – this interaction occurs when one organism benefits at the expense of another ('Encyclopedia Britannica | Britannica' n.d.). In plant-animal relationship, antagonistic interactions usually arise when the plant serves as a food resource for the animals (Del-Claro and Torezan-Silingardi 2021). However, this is not always the case. Antagonistic interactions between plants and animals include parasitism, where one organism resides within or is attached to the host and draws nourishment, and predation, when one organism obtains energy or nutrients from another organism by killing it (Abrahamson 1989).
- **Mutualistic** – an interaction that is beneficial for both participating species (Krebs 2009). A typical mutualistic interaction between plants and animals is the relationship between a pollinator and a flower, where an animal is rewarded with nectar or brood-place, and the flower benefits from the transport of pollen to another blossom (Abrahamson 1989).

- Commensalism – an interaction where one organism benefits while the other remains unaffected (Mathis and Bronstein 2020). A common example is when animals utilize habitats provided by plants, such as bird nesting in a tree (Abrahamson 1989).

However, the interactions between plants and animals are not always strictly mutualistic or antagonistic (Rodríguez-Rodríguez, Jordano, and Valido 2017) and can change with ecological context (Strauss and Irwin 2004). Such conditional interactions can vary both in magnitude (from weak to strong) and sign (from negative to neutral to positive) (Perea et al. 2013). Different features of a given relationship between plant and animal shape the structure and the dynamics of ecological systems (Bascompte 2010; Suweis et al. 2013).

The seed stage is a particularly hazardous phase in plant's life cycle (Fenner and Thompson 2005). Seeds suffer predation primarily from insects, birds, and mammals, with the interaction coevolving at the chemical, spatial, and temporal level (Janzen 1971). Typically, we categorize seed predation into two types: pre-dispersal and post-dispersal seed predation (Janzen 1971; Fenner and Thompson 2005). The main driver of pre-dispersal seed predation is the higher abundance of seeds near the parent plant, which provides an easily accessible food source for pre-dispersal seed predators (Comita et al. 2014). The magnitude of pre-dispersal predation can vary from negligible to extremely severe, potentially leading to the consumption of the entire seed yield (Preisser and Bastow 2005; Kolb, Ehrlén, and Eriksson 2007). The majority of pre-dispersal seed predators are small, highly specialized insects, many of which develop inside the seed (Crawley 2000).

Seeds that escaped increased mortality near the parent plant are, however, susceptible to predation from post-dispersal predators (Hulme 1994). The vast majority of dispersed seeds, found by animals on the ground, are consumed (Vander Wall, Kuhn, and Beck 2005). There are several factors that influence the probability of seed consumption after dispersal. For example, seeds that are less accessible, such as located in dense vegetation (Schoepf et al. 2015) or cached underground, might be less likely to be harvested (Bogdziewicz, Crone, and Zwolak 2020). Additionally, isolated seeds scattered on the ground have higher chances of survival than seeds aggregated around parent plant (Chapman and Chapman 1996). Moreover, some

granivores have preferences towards seeds of specific sizes (Perea, Miguel, and Gil 2011; Lichti, Steele, and Swihart 2017; Wang and Ives 2017), usually choosing larger seeds for storage (Wang and Chen 2009) and smaller seeds for immediate consumption (Wang and Ives 2017).

In response to predation, plants have evolved specific mechanisms that increase seeds survival (Preisser and Bastow 2005). To prevent immediate consumption, some seeds have defence mechanisms that involve chemical compounds such as poisonous alkaloids, or saponins that reduce the nutritive value of the seed (Janzen 1969; Preisser and Bastow 2005). Additionally, seeds may produce a hard coat that forms a physical barrier to prevent oviposition or larval entry (Preisser and Bastow 2005). However, the cost of defence allocation may create a trade-off between investments in different types of anti-predator defence (Koricheva, Nykänen, and Gianoli 2004).

Another adaptive strategy involves the ability to germinate even if the seed has been severely damaged. There is evidence that some seeds can germinate even if up to 70% of the cotyledon has been consumed (Giertych and Suszka 2011; Perea, San Miguel, and Gil 2011). Increased seed survival might also be a selective benefit of masting (Silvertown 1980), i.e. the synchronous and variable production of seed crops (Kelly 1994). This is explained by the predator satiation hypothesis, which suggests that the evolution of abundant, intermittent seed crops helps to overflow predators with seeds, so that they are unable to consume all available seeds during mast years, and starve between mast events (Solomon 1949; Kelly 1994).

Seed dispersal represents another crucial relationship between plants and animals (Herrera et al. 1994; Schupp and Fuentes 1995). Dispersal is a process by which offspring or propagules move away from their parents to settle in a more distant area, or when individuals move from one breeding population to another (Ronce 2007). The process is present in both plant and animal species, but it differs substantially in the way it is executed. While most animals move on their own, plants depend on other dispersal agents, such as wind, water or animals, to move their propagules away from parent individual (Herrera 2002). Animal-mediated dispersal (zoochory) is substantially more widespread than other modes of seed dispersal, with the average of 90% of woody plants in tropical forest and up to 62% of temperate forest species being dispersed by animals (Howe and Smallwood 1982; Herrera 1984), mostly birds and

mammals (Fenner and Thompson 2005). There are several processes by which animals can disperse seeds: ectozoochory, when seeds attach to an animal's skin, fur or feathers; endozoochory, when animals consume seeds or fruits and later regurgitate or defecate them; and synzoochory (a. k. a. scatter-hoarding), where animals such as rodents and corvids disperse and store seeds, which can germinate and establish if not retrieved (Herrera 2002; Steele 2021).

Plants evolved numerous adaptations promoting attraction of the disperser or facilitating the attachment and movement by the disperser (Herrera 2002; Lengyel et al. 2010). Some seeds are being transported without the animal knowing it (Steele 2021), which can result in dispersal over great distances (Sorensen 1986). Adhesive seeds attach to the animal by means of hooks, burrs or sticky secretion (Van Der Pijl 1982; Sorensen 1986). Other dispersal strategies require some kind of reward to attract an animal (Edwards, Dunlop, and Rodgerson 2006; Schupp et al. 2019). It usually involves nutritious pulp, rich in sugar, fat or protein (Fenner and Thompson 2005). To complicate matters, some seeds transported by animals apparently have not evolved any particular adaptation to increase the probability of being dispersed (Fenner and Thompson 2005).

Seed dispersal plays a vital role in both seed survival and the probability of germination (Howe and Smallwood 1982; Wenny 2001). Seeds can experience high mortality near the parent plant (Hyatt et al. 2003; Comita et al. 2014) due to increased pathogen density (Bell, Freckleton, and Lewis 2006), predation (Bell, Freckleton, and Lewis 2006), and competition for resources (Comita et al. 2014). Thus, moving seeds away enables to evade these unfavourable factors (Schupp 1988; Comita et al. 2014; Schupp et al. 2019). Beyond this, seed dispersal offers other advantages. When dispersed, seeds can colonize distant, vacant sites (Howe and Miriti 2004). Moreover, animals that disperse seeds often take them to non-random locations, some of which may be highly suitable for germination and seedling establishment (Howe and Smallwood 1982).

For many animals, seeds, fruits, and nuts are the main food resource (Fenner and Thompson 2005). As a consequence, granivore population size strongly depends on the seed crop. Their populations can grow in years following an abundant seed crop, and drastically decline in years after a crop failure (Wolff 1996; Selva et al. 2012;

Zwolak, Bogdziewicz, and Rychlik 2016). There are two main strategies that are used by some granivores to buffer these fluctuations in food resources and survive periods of scarcity. Animals that are capable to defend their supplies store all their resources in one location, and are called ‘larder-hoarders’ (Vander Wall 1990). Larder-hoarding is found, for instance, in eastern chipmunks (*Tamias striatus*) (Clarke and Kramer 1994), common hamsters (*Cricetus cricetus*) (Hędrzak, Badach, and Kornaś 2021), and bank voles (*Myodes glareolus*) (Hansson 1986). From a plant’s perspective, larder-hoarding rarely provides appropriate germination conditions because larders tend to be located in deep burrows. A contrasting strategy, called ‘scatter-hoarding’, occurs when an animal stores seeds in many undefended caches, typically one food item per cache. This strategy is employed by many species from rodent families Sciuridae, Muridae or Dasyproctidae, and bird species from Corvidae, Paridae, Sittidae and Picidae families (Vander Wall 1990). Typically, seed burial by scatter-hoarders is highly beneficial for plant recruitment (Briggs et al. 2009, Zwolak and Crone 2012).

However, variation in plant-animal interactions is not limited to species-level relationships (Zwolak 2018). In animals, individuals of the same species differ in their behavior, age, body mass, and sex (Bolnick et al. 2011), which can impact their performance in interspecific interactions (Moran et al. 2022). Individuals with certain traits can also provide rare dispersal outcome that might be masked when we focus on species averages (McConkey and O’Farrill 2015; González-Varo and Traveset 2016). Yet, in plants, variation can be considered even at the intra-individual level due to a plant’s modular construction. This results in certain variability in copies of the same organ, such as leaves, flowers or seeds, produced by the same individual (Herrera 2017). Such variation, both in plants and animals, might be an important driver of ecological dynamics (Des Roches et al. 2018).

In my dissertation I aim to explore the dynamics of plant-animal interactions, using trees and granivores as a model. I am investigating the mechanisms employed by plants to increase seed survival, both on a global scale through the meta-analysis of large-scale patterns in seed production and predation, and at the individual level, by exploring the consequences of intra-individual variation in acorn production. Additionally, I am investigating seed dispersal patterns and seed fate in relation to the varying traits of granivores. My objective is to offer a holistic approach to the study of

plant-animal interactions, an approach that ranges from synthesizing worldwide datasets to conducting case studies that incorporate the variation observed at the individual level in both plants and granivores, and its consequences for seed survival.

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5. Doctoral dissertation

Below are given the full texts of publications included in my dissertation.

5.1 Global patterns in the predator satiation effect of masting: A meta-analysis

Zwolak, R., **Celebias P**, Bogdziewicz M. 2022. 'Global Patterns in the Predator Satiation Effect of Masting: A Meta-Analysis'. *Proceedings of the National Academy of Sciences* 119 (11): e2105655119.

5.2 Consequences of intraspecific variation in seed size: does the presence of small seeds reduce predation on large ones?

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

5.3 Behavior, body mass, and sex: how intraspecific variation influences seed dispersal by a scatterhoarding rodent

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Abstract

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. We explored how individual traits (sex, body mass, exploration levels) of yellow-necked mice (*Apodemus flavicollis*) impact the dispersal of common oak (*Quercus robur*) acorns. 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 and reproductive state 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. These 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, conditional mutualism, context-dependence, individual variation, scatterhoarding, seed dispersal, synzoochory

5.3.1 Introduction

Intraspecific variation, a vital driver of ecological dynamics (Des Roches et al. 2018), has the potential to influence species interactions (Wolf and Weissing 2012), community composition (Hausch, Vamosi, and Fox 2018), and ecosystem functioning (Bonaldo and Bellwood 2008). Intraspecific variation frequently manifests as ecologically significant differences in the morphology, physiology or behavior of animals (Bolnick et al. 2003; Sih, Bell, and Johnson 2004), stemming from factors such as sexual dimorphism (Shine 1989), ontogenetic shift (Nakazawa 2015) or personality traits (Sih, Bell, and Johnson 2004). As a result, different individuals may assume quantitatively or qualitatively different roles in interspecific interactions (McConkey and O’Farrill 2015; Poisot, Stouffer, and Gravel 2015, Moran et al. 2022). 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.

Seed dispersal is a critical ecological interaction that could be particularly affected by intraspecific variation. 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 (Zwolak 2018). The influence of animal traits on seed dispersal is complex, as individuals within the same species can differ in multiple ways (Zwolak 2018). Males and females, for example, may exhibit distinct seed dispersal patterns due to variations in morphology and behavior (Clarke and Kramer 1994; Karubian et al. 2012). Sex can affect roaming patterns and home range size (Cutrera et al. 2006), which in turn impact seed dispersal distance (Oleksy, Racey, and Jones 2015). Additionally, reproductive roles, particularly during mating season, can shape seed dispersal decisions (Karubian et al. 2012). 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; Muñoz and Bonal 2008; Larsen and Burns 2012) and consume more seeds (Herrel et al. 2004), leading to increased quantities of dispersed seeds (Eisenhauer et al. 2010; Larsen and Burns 2012; Correa et al. 2015, but see Tulipani and Lipcius 2014). Finally, recent studies have highlighted the critical impact of individual behavioral types on seed dispersal (Dochtermann and Jenkins 2007; Brehm et al. 2019, Feldman et al. 2019; Zwolak and Sih 2020; Brehm and Mortelliti 2022) which have largely been ignored until recently.

The consequences of individual behavioral variation have been well studied at the individual level, such as its impact on survival or fitness (Boon et al. 2007, Guilette et al. 2011, Moiron et al. 2020). However, its effects at higher levels, such as interactions among species, remain less explored (Sih et al. 2012). In the case of seed dispersal, individuals with different behavioral traits can exhibit varying effectiveness (Zwolak 2018). Bolder and fast-exploring individuals are thought to be more inclined to cache seeds in riskier environment (Zwolak and 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 (Zwolak and 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 (Lichti, Steele, and Swihart 2017, Gómez et al. 2019). 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 (Schupp and Fuentes 1995; Zwolak and Crone 2012; Pesendorfer et al. 2018). 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.

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 first hypothesis (**H1**) posited that larger individuals would cache fewer seeds compared to their smaller counterparts, as their decision to consume seeds instead of caching may be driven by higher energy requirements (Lichti, Steele, and Swihart 2017). Additionally, we hypothesized (**H2**) that larger individuals will carry seeds farther because the cost of seed transport decreases with body mass (Munoz and 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, particularly in reproductively active (scrotal) males, as they expand their home ranges to encompass multiple female territories (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 and 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, Zwolak and Sih 2020).

5.3.2 Methods

5.3.2.1 Study site and small mammal trapping

We conducted this study in Puszcza Zielonka Landscape Park (52.6N, 16.9E), 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*). 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 10 m spacing. We baited traps with oat flakes and sunflower seeds and checked twice per day. We conducted five 4-day long trapping sessions at three-week intervals from June to September in 2020, 2021, and 2022, totalling 36 000 trap-nights. During each session, we assessed the sex, weight, and reproductive status of each trapped animal. We double-marked all individuals with unique ear tags and passive integrated transponder (PIT) tags.

5.3.2.2 Animal personality test

We tested each captured individual for behavioral type using two tests: an open-field test to measure activity and exploration in a new environment (Montiglio et al. 2012, Bednarz and Zwolak 2022) 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 minute. 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 two minutes, 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-handled digital cameras.

5.3.2.3 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 three-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 30 m apart. At each depot, we placed five acorns marked with a red plastic tag (20×40 mm) attached to the acorn with a thin steel wire (length 100 mm, \varnothing 0.2 mm). We placed the acorns in the loop of a PIT-tag reader's antenna, with a ReconyxTM 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, 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 and 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.

5.3.2.4 Statistics

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 behavioral 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 behavioral observations. For each individual, we calculated the mean best linear unbiased predictor (BLUP) over simulations glmmTMB’ package (Brooks et al. 2017). Due to 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 farther 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.

The impact of the yellow-necked mouse’s exploration rate, sex, body mass, and year of study on the distance of seed dispersal (for seeds that were removed and either cached or left on ground surface), was tested using Gaussian-family generalized linear mixed models (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. In this analysis, we tested hypothesis (H4) by categorizing the “sex” variable into three groups: females, reproductively active (scrotal) males, and non-reproductively active males. In the initial GLMM models, we included two-way interactions between the year and other explanatory variables. These interactions were retained in the final models only if they were statistically significant.

We tested for the statistical significance of fixed factors with Wald type II chi-square tests ('Anova' function from the 'car' package, Fox and 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.

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. Again, the initial GLMM models included all possible two-way interactions between the year and other explanatory variables.

5.3.3 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 ($\beta \pm SE = -0.029 \pm 0.040$, $p = 0.464$), but increased with mouse's body mass ($\beta \pm SE = 0.065 \pm 0.020$, $p = 0.001$). Moreover, the exploration rate varied across the years of the study (Chi-square = 14.483, $df = 2$, $p < 0.001$) and was decreasing over repeated tests ($\beta \pm SE = -0.04 \pm 0.011$, $p < 0.001$). 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, $p < 0.001$).

5.3.3.1 Impact of individual traits on seed dispersal

Over the three years of the study, we recorded 196 marked and behaviorally 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.

5.3.3.1.1 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 1; estimates and standard errors are provided in Appendix Table A1). 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: $p = 0.263$) (Fig. 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 ($p = 0.371$).

Table 1. Summary of model output examining the relationship between the probability of seed consumption 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.

Effects	Chi-square	Df	P- value
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	0.017
Sex:Year	7.451	2	0.024
Body mass:Year	7.930	2	0.019

5.3.3.1.2 Seed caching

The impact of exploration rate, sex, and body mass on seed caching also varied across years (Table 2; Appendix Table A2). The impact of body mass was negative in 2020 ($p = 0.031$), but positive in 2021 ($p = 0.015$) and 2022 ($p < 0.001$) (Fig. 1B). The impact of exploration rate was positive in 2021 ($p < 0.001$; Fig. 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 ($p = 0.002$) (Fig. 1D).

Table 2. Summary of model output examining the relationship between the probability of seed caching 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.

Effects	Chi-square	Df	P- value
Exploration rate	5.367	1	0.021
Year	26.027	2	<0.001
Sex	0.514	1	0.474
Body mass	0.344	1	0.558
Exploration rate:Year	21.751	2	<0.001
Sex:Year	22.691	2	<0.001
Body mass:Year	27.319	2	<0.001

5.3.3.1.3 Distance of dispersal

On average, dispersed seeds were transported 6.2 m from the depots (range: 0.1 – 49.7 m). The distance of dispersal was unaffected by the sex of the mice nor male reproductive status (Table 3; Appendix Table A3). Furthermore, exploration rate had no effect on the distance of seed dispersal (Table 3). The effect of body mass on the distance of seed dispersal, however, varied annually (body mass × year interaction in Table 3; Fig. 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 ($p = 0.197$) and 2021 ($p = 0.681$).

Table 3. Summary of model output examining the relationship between distance of dispersal from the seed depot and the following variables: exploration in an open-field test, year (2020, 2021 and 2022), sex, and body mass.

Effects	Chi-square	<u>Df</u>	P- value
Exploration rate	0.446	1	0.504
Year	38.059	2	<0.001
Sex†	4.335	1	0.114
Body mass	1.443	1	0.230
Body mass:Year	18.297	2	<0.001

†In this analysis, variable “Sex” included three groups: females, reproductively active (scrotal) males, and non-reproductively active males

5.3.3.1.4 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 4). 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 4; Appendix Table A4; Fig. 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: $p = 0.114$).

Table 4. Summary of model output examining the relationship between distance of seed dispersal from the nearest tree and the following variables: exploration in an open-field test, year (2020, 2021, and 2022), sex, and body mass.

Effects	Chi-square	<u>Df</u>	P- value
Exploration rate	6.505	1	0.011
Year	14.112	2	0.001
Sex	0.759	1	0.384
Body mass	5.971	1	0.015
Body mass:Year	6.127	2	0.047

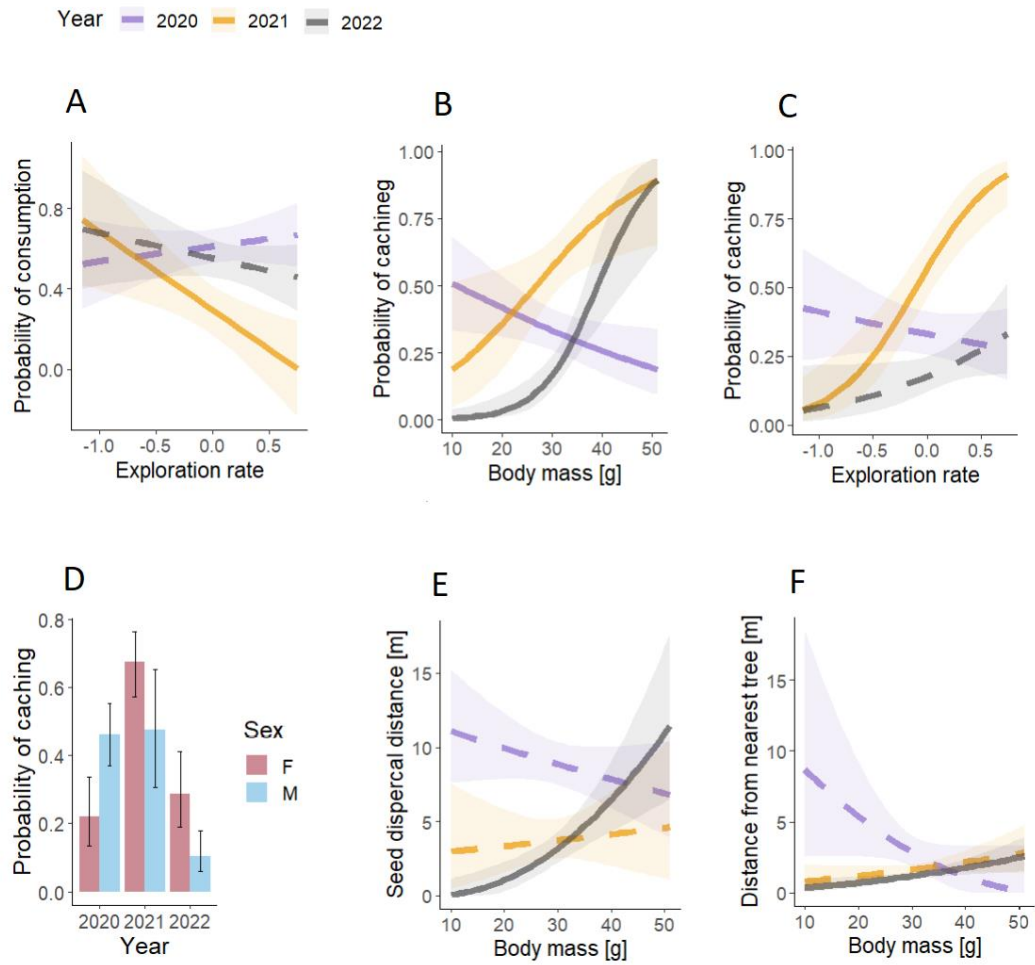


Figure 1. Impact of different traits of yellow-necked mice on probability of consumption (A), probability of caching (B, C and D), distance of dispersal from the seed depot (E) and the distance of dispersal from the nearest tree (F). Lines denote estimates from generalized linear mixed models (solid line for significant relationship and dashed line for non-significant relationship), shading corresponds to 95% CI, and colors indicate relationships in years 2020-2022.

5.3.4 Discussion

Our study reveals that the relationship between individual traits and seed dispersal is not static but varies from year to year, implying that environmental conditions could play a decisive role 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.

Despite the predicted decrease in probability of seed caching with body mass (H1; Table 5), this effect was observed only in one year of the study (2020). In the subsequent years (2021 and 2022), the opposite effect was found. Perhaps seed handling challenges are more significant than the energetic requirements we initially focused on. Caching behavior often involves carrying seeds over longer distances (Steele, Hadj-Chikh, and Hazeltine 1996), a task possibly more challenging for smaller and more manageable for larger individuals (Muñoz and 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 5).

The results for hypothesis H3 (regarding a higher seed caching propensity in males compared to females) were mixed. Over one of the study years, males demonstrated a higher likelihood to cache seeds compared to females, but this trend inverted in the remaining years. Furthermore, hypothesis H4, which predicted that sex and reproductive status would influence seed dispersal distance, was not supported. Despite the well-established differences in the spatial behavior of male and female yellow-necked mice (Stradiotto et al. 2009, Bogdziewicz et al. 2016), neither sex nor reproductive status had any discernable impact on seed dispersal distance in our study. 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. Nevertheless, 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 behavior (Koolhaas et al. 1999; Sih et al. 2004). Such behavior can have important consequences for plant recruitment because seeds deposited farther away from adult

plants often escape density-dependent mortality, and thus can be more likely to germinate (Bell, Freckleton, and Lewis 2006; Comita et al. 2014; but see Bogdziewicz, Crone, and Zwolak 2020).

Our results also diverge from previous studies by Brehm et al. (2019) and Brehm and Mortelliti (2022). In these studies, scatterhoarding 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 to their reactive counterparts. Yet, our study unveils high 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.

Seed-granivore interactions are highly context-dependent (Ostoja, Schupp, and Klinger 2013; Lichti, Steele, and Swihart 2017; Celebias and Bogdziewicz 2023). Several factors, such as the quality of the patch (Caccia et al. 2006), population size of granivores (Janova, Heroldova and Cepelka 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 scatterhoarders under different environmental conditions (i.e., considered by averaging out intraspecific variation among animal seed dispersers (Zwolak 2018). Additionally, our data imply that the influence of scatterhoarders' individual traits is equally contingent on ecological context.

Though mechanisms behind the context-dependency are unclear we suggest potential explanations for annual variation. Environmental factors like weather (Wróbel and Bogdziewicz 2015) and food availability (Fletcher et al. 2010) can impact the energy levels and foraging behavior of mice, potentially interacting with individual traits to affect seed dispersal behavior. Although we controlled for tree nut abundance by conducting our experiments before seed fall, 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 behaviors, 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 behaviors 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 behaviors, as individuals with specific trait combinations differentiate their foraging strategies to reduce competition. However, despite considerable variation in mouse abundance, it did not appear to drive the context-dependence in our results (see supplementary analysis in Appendix B: Impact of mouse abundance on seed fate). Predation risk can also impact traits' influence. For instance, in years with higher predation risk, the influence of traits related to risk-taking behaviors, 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 (Chamberlein, Bronstein and Rudes 2014), and single-year studies may overestimate effects or miss context-dependency (Nosek, Spies, and Motyl 2012).

Future research should aim to uncover the specific mechanisms responsible for the varying effects of individual traits on seed dispersal and investigate the influence of environmental and ecological factors on this process. 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 necessity of incorporating both individual variation and environmental context when exploring factors that shape seed dispersal patterns.

In conclusion, our study underscores that seed dispersal research must account for year-to-year variations, which are likely tied to environmental shifts. 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 and its pivotal role in shaping and maintaining ecosystems.

Table 5 Summary of tested predictions and results

	Prediction	Is prediction supported?	Result
H1	Larger individuals cache fewer seeds compared to smaller individuals.	Partially	The impact of body mass on caching behavior 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, especially reproductively active, transport seeds farther than females.	No	Sex and reproductive status had no effect on seed dispersal distance.
H5	More exploratory individuals are more likely to consume acorns rather than cache them compared to 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 than less exploratory individuals distances.	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.

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APPENDIX A

Appendix Table A1. Summary of model output examining the relationship between the probability of seed consumption by yellow-necked mice (*Apodemus flavicollis*) and the following variables: exploration in the open-field, year (with 2020 as the reference level), sex (with females as the reference level), and body mass.

<i>Predictors</i>	Probability of consumption		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.48	0.23 – 0.72	<0.001
Exploration_rate	0.08	-0.10 – 0.25	0.407
Year2021	0.10	-0.46 – 0.65	0.731
Year2022	0.31	-0.12 – 0.75	0.156
SexM	-0.17	-0.32 – -0.03	0.019
Body_mass	0.01	0.00 – 0.01	0.047
Exploration_rate:Year2021	-0.47	-0.79 – -0.14	0.005
Exploration_rate:Year2022	-0.20	-0.48 – 0.08	0.159
Year2021:SexM	0.29	0.04 – 0.55	0.023
Year2022:SexM	0.24	0.03 – 0.45	0.022
Year2021:Body_mass	-0.02	-0.04 – -0.00	0.045
Year2022:Body_mass	-0.02	-0.03 – -0.00	0.018
ICC	0.18		
Observations	737		
Marginal R ² / Conditional R ²	0.123 / 0.284		

Appendix Table A2. Summary of model output examining the relationship between the probability of seed caching by yellow-necked mice (*Apodemus flavicollis*) and the following variables: exploration in the open-field, year (with 2020 as the reference level), sex (with females as the reference level), and body mass.

<i>Predictors</i>	Probability of caching		
	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.28	0.16 – 0.52	<0.001
Exploration_rate	0.71	0.34 – 1.45	0.342
Year2021	7.11	3.17 – 15.97	<0.001
Year2022	1.41	0.64 – 3.11	0.396
SexM	3.03	1.52 – 6.04	0.002
scale(Body_mass)	0.77	0.61 – 0.98	0.031
Exploration_rate:Year2021	21.89	5.86 – 81.73	<0.001
Exploration_rate:Year2022	4.49	1.00 – 20.13	0.050
Year2021:SexM	0.14	0.05 – 0.43	0.001
Year2022:SexM	0.10	0.03 – 0.27	<0.001
Year2021:scale(Body_mass)	2.42	1.39 – 4.21	0.002
Year2022:scale(Body_mass)	4.61	2.42 – 8.81	<0.001
Observations	737		
Marginal R ² / Conditional R ²	0.337 / NA		

Appendix Table A3. Summary of model output examining the relationship between distance of dispersal from the seed depot and the following variables: exploration in the open-field, year (with 2020 as the reference level), sex (with females as the reference level, M denoting non-scrotal males, and MS denoting scrotal males), and body mass.

<i>Predictors</i>	Distance of dispersal from the station		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	3.65	2.79 – 4.52	<0.001
Body_mass	-0.02	-0.04 – 0.01	0.194
Year2021	-1.88	-3.53 – -0.24	0.025
Year2022	-4.00	-5.43 – -2.58	<0.001
Exploration_rate	0.14	-0.26 – 0.53	0.504
SexM	-0.43	-0.91 – 0.04	0.074
SexMS	-0.01	-0.36 – 0.35	0.969
Body_mass:Year2021	0.03	-0.03 – 0.08	0.306
Body_mass:Year2022	0.09	0.05 – 0.14	<0.001
Observations	385		
Marginal R ² / Conditional R ²	0.310 / NA		

Appendix Table A4. Summary of model output examining the relationship between distance of seed dispersal from the nearest tree and the following variables: exploration in the open-field, year (with 2020 as the reference level), sex (with females as the reference level), and body mass.

<i>Predictors</i>	Distance of dispersal from the nearest tree		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.68	1.35 – 2.01	<0.001
scale(Body_mass)	-0.45	-0.92 – 0.03	0.064
Year2021	-0.38	-0.72 – -0.03	0.032
Year2022	-0.56	-0.90 – -0.23	0.001
SexM	-0.07	-0.24 – 0.09	0.384
Exploration_rate	0.29	0.07 – 0.51	0.011
scale(Body_mass):Year2021	0.59	0.07 – 1.10	0.025
scale(Body_mass):Year2022	0.62	0.13 – 1.12	0.013
Observations	290		
Marginal R ² / Conditional R ²	0.214 / NA		

APPENDIX B

Impact of mouse abundance on seed fate

We investigated whether mouse abundance modified the impact of mouse's individual traits on seed consumption, caching, and dispersal distance. As an index of population abundance, we used the number of unique individuals captured during a given trapping session at a particular study site.

We conducted statistical analyses as outlined in the Methods section, substituting the 'Year' variable with mouse abundance because we hypothesized that shifts in abundance might account for the observed annual variation in the relationship between individual traits and seed dispersal parameters. Notably, the years showed significant differences in mouse abundance levels, thus including both variables would lead to collinearity.

We found that 'Year' consistently outperformed 'Abundance' as an explanatory variable in terms of both AIC (Burnham and Anderson 2002) of models with either year or abundance, and the statistical significance of their interaction terms with individual traits (Appendix Tables B1-B4). Although comparing phenomenological (with 'Year') and mechanistic (with 'Abundance') models is generally discouraged due to the tendency of the former to describe data well while the latter offers more biological insight (Beissinger and Snyder 2002), it's worth noting that interactions involving 'Abundance' were only statistically significant in three cases (Exploration rate:Abundance' effects in Appendix Tables B1 and B2, and 'Body mass:Abundance' effect in Appendix Table B2). Consequently, in the best-case scenario (keeping in mind that this is a post-hoc analysis as we had no a priori reasons to anticipate the modifying influence of abundance on individual traits), variations in abundance may only explain some of the variability in the influence of individual traits of yellow-necked mice on their seed dispersal patterns.

Appendix B References

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Appendix Table B1. Summary of model output examining the relationship between the probability of seed consumption by yellow-necked mice (*Apodemus flavicollis*) and the following variables: exploration in an open-field test, population abundance, sex, and body mass. The AIC value of this model was higher by 11.9 compared to the model that incorporated 'Year' instead of 'Abundance'.

Effects	Chi-square	Df	P- value
Exploration rate	0.277	1	0.598
Abundance	11.393	1	0.001
Sex	0.03	1	0.959
Body mass	0.006	1	0.939
Exploration rate:Abundance	4.693	1	0.030
Sex:Abundance	1.532	1	0.216
Body_mass:Abundance	2.786	1	0.095

Appendix Table B2. Summary of model output examining the relationship between the probability of seed caching by yellow-necked mice (*Apodemus flavicollis*) and the following variables: exploration in an open-field test, abundance, sex, and body mass. The AIC value of this model was higher by 55.8 compared to the model that incorporated 'Year' instead of 'Abundance'.

Effects	Chi-square	Df	P- value
Exploration rate	<0.001	1	0.994
Abundance	1.315	1	0.252
Sex	0.334	1	0.563
Body mass	1.070	1	0.301
Exploration rate:Abundance	5.216	1	0.022
Sex:Abundance	3.321	1	0.068
Body mass:Abundance	6.104	1	0.013

Appendix Table B3. Summary of model output examining the relationship between distance of dispersal from the seed depot and the following variables: exploration in an open-field test, abundance, sex, and body mass. The AIC value of this model was higher by 24.6 compared to the model that incorporated ‘Year’ instead of ‘Abundance’.

Effects	Chi-square	<u>Df</u>	P- value
Exploration rate	0.281	1	0.596
Abundance	15.451	1	<0.001
Sex†	0.354	1	0.838
Body mass	2.082	1	0.149
Sex:Abundance	3.518	1	0.061

†In this analysis, variable “Sex” included three groups: females, reproductively active (scrotal) males, and non-reproductively active males.

Appendix Table B4. Summary of model output examining the relationship between distance of seed dispersal from the nearest tree and the following variables: exploration in an open-field test, abundance, sex, and body mass. The AIC value of this model was higher by 12.3 compared to the model that incorporated ‘Year’ instead of ‘Abundance’.

Effects	Chi-square	<u>Df</u>	P- value
Exploration rate	0.672	1	0.412
Abundance	0.941	1	0.332
Sex	1.601	1	0.206
Body mass	4.178	1	0.041
Body mass:Abundance	0.955	1	0.328

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Declaration of authorship statements of the doctoral candidate

Zwolak, Rafał, **Paulina Celebias**, and Michał Bogdziewicz. "Global patterns in the predator satiation effect of masting: A meta-analysis." *Proceedings of the National Academy of Sciences* 119.11 (2022): e2105655119.

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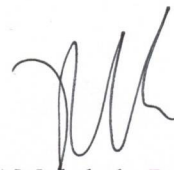
Contribution

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- Collecting and reviewing literature for meta-analysis
- Writing the manuscript

Paulina Celebias

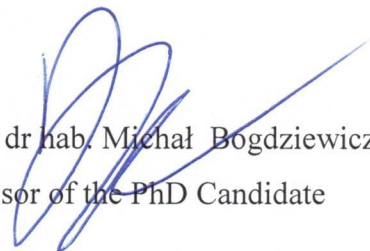
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Contribution

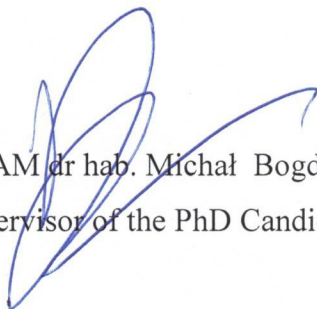
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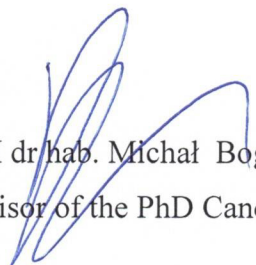
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I declare that my contribution to this paper included:

- Design of the study
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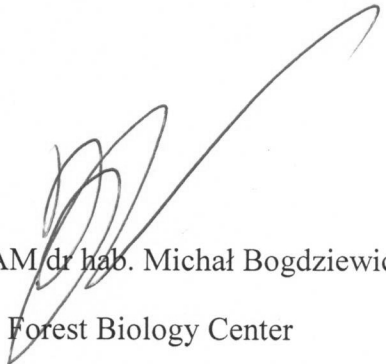
I confirm that I am the co-author author of the paper: **Celebias, Paulina**, Aleksandra Wróbel, Milena Zduniak, Michael Steele, Michał Bogdziewicz, Rafał Zwolak. „Behavior, body mass, and sex: how intraspecific variation influences seed dispersal by a scatterhoarding rodent”. Unpublished

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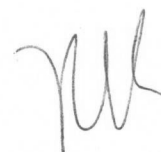
I confirm that I am the co-author author of the paper: **Celebias, Paulina**, Aleksandra Wróbel, Milena Zduniak, Michael Steele, Michał Bogdziewicz, Rafał Zwolak. „Behavior, body mass, and sex: how intraspecific variation influences seed dispersal by a scatterhoarding rodent”.
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