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SHORT COMMUNICATION

The hidden truth: unexpected acorn caching sites by Eurasian Jays (*Garrulus glandarius* L.) re-examined

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Abstract

Eurasian Jays (*Garrulus glandarius*) typically store seeds on the ground in shallow caches, promoting tree recruitment. However, speculation exists that Eurasian Jays occasionally store a portion of seeds in microhabitats unsuitable for proper germination. Here, we report that unexpected caching sites in Eurasian Jays can be much more widespread than previously considered and despite their accidental character it seems to be a durable aspect of Eurasian Jay's hoarding behavior. Out of 259 removed acorns of Pedunculate Oak (*Quercus robur*), we localized 31 consumed and 222 stored acorns. Six experimental acorns (3% of stored acorns) were found stored by jays in unexpected caching sites: (i) above the ground on individuals of Scots Pine (*Pinus sylvestris*), (ii) inside the woody stems of *Reynoutria* sp. individuals, (iii) in a rotten trunk, and (iv) among ruin debris. Our findings suggest the need to revise our understanding of so-called unexpected caching in Eurasian Jays. This highlights a previously overlooked aspect of oak-jay interactions, offering a valuable piece to the puzzle.

Keywords Acorn dispersal · Caching · Granivorous bird · Plant-granivore interactions · *Quercus* · Radio-tracking

Zusammenfassung

Die versteckte Wahrheit: unerwartete Eichelverstecke des Eichelhähers (*Garrulus glandarius* L.) unter der Lupe

Eichelhäher (*Garrulus glandarius*) lagern Samen üblicherweise in oberflächlichen Verstecken auf dem Boden und fördern so die Vermehrung von Bäumen. Es gibt jedoch die Vermutung, dass Eichelhäher gelegentlich einen Teil der Samen in Mikrohabitaten ablegen, die für eine gute Keimung ungeeignet sind. Hier berichten wir, dass unerwartete Samenverstecke des Eichelhähers viel verbreiteter sind als bisher angenommen, und dass sie trotz ihres zufälligen Charakters ein dauerhafter Aspekt des Hortungsverhaltens von Eichelhähern zu sein scheinen. Von 259 markierten Eicheln der Stieleiche (*Quercus robur*), die zuvor von den Eichelhähern weggetragen wurden, fanden wir 31 angefressene und 222 gelagerte Eicheln wieder. Sechs der Versuchseicheln (3% der gelagerten Eicheln) wurden von Eichelhähern in unerwarteten Verstecken gelagert: (i) über den Boden auf einzelnen Waldkiefern (*Pinus sylvestris*), (ii) im Inneren der holzigen Stämme von *Reynoutria* sp., (iii) in Totholz und (iv) inmitten von Schutt. Unsere Ergebnisse lassen vermuten, dass wir unser Verständnis vom sogenannten unerwarteten Verstecken bei Eichelhähern überdenken müssen. Dies unterstreicht einen bisher übersehenen Aspekt der Wechselwirkungen zwischen Eiche und Eichelhäher und liefert ein wertvolles Teil des Puzzles.

Introduction

Seed dispersal plays a pivotal role in shaping the demographic structure of plants and ensuring population sustainability (Bossema 1979; Vander Wall 1990; Gómez et al. 2019). In animal-dispersed plants, the landscape pattern of seed deposition is contingent upon disperser activity (Gómez et al. 2019). Despite extensive research, the specific contribution of avian dispersers to plant recruitment remains unclear, partly due to the difficulty of tracking bird-dispersed seeds in the wild (Pons and Pausas 2007; Wróbel

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et al. 2021, 2022; Sorensen et al. 2022). Eurasian Jays (*Garrulus glandarius*; hereafter "jays") typically store food items like acorns (*Quercus* spp.) on the ground in shallow caches, promoting tree recruitment (Bossema 1979; Vander Wall 1990; Pérez-Camacho et al. 2023). However, in Wróbel et al. (2021), it has been speculated, that jays sometimes store a certain proportion of acorns in microhabitats clearly detrimental for proper development into the adult plant. For example, jays store some acorns in tree cavities, and such decisions resulted from the availability of microsites for caching. Here, we report that unexpected caching sites in jays can be much more widespread than previously considered (Wróbel et al. 2021) and despite their accidental character it seems to be a durable aspect of jay's hoarding behavior. We note, however, that the term "unexpected" only refers to a human perspective based on current knowledge.

Methods

In October and November 2023, we were conducting research on dispersal of Pedunculate Oak (*Quercus robur*) by jays in abandoned post-agricultural sites with mid-field afforested patches. We used Telenax™ radio transmitters inserted into each acorn, and were thus able to determine the exact fate of removed acorns (see e.g., Pons and Pausas 2007; Kurek et al. 2019, 2023; Wróbel et al. 2021, 2022 for a similar approach). We offered marked acorns on feeders fixed to 3-m-high branches of oak trees during the daytime (7:00 am to 5:00 pm). The study sites were located in three geographical regions in southern Poland: Dynowskie Foothills, Sandomierska Basin, and Silesian Upland (two sites per region, one or two feeders per site; nine feeders in total). Through direct observation and camera traps, we verified that the sole species engaging in acorn removal included in the analyses was the jay. Each feeder was visited by at least a few jays. Following the removal of an experimental acorn by a jay, we initiated radio-tracking to locate the seed as well as to determine its fate (consumed vs. stored) and microhabitat of caches. The experimental acorns were found within a few hours after removal (usually after several minutes).

Results and discussion

We located 253 out of the initial 259 marked acorns. Of the located acorns, 31 were consumed and 222 were stored; the signal of three radio transmitters was never found. Although most of stored seeds were hidden in either litter, the topsoil or short vegetation, six acorns offered at five different feeders were found located: (i) ~ 3 m above the ground on two individuals of Scots Pine (*Pinus sylvestris* L.) (two acorns), (ii) inside the woody stems of *Reynoutria* sp. individuals (two acorns; Fig. 1a and electronic supplementary material Video S1), (iii) in a rotten trunk of the Goat Willow (*Salix caprea*) (one acorn; Fig. 1b), and (iv) among ruin debris (one acorn; Fig. 1c). Therefore, 3% of cached acorns (six out of 222 acorns) were stored in unexpected caching sites (i.e., other than those on the ground, typically reported for jays). Additionally, we never found another three radio transmitters, but the signal strength suggested they were placed at elevated positions in the trees (one per each of the following tree species: Scots Pine, European White Birch *Betula pendula*, and Black Locust *Robinia pseudoacacia*) at heights exceeding four meters, too high to reach. We cannot exclude the possibility that those were intact seeds, stored in tree cavities, bark crevices or in the branch axils. Consequently, the share of unexpected caches could be 4% ($n = 9$).

Plant–granivore interactions are usually placed somewhere on an interaction continuum, are highly context-dependent (i.e., they are strongly affected by environmental conditions and habitat features), and can vary in space and time (Zwolak et al. 2016; Gómez et al. 2019). Jays use sophisticated cache-protection strategies as they are highly attuned to the possibility of pilferage, particularly from conspecifics (Shaw and Clayton 2012, 2013) and rodents (Zwolak et al. 2016), and make caching decisions based on their perception of competition and potential seed losses (Shaw and Clayton 2012, 2013). It is well-documented that seed hoarding in ground caches by jays enhance oak recruitment (Bossema 1979; Gómez 2003; Gómez et al. 2019). However, acorn storage by jays in tree cavities was first described by Wróbel et al. (2021), and confirmed later by Pérez-Camacho et al. (2023). While storing seeds in tree cavities or woody dead plant material could potentially benefit jays, such as by reducing the probability of seed pilferage or germination (see more in Wróbel et al. 2021), from the plant's perspective, these sites are unsuitable for growth.

Reports on jays hoarding food in unexpected caching sites are very rare and are rather considered as accidental events that occur only under specific environmental conditions (Wróbel et al. 2021; Pérez-Camacho et al. 2023). Only more systematic observations or long-term investigations may fundamentally change our knowledge and approach to this seemingly rare phenomenon. For example, the first study of primary seed dispersal (i.e., directly after a seed removal event) of radio-tracked acorns were conducted in pure Scots Pine monocultures covering hectares of woody areas, lacking specific microhabitats like crevices or tree holes for unexpected acorn storage like those found in this study (Kurek et al. 2019). Jays in these environments only had the option to store acorns in the moss layer under the forest canopy, making any other caching behavior appear unexpected (Wróbel et al. 2021).

Previous experiments conducted in forest-dominated landscapes (Wróbel et al. 2021) showed that unexpected

Fig. 1 The microsites of Eurasian Jays' (*Garrulus glandarius*) caches of the experimental acorns stored in **a** a *Reynoutria* sp. stem, **b** a rotten trunk of Goat Willow (*Salix caprea*), and **c** ruin debris. The arrows show: the exact *Reynoutria* sp. stem with the radio-tagged acorn hidden inside (not visible in the picture) (white arrow), and the antenna protruding from the acorn (blue arrow)

caching sites can be more common than expected. Our study confirms this finding, recording such sites in semi-open areas within post-agricultural lands [see also acorn storage in tree cavities reported in similar landscape in Pérez-Camacho et al. (2023)]. Notably, in other studies conducted on tracking acorns dispersed by jays, some fraction of radio-tagged seeds was never found, e.g., 4.5% in Pons and Pausas (2007) and 5.8% in Kurek et al. (2019), or the directly observed activity in forest canopy could have been determined as non-hoarding behavior (Gómez 2003). Therefore, acorn storage in tree cavities or other unexpected structures might have been overlooked.

In our study, we aimed to further demonstrate that jay hoarding behavior can be more nuanced than previously thought. This is especially true in environments with higher microhabitat heterogeneity, such as forest stands with more natural features and high amounts of dead wood and old trees, which offer more opportunities for jays to use these objects for hoarding seeds. Caching seeds alone may not be sufficient for oak recruitment if they end up in microhabitats unsuitable for germination and this becomes even more crucial considering the extensive landscape changes caused by humans. While research in mixed- and deciduous, managed forests in moraine landscapes revealed unexpected caching at a low frequency (Wróbel et al. 2021), our study in forest patches located within an agro-pastoral landscape provides further evidence of such caching behavior. While the low proportion of acorns cached this way suggests minimal impact on the population level, we speculate that this behavior's frequency depends heavily on the ecological context. Specifically, factors like the availability of suitable caching sites and the effectiveness against pilferage might influence how often jays utilize this strategy. Beyond environmental variables, individual learning and experience likely play a role as well. Jays, as shown by Shaw and Clayton (2012, 2013), can learn to estimate pilferage risk, potentially leading to intraspecific variation in caching behavior. Our findings reveal other types of unexpected caches, suggesting that this behavior, previously considered accidental, might be a more common and fundamental aspect of jay hoarding. Therefore, our understanding of so-called unexpected caching still needs revision for having a deeper insight into seed dispersal in one of the major animal-dispersed tree genus in the northern temperate zone. This finding highlights a previously overlooked aspect of oak-jay interactions, adding a valuable piece to the puzzle.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-024-02181-0.

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Data availability The datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work did not include handling animals nor substantially affecting animals.

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