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Influence of body size on the dual role of isopod *Porcellio scaber* in seed dispersal and predation of the mycoheterotrophic plant *Monotropastrum humile*

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Running title: Role of isopods in seed dispersal and predation

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Author contributions
KS designed the project and conducted the feeding experiments. MY and KS analyzed the data. KS wrote the initial draft. All authors revised the manuscript and approved the final version.

Conflict of interest
The authors declare no conflict of interest.

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Abstract

1. Endozoochorous seed dispersal by invertebrates, although infrequently documented, is gaining attention for its feasibility in plants with small seeds. Recent studies have highlighted terrestrial isopods as potential dual agents, acting both as seed dispersers and predators, especially for herbaceous plants with fleshy fruits and tiny seeds. However, the determinants of these contrasting roles are not well understood.
2. The present study explores intraspecific variation in *Porcellio scaber*, examining its dual role as a seed predator and disperser for *Monotropastrum humile* (Ericaceae), a plant with fleshy fruits and minute seeds (0.30–0.35 mm in length). We particularly focus on the impact of the sex and body size (5.44–11.99 mm) of the isopod *P. scaber* on seed dispersal or predation.
3. Our results indicate a significant correlation between seed dispersal effectiveness and isopod body size, with some variation attributed to sex differences. Smaller *P. scaber* individuals predominantly prey on seeds, while larger individuals are more likely to facilitate seed dispersal, maintaining seed viability.
4. Overall, our findings reveal that body size is a crucial factor in defining the ecological role of *P. scaber*. This challenges the conventional approach of using species-level average data in seed dispersal studies, emphasizing the need to consider intraspecific variations for a comprehensive understanding of seed dispersal.

KEYWORDS: endozoochorous seed dispersal, dust seed, intraspecific variation, *Porcellio scaber*, seed dispersal, terrestrial isopods

Introduction

Seed dispersal is a crucial mechanism that shapes biodiversity, with animals playing a pivotal role as dispersal agents (Wang & Smith, 2002). While seed dispersal efficiency is often quantified using species-level averages and associated errors (Zwolak, 2018), reliance on such averages may lead to inaccurate conclusions about plant-seed dispersal interactions, particularly if only individuals with extreme trait values are involved in dispersal activities (González-Varo & Traveset, 2016). Indeed, several studies have highlighted the significant impact of individual variations, such as growth stages, on seed dispersal effectiveness (King *et al.*, 2011; Larsen & Burns, 2012; Correa *et al.*, 2015).

Recent research has revealed that the isopod species *Porcellio scaber* can act as both seed predators and dispersers for *Monotropastrum humile* (Ericaceae), a plant with fleshy fruits and minute seeds (Suetsugu *et al.*, 2024). Although *P. scaber* is an introduced species, it has become one of the most common crustaceans in Japan (Tanaka & Udagawa, 1993), where this study was conducted. This finding challenges the traditional view that small invertebrates are ineffective endozoochorous seed dispersers due to size-related biophysical constraints (de Vega *et al.*, 2011). Notably, adult *P. scaber*, with body lengths ranging from 8–12 mm, are currently the smallest recorded internal seed dispersal agents. The previous study also indicated significant variability in seed fate (i.e., dispersal vs. predation) (Suetsugu *et al.*, 2024), yet the factors influencing these outcomes remain inadequately explored.

In this study, we experimentally evaluated the effects of body size and sex on the seed dispersal effectiveness of *M. humile* by *Porcellio scaber*. We specifically investigated whether (i) seeds dispersed by larger individuals are more likely to survive gut passage and (ii) there are differences in seed survival rates after gut passage between male and female individuals.

Materials and Methods

To assess the variation in the proportion of ingested seeds that were dispersed intact, differentiated by sex and body size, we conducted laboratory feeding experiments with *Porcellio scaber* at Kobe University (Kobe, Hyogo, Japan) in late July 2018. These specimens were collected in mid-July 2018 from the same population (Sapporo, Hokkaido, Japan; Suetsugu *et al.*, 2024) where we previously studied the interaction between *P. scaber* and *M. humile*. Each individual was housed separately in a plastic Petri dish (90 mm × 20 mm) throughout the experiment duration. When not participating in feeding trials, they were provided with litter from several plant species, including *Quercus glauca*. Petri dishes were maintained in laboratory conditions at an average temperature of 25°C.

Seeds (0.30–0.35 mm in length) were extracted from the fleshy fruits of *M. humile* collected in the field. Seventy seeds were remixed with the fleshy portions of the fruit without seeds. This mixture was then placed on moist filter paper in each Petri dish within each enclosure. When the isopod individuals molted during feeding experiments, they consumed almost no food, and these instances were excluded from further analysis. For other cases (16 males and 20 females), any unconsumed fruit with seeds was removed after 12 hours, and the remaining seeds were counted.

Fecal pellets were collected at 6-hour intervals for 48 hours post-consumption, based on preliminary findings that food typically passes through *P. scaber* individuals within 24 hours of consumption. The pellets were examined under a dissecting microscope for intact seeds. After the feeding experiments, the length of each isopod was measured from the apex of the cephalothorax to the posterior of the pleotelson. The length was determined to the nearest 0.01 mm under a stereomicroscope (M165C; Leica Microsystems, Cambridge, UK). The viability of the intact seeds was subsequently tested using TTC staining, as previously described for dust-like seeds (de Vega *et al.*, 2011). The viability of seeds by both male and female *P. scaber* individuals was compared to that of 50 control seeds collected directly from 10 intact fruits (Table S1).

A Generalized Linear Model (GLM) with a binomial error structure and logit link was used to analyze the effect of body size and sex on the proportion of intact seeds. Another GLM with the same structure was employed to compare the proportion of viable seeds among intact seeds, seeds consumed by male individuals, and seeds consumed by female individuals. Statistical analyses were conducted using R software version 4.2.3.

Results and Discussion

Our experiments revealed that some seeds remained intact after passing through the digestive systems of both male and female individuals, with averages of 34.8 ± 15.0% (mean ± SD; n = 16) and 31.6 ± 17.5% (mean ± SD; n = 20; Table S1), respectively. There was no significant difference in seed viability between seeds excreted by male (51.9 ± 8.6%; mean ± SD; n = 16) and female (54.1 ± 6.1%; mean ± SD; n = 19) *P. scaber* individuals, and those extracted directly from intact fruits (56.8 ± 7.6%; mean ± SD; n = 10). Importantly, our analyses demonstrated a significant positive correlation between the body size of *P. scaber* (5.44–11.99 mm) and the proportion of intact seeds (0–59.01%; $P < 0.001$, Table S2), suggesting that smaller individuals predominantly act as seed predators, while larger ones tend to serve as seed dispersers (Figs. 1–2). This indicates that intraspecific variations in body size are key determinants of the role an isopod species plays as either a seed predator or disperser. Although *P. scaber* individuals of various sizes and sexes readily consume *M. humile* seeds, smaller individuals reduce the likelihood of seeds remaining intact, possibly due to their smaller chewing mouthparts that necessitate comminution of food. Other studies corroborate that larger individuals generally disperse seeds more effectively than smaller ones (King *et al.*, 2011; Larsen & Burns, 2012; Correa *et al.*, 2015). For example, seed dispersal capability of *Gaultheria depressa* (Ericaceae) whose seed size is 0.40–0.65 mm by the alpine scree weta *Deinacrida connectens* varied significantly, correlating closely with body size (Larsen & Burns, 2012).

Sexual dimorphism in seed-dispersing animals also affects seed fate through various mechanisms (Zwolak, 2018). For instance, studies on rabbits have shown that more intact seeds pass through the guts of females than males, possibly due to differences in jaw structure (Mancilla-Leytón *et al.*, 2013). Similarly, our study suggests that seeds consumed by female *P. scaber* individuals are more likely to remain intact compared to those consumed by males of the same size ($P < 0.001$, Fig. 2; Table S2), despite no apparent morphological differences in the isopod mouthparts. Our results support the growing evidence suggesting that the traditional dichotomy of seed predator versus seed disperser oversimplifies the complex interactions between seed-consuming animals and plants (Corlett & Lucas, 1990; Norconk *et al.*, 1998). Notably, we demonstrated that a *P. scaber* nymph, as small as 6.02 mm, is capable of dispersing viable seeds, albeit at a lower rate. Considering *P. scaber* adults (larger than 8 mm) were previously recognized as the smallest endozoochorous seed dispersers (Suetsugu *et al.*, 2024), this record updates the size threshold for such dispersal mechanisms.

It should be noted that *P. scaber* is an exotic species in Japan, and even larger individuals are probably less efficient as seed dispersers compared to camel crickets with a higher proportion of intact defecated seeds and higher mobility (Suetsugu, 2018). However, non-native species, often being opportunistic, can play important roles in ecosystems, particularly in situations where native species are declining due to habitat disturbance (Alpert, 2006; Stavert *et al.*, 2018). Consequently, given its abundant nature even in disturbed landscapes (Karasawa, 2022), *P. scaber* could be an important seed disperser of *M. humile* in disturbed habitats, compensating for the loss of native species that are more dependent on natural settings. Additionally, even under conditions with a sufficient camel cricket population, incorporating a variety of seed dispersal agents might enhance seed dispersal efficiency.

In conclusion, our findings reveal that body size significantly influences the ecological role of *P. scaber*, determining whether it acts as a seed disperser or predator for *M. humile*. Our results, along with some recent studies (Bolnick *et al.*, 2011; Denny, 2017), challenge the conventional approach of using species-level average data in seed dispersal studies, emphasizing the need to consider intraspecific variations for a comprehensive understanding of seed dispersal. Further research on invertebrate seed consumers, incorporating intraspecific variations in body size and sex, could provide deeper insights into seed dispersal and predation.

Data Availability

The data that support the findings of this study are available in the supplementary material of this article.

Ethics approval statement

This work did not require ethical approval from human subjects or animal welfare committees. The plant and animal materials used in this study did not involve endangered or protected species.

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Figure legends

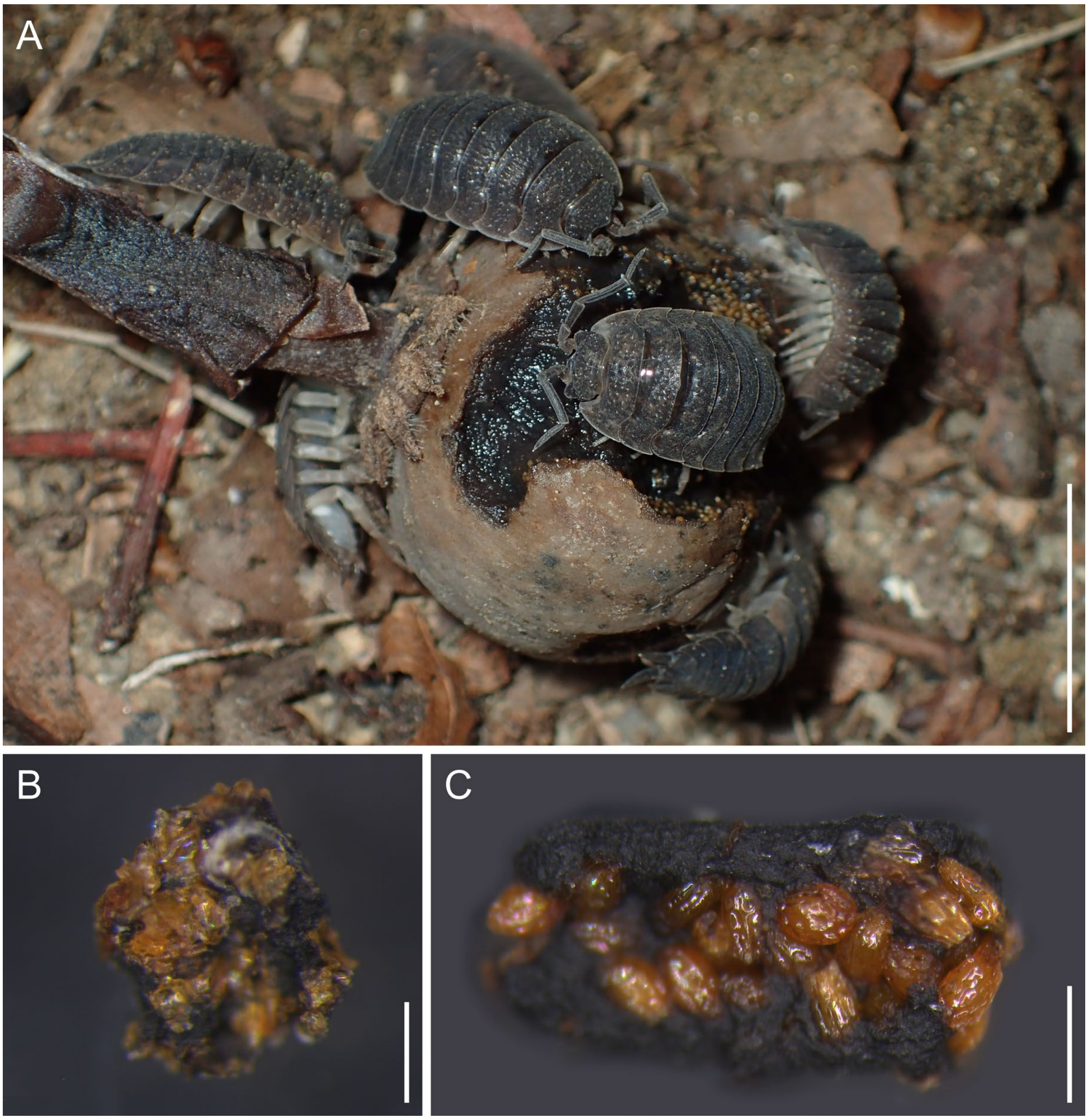

Figure 1. Interaction between *Monotropastrum humile* and its fruit feeder *Porcellio scaber*. (A) Some *P. scaber* individuals consuming the fruit. (B) Feces defecated by a small *P. scaber* individual, with most seeds broken. (C) Feces defecated by a large *P. scaber* individual, with most seeds remaining intact. Scale bars: 1 cm (A), 200 µm (B), and 500 µm (C).

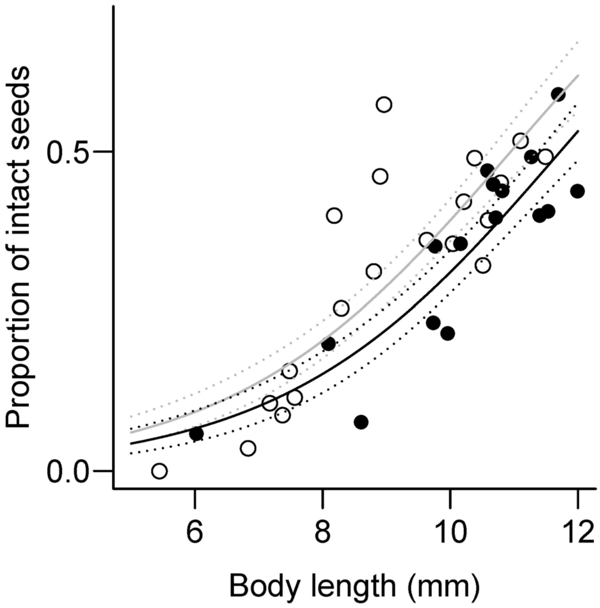

Figure 2. Effect of body size and sex on the proportion of intact seeds. Closed circles represent males. Open circles represent females. The black solid line represents the regression curve for males. The gray solid line represents the regression curve for females. The dotted lines represent the 95% confidence interval.