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Unlikely allies: Camel crickets play a role in the seed dispersal of an Asian autotrophic shrub

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Societal Impact Statement

Dust seeds, which are minute and contain minimal energy reserves, are often associated with heterotrophy (plants that obtain carbon without photosynthesis). Consequently, previous studies have mainly focused on the relationships between dust seeds and heterotrophy. However, dust seeds are also found in green plants. This manuscript focuses on the seed ecology of the apparently autotrophic shrub *Rhynchotechum discolor* that produces dust seeds. Using time-lapse photography, feeding experiments, and germination tests, we show that camel crickets effectively disperse the seeds of this autotrophic shrub. This is the first study to document insect-mediated internal seed dispersal of an autotrophic plant in regions inhabited by terrestrial mammals, offering new insights into the evolutionary ecology of dust seeds.

Summary

- Although angiosperms exhibit a wide range of seed sizes, the mechanisms driving these differences are poorly understood. The evolution of dust seeds, which contain minimal energy reserves, is traditionally linked to heterotrophy, in which external carbon sources are provided to the embryo or seedling. Dispersal by small animals may be another important but underexplored evolutionary driver of minute seed size. However, insect endozoochory has been documented only in the seeds of heterotrophic species and autotrophic species in New Zealand (i.e., in communities without native terrestrial mammals).
- Here, we investigate this seed dispersal mechanism in the Japanese shrub *Rhynchotechum discolor* (Gesneriaceae), which produces white berries with numerous tiny ellipsoid seeds, using time-lapse photography, feeding experiments, and germination tests, particularly focusing on potential interactions with insect internal seed dispersers.
- Our time-lapse photography indicated that camel crickets predominantly feed on fallen fruits of *R. discolor*. Field sampling revealed that camel crickets excreted numerous intact *R. discolor* seeds. Feeding experiments confirmed that some camel crickets excreted a high proportion of intact seeds, many of which successfully germinated into autotrophic seedlings.

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- The present study provides the first evidence of insects acting as endozoochorous seed dispersers in fully autotrophic plants within regions inhabited by terrestrial mammals. Our findings suggest that orthopteran-mediated seed dispersal is more widespread than previously thought, and that dust seeds can evolve from selective pressures beyond heterotrophy, specifically through insect-mediated seed dispersal.

KEYWORDS
autotrophic plant, camel cricket, dust seed, endozoochory, seed disperser, seed ecology

1 | INTRODUCTION

Angiosperms display an extensive range of seed sizes, spanning over 10 orders of magnitude in weight, which has spurred significant interest in the evolutionary ecology of seed size (Harper et al., 1970). Seed size is a critical factor influencing recruitment, with dust seeds, particularly small seeds, representing an extreme trade-off between seed size and quantity. Larger seeds offer advantages in resource-scarce environments, such as shaded or drought-prone areas, and in recovery from damage caused by herbivores or pathogens, but this benefit is offset by a decrease in seed production (Moles & Westoby, 2004). Conversely, producing many smaller seeds enhances dispersal and increases the chances of seeds reaching suitable microsites for recruitment, but this strategy results in lower recruitment success per seed (Eriksson & Kainulainen, 2011).

Dust seeds are characteristic of orchids and several other plant families (Eriksson & Kainulainen, 2011). A widely accepted hypothesis regarding the evolution of dust seeds suggests their association with heterotrophy, where external organic carbon sources are supplied, at least during the initial stages of seedling development (Figura et al., 2019; Hashimoto et al., 2012; Johansson et al., 2017). This connection has spurred increased research into the relationships between the evolution of dust seeds and heterotrophy (Leake, 1994; Merckx, 2013; Miura et al., 2024). However, heterotrophic status during the recruitment phase has not yet been described for plants with dust seeds in the families Rubiaceae, Buddlejaceae, and Gesneriaceae (Merckx, 2013). Therefore, further studies are needed to explore other evolutionary aspects of dust seed ecology.

Another plausible factor in the evolution of dust seeds is their role in seed dispersal. Dust seeds often have a low weight-to-volume ratio and may possess an elongated shape or wing-like structures, traits selected for wind dispersal (Eriksson & Kainulainen, 2011). Moreover, endozoochory, or internal seed dispersal through the digestive tracts of animals, is plausible whenever seeds are small enough for ingestion by frugivorous animals, suggesting that smaller seeds increase their chances of being adopted by diverse frugivores as seed dispersers (Suetsugu, 2018a; Suetsugu et al., 2017). In fact, insects have been known to contribute as seed dispersers in heterotrophic plants, although vertebrates, primarily birds and mammals, are recognized as the principal seed dispersers of almost all plants. For instance, beetle endozoochory is reported in the holoparasitic *Cytinus hypocistis* (Cytinaceae) (de Vega et al., 2011). Remarkably, camel crickets are the primary dispersers for three unrelated fully mycoheterotrophic plant genera, *Yoania* (Orchidaceae), *Monotropastrum* (Ericaceae), and *Phacellanthus* (Orobanchaceae), all producing fleshy, indehiscent fruits (Suetsugu, 2018b,a; Suetsugu et al., 2024).

Moreover, in New Zealand, the large, flightless orthopterans known as weta have been identified as endozoochorous seed dispersers of autotrophic plants with relatively minute seeds (Duthie et al., 2006; Larsen & Burns, 2012). Yet, this phenomenon has been thought to be unique to New Zealand, where terrestrial native mammals are absent. Indeed, weta, referred to as New Zealand's invertebrate mice, are known to fulfill ecological niches typically occupied by mammals (Duthie et al., 2006; Larsen & Burns, 2012). Therefore, whether insect-mediated internal seed dispersal systems can be found among autotrophic plants outside New Zealand remains an open question.

The current study focuses on the seed dispersal system of *Rhynchotechum discolor* (Gesneriaceae), an apparently autotrophic shrub species found across tropical and subtropical regions of Asia (Anderson & Middleton, 2013). Notably, although all 16 species within this genus produce white berries with numerous tiny ellipsoid seeds (approximately 0.3 mm in length) (Anderson & Middleton, 2013), seed dispersal mechanisms have remained unidentified in any species. Based on the similarity in fruit and seed morphology to those dispersed by camel crickets, such as in *Monotropastrum* and *Phacellanthus* (Figure 1; Suetsugu, 2018a; Suetsugu et al., 2024), we hypothesized that *R. discolor* might also be dispersed by camel crickets. Actually, during our preliminary field observation, we observed fallen *R. discolor* fruits with potential feeding marks from camel crickets on Amami-Oshima Island, Ryukyu Islands, Japan. The indirect observations suggested a previously unidentified interaction between camel crickets and this shrub. In this study, we investigated the seed dispersal mechanism of *R. discolor*, focusing primarily on the potential role of camel crickets.

2 | MATERIALS AND METHODS

2.1 | Study species and site

Our study was conducted in the understory of a densely vegetated evergreen forest in Naze, Amami City, on Amami-Oshima Island, central Ryukyu, Japan.

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FIGURE 1 Heterotrophic plants (*Phacellanthus tubiflorus* (a), *Cytinus hypocistis* (b), *Monotropastrum humile* (c, d), *Yoania amagiensis* (e), and *Apostasia nipponica* (f–h)) and their internal seed dispersers. (a) *Diestrammena japanica* feeding on a *P. tubiflorus* fruit. (b) *Pimelia costata* feeding on a *C. hypocistis* fruit. (c) *Diestrammena elegantissima* feeding on a *M. humile* fruit. (d) *Porcellio scaber* and *D. japonica* feeding on a *M. humile* fruit. (e) *Diestrammena elegantissima* feeding on a *Y. amagiensis* fruit. (f) *Diestrammena yakumontana* feeding on an *A. nipponica* fruit. (g) *Duolandrevus ivani* feeding on an *A. nipponica* fruit. (h) An *A. nipponica* plant with a fruit eaten by *D. ivani*. The arrow indicates the feeding mark. Despite its leafy habits, *A. nipponica* is known as a partially mycoheterotroph, obtaining most carbon from its fungal association (Suetsugu & Matsubayashi, 2021). Scale bars: 1 cm. Photographs: Kenji Suetsugu (a, c, e–h), Clara de Vega (b), and Osamu Kimura-Yokoyama (d).

R. discolor (Gesneriaceae) is characterized by its alternate leaves, linear calyx lobes, and few-branched inflorescences (Anderson & Middleton, 2013). It is distributed across a broad range, from the Ryukyu Islands of Japan in the north to Papua New Guinea and Flores in the south. The plant is commonly found in primary and secondary forests, swamps, thickets, and along trailsides, with a preference for moist and shady conditions (Anderson & Middleton, 2013). The mature fruits of *R. discolor* are typically round or oval in shape and have an average diameter of 7.8 ± 0.8 mm ($n = 10$, mean ± SD) (Figure 2a–c). Each fruit contains an average of 887.7 ± 287.4 seeds ($n = 6$) embedded within its fleshy pulp (Figure 2d). These small seeds, which lack elaiosomes for dispersal by ants, measure 0.29 ± 0.03 mm ($n = 11$) in length and 0.17 ± 0.01 mm ($n = 11$) in width. Once ripe, the fruits detach from the persistent calyx and drop to the ground, where they are accessible at ground level (Figure 2e). The ripe fruits, which lacked a distinct scent, are translucent white in color. The fruit sugar concentration based on a portable refractometer (A141-831; Shimadzu, Kyoto, Japan) is 3.7 ± 0.2% ($n = 10$), while the pulp is hardly sweet to humans.

2.2 | The assemblages of fruit consumers

An investigation was conducted on the assemblages of fallen fruit consumers during the fruiting season of *R. discolor* between early to late January 2022. To capture images of fruit consumers, we used the interval-programming function of a waterproof digital camera (Pentax Optio WG-1, RICHO, Tokyo, Japan). This method has been validated

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FIGURE 2 *Rhynchotechum discolor* and the camel crickets dispersing its seeds. (a, b) Fruiting plant in its habitat. (c) Fruits on the plant. (d) Longitudinal section of the fruit. (e) Fruit with feeding marks by camel crickets. (f) *Diestrammena gigas* feeding on a fallen fruit. (g) *Neotachycines bimaculatus* feeding on a fallen fruit. (h) *Neotachycines politus* feeding on a fallen fruit. (i) Fecal pellet of *D. gigas* containing numerous seeds. (j) Germinated seed recovered from *D. gigas* fecal pellet. (k) Seedlings with developed cotyledons. Scale bars: 100 mm (a, b), 10 mm (c), 5 mm (d–h), 1 mm (i), 0.2 mm (j), and 3 mm (k). Photographs: Yohei Tashiro (a–c, e, f–h) and Kenji Suetsugu (d, i–k).

as an effective alternative to direct observation of rare pollination and seed dispersal occurrences (Hattori et al., 2020; Suetsugu, 2020). The camera was mounted on a flexible tripod (Gorillapod, Joby, San Francisco) and placed directly in front of *R. discolor* fallen fruits (at a distance of approximately 30 cm). Time-lapse photographs were taken at five sites within the investigated forest between sunset and sunrise, given that our preliminary direct observation indicated that the consumption of fallen fruits occurred primarily at night. Additionally, because direct observation revealed that most fruit consumers spent at least several minutes feeding on a single fruit, each camera was set to acquire photographs at 50-s intervals. Moreover, to increase the frequency of recording fruit consumers, we collected up to 10 fallen fruits within each camera angle, even though it was uncommon for more than a few fruits to fall naturally in the area.

Our monitoring efforts spanned approximately 644 h, resulting in the capture of approximately 46,500 photographs. We focused solely on animals that fed on *R. discolor* fruits, and visitors of the same species captured in consecutive frames were considered to be a single individual, except in cases where it was evident from body size or other distinguishing features that they were different individuals.

2.3 | Field sampling of camel crickets and harvestman

As camel crickets were identified as the primary consumers of *R. discolor* fruits (see main text), we deployed three traps targeting camel crickets. These traps were constructed from plastic boxes (100 × 230 × 90 mm) with a one-way entrance (23 mm in diameter). Each trap contained a 10-mL solution comprising a 1:1 ratio of beer (Kirin Tanrei, Kirin Brewery, Hyogo, Japan) and soft drink (Calpis, Osaka, Japan) and was placed 5 m away from a target *R. discolor* plant

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for 1 day. After capturing the camel crickets (*Diestrammena gigas* [$n = 12$], *Neotachycines bimaculatus* [$n = 5$], and *Neotachycines politus* [$n = 3$]), we transferred them to individual plastic containers. We then collected all fecal pellets every 24 h for 96 h and inspected them under a stereomicroscope (Leica M165C, Leica Microsystems Ltd, Germany) to identify the presence or absence of *R. discolor* seeds. If present, we assessed the mechanical damage and counted the number of intact (nondeformed) seeds.

Given that *Nelima okinawaensis* visited with a frequency similar to that of camel crickets, we also collected the harvestman individuals ($n = 12$) near the investigated population for feeding experiments.

2.4 | Feeding experiments in the laboratory

To investigate whether viable seeds could be defecated by camel crickets or harvestmen, we conducted feeding experiments on the camel crickets *D. gigas* ($n = 8$) and *N. bimaculatus* ($n = 4$), as well as the harvestman *N. okinawaensis* ($n = 12$). This experiment aimed to determine potential differences in the proportion of viable seeds between those defecated by these consumers and seeds recovered directly from fruits. In each feeding trial, a mixture of 200–250 seeds and cheese was provided on moist filter paper within each enclosure. After 24 h, any unconsumed seeds were recovered and counted. Fecal pellets were collected every 24 h for a total of 96 h and examined under a Leica M165C stereomicroscope to count the number of *R. discolor* seeds defecated.

The germinability of the defecated seeds was compared with the viability of 100 seeds directly collected from each fruit ($n = 12$). These seeds were sown on rockwool (Nitto Boseki, Tokyo, Japan), watered daily, and grown under controlled conditions of a 16/8 h light/dark cycle with white light fluorescent lamps at approximately 50 µmol m^{-2} s^{-1} and 25°C. The emergence of the radicle from the seed coat was considered the criterion for determining seed germination. The number of germinated seeds was recorded weekly for 8 weeks. Using the count data, we calculated the cumulative germination rate as the ratio between the number of germinated seeds and the total number of seeds. The germination rate of defecated seeds was compared with that of nondefecated seeds using analysis of variance (ANOVA), followed by a post hoc Tukey–Kramer test.

3 | RESULTS AND DISCUSSION

Here, we reveal that camel crickets serve as seed dispersers of the autotrophic shrub *R. discolor* on Amami-Oshima Island, Ryukyu Islands, Japan. This is the first evidence of insect endozoochory in autotrophic plants within regions inhabited by terrestrial mammals.

Based on our intensive time-lapse photography spanning approximately 644 h, we discovered that camel crickets, including *Diestrammena gigas*, *N. bimaculatus*, and *Neotachycines politus*, predominantly feed on fallen fruits of *R. discolor* (Figure 2f–h, Table 1). While the harvestman *Nelima okinawaensis* visited with a frequency similar to that of camel crickets, the volume of fruit consumed per visit was notably greater in camel crickets. Thus, we determined that camel crickets serve as the primary feeders of fallen fruits. The small seeds, encased in a fleshy endocarp, are likely consumed along with the fruits, providing a reward for the insects. Field sampling showed that some camel cricket individuals (3/12 in *D. gigas*, 1/5 in *N. bimaculatus*, and 1/3 in *N. politus*) captured in traps placed near the plants excreted numerous morphologically intact *R. discolor* seeds (36.7 ± 17.0 [average ± SD, $n = 3$] in *D. gigas*, 11 in *N. bimaculatus*, and 27 in *N. politus*; Dataset S1), indicating that they actively sought out the ripe fruits.

In our feeding experiments, we observed that camel crickets excreted a high proportion of intact seeds (78.7 ± 6.7% [$n = 8$] in *D. gigas* and 44.9 ± 11.4% [$n = 4$] in *N. bimaculatus*; Figure 2i, Dataset S2). Microscopic examination showed that most seeds from camel cricket feces were intact, with normal embryos, similar to those from uningested fruits, although some broken seeds were also

TABLE 1 Fruit feeders to *Rhynchotechum discolor* with the total number of frames capturing each species of visitors.

Taxon	*n*
Insecta	
Orthoptera	
Rhaphidophoridae	
Neotachycines bimaculatus	6825 (366)
Neotachycines sp.	2832 (215)
Neotachycines politus	310 (21)
Diestrammena gigas	1296 (111)
Diestrammena sp.	72 (8)
Coleoptera	
Unidentified coleopteran larva	140 (17)
Blattodea	
Blattellidae	
Centrocolumna japonica	29 (4)
Arachnida	
Opiliones	
Sclerosomatidae	
Nelima spp.	3072 (382)
Crustacea	
Decapoda	
Potamidae	
Amamiku amamensis	100 (6)
Geothelphusa	
Geothelphusa sakamotoanus	21 (13)
Aves	
Passeriformes	
Turdidae	
Turdus pallidus	2 (1)

Note: Numbers in parentheses: the number of individuals feeding on fruits. For each species, fruit feeders captured in consecutive frames were considered the same individuals.

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observed. Therefore, the thickened seed coat of *R. discolor* likely provides some protection during passage through the digestive tract of these camel crickets. We found that both intact and defecated seeds germinate with only water, developing into autotrophic seedlings within 2 months after defecation (Figure 2j–k), albeit with a reduced germination rate (35.9 ± 9.0% [$n = 12$] in the seeds directly collected from fruits, 19.4 ± 8.0% [$n = 8$] in those defecated by *D. gigas*, and 6.8 ± 2.7% [$n = 4$] in those defecated by *N. bimaculatus*; Dataset S2) ($p < .001$). The seeds defecated by *D. gigas* had a significantly higher germination rate than those from *N. bimaculatus* ($p < .05$). As *D. gigas* is larger than *N. bimaculatus*, these findings corroborate previous research indicating that the efficacy of weta as seed dispersers varies significantly with their body size: smaller weta primarily function as seed predators, whereas larger weta are effective seed dispersers (Larsen & Burns, 2012). The harvestman *N. okinawaensis*, although the next significant fruit consumer following the camel cricket, did not expel any intact seeds.

To date, outside of New Zealand, insect-mediated endozoochory has only been documented in at least partially heterotrophic plants with extremely minute seeds that require external organic carbon sources for germination (de Vega et al., 2011; Suetsugu, 2018a, 2018b, 2020; Suetsugu & Matsubayashi, 2021). In contrast, as we demonstrated (Figure 2j–k), *R. discolor* seeds rapidly germinate with just water, developing into autotrophic seedlings. This challenges the assumption that all plants with dust seeds depend on external organic carbon sources. It is also noteworthy that Amami-Oshima Island is home to abundant terrestrial mammals, such as the Amami rabbit *Pentalagus furnessi* and the Ryukyu long-haired rat *Diplothrix legata*, which could potentially function as seed dispersers (Suetsugu & Hashiwaki, 2023).

Our study is the first to provide evidence of insects acting as endozoochorous seed dispersers in fully autotrophic plants within regions inhabited by terrestrial mammals. The widespread presence of camel crickets in Japan (Sato et al., 2012) likely supports the feasibility of their being effective seed dispersers. Our discovery of camel crickets dispersing seeds of an autotrophic plant implies that orthopteran-mediated seed dispersal is more prevalent than previously thought. This underscores the importance of further research into the role of insects as potential seed dispersers even in regions where terrestrial mammals exist.

While our study confirms camel crickets as effective dispersal agents for *R. discolor*, the plant likely employs multiple dispersers. Observations of the pale thrush *Turdus pallidus* consuming some fruits indicate that birds could be more efficient dispersers than camel crickets, considering their ability to transport seeds over greater distances. Actually, some researchers have suggested that birds might disperse these fruits due to their resemblance to bird-dispersed *Cyrtandra* (Gesneriaceae) fruits (Möller et al., 2009). Nonetheless, *R. discolor* fruits are concealed by leaves (Figure 2a–c), making them difficult for flying birds to spot. Additionally, ripe fruits fall off the tree due to an abscission layer, suggesting adaptation to endozoochory by ground-dwelling animals. Furthermore, the white coloration of *R. discolor* fruits contrasts with the typical red or black fleshy fruits dispersed by birds (Willson & Whelan, 1990).

Interestingly, weta-dispersed New Zealand plants also have translucent white fruits located deep within the plant canopy (Burns, 2006; Fadzly & Burns, 2010; Suetsugu, 2018b; Suetsugu et al., 2024). *R. discolor* also shares fruit and seed morphology with heterotrophic plants utilizing insect endozoochorous seed dispersal systems, including (i) inconspicuous fruit display, (ii) fruits presented at ground level, (iii) small seed size allowing seeds to be ingested whole, and (iv) a hard testa ensuring the viability of ingested seeds. The similarity suggests a potential insect-mediated seed dispersal syndrome (Figures 1 and 2). On the other hand, we note the considerably higher germination rate observed in seeds directly collected from fruits compared to those defecated by camel crickets. Although low seed viability does not immediately exclude the possibility of mutualistic relationships (Cosyns et al., 2005; Janzen, 1984; Suetsugu & Hashiwaki, 2023), camel crickets might act as commensals or antagonists when more effective seed dispersers, likely birds, are abundant. Further research is essential to understand the roles of these additional seed dispersers, each with potentially distinct dispersal patterns.

Overall, this study represents the first documentation of insect-mediated internal seed dispersal in a fully autotrophic plant outside New Zealand. The photosynthetic seedling growth in *R. discolor* suggests that selective pressures beyond reliance on heterotrophy may have influenced the evolution of dust seeds. Given that smaller seeds are more likely to escape mastication and survive digestive processes, a small seed size could have evolved as an adaptation to convert seed predators into seed dispersers. The fruit and seed morphology and coloration of other members of *Rhynchotechum* parallel those seen in *R. discolor*, suggesting that seed dispersal by camel crickets is widespread within the genus, which comprises 16 species (Anderson & Middleton, 2013). In a broader ecological context, similar seed dispersal systems might be found among plants with dust seeds, which are present in at least 13 families (Eriksson & Kainulainen, 2011). Further research is crucial to understand the global significance of insect-mediated seed dispersal through gut passage.

AUTHOR CONTRIBUTIONS

Kenji Suetsugu and Hirokazu Tsukaya designed the project. Kenji Suetsugu conducted time-lapse photography, reviewed the images captured by time-lapse photography, conducted the feeding experiments, and wrote the initial draft. Hirokazu Tsukaya revised the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supporting Information of this article.

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