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Spore Dispersal of Fetid *Lysurus mokusin* by Feces of Mycophagous Insects

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Abstract The ecological roles and biological mechanisms of zoochory in plants have long been foci in studies of co-evolutionary processes between plants and animals. However, the dispersal of fungal spores by animals has received comparatively little attention. In this study, the dispersal of spores of a selected fetid fungus, *Lysurus mokusin*, via feces of mycophagous insects was explored by: collecting volatiles emitted by the fungus using dynamic headspace extraction and analyzing them by GC-MS; testing the capacity of mycophagous insects to disperse its spores by counting spores in their feces; comparing the germinability of *L. mokusin* spores extracted from feces of nocturnal earwigs and natural gleba of the fungus; and assessing the ability of *L. mokusin* volatiles to attract insects in bioassays with synthetic scent mixtures. Numerous spores were detected in insects' feces, the bioassays indicated that *L. mokusin* odor (similar to that of decaying substances) attracts diverse generalist mycophagous insects, and passage through the gut of *Anisolabis maritima* earwigs significantly enhanced the germination rate of *L. mokusin* spores. Therefore, nocturnal earwigs and diurnal flies probably play important roles in dispersal of *L. mokusin* spores, and dispersal via feces may be an important common dispersal mechanism for fungal reproductive tissue.

Keywords Butanoic acid · *Lysurus* · Mycophagous · Sapromyiophily · Dispersal strategy · Phallaceae

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Introduction

The relationships between insects and fungi, both antagonistic and mutualistic, play key roles in natural communities (Blackwell 2000; Pirozynski and Malloch 1988). Typical antagonistic interactions include insects' use of fungi as food without spore dispersal and fungal parasitic exploitation of insects (Fäldt et al. 1999; Guevara et al. 2000; Hedlund et al. 1995), while typical mutualistic interactions include external transfer of fungal spores by insects (or facilitation of fungal cross-fertilization) in return for food (Bultman et al. 1998; Roy 1993; Schiestl et al. 2006). Another type of mutualistic interaction of particular interest here is the dispersal of fungal spores ingested by various insect species while eating their fruiting bodies (Bultman et al. 1995; Tuno 1998, 1999).

Lysurus mokusin (L.) Fr. (Phallaceae) is one of the most common fungi in China (Mao 1998). The mature fruiting body of *L. mokusin* consists of long red arms covered with brown mucilaginous gleba (Fig. 1a), which can last 1–2 days in the field. Its sporocarps, which mature at night and release brown spores, have a dung-like odor that attracts various saprophagous insects, including earwigs, flies, nitidulids, and rove beetles according to field observations (Fig. 1b–e) at the Kunming Institute of Botany (KIB), the Chinese Academy of Sciences (25°8′48.9″ N, 102°44′41.2″ E, 1,788 m).

The mechanism of spore dispersal by insects remains poorly explored compared with pollen or seed dispersal by insects. To our knowledge, spore dispersal through digestive systems of insects has been substantiated only in a limited number of diurnal fly visitors (Bultman et al. 1995; Tuno 1998, 1999), although some nocturnal visitors, such as common omnivorous earwigs (Dermaptera), may play similar roles. In preliminary observations, we noted that nitidulidae or rove beetles often eat hyphostroma of *L. mokusin*, but flies and earwigs eat its mucilaginous gleba. Therefore, we hypothesized that: both diurnal and nocturnal mycophagous insects disperse

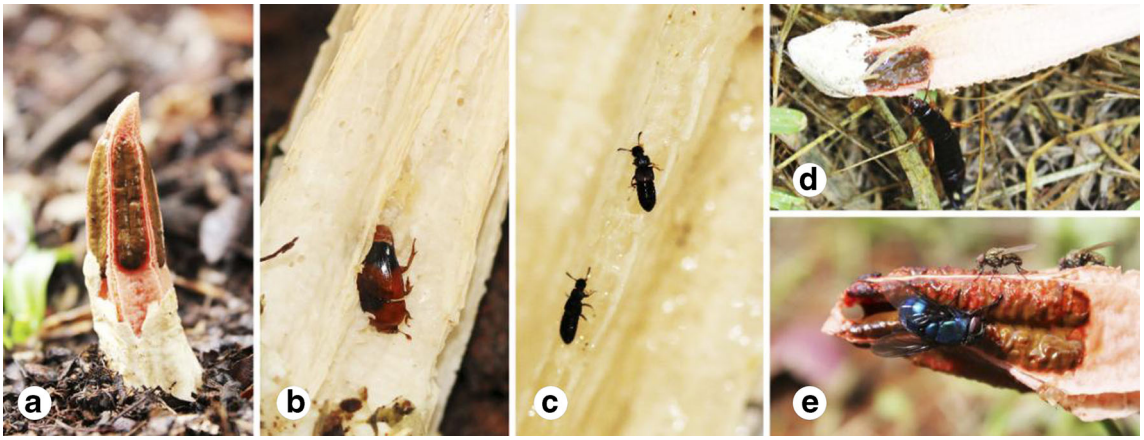

Fig. 1 *Lysurus mokusin* and its visitors: **a** *L. mokusin* sporocarp; **b** nitidulidae; **c** rove beetles; **d** earwig; **e** saprophagous flies

L. mokusin spores; attraction by volatiles emitted by the fungus may play a key role; and the spores' germination rate may be enhanced by passage through earwigs' digestive tracts. To test these hypotheses, we analyzed the fetid scent of *L. mokusin*, counted its spores in feces of mycophagous earwigs and flies, and compared the germinability of *L. mokusin* spores extracted from feces of earwigs and fruiting bodies.

Methods and Materials

Scent Collection of *L. mokusin* Volatiles

Three samples of volatiles emitted by *L. mokusin* sporocarps, growing naturally in the KIB location, were collected by dynamic headspace extraction and analyzed by gas chromatography/mass spectrometry. Headspace samples were taken by enclosing the fungus in Tedlar bags (Dupont, USA) prior to sampling, and subsequently pumping air for 3 hr through filters containing 150 mg of Porapak Q (mesh 60/80, Waters Associates, Inc.) using a pump with an inlet flow rate of 300 ml/min. Before use, the adsorbent cartridges were cleaned with 2 ml of diethyl ether and dried with nitrogen gas. Trapped volatiles were eluted with 400 μl dichloromethane, and concentrated to one-sixth the original volume by a gentle stream of nitrogen. An empty bag was used as a control and the samples were stored at −20 °C before analysis.

Analysis of *L. mokusin* Volatiles

The sampled volatiles were analyzed using an Agilent Technologies HP 6890 gas chromatograph (carrier gas, helium, 1 ml/min; injector temperature, 260 °C; column temperature initially 40 °C increasing by 3 °C/min to 260 °C after injection), equipped with an HP-5MS column (30 m×0.25 mm, 0.25 μm film thickness), linked to an HP 5973 mass spectrometer. Compounds were identified by comparing mass spectra and relative retention times with those of authentic standard compounds and entries in the Wiley NIST 05 mass spectral database, and their relative quantities were determined by peak area measurements.

Collection of *L. mokusin* Sporocarps' Earwig and Fly Visitors

To evaluate frequencies of visitations of *L. mokusin* sporocarps by diurnal flies, flies visiting a naturally growing sporocarp of the fungus were collected for 30 min per day, from 13:00 to 13.30, and those visiting another sporocarp from 13.30 to 14:00. This procedure was repeated on each of 6 d, from 17 to 23 July, 2011, using a different pair of sporocarps every day. In total, 151 flies visiting the 12 selected *L. mokusin* sporocarps were collected and identified. In addition, frequencies of earwig visitations to 172 *L. mokusin* sporocarps were recorded, and all of the earwigs were collected in 2010–2012; voucher specimens were deposited in the KIB archives. Because earwigs often stayed by *L. mokusin* sporocarps when they located them (as potential foods), we collected earwig visitors, at 08:00 in the morning, from 104, 36, and 32 *L. mokusin* sporocarps from 26 July to 13 August in 2010, 2011, and 2012, respectively.

Spore Dispersal via Earwig and Fly Feces

Sixteen mature, naturally growing *L. mokusin* sporocarps were collected and separately crushed in 500 ml of 70 % ethanol, and 50 μl portions of the homogenized suspension were diluted 300-fold. Then 100 μl samples were dropped on a hemocytometer and examined under an Olympus microscope (1,000×) to record the spore number. To test the ability of earwigs to disperse spores of the fungus, 22 *Anisolabis maritima* Bonelli visitors were collected. Each earwig was left in a Petri dish with distilled water but no food for 72 hr under natural environmental conditions to clear residual food. Then, mature *L. mokusin* gleba was provided, and the earwig was allowed to feed on it for 48 hr. During this treatment, the

number of defecations, was recorded, and the feces were collected to count spore numbers in them. The spore number in feces of wild earwigs, caught on naturally growing *L. mokusin* sporocarps (after eating) and kept in a Petri dish, were used as control. Numbers of *L. mokusin* spores defecated by fly visitors were not counted directly, but the potential spore load of flies was evaluated by counting spores within the recta of flies visiting *L. mokusin* sporocarps. Selected *Lucilia sericata* flies were dissected under a stereomicroscope to removed their recta (N=12), each extracted rectum was crushed in 1 ml 70 % ethanol, then the number of spores in it was counted as described above. Morphological characteristics of *L. mokusin* spores taken from sporocarps, and feces were compared by scanning electron microscopy (SEM) to assess effects on them of passage through the earwigs' digestive system. Minute pieces of materials were mounted on stubs using double-sided adhesive tape and allowed to air-dry overnight. After gold sputtering, specimens were examined and photographed under a Hitachi S-520 scanning electron microscope (Nissei Sangyo America, Ltd, Pleasanton, CA, USA).

Viability of Spores from Earwig Feces and Fruiting Bodies

Feces from *A. maritima* fed with gleba were surface-sterilized by dipping in 70 % ethanol for 30 sec, rinsed four times with 3 ml sterilized water, then crushed in 100 μl sterilized water. Portions (10 μl) of each homogenized suspension were spread on Potato Dextrose Agar (PDA) medium with 40 mg/L ampicillin and tetracycline in a 50 ml conical flask to examine the germinability of spores in the feces. Suspensions of gleba from naturally growing sporocarps were used as controls. All procedures for both fecal samples and controls (eight replicates in each case) were conducted on a clean bench to avoid contamination with other fungi. The conical flasks were incubated at 25 °C under 12/12 hr L/D cycles, and the proportion of germinated spores in each conical flask was examined after 48 and 96 hr. The germination of spores extracted from feces of drosophilid and muscid flies has already been substantiated in other fungal species by Tuno (1998, 1999). Thus, we only investigated the viability of spores obtained from feces of nocturnal earwig in this study.

Bioassay of *L. mokusin* Volatiles' Ability to Attract Insects

The ability of volatiles emitted by *L. mokusin* to attract flies and earwigs was tested in bioassays, as follows. A solution containing four typical volatiles of *L. mokusin* (in proportions similar to those of natural *L. mokusin* extracts, as verified by GC analyses) was prepared. This synthetic scent mixture consisted of 20.2 mg butanoic acid, 16.7 mg *p*-cresol, 16.4 mg phenol, and 7.5 mg indole (95–99 % purity, Sigma-Aldrich) in 2 ml dichloromethane. Odorless degreased cotton balls (soaked with dichloromethane for 24 hr and dried at room temperature, three replicates) were impregnated with 200 μl samples of the scent mixture or mock (dichloromethane) and placed in GC vials. A pair of scented and control vials was placed in a patrolling area of flies (Fig. 2), 30 cm apart, after the solvent had evaporated (13:00–14:00, from 18 to 24 in August, 2011). If flies approached (within 3 cm) or landed on the vials (Fig. 2a, b), we assumed that they were attracted by the sample or control. Every 5 min, the positions of the sample and control were changed to avoid location effects. Each test lasted 30 min, and the bioassays were performed six times. Each vial was used only once for bioassay.

To assess the ability of the synthetic mixture to attract earwigs, we designed traps consisting of modified PET bottles (Fig. 2c) containing GC vials with scented and control cotton balls, as described above, to collect nocturnal earwigs. Seven scented and seven control traps were placed in the KIB grounds, spaced at least 3 m apart. Earwigs captured in these traps were recorded daily, and the process continued for 5 d until we could not smell any fetid odor from the scented traps.

Statistical Analyses

Values of measured variables presented below are means and standard errors. Effects of the treatments on the variables were assessed using One-Sample *t* tests and Independent-Samples *t* tests. SPSS 13.0 software (SPSS Inc., Armonk, NY, USA) were used for all the analyses.

Results

Composition of *L. mokusin* Scent

We identified 15 volatiles (as described in "Materials and methods") in extracts of mature *L. mokusin* sporocarps. The major constituents were butanoic acid, *p*-cresol, phenol, pentanoic acid, and indole in the following relative proportions (N=3): 20.21±2.24 %, 16.71±3.05 %, 16.39±3.10 %, 10.22±4.18 %, and 7.49±1.86 %, respectively (Table 1). Several main odor compounds, such as butanoic acid, *p*-cresol, phenol, and indole were identified on the basis of GC retention time and mass spectrum identical to standard compounds purchased from Sigma-Aldrich, USA. For the other compounds, putative names are provided according to the Wiley NIST 05 mass spectral database.

Relationships Between *L. mokusin* and Mycophagous Insects

All earwigs (N=76) observed visiting *L. mokusin* sporocarps during the study period were *Anisolabis* spp., and 94.7 % were

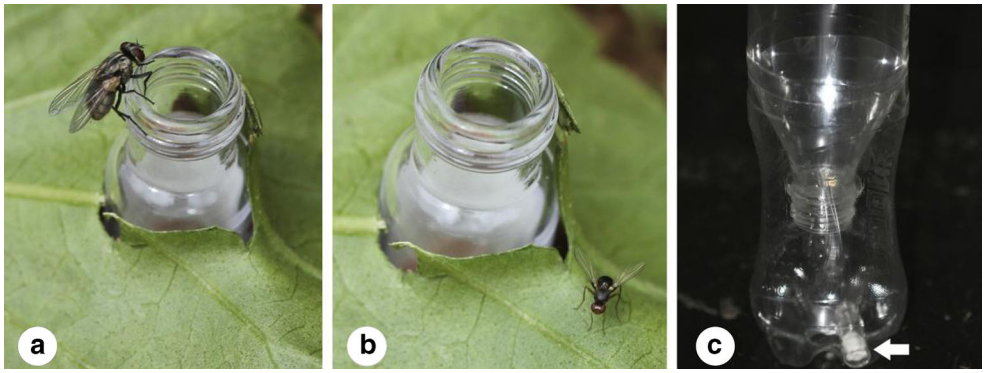

Fig. 2 Bioassay of the ability of volatiles emitted by *Lysurus mokusin* to attract flies and earwigs. **a & b** illustration of the fly attraction bioassay using a GC vial with scent sample, disguised by a leaf; **c** scent trap used to capture earwigs, constructed from a modified PET bottle. The top of the bottle was cut and inserted backwards into the lower part of the bottle. A GC vial with a synthetic scent mixture was placed at the bottom of the bottle (*arrow*), or with no scent for controls. The trap was buried in the soil with its top even to the soil surface

identified as *A. maritima* individuals (Fig. 3a). The frequencies of earwig visitations to 172 *L. mokusin* individuals were 39.4 % (41/104), 58.3 % (21/36), and 43.8 % (14/32) in 2010–2012, respectively.

The mature fruiting bodies of *L. mokusin* we examined contained $7.53\pm1.00\times10^9$ spores (N=16), the *A. maritima* individuals defecated 7.22±0.66 times per day (N=22), and we recorded significantly more (df=88, t=9.719, P<0.001) spores in feces of *A. maritima* individuals fed with *L. mokusin* ($8.08\pm0.52\times10^6$, N=55) than in feces of counterparts caught in the wild ($1.63\pm0.14\times10^6$, N=35).

The scanning electron microscopy results show that spores extracted from *L. mokusin* sporocarps and from feces had rough and smooth surfaces, respectively (Fig. 3b, c). After 4 d incubation, the germination rates of spores extracted from feces and sporocarps were 74.00±3.43 % (N=8) and just 8.15 ±0.86 % (N=8), respectively (Fig. 3d, e): a highly significant difference (df=14, t=−18.615, P<0.001).

The collected fly visitors (151 individuals) represented 11 genera and three families: Calliphoridae (86), Sarcophagidae (57), and Muscidae (8). The main visitors were *Lucilia sericata* (Meigen) (44) and *Ravinia striata* F. (30), and estimated number of spores in the recta of *L. sericata* flies was $9.90\pm1.21\times10^5$ (N=12).

Bioassay of *L. mokusin* Volatiles' Ability to Attract Insects

Bioassays showed that synthetic scent consisting of butanoic acid, *p*-cresol, phenol, and indole attracted diverse flies to approach or land on the sample vials. Seventy-three flies representing ten genera and five families—Sarcophagidae (28), Calliphoridae (23), Muscidae (18), Sepsidae (3), and Drosophilidae (1)—were caught and identified. The main

Table 1 Average relative amounts (%) of volatiles emitted by *Lysurus mokusin* sporocarps (N=3)

No.	Compound	R*t*	RI	CAS	Mean±S.E. (%)
1	3-Hydroxy-2-butanone	3.62	709	513-86-0	4.05±3.06
2	Propanoic acid	3.79	717	79-09-4	0.77±0.40
3	3-Methyl-1-butanol	4.08	730	123-51-3	0.83±0.58
4	2-Methyl-propanoic acid	4.77	761	79-31-2	0.35±0.35
5	Butanoic acid ethyl ester	5.55	797	105-54-4	7.13±4.10
6	Propanoic acid propyl ester	5.78	805	106-36-5	2.90±1.55
7	Butanoic acid*	6.57	829	107-92-6	20.21±2.24
8	n-Propyl isobutyrate	7.24	849	644-49-5	0.69±0.37
9	3-Methyl-butanoic acid	7.67	862	503-74-2	0.88±0.88
10	2-Methyl-butanoic acid	8.38	884	116-53-0	4.22±1.29
11	Pentanoic acid ethyl ester	8.87	899	539-82-2	2.28±0.75
12	Pentanoic acid	10.17	931	109-52-4	10.22±4.18
13	Phenol*	12.94	999	108-95-2	16.39±3.10
14	*p*-Cresol*	16.82	1,092	106-44-5	16.71±3.05
15	Indole*	23.99	1,308	120-72-9	7.49±1.86

*RI and R*t retention index and time on the HP-5MS column, respectively, *CAS* registry number in the Chemical Abstracts Service database

Compounds marked with asterisks (*) were identified on the basis of similarities of GC retention times and mass spectra to those of standard compounds purchased from Sigma-Aldrich, USA. For the other compounds, putative names are provided according to the Wiley NIST 05 mass spectral database

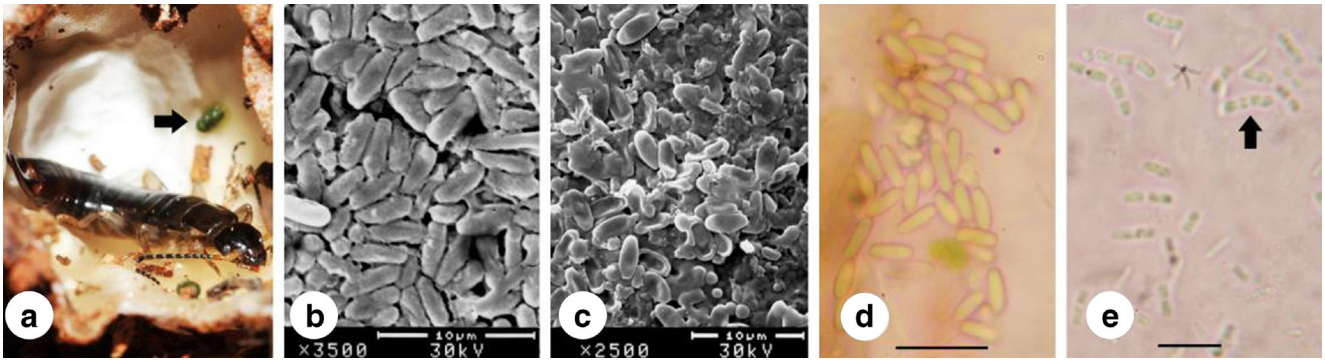

Fig. 3 Earwig dispersal of *L. mokusin* spores. **a** *Anisolabis maritima* and its feces (*arrow*); **b & c** natural spores and spores extracted from feces of *A. maritima*; **d & e** spores extracted from feces of *A. maritima*, which had enhanced germinability on Potato Dextrose Agar medium (*arrow*). Scale bar, 5 μm in **d & e**

visitors were *Musca sorbens* Wied. (19) and *Parasarcophaga albiceps* (Mg) (13). In stark contrast, only two flies landed on control vials. However, we caught no earwigs in our devised traps.

Discussion

In a sapromyiophilous pollination syndrome, floral scents attract saprophagous, coprophagous, and necrophagous insects by mimicking the odors of decaying organic matter, typifying the insects' food or brood sites (Jürgens et al. 2006, 2013). Similarly, some fungi and mosses emit fetid odors that attract flies and thus enhance their spore dispersal (Fischer and Vicha 2003; Marino et al. 2009; Tuno 1998). Indeed, previous studies have indicated that convergent evolution of carrion or fecal scent mimicry in angiosperms and fungi may continually occur in natural communities (Johnson and Jürgens 2010; Vereecken and McNeil 2010).

Here, we report the first characterization of the fetid odor emitted by fruiting bodies of *L. mokusin*, its effects on insects, and insect visitors' ability both to disperse its spores and enhance their germinability. Our results show that gleba of *L. mokusin* produces a dung-like odor, the main volatiles being butanoic acid (20.21 %), *p*-cresol (16.71 %), phenol (16.39 %), pentanoic acid (10.22 %), and indole (7.49 %), with aliphatic acids accounting for 37.6 % of the total contents. This is consistent with previous indications that scents mimicking those of herbivore feces have high *p*-cresol and/or aliphatic acid contents, which are typical characteristics of odors associated with decaying materials (Jürgens et al. 2006, 2013). Phenol is a common metabolite in excreta of animals and known to attract flies (Foster and Harris 1997; Lane and Fraser 1999; Liu et al. 2005), while indole has been identified in volatiles emitted by feces of mustelids and wolves (Brinck et al. 1983; Raymer et al. 1985). Numerous saprophagous and coprophagous visitors (and hence potential spore dispersers) were observed on the fetid fungus, including earwigs, flies, nitidulids, and rove beetles (Fig. 1). Therefore, we hypothesized that the strong odor of *L. mokusin*, similar to that of feces, attracts diverse generalist mycophagous insects. Accordingly, our bioassays indicated that the synthetic scent can attract various flies to approach or land on sample vials, implying that the fetid odor of *L. mokusin* plays an important role in attracting fly visitors. By contrast, nocturnal earwigs were not apparently attracted by the synthetic scent compounds placed in our traps, but the traps may not be effective for catching earwigs, and/or the selected 'cocktail' of scent compounds may not include substances that are attractive for earwigs.

Our results, however, provide clear indications that earwigs ingest gleba of *L. mokusin* and disperse spores through their feces, since we detected large numbers of viable spores of the fungus in *A. maritima* feces (and higher numbers in feces of individuals that had been fed with *L. mokusin* gleba than in feces of earwigs caught in the wild). This is consistent with previous findings that although many fungi may disperse their spores by wind or water (Ingold and Hudson 1993), spores of some fungi may be dispersed by various animals, such as flies, turtles, rodents, and marsupials (Janos et al. 1995; Jones et al. 2006; Reddell et al. 1997; Shaw 1992; Tuno 1999). Only mucus of the gleba appears to be digested by *A. maritima*, and scanning electron microscopy revealed that a layer of coating matter on the surface of the spores was removed by the earwigs' digestive tract (Fig. 3b, c). Nicholson and Epstein (1991) reported that extracellular mucilage or glycoproteins are commonly present on fungal germlings, and Stoffolano et al. (1990) demonstrated that the gleba from *Mutinus caninus* (Persoon) can promote egg development of *Phormia regina* (Meigen). The nutritional substances contained in spores and gleba of *L. mokusin* is unknown, but our results infer that the relationship between earwigs and *L. mokusin* may be mutualistic. However, whether consumption of gleba can enhance fitness of earwigs, needs to be tested in future work.

Previous studies with other fungi have indicated that the germinability of spores of various fungi may be enhanced by passage through the guts of animals (Claridge et al. 1992; Cork and Kenagy 1989; Jones et al. 2006; Tuno 1998, 1999). Accordingly, we found that the germination rate of *L. mokusin* spores significantly increased after passage through the *A. maritima* gut. Furthermore, we found that the sticky gleba of *L. mokusin* was rarely attached to the body of *A. maritima*, in accordance with the hypothesis that *Dictyophora* spores are largely dispersed via guts of visitors rather than by adhering to insect bodies (Tuno, 1998). Advantages of spore dispersal by animals may include extension of dispersal range, access to new nutrient sources, and enhancement of gamete transfer for mating (Ingold and Hudson 1993; North et al. 1997; Steinebrunner et al. 2007). We found that *L. mokusin* provides food in the form of gleba to the earwig *A. maritima*, which may excrete about 1.18×10^7 spores of *L. mokusin* per day (far more than the numbers, ca. 9.90×10^5, found in recta of *L. Sericata* flies), and not only disperse the spores far from parental individuals (sticky spores in gleba often fall on ground and earwigs disperse spores as their crawl) but also enhance the spores' germinability. Thus, nocturnal *A. maritima* earwigs probably play an important role in dispersing *L. mokusin* spores, and fungal spore dispersal via insect feces may be a common important element of fungus-insect interactions in complex ecological communities.

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