Spore consumption and life history of *Zearagytodes maculifer* (Broun) (Coleoptera: Leiodidae) on *Ganoderma,* its fungal host

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Abstract: Spore consumption and aspects of the life history of *Zearagytodes maculifer* (Coleoptera: Leiodidae) were studied on the bracket fungi *Ganoderma* cf. *applanatum* and *G. australe* in the Waitakere Ranges, New Zealand. Eggs, the four larval instars and their duration are described. The 25-day development time found (egg to adult) is short compared with other mycophagous beetles inhabiting bracket fungi. Numbers of larvae and adult beetles found on hosts were only weakly associated with season, and both larvae and adults were active in winter. Rate of spore consumption did not depend on larval instar, or which fungal species was host. However, fewer larvae and adult beetles were found per sporocarp on *G. australe*, whose ingested spores appeared to be less easily broken. The impact of *Z. maculifer* on host fitness appeared to be neutral as larvae consumed a very small proportion of discharged spores.

Keywords: bracket fungi; fungus–insect interactions; Leiodidae; mycophagous beetle; spore-feeder

Introduction

Fungus–insect relationships have been studied for decades (Scheerpeltz & Höfler 1948; Benick 1952; Wheeler & Blackwell 1984; Komonen 2003), but their roles in shaping life history traits and host selection of mycophagous insects remain unclear. For ephemeral mushrooms, mycophagous insects may possess rapid larval development (Sevenster & van Alphen 1993; Leschen 1994; Toda & Kimura 1997), parental care of eggs (Setsuda 1994), and small clutch size to enhance risk-spreading (Hackman 1979; Bruns 1984; Hanski 1989). In such spatially and temporally unpredictable habitats, adult mycophagous insects develop a wider host range (i.e. they are polyphagous); enabling ovipositing females to maximise reproductive success (Hanski 1989; Sevenster & van Alphen 1993; Toda & Kimura 1997; see also Leschen 1990). In contrast, bracket fungi offer long-lasting larval habitats and spatially and temporally predictable adult habitats (Pace 1967; Hanski 1989); insects may grow slowly on them (Liles 1956), have larger clutch sizes (Hanski 1989) and evolve obligate host associations (Lawrence 1973; Hanski 1989). Two comparative analyses (Ashe 1984; Hanski 1989) showed that chemical defence by fungi plays a minor role in governing fungus–insect interactions. However, most empirical studies on fungus–insect interactions have been limited to inferential evidence of host records (Jonsell & Nordlander 2004; Yamashita & Hijii 2007), have produced negative or enigmatic results (Hanski 1989; Leschen 1994), and have not considered phylogenetic effects. Furthermore, life history and host selection studies have rarely been experimental.

Spore-feeding insects and their host fungi are excellent models for examining life history traits and host selection, especially as the insects are external feeders that can be observed easily and manipulated, experimentally. The New Zealand species *Zearagytodes maculifer* (Broun) (Leiodidae: Camiarinae: Agyrtodini) is one of the most common spore-feeders on long-lived bracket fungi of the genus *Ganoderma* (Newton 1984). Both *G.* cf. *applanatum* (referred to hereafter as *G. applanatum*) and *G. australe* act as hosts for both adult and larval beetles, which feed on spores on the hymenial surface of sporocarps (the fruiting bodies of fungi) (Fig 1a, b).

An ideal test of host selection requires the direct measurement of fitness-related parameters (e.g. survival, larval development time, or pupal size), but the rearing of specialist mycophagous insects is difficult (Hanski 1989). We therefore focused on two short-term parameters that could be readily measured: larval spore consumption rate and spore-breaking ability. Since larvae do not move between sporocarps, their ability to break spores to obtain nutrient may have consequences for fitness. Hence, one might expect greater ability of larvae to break spores of more preferred fungal species.

The host fungus *G. applanatum* has two morphotypes, which differ in the structure of their hymenial surfaces and once were considered to be separate species (Cunningham 1965). One type has an even, smooth pore surface; the other has a distinctly pitted and rugose surface (Buchanan & Wilkie 1995). In small patches of bush in suburban Auckland where *Z. maculifer* is absent, the pore surface always appears to be smooth, but in the Waitakere Ranges almost all sporocarps have a rugose surface (KK, pers. obs.). Newton (1984) noted that adult *Z. maculifer* also fed on hyphae, and it is possible that its feeding on hymenial tissue induces a pitted, rugose surface.

The aim of this paper is to describe aspects of the life history and feeding behaviour of *Z. maculifer*. Seasonal abundance and host relationships of *Z. maculifer* with *Ganoderma* species are reported, and we determined the duration and number of larval instars using a combination of field experiments and laboratory observations. Spore consumption rates and host selection patterns were tested using the two *Ganoderma* species and then related to field observations. Finally, we considered the effects of larval spore-feeding on fungal host fitness, and whether adult grazing induces a change in host morphotype of *G. applanatum*.

Methods

Study area

The Waitakere Ranges (16 000 ha) are 25 km west of central Auckland City, New Zealand, and rise from sea level to 400 m

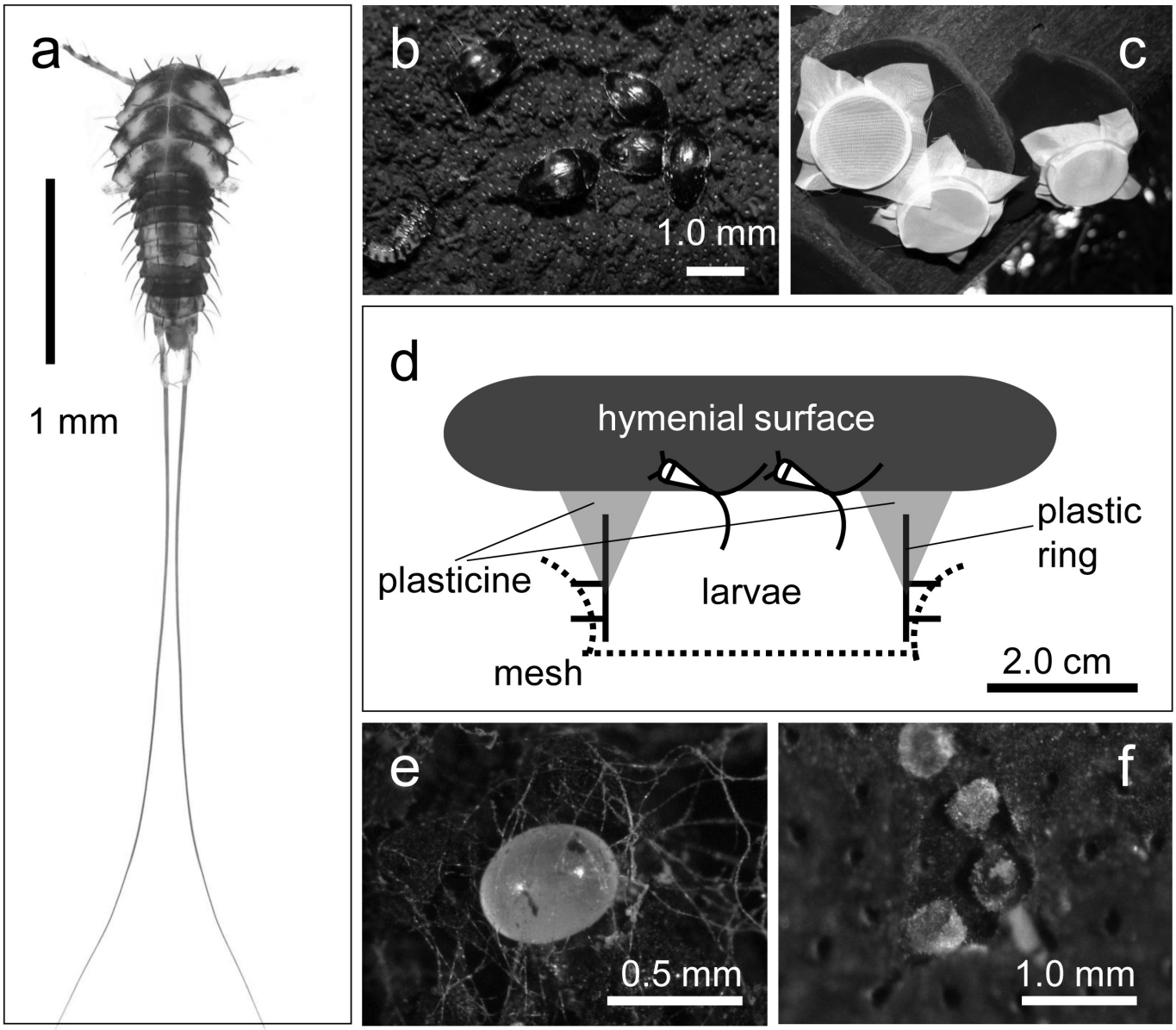

Figure 1. The spore-feeding beetle *Zearagytodes maculifer*: (a) dorsal view of a larva, (b) adults and larvae, (c) experimental arenas for rearing, (d) schematic representation of the structure of an experimental arena, (e) egg, (f) physical egg protection with faecal pellets (spore mass).

a.s.l. Two large plots, designated Cascade Kauri Park (36˚53' S, 174˚31' E) and Upper Huia Dam (36˚56–57' S, 174˚30–32' E), were chosen as field survey and experimental sites (Fig. 2). The vegetation is dense regenerating native forest but differs between sites: Cascade Kauri Park is *Agathis*-dominated forest, whereas Upper Huia Dam has mixed broadleaved–conifer forest.

Study system

The genus *Zearagytodes* contains three described species (and four or more undescribed species) and is endemic to New Zealand (Newton 1984, 1989; Seago 2005). *Zearagytodes maculifer* is found throughout the North Island, and occurs in kauri-dominated forests and small suburban reserves within the Auckland region (Kuschel 1990).

Species of the bracket fungus *Ganoderma* (Ganodermataceae, Basidiomycota) produce conspicuous perennial sporocarps on a variety of woody hosts (Buchanan & Wilkie 1995); three species have been recognised in New Zealand. Two of them, *G. applanatum* and *G. australe*, are common (Buchanan & Wilkie 1995). However, because of variation in some morphological features, distinguishing between these species can be confusing. Buchanan and Wilkie (1995) showed that *G. australe* has a smooth pore surface, softer context than *G. applanatum*, indistinctly stratose to non-stratose tubes, and larger, reddish-brown (rusty-brown) spores. In contrast, both rugose and smooth pore surfaces are found in *G. applanatum*, whose spores are yellowish-brown. Spores of *Ganoderma* species are uniquely double-walled, typically ovoid, echinulate, and enlarged or truncated at the apex (Moncalvo et al. 1995). Those of *G. applanatum* measure 9.0–11.0 × 6.0–7.5 µm, whereas spores of *G. australe* are 11.5–14.5 × 6.5–9.0 µm (Buchanan & Wilkie 1995).

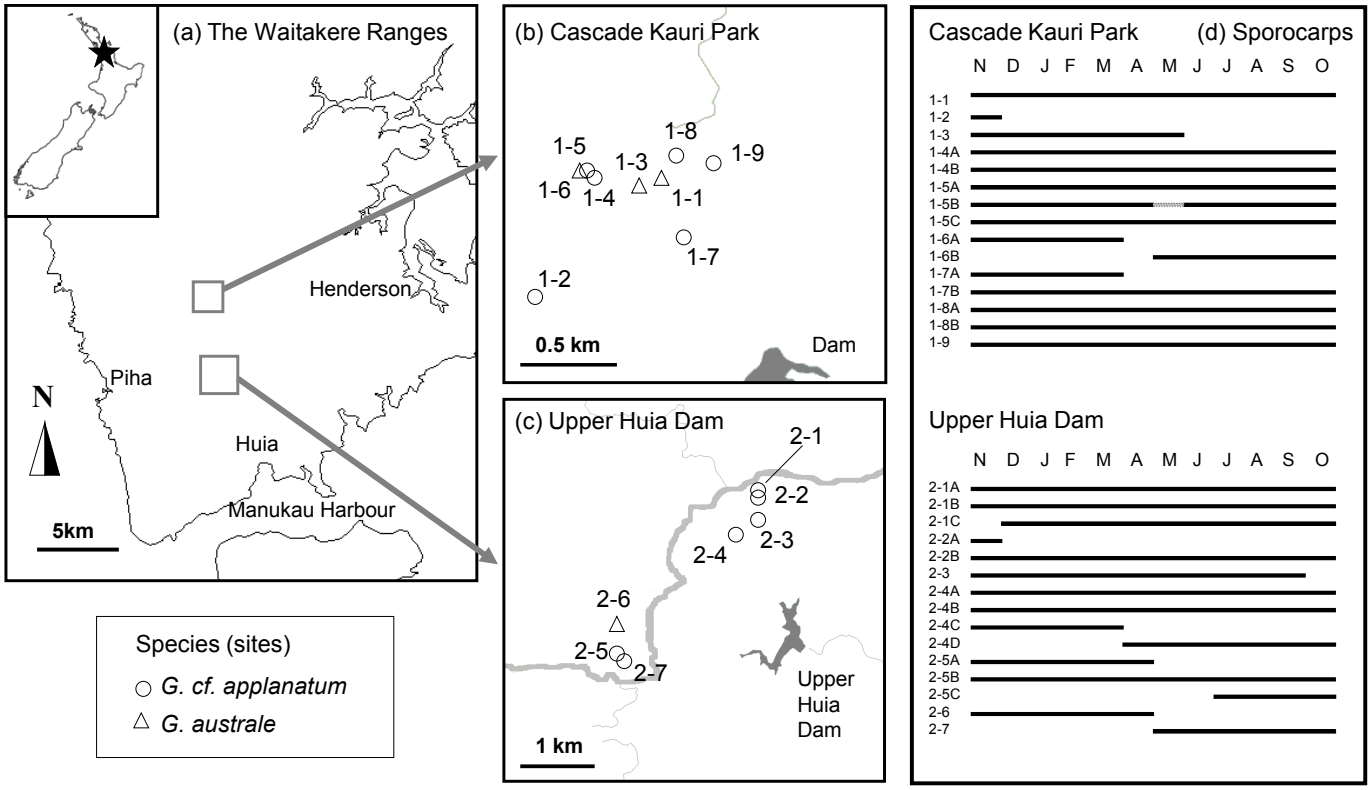

Figure 2. (a) Location of the two study areas, Cascade Kauri Park and Upper Huia Dam, in the Waitakere Ranges, Auckland Region, New Zealand; (b, c) location of patches where fungi were observed in the two study areas; (d) months in which sporocarps were found in each patch between November 2007 and October 2008 – the grey zone in sporocarp 1-5 at Cascade Kauri Park indicates where the sporocarp was perturbed by mould but rejuvenated in a month.

Field and laboratory experiments

Seasonality and host relationship

We examined the number of individuals of *Z. maculifer* (both larvae and adults) and daily spore release patterns over a total of 25 *Ganoderma* sporocarps at monthly intervals from November 2007 to October 2008. We selected nine logs with *Ganoderma* sporocarps at a site in Cascade Kauri Park (Fig. 2b, d) and seven logs at the Upper Huia Dam (Fig. 2c, d). The mean distance between logs was 0.6 km at Cascade Kauri Park and 1.8 km at the Upper Huia Dam. Due to sporocarp deaths or emergence, sporocarp number was 25 at the start of the study and 21 at the end, with a total of 30 studied overall (n = 15 per site) (Fig. 1d), comprising 25 sporocarps of *G. applanatum* and 5 of *G. australe*. A sporocarp of study was replaced when a new sporocarp emerged from the same log. The initial mean area of hymenial surface was approximately 192 cm^2 ± 31.2 (mean ± SE, n = 25). Fortunately, larvae and adults of *Z. maculifer* are always visible on hymenial surfaces, and therefore we obtained an absolute count of *Z. maculifer* populations. We measured daily spore release by setting a plastic plate underneath the hymenial surface for 24 h, and then in the laboratory counting the number of spores collected per square centimetre. The detailed methods and results are reported elsewhere (Kadowaki et al. in press).

Eggs

We measured egg size and hatching time. Eight eggs were collected from the three sporocarps located at 1-5 at Cascade Kauri Park (Fig. 2b, d) on 7 March 2009 and preserved in 70% ethanol for size measurements. We collected a further 18 eggs from the same sporocarps on 10 March 2009 to rear individually on wet filter paper in a Petri dish at ambient conditions, which were checked daily for hatchlings. The exact age of the latter eggs at the time of collection (10 March 2009) was not known, but as they were not seen on 7 March, we assumed they were less than 3 days old.

Larvae

Larval morphometrics were quantified by examining 60 ethanol-preserved specimens that were collected haphazardly from Cascade Kauri Park (patches 1-4, 1-5 and 1-9; Fig. 2b) from November 2008 to February 2009. Three measurements (head capsule width, body length and urogomphal length) were made on each larva, to the nearest 0.01 mm, using a linear micrometer inserted into the eyepiece of a Leica MZ16 microscope. Four final-instar larvae were excluded from analysis because the urogomphi had been detached and could not be measured. We visually assessed the peaks in frequency distributions of the three measured body parts.

Larval development

We conducted field trials to determine the rate of larval development in *Z. maculifer*. Experimental arenas (n = 16) were set up on nine *G. applanatum* sporocarps: 5 arenas on five sporocarps at Cascade Kauri Park, and 11 arenas on four sporocarps at Upper Huia Dam (2 or 3 arenas per sporocarp). An arena was built by attaching a plastic ring (diameter = 4 cm, height = 1.5 cm) to the rough hymenial surface using 10.5 g of brown plasticine (Fig. 1c, d). At least 3 days were required for

the plasticine to become tightly attached to the surface. The top of each arena was covered by a square sheet (7.5 × 7.5 cm) of fine white mesh fabric (0.2-mm mesh) secured by a rubber band to prevent larvae moving into and out of the arena. The hymenium was brushed lightly before affixing an arena and left for 2 weeks, allowing any newly hatched beetle larvae or other insects to be removed. Two first-instar larvae of *Z. maculifer* obtained from other sporocarps were then introduced to each arena with a soft brush on 10 and 11 March 2009, at Cascade Kauri Park and Upper Huia Dam, respectively. Instar development and survival were recorded every 3 or 4 days based on numbers of exuviae present and body size. Mesh coverings were replaced after each observation. The trial was terminated either after 4 weeks or when all larvae had pupated or died. Mean daytime temperature was 21.4°C, and humidity 67%, during the observation periods (1100–1300 hours).

Spore consumption and spore-breaking capability

Spore consumption and spore-breaking ability were measured in a two-way factorial experiment using four instars of *Z. maculifer* and two *Ganoderma* species, replicated four times in an array of 32 Petri dishes. Spores were collected on 5–8 August 2008 from 12 *G. applanatum* sporocarps and one *G. australe* sporocarp at Cascade Kauri Park. Only fresh, unbroken spores were used. Larvae were collected at the same site and kept together in a large plastic container with a wet paper towel flooring on 14 September 2008. Immediately before the experiment larvae were starved for 4 h and gently sprayed with water for 30 s to remove spores adhering to their bodies. A single larva was placed in each Petri dish (3-cm diameter, 1 cm high) that contained 10 mg of spores on damp filter paper and was kept at ambient temperature (c. 15°C). After 24 h, the total number of faecal pellets per individual was examined, and larvae were then preserved in 70% ethanol to measure head capsule width.

The spore-breaking capability of each larva was calculated by counting the number of broken spores out of 150 randomly selected spores in each of five faecal pellets. For assessing broken spores, faecal pellets were mounted individually on glass slides and viewed at 200× magnification. Spores were regarded as broken if they lacked full contents (Nakamori & Suzuki 2005).

An approximate estimate of the average number of spores consumed by a single larva over its entire life was estimated by multiplying larval development time (field trial) by daily spore consumption rate (laboratory experiment) and the mean number of spores per faecal pellet. The latter factor was estimated using data from fourth-instar larvae (averaged from five faecal pellets), since it was too labour intensive to estimate these for all the four instars. We then obtained an estimate of the maximum number of spores consumed by *Z. maculifer* larval populations in relation to the total number of spores discharged by a sporocarp.

Spore consumption data were analysed using generalised linear models. Two explanatory variables were used: larval instar (three levels, 1, 2, and 3–4 instars combined, ordinal) and fungal species (two *Ganoderma* species, categorical). Third and fourth instars were pooled because limited numbers of fourth-instar larvae were available at the time of collection. Because the variance of residuals increased with the mean level of the response, the assumption of constant variance was problematic. Hence, a quasi-Poisson error term with a log-link was used for analysis (Ver Hoef & Boveng 2007). The baseline constraint of the fungal species variable was set to *G. applanatum*.

Logistic regression was used to model the cumulative frequency of broken spores (Lindsey 1995). Although we conducted multiple counts from faecal pellets produced by each larva, we were primarily interested in the variability among faecal pellets from different individuals. Therefore, a mixed-effect approach was used by incorporating 'individual larva' as random intercepts (i.e. repeated measurements). The same two explanatory variables (larval instar and fungal species) were used as above.

Grazing effect on host morphotypes

To determine whether adults of *Z. maculifer* induced a rugose hymenial surface in *G. applanatum*, we established 12 new arenas on six sporocarps, which were located at sporocarps 1-5 and 2-4 (Fig. 2). Hymenial surfaces were initially smooth. Three adult *Z. maculifer* were introduced into six arenas and left to feed for five weeks (7 May to 13 June 2009), while the other six arenas were controls lacking beetles. Survival of beetles was checked weekly when mesh covers were replaced. Morphology of the hymenial surface at the beginning and end of the trial was assessed as smooth, slightly rugose, or highly rugose, by moulding plasticine over it to record microstructure.

All statistical analyses were implemented in R.2.7.1. (R Development Core Team 2008) with the lme4 package (Pinheiro & Bates 2000).

Results

Seasonality and host relationship

A total of 11 731 larvae and 8906 adults of *Z. maculifer* were recorded. Seasonal abundance of *Z. maculifer* showed no clear pattern for adults, but larval abundance tended to be higher in winter (Fig. 3). The average number of months in which larval populations were found was 8.15 across 16 sporocarps that persisted for 12 months. Overall, 99.6% of larvae were found on *G. applanatum* and only 0.4% on *G. australe*. Adults were also very rare on *G. australe* (0.06 – 0.07%).

Eggs

Eggs were ovoid (length = 0.52 ± 0.044 mm SD, maximum width = 0.39 ± 0.040 mm SD, n = 8), lacked micro-sculpture, and were white to grey at maturity (Fig. 1e). Egg surfaces were partly covered by masses of fungal spores. Eggs were deposited singly in gaps on the fungal hymenium, and were concealed by faecal pellets of females (Fig. 1f). Eggs were also deposited on plasticine in the field trial. In the laboratory, duration of the egg stage was 5–7 days (n = 16). One egg failed to hatch and another died after 7 days. Survival from egg to first instar was 88.9%.

Larval instars and development time

The frequency distribution of head capsule width measurements showed four discrete, non-overlapping peaks corresponding to 'observed' instars 1-4 (Fig. 4a). Although the first instar was well defined by urogomphus length, later instars were not clearly separated (Fig. 4b). The overlapping distribution of body length was not concordant with the distribution of head capsule width (Fig. 4c). The field trial observed four larval intervals (Table 1). Total development time for the combined egg, larval and pupal stages was approximately

25 days (Table 1). However, only four individuals completed pupation, which averaged 4–8 days (Table 1). Most larvae died on the mesh cover while searching for an appropriate place to pupate. Larvae that successfully pupated were found on the hymenial surface, or in gaps between the hymenium and the plasticine. Survival from first to fourth instar in the field trial was 60% (n = 30).

Spore consumption and spore-breaking capability

A generalised linear model showed that neither larval instar nor *Ganoderma* species influenced larval spore consumption rates over a 24-h period (P = 0.348 and 0.117, respectively; Fig. 5a, b). The mean proportion of spores broken by *Z. maculifer* was less than 10%, and the spores of *G. australe* were significantly more difficult to break than those of *G. applanatum* (P < 0.0001; Fig. 5d). Instar number did not affect larval spore-breaking capability (P = 0.458; Fig. 5c). The number of spores found per faecal pellet produced by fourth-instar larvae was 318 ± 129 SD.

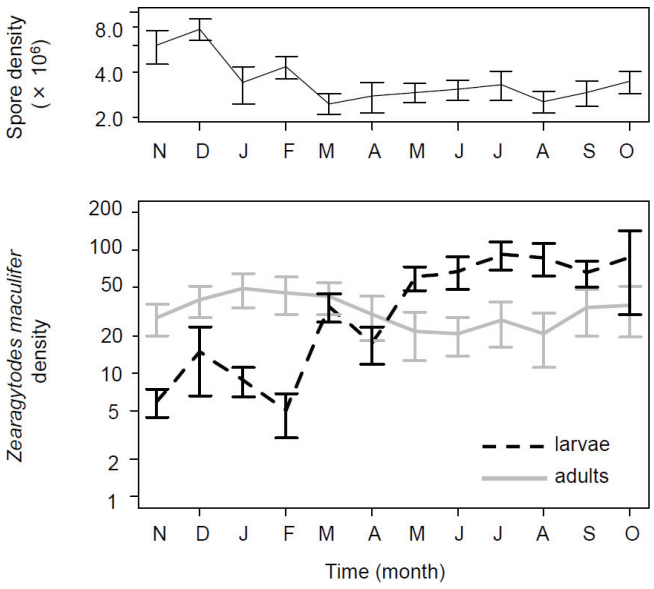

Figure 3. (a) Mean (±SE) spore density per pore surface area (cm^2) each month for all sporocarps examined in two study areas in the Waitakere Ranges, Auckland Region, New Zealand; (b) mean (±SE) monthly abundance per sporocarp of larvae and adults of *Zearagytodes maculifer*.

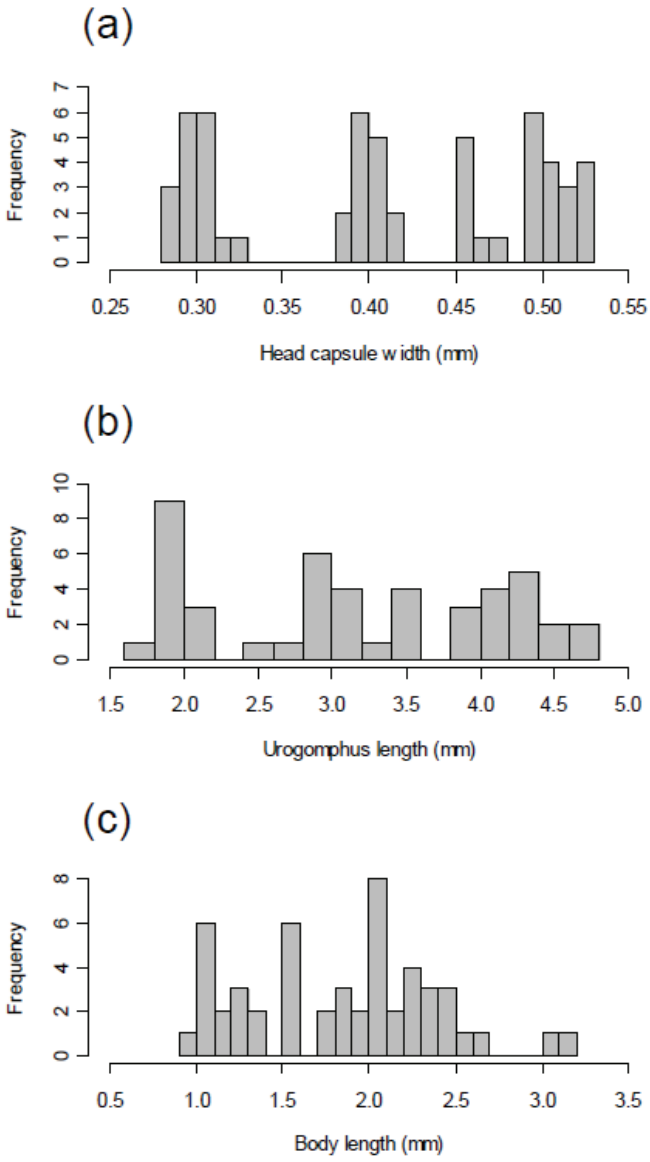

Figure 4. Frequency distribution of (a) head capsule width, (b) urogomphus length and (c) body length measurements for *Zearagytodes maculifer*.

Table 1. Mean (SD) larval body length, head width, urogomphus length and instar duration (larvae and pupae) for *Zearagytodes maculifer*. n^1 = larvae measured; n^2 = larvae reared in the field.

Instar	Body length (mm)	Head width (mm)	Urogomphus length (mm)	n^1	Instar duration (days)	n^2
1	1.2 (0.18)	0.30 (0.01)	2.0 (0.20)	17	4.9 (2.0)	28
2	2.0 (0.42)	0.40 (0.01)	3.15 (0.31)	15	5.2 (2.2)	27
3	2.2 (0.30)	0.46 (0.01)	4.2 (0.38)	7	4.4 (2.4)	24
4	2.3 (0.32)	0.51 (0.01)	4.3 (0.20)	17	6.2 (2.9)	18
Pupa					4.6 (1.3)	4

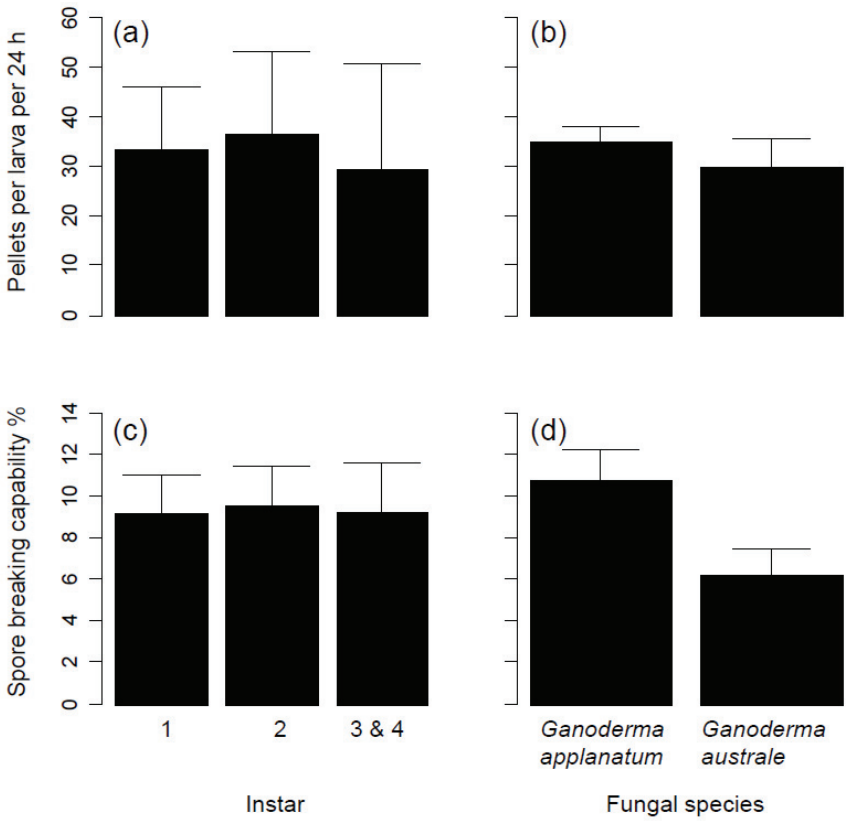

Figure 5. Effects (mean ± SE) of instar and *Ganoderma* species on (a, b) faecal pellet egestion rate (number of pellets per larva per 24 h), and (c, d) spore-breaking capability of *Zearagytodes maculifer* larvae.

Effect of sporophagy on host morphotype

The hymenial surfaces of both control and treatment sporocarps were visually similar at the end of the experiment and all were scored as smooth.

Discussion

Life history

The number of larval instars in Leiodidae ranges from two in cave-dwelling Leptodirini to five in *Leptinus* species parasitic on mammals (Newton 2005). *Zearagytodes maculifer* had four larval instars, and therefore fell within the known range. First to third instars had distinct, non-overlapping peaks in head capsule width distribution. Fourth instars were only slightly larger in body length than third instars, although a field-rearing trial showed four instar intervals. We could not convincingly exclude the possibility that the beetle has three instars, since the apparent four 'numeric' instars might be due to heterogeneous larval growth patterns between sexes or related to nutrient uptake.

Few data are available about the size of leiodid eggs (Newton 2005), but those of *Z. maculifer* were larger in size than the eggs of *Phanerota fasciata* (Staphylinidae) (Ashe 1981) and *Scaphisoma impunctatus* (Leschen 1988), and were similar to those of *Bolitophagus reticulates* (Jonsson 2003). Deposition of eggs singly, as found in *Z. maculifer*, has also been reported in several other fungal-feeding beetles, e.g. *Bolitotherus cornutus* (Tenebrionidae) (Pace 1967), *Pleurotobia tristigmata* (Staphylinidae) (Ashe 1990), and *Gyrophaena* (Staphylinidae) (White 1977). Physical egg protection by faecal matter is also known from *Scaphisoma* (Staphylinidae), *Endomychus* (Endomychidae), *Bolitotherus* (Tenebrionidae) (Leschen 1994). Time taken for development of *Z. maculifer* from egg to adult in the field (25 days) was similar to that of *Endomychus biguttatus* (Endomychidae) on the fungus *Schizophyllum commune* (Leschen & Carlton 1988), but was much shorter than reported for *Bolitotherus cornutus* on *G. applanatum* (88 days; Liles 1956) and *Cis bilamellatus* (Ciidae) (56 days; Paviour-Smith 1968). Thus, the egg-to-adult period was equivalent to, or shorter than, that of other fungivorous beetles living on bracket fungi.

The life cycle of *Z. maculifer* showed little indication of seasonality and both adults and larvae were present throughout the year, though larval abundance peaked during winter. This weak seasonality is unusual for Leiodidae. Chandler and Peck (1992) showed that leiodid beetles living on slime moulds and fungi in a New Hampshire (USA) forest had a narrow, unimodal peak in adult emergence, whereas a univoltine life cycle with summer diapause was found in *Catops nigricans*, a saprophagous species of European leiodid (Topp 1990). The persistence of bracket fungi, and the mild environment of forests in northern New Zealand, may facilitate continuous breeding in *Z. maculifer*.

Host selection

Spore consumption rates did not differ significantly among larval instars, or on the two *Ganoderma* species, though rates showed considerable variation. In fourth-instar larvae this variation may have been partly due to cessation of feeding prior to pupation.

Spore-breaking ability of *Z. maculifer* larvae was low (<10%) compared with the 50–90% recorded by Nakamori and

Suzuki (2005) for a collembolan *Hypogastrura* fed spores of *Hypsizygus marmoreus*, and suggests that *Ganoderma* spores may be better defended than those of *H. marmoreus*. However, the relative efficiency of the spore-crushing mechanisms of the respective collembolan and coleopteran species is not known. As *Z. maculifer* larvae are spore-feeding specialists (Lawrence 1989) it would be particularly interesting to know whether a low percentage of spore breaking can limit nutrient uptake and whether spore-breaking ability provides a robust measure of nutrient uptake from its fungal host.

The impact of spore feeding by *Z. maculifer* on fitness of its fungal hosts is likely to be neutral. The average number of spores consumed by a larva in its life is estimated to range from 7.87×10^4 to 2.98×10^5, and when multiplied by 118 (the maximum number of larvae per sporocarp) represents a very small percentage (0.1–0.4%) of the spores discharged by an intermediate-sized sporocarp (c. 192 cm^2) of *G. applanatum*. Our results contrast with those of Guevara et al. (2000), who showed that feeding by ciid beetles had a negative impact on the fitness of the fungus *Trametes versicolor* by reducing its short-term reproductive potential. However, they are similar to those of Økland & Hågvar (1994), who argued that the sporulating sporocarp of *Fomitopsis pinicola* was able to tolerate high grazing pressure by a spore-feeding staphylinid beetle *Gyrophaena boleti*. In contrast to *Z. maculifer* and *G. boleti*, ciid beetles feed almost entirely on the stroma, rather than the spores and hymenium, respectively. Finally, grazing by adults of *Z. maculifer* did not induce a change in the morphology of *G. applanatum* from smooth to rugose. Its polymorphism therefore remains unexplained.

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