



Competition as possible driver of dietary specialisation in the mushroom harvesting ant *Euprenolepis procera* (Hymenoptera: Formicidae)

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Abstract

Competition between co-existing species for limited resources is considered a main driving force of niche differentiation, including dietary specialization. Responses to interference competition vary, ranging from combat in dominant species to avoidance in submissive ones. Submissive species often show alternative strategies to avoid competition such as quick and efficient resource exploitation or shifts to less competitive resources. In the present study, we have evaluated the potential role of interference competition as driver of dietary specialisation in the mushroom-harvesting formicine ant *Euprenolepis procera* (EMERY, 1900). This ant harvests a broad spectrum of wild-growing mushroom fruiting bodies – an exceptional diet among ants. We asked whether competition avoidance for more typical ant diets could explain the high degree of dietary specialization in *E. procera*. In baiting experiments at the Ulu Gombak field station, Malaysia, we first showed that *E. procera* also utilizes alternative food sources (tuna and honey) demonstrating that mushroom-harvesting is not a hard-wired foraging strategy. In contrast to expectations, *E. procera*'s competitive ability for these resources was relatively high compared with other ants in the community. In a second experiment, we offered three resources (honey, tuna, mushroom) simultaneously and close to each other in baiting stations. In the absence of other ants, all three resources were exploited at similarly high rates by *E. procera* workers. However, *E. procera* avoided foraging on tuna and honey baits when those baits were utilized by other ants. This context-dependent food choice behaviour in *E. procera* suggests that the exceptional dietary specialization on wild-growing mushrooms represents a case of competition-induced niche differentiation. Finally, we provide new data about the geographic distribution and about variability in seasonal dietary preferences of *E. procera*.

Key words: Niche differentiation, competition avoidance, mushroom harvesting, dietary specialisation, mycophagy.

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Introduction

Competition for limited resources constitutes a main driving force of evolution, potentially shaping the morphology, the behaviour, and the life history of organisms (SCHLUTER 2000, MITTELBACH 2012). Food, since it provides nutritional support for survival and growth, is among the most contested resources among animals (STEPHENS & al. 2008). In ecological theory the coexistence of sympatric

species is facilitated if species adopt alternative foraging strategies or occupy complementary food niches, ultimately leading to competitive release and decreased interference (MITTELBACH 2012). In many cases, exceptional dietary specializations in animals supposedly evolved due to strong, long-lasting competition for other food resources (e.g., SCHLUTER 2000). Remarkable examples

of food specialization and dietary niche differentiation are known among ants, particularly in the tropics (HÖLLEDOBLER & WILSON 1990). This includes mass predation of other social insects in army ants (SCHNEIRLA 1971, GOTWALD 1995) and fungus-farming in attine ants (MUELLER & al. 2001, HÖLLEDOBLER & WILSON 2010). For instance, fungus-farming involved a dramatic shift, switching from typical ant diets to cultivating and feeding on a symbiotic, cellulose-digesting fungi. This shift opened up a new dietary niche space – the exploitation of otherwise indigestible plant material.

Harvesting of wild-growing fungal fruiting bodies (sporocarps), commonly referred to as mushrooms, constitutes another exceptional dietary specialization in ants (WITTE & MASCHWITZ 2008). As yet, reliance on wild-growing mushrooms as primary dietary resource has only been demonstrated in the Old World formicine ant *Euprenolepis procera* (EMERY, 1900) whose natural diet is based almost exclusively on mushrooms (WITTE & MASCHWITZ 2008, VON BEEREN & al. 2014). The related species *Euprenolepis wittei* LAPOLLA, 2009 likewise harvests and process mushrooms within its nest, but its dependency on a mushroom diet remains questionable (VON BEEREN & al. 2014). While occasional harvesting of wild-growing mushrooms has additionally been described in several ant species (e.g., CARROLL & al. 1981, PFEIFFER & LINSÉNMAIR 2000, MUELLER & al. 2001, LECHNER & JOSENS 2012, MASIULIONIS & al. 2013, EPPS & PENICK 2018), most ants do not harvest mushrooms. This absence of mycophagy in ants might seem surprising at first hand, particularly as potentially nutrient-rich fungi constitute a major component of many terrestrial ecosystems (PIMENTEL & al. 1992, CLARIDGE & MAY 1994, WALLIS & al. 2012). In fact, mycophagy is widespread among a diversity of other invertebrates and some vertebrates (WILDING & al. 1989, CLARIDGE & TRAPPE 2005). However, several characters of mushroom fruiting bodies have been suggested to hamper a dietary specialization on this resource. First, digestion of mushrooms is considered challenging because nutrients are enclosed in non-digestible chitinous cell walls (MARTIN 1979, CLARIDGE & TRAPPE 2005). Consequently, a diet based primarily on mushrooms is considered unfavourable for species lacking appropriate adaptations for efficient mushroom digestion (CLARIDGE & TRAPPE 2005, HANSON & al. 2006, D'ALVA & al. 2007). Second, many mushroom species evolved potent toxins as chemical defences (SPITELLER 2008). Third, the fruiting bodies of many fungi grow unpredictably in space and time – a challenge for efficient food retrieval (CLARIDGE & TRAPPE 2005, VON BEEREN & al. 2014).

The mushroom-harvesting specialist *Euprenolepis procera* appears to possess specific adaptations to overcome these impediments, among others an elaborate foraging strategy to exploit mushroom fruiting bodies (VON BEEREN & al. 2014), conservation of mushroom material inside the nest through intensive processing, and possibly fermentation of fungal material as indicated by a characteristic sweetish-sour smell (WITTE & MASCHWITZ

2008). However, details about digestive processes and possible detoxification mechanisms remain unknown to date (WITTE & MASCHWITZ 2008, VON BEEREN & al. 2014). Despite these specific adaptations to a mushroom diet *E. procera* colonies readily accepted other food in laboratory nests (WITTE & MASCHWITZ 2008). Several colonies were kept successfully for more than three months under a typical ant diet exclusively consisting of crickets and honey (WITTE & MASCHWITZ 2008; S. Lizon à l'Allemand & C. von Beeren, unpubl.). This prompted the question why *E. procera* almost exclusively feeds on mushrooms under natural conditions.

We hypothesized that *Euprenolepis procera* avoids interspecific competition for more easily digestible sugar-rich and protein-rich resources by focussing on mushrooms as a less competitive resource. We tested this hypothesis by evaluating *E. procera*'s dietary preferences and by inferring their competitive abilities using two complementary baiting experiments. In a “single-resource experiment” we offered the following resources one at a time: honey as a carbohydrate-rich resource, tuna as a protein-rich resource, and mushroom as *E. procera*'s main natural diet. This experiment allowed us to assess natural resource preference of *E. procera*, to infer the level of competition in the ant community for each of these resources, and to evaluate the competitive ability of *E. procera* relative to other ants in the community. In the “multi-resource experiment” all three resources were offered simultaneously to investigate the food choice of *E. procera* under competition when alternative resources are directly available. Due to its natural preference for mushrooms, we expected *E. procera* to preferentially utilize mushrooms and to avoid competition for other resources. Besides competition experiments, we also provide new data about the geographic distribution and seasonal variability in dietary preferences of *E. procera*.

Material and methods

The study was carried out at the secondary lowland rainforest of the Field Studies Centre of the University Malaya in Ulu Gombak (03° 19.4796' N, 101° 45.1630' E, ca. 230 m above sea level, a.s.l.). All experiments were carried out during 20:00 h - 04:00 h as foraging activities of *Euprenolepis procera* are strictly nocturnal (WITTE & MASCHWITZ 2008). We investigated resource preferences and competitive abilities of *E. procera* through a single-resource and a multi-resource baiting experiment, each of the two experiments touching slightly different aspects of *E. procera*'s foraging ecology (see below). As baits we offered three different food resources, which we offered *ad libitum*: approx. 15 - 20 g of tuna (protein-rich), approx. 10 - 15 g of honey (carbohydrate-rich), and approx. 15 - 25 g (one large) *Pleurotus* sp. mushroom (mimicking the natural diet of *E. procera*; Fig. 1). In rare cases, resources were going to be depleted within the experimental period. In these cases, we carefully refilled the bait with the respective resource. We chose tuna as protein-rich resource and honey as carbohydrate-rich resource because they



Fig. 1: Bait use by *Euprenolepis procera*. Shown are *E. procera* workers at (A) a mushroom bait, (B) a tuna bait, and (C) a honey bait (single-resource experiment).

have been shown to attract a high diversity of ants (e.g., ROMERO & JAFFE 1989, HAHN & WHEELER 2002, NARENDRA & al. 2011). Note that tuna is also rich in fat and salt so that preferences for tuna cannot be solely assigned to a high protein content (see also KASPARI & YANOVIK 2001). We offered tuna stored in water instead of salty solution to avoid having an artificially high salt content.

Single-resource experiment: The aims of the single-resource experiment were threefold. First, we aimed to experimentally quantify to what extent *Euprenolepis procera* feeds on experimentally offered food resources which represented typical ant diets and mushrooms as its natural diet. Second, we evaluated the level of utilization among ants in the community for each of these resources as a measure indicative of competition intensity. Third, we assessed the utilization efficiency of *E. procera* relative to other ants in the community, measured in bait discovery efficiency, monopolization ability, and dominance, thus inferring *E. procera*'s competitive abilities relative to other ants.

Single-resource experiments were carried out in March and July - September 2008 and in February - April 2009 (N = 15 nights). On a given night, 16 - 20 baits of one of the three resources were randomly distributed on the forest floor between 20:00 h - 21:00 h, with at least 10 m distance between baits. We altered the location of baits between nights with a minimum distance of 5 m from baits installed in previous nights to avoid the establishment of permanent ant trails across nights. Mushroom and tuna baits were placed on leaves on the forest floor, while honey baits were offered in Petri dishes (Sigma-Aldrich; Fig. 1). For a period of four hours, we checked the baits hourly for the presence of ants and other invertebrates, resulting in four observations per bait per night. Note that mushroom baits were inspected visually so that small ants, flies or staphylinid beetles hiding in between gills might have been missed. If ants were present, we assessed the number of workers per morphospecies at the bait and carefully collected a few specimens of each morphospecies for later genus identification using the key of Hashimoto (HASHIMOTO 2003). A morphospecies was simply defined as ant workers that appeared morphologically similar to each other. We decided to constrain our identification to the

genus level as many of the collected specimens could not be reliably identified to the species level (e.g., in the genera *Camponotus* and *Pheidole*). We did this as genera tend to be groups of ecologically very similar species, hence having similar feeding preferences and strategies. Nonetheless, readers should be aware that a genus-level identification clearly sets limitations on the community-wide inferences about competitive ability patterns in bait-exploiting ants, in particular as sometimes strong variation of foraging strategies and competitive abilities can exist within a single genus. The only ants we identified to the species level were those belonging to the genus *Euprenolepis* (i.e., *E. procera* and *E. wittei*; for species key, see LAPOLLA 2009) to test for differences in competitive abilities of the two mushroom-harvesting ants. It should be noted here that competition in its strict sense is a process affecting populations (e.g., CERDÁ & al. 2013), which can hardly be studied with baiting experiments. In the present study, we thus use the terms "competition" and "competitive ability" in a loose sense referring to features solely related to bait exploitation (see next paragraphs).

As the competitive abilities of ants are usually considered a multi-faceted aspect of ant ecology (e.g., WILSON 1971, PARR & GIBB 2012, CERDÁ & al. 2013, STUBLE & al. 2017), we applied several indices to infer the relative competitive ability of *Euprenolepis procera*. Competitive interactions can take place in direct interactions (interference competition), or indirectly in the context of resource discovery time and exploitation efficiency (exploitation competition). For each resource, we thus inferred the exploitation efficiency and the competitive ability of *E. procera* relative to other ants in the community by calculating the following indices for each genus (see also CERDÁ & al. 1997, SANTINI & al. 2007). A **first discoverer index (FDI)** was used as a measure for discovery abilities compared to other ants in the community. The FDI of a given genus / *Euprenolepis* species is defined as the ratio between the numbers of baits discovered as the first approaching ants and the total number of discovered baits of that genus / *Euprenolepis* species. If two genera / *Euprenolepis* species were simultaneously present at a given bait during the first count, the discovery as first ants at baits was assigned to both genera. We furthermore

determined temporal aspects of the ants' foraging efficiency by determining the **bait discovery time**, which was defined as the time span between bait installation and detection of first ant workers at a bait (measured in hours), and the **exploitation duration**, which was the time spent at a given bait (measured in hours – maximum four hours). Note that one hour in between observations does only allow us to assess the bait discovery time and exploitation duration with relatively low precision.

As a measure for exclusive occupation of baits by certain genera / *Euprenolepis* species we used a **monopolisation index (MI)**. The MI of a given genus / *Euprenolepis* species is defined as the ratio between the number of baits that were exclusively occupied (no other ant genus was present throughout the duration of 4h) and the total number of baits discovered by this genus. If more than one genus occurred at a given bait, we classified the genera / *Euprenolepis* species into the following three categories: (a) dominant if a genus / *Euprenolepis* species replaced another genus / *Euprenolepis* species at a bait; (b) subordinate if a genus / *Euprenolepis* species was replaced at a bait; (c) peaceful if a genus / *Euprenolepis* species co-occurred with other ants at a bait without being displaced or displacing other ants. Based on this data, a **dominance index (DI)** was calculated to quantify interference abilities, defined as the ratio of observations as a dominant competitor to the total number of encounters with other ant genera / *Euprenolepis* species. Note that dominance as defined here does not necessarily imply that ants interacted with one another, for example by aggressive behaviour. As a measure of competitive ability, we also determined the maximum number of ants for each genus / *Euprenolepis* species at a given bait within the four hours observation period. For limitations of an index-based approach for assessing competitive abilities in ant communities, see, for example, STUBLE & al. (2017).

We used non-parametric statistics to test for differences in the maximum number of workers at baits and the exploitation duration at baits. We refrained from using parametric statistics for these comparisons as data distributions did not meet the assumptions of normality, even after transformations. Hence, we used Mann-Whitney *U* tests (MANN & WHITNEY 1947) and Kruskal-Wallis tests (KRUSKAL & WALLIS 1952). As post-hoc analyses for Kruskal-Wallis tests we used Dunn's multiple comparisons rank sum test (DUNN 1964) with false discovery rate correction to account for type I error-accumulation (BENJAMINI & HOCHBERG 1995) as implemented in the R package "PMCMRplus" (POHLERT 2018). All statistics were done in R 3.5.1 (R CORE TEAM 2018) and PAST 3.2.2 (HAMMER & al. 2001).

Multi-resource experiment: This experiment aimed to investigate two aspects of *Euprenolepis procera*'s foraging behaviour. First, we assessed if *E. procera* shows preferences for any of the simultaneously offered resources in absence of competition. Second, we aimed to evaluate whether these dietary preferences change under competition and in a situation where alternative food resources

were readily accessible. This allowed us to evaluate if and to what extent *E. procera* exploits resources in competitive situations. Because of *E. procera*'s natural dietary preference for mushrooms, we expected *E. procera* to avoid competition for tuna and honey resources.

This experiment was carried out in March 2010 at the Ulu Gombak Field Station (N = 7 nights). One tuna bait, one honey bait, and one mushroom bait were simultaneously offered in a baiting station. Baits within such a station were arranged in a triangular shape with a distance of 30 cm to each other. Six to ten of such baiting stations were set up per night with at least 10 m distance from each other. Each baiting station was assigned a unique identification number ("baiting station ID"). Baiting stations were installed between 20:00 h - 21:00 h and localities of stations were altered between nights. We visited baiting stations every 30 min over the course of five hours, resulting in ten repeated observations per baiting station per night ("replicates"). We noted the number of ants per morphospecies at each resource and carefully collected a few specimens per morphospecies for genus identification as described above.

We tested for differences in the presence or absence of *Euprenolepis procera* workers at baits of different resources with respect to whether competitors were absent (no competitors) or present at honey, tuna, or honey and tuna. We analysed the data with a generalized linear mixed effect model (GLMM) based on a binomial error distribution and logit as link-function. We fitted *E. procera* "presence or absence" at baits as a binomial response variable with "resource type" (tuna, honey, mushroom) and "presence of competitors" (absent / competitor at tuna / competitor at honey / competitor at tuna and honey) as fixed explanatory variables, as well as "replicate" in "baiting station ID" as nested random factor and "baiting station ID" as crossed random factor. For GLMM calculation we used the R packages "lme4" (BATES & al. 2015), "car" (FOX & WEISBERG 2011), "effects" (FOX 2003), "MuMIn" (BARTON 2018), "multcomp" (HOTHORN & al. 2017), and "nlme" (PINHEIRO & al. 2018). We subsequently controlled the models normality of residuals, variance heteroscedasticity and overdispersion using the R-package "DHARMA" (HARTIG 2019) and found that all criteria were met. Lastly, we applied marginal and conditional r^2_{GLMM} as coefficients to describe the proportion of variance explained by fixed and random factors, respectively (NAKAGAWA & SCHIELZETH 2013).

Natural history data – seasonal dietary preferences and geographical distribution: Besides evaluating food preferences and competitive abilities of *Euprenolepis procera*, we additionally collected natural history data about potential seasonal dietary differences and about the geographic distribution of *E. procera*. These data are thematically not directly linked to the competition experiments described above. Nonetheless, we decided to include the natural history data in the present article, because they constitute valuable information about the biology of the mushroom-harvesting ant *E. procera*.

Seasonal dietary preferences. We evaluated *Euprenolepis procera*'s natural food intake at Ulu Gombak during two different times of the year, from March to April 2008 (from hereon called "early season") and from August to September 2008 (from hereon called "late season"), to investigate the possibility that resource use might differ between seasons. The two observation periods differed in rainfall. We analysed precipitation data of the two observation periods through data that were kindly provided by the company Greenspan Technology. This company had a weather data logger at the Ulu Gombak field site. We calculated the daily average precipitation (raw data consisted of precipitation measurements for every minute per day) and compared the precipitation data per day between early season and late season. We detected more rainfall in the early season (median = 3.75 mm / day) compared to the late season (median = 1.5 mm / day; Mann-Whitney *U* test, $U = 986.5$, $p = 0.006$, early season: $N = 44$ days, late season: $N = 45$ days). Note that this study does not allow us to draw conclusions about general differences in these two times of the year as we only sampled once in early season and once in late season. Nonetheless, the data allow us to show that *E. procera*'s dietary preferences can vary temporally.

In total, 14 *Euprenolepis procera* colonies were studied in the early season and 12 colonies in the late season. First, we located field colonies by attracting *E. procera* workers to mushroom baits (*Pleurotus* sp.) and by tracking foraging columns back to the nest site. On any given observation day, the nest site of each colony was visited one to three times with at least 2 h between visits. To evaluate if the ants showed foraging activity at all, we first observed foraging trails at the nest entrance. Foraging trails with ten or more passing ants per minute were considered for dietary observations. We then followed the foraging column to potential food sources, which were either mushrooms, fruits, or dead invertebrates. A given food item was only recorded once per day to avoid over-representation. The number of colonies under observation varied between seasons (early season: mean \pm SD = 6 ± 1 colonies surveyed per night, number of observation days = 28d; late season: mean \pm SD = 9 ± 1 colonies surveyed per night, number of observation days = 23d; Mann-Whitney *U* test, $U = 22$, $p < 0.001$). For a better comparison of *E. procera*'s diet between seasons, we standardized the number of discovered food items for each night with the number of colonies under surveillance (e.g., 0.5 mushrooms per colony per night). The influence of season on *E. procera*'s utilized resources (either mushroom, fruit or invertebrate carcass) was analysed using a one-way multivariate analysis of variance (Wilk's lambda MANOVA), due to the non-independence of resource use per night. We used univariate protected ANOVAs (SCHEINER & GUREVITCH 2001) to test for differences in resource use between the two seasons. The response variables were arcsin-square root transformed to ensure multivariate normality.

Geographical distribution. We searched for mushroom-harvesting ants in other regions of peninsular

Malaysia to unveil if *Euprenolepis procera* is a common species in these lowland tropical rainforests. Using *Pleurotus* sp. mushroom baits, we searched for *Euprenolepis* species at four locations: Endau Rompin (August 2008; $02^{\circ} 31.882' N$, $103^{\circ} 24.911' E$, 49 m a.s.l.), Bukit Rengit (February 2009; $03^{\circ} 35.779' N$, $102^{\circ} 10.814' E$, 72 m a.s.l.), Kuala Lompat (February 2009; $03^{\circ} 42.738' N$, $102^{\circ} 17.196' E$, 52 m a.s.l.) and Lentang (February 2011; $3^{\circ} 22.871' N$, $101^{\circ} 53.218' E$, 176 m a.s.l.). The latter site was chosen as a sampling site in close vicinity (25 km) to Ulu Gombak with similar characteristics regarding soil, topography and vegetation (S. Lizon à l'Allemand, unpubl.; see also Tab. S1, as digital supplementary material to this article, at the journal's web pages). Located on the other side of the Genting mountain range, however, it differs in local climate. The remaining three sites were geographically less close to Ulu Gombak (range: 55 km - 203 km distance to Ulu Gombak) and additionally showed differences in local climate as well as soil and plant composition (Tab. S1). Data about the geographic distribution of the second mushroom harvesting ant *E. wittei* were published previously (VON BEEREN & al. 2014).

Results

Single-resource experiment: *Euprenolepis procera* exploited all three resources (Tab. 1; Fig. 1) and utilized them for an equally long time (Kruskal-Wallis test, $\chi^2 = 0.29$, $df = 2$, $p = 0.855$; see Tab. 1 for sample size; Tab. 2) and with similar number of workers (Kruskal-Wallis test, $\chi^2 = 0.69$, $df = 2$, $p = 0.704$; see Tab. 1 for sample size; Tab. 2). Considering the entire ant community, however, resource use differed considerably (Tab. 1). While all tuna and most honey baits were discovered and utilized by ants within the 4h observation period, only 61% of mushroom baits were utilized (77 out of 125 mushroom baits). Most obviously, the diversity of ants at different food resources differed in that more ant genera appeared at honey ($N = 11$ genera) and tuna baits ($N = 12$ genera) than at mushroom baits ($N = 1$ genus; Tab. 1). As expected, we only detected two *Euprenolepis* species at mushroom baits, with *E. procera* being more often detected than *E. wittei* (54% vs. 6% of mushroom baits utilized, respectively; Tab. 1). Other arthropods such as harvestmen and crickets appeared only occasionally at tuna and mushroom baits, while no other animals than ants were detected at honey baits (Tab. 1). In the following, we relate the competitive ability of *E. procera* for each resource to other ants in the community.

Tuna baits. With 61% of tuna baits utilized, *Euprenolepis procera* was the most abundant ant at this resource (Tab. 1). The maximum number of ants at tuna baits differed considerably among the observed genera / *Euprenolepis* species (Kruskal-Wallis test, $\chi^2 = 75.56$, $df = 10$, $p < 0.001$, for sample size see Tab. 1) and *E. procera* was among the ants with highest number of workers at tuna baits (Tab. 2; Fig. S1). Ant genera / *Euprenolepis* species also differed in the exploitation duration at tuna baits (Kruskal-Wallis test, $\chi^2 = 27.88$, $df = 10$, $p = 0.001$;

Tab. 1: Percentage of baits utilized by a given ant genus / *Euprenolepis* species for each resource (single-resource experiment). The numbers of occurrences at baits are given in parentheses. Abbreviations: n.d. = not detected at this resource.

Species / genus	Tuna (N=74 baits)	Honey (N=74 baits)	Mushroom (N=125 baits)
<i>Euprenolepis procera</i>	61% (45)	28% (21)	54% (69)
<i>Euprenolepis wittei</i>	9% (7)	5% (4)	6% (7)
<i>Camponotus</i>	32% (24)	4% (3)	n.d.
<i>Crematogaster</i>	5% (4)	1% (1)	n.d.
<i>Lophomyrmex</i>	16% (12)	5% (4)	n.d.
<i>Meranoplus</i>	n.d.	3% (2)	n.d.
<i>Odontomachus</i>	12% (10)	15% (11)	n.d.
<i>Odontoponera</i>	16% (12)	11% (8)	n.d.
<i>Paratrechina</i>	1% (1)	n.d.	n.d.
<i>Pheidole</i>	5% (4)	18% (14)	n.d.
<i>Pheidologeton</i>	3% (2)	5% (4)	n.d.
<i>Pseudolasius</i>	n.d.	8% (5)	n.d.
<i>Tapinoma</i>	12% (9)	35% (25)	n.d.
other animals	15% (11)	n.d.	8% (10)

Tab. 2: Exploitation duration and maximum number of ants at baits (single-resource experiment). Exploitation duration and maximum numbers of individuals at baits of the three resources are given for different genera / *Euprenolepis* species. Abbreviations: n.d. = not detected at this resource; SD = standard deviation.

Species / genus	Exploitation duration (mean ± SD in hours)			Maximum number of ants at a given bait over time (mean ± SD)		
	Tuna	Honey	Mushroom	Tuna	Honey	Mushroom
<i>Euprenolepis procera</i>	2.82 ± 1.00	2.71 ± 1.01	2.74 ± 0.99	76 ± 43	66 ± 36	74 ± 41
<i>Euprenolepis wittei</i>	1.71 ± 1.11	2.50 ± 1.29	2.57 ± 1.51	14 ± 14	28 ± 15	30 ± 18
<i>Camponotus</i>	1.63 ± 0.82	2.00 ± 1.00	n.d.	13 ± 36	6 ± 4	n.d.
<i>Crematogaster</i>	2.50 ± 1.73	2.00	n.d.	55 ± 31	150	n.d.
<i>Lophomyrmex</i>	1.67 ± 0.99	3.50 ± 1.00	n.d.	47 ± 30	93 ± 67	n.d.
<i>Meranoplus</i>	n.d.	2.50 ± 2.12	n.d.	n.d.	15 ± 7.07	n.d.
<i>Paratrechina</i>	4.00	n.d.	n.d.	250	n.d.	n.d.
<i>Odontomachus</i>	2.22 ± 1.40	2.09 ± 1.30	n.d.	9 ± 10	8 ± 14	n.d.
<i>Odontoponera</i>	2.08 ± 1.24	2.38 ± 1.41	n.d.	3 ± 3	4 ± 3	n.d.
<i>Pheidole</i>	2.50 ± 1.73	1.85 ± 1.28	n.d.	30 ± 14	25 ± 39	n.d.
<i>Pheidologeton</i>	2.50 ± 0.71	2.00 ± 1.41	n.d.	145 ± 148	76 ± 64	n.d.
<i>Pseudolasius</i>	n.d.	2.00 ± 1.55	n.d.	n.d.	12 ± 6	n.d.
<i>Tapinoma</i>	1.78 ± 1.09	3.46 ± 1.03	n.d.	20 ± 18	72 ± 50	n.d.

for sample size see Tab. 1) with *E. procera* being among the ants staying longest (Tab. 2). Compared to other ant genera, *E. procera* showed an intermediate first discovery index for tuna baits, an intermediate monopolization index for tuna baits, and together with *Pheidole* and *Pheidologeton* the highest dominance index for tuna baits (*E. procera*: dominant interactions = 25; subordinate interactions = 8; peaceful interactions = 6; Tab. 3).

Honey baits. *Euprenolepis procera* discovered 28% of honey baits and only ants of the genus *Tapinoma* discovered more (35% of honey baits; Tab. 1). Ant genera / *Euprenolepis* species differed in the maximum number of ants at honey baits (Kruskal-Wallis test, $\chi^2 = 53.42$, $df = 11$, $p < 0.001$, for sample size see Tab. 1; Fig. S1) and *E. procera* together with ants of the genera *Tapinoma*, *Lophomyrmex* and *Pheidologeton* showed highest worker

Tab. 3: First discoverer index (FDI), monopolization index (MI) and dominance index (DI) for different genera / *Euprenolepis* species (single-resource experiment). Sample sizes are given in Table 1. Abbreviations: n.d. = not detected at this resource.

Species / genus	FDI			MI			DI		
	Tuna	Honey	Mushroom	Tuna	Honey	Mushroom	Tuna	Honey	Mushroom
<i>Euprenolepis procera</i>	0.53	0.67	0.97	0.33	0.38	0.92	0.64	0.59	1.00
<i>Euprenolepis wittei</i>	0.29	0.25	0.86	0.00	0.00	0.71	0.10	0.34	0.00
<i>Camponotus</i>	0.29	0.33	n.d.	0.04	0.00	n.d.	0.26	0.00	n.d.
<i>Crematogaster</i>	0.50	n.d.	n.d.	n.d.	n.d.	n.d.	0.00	n.d.	n.d.
<i>Lophomyrmex</i>	0.67	1.00	n.d.	0.00	0.75	n.d.	0.28	n.d.	n.d.
<i>Meranoplus</i>	n.d.	1.00	n.d.	n.d.	0.50	n.d.	n.d.	0.50	n.d.
<i>Paratrechina</i>	1.00	n.d.	n.d.	1.00	n.d.	n.d.	0.00	n.d.	n.d.
<i>Odontomachus</i>	0.90	0.45	n.d.	0.50	0.27	n.d.	0.00	0.56	n.d.
<i>Odontoponera</i>	0.50	0.25	n.d.	0.08	0.25	n.d.	0.27	0.11	n.d.
<i>Pheidole</i>	0.75	0.86	n.d.	0.00	0.43	n.d.	0.60	0.22	n.d.
<i>Pheidologeton</i>	0.00	0.50	n.d.	0.00	0.25	n.d.	0.67	0.50	n.d.
<i>Pseudolasius</i>	n.d.	0.40	n.d.	n.d.	0.20	n.d.	n.d.	0.00	n.d.
<i>Tapinoma</i>	0.56	0.80	n.d.	0.00	0.77	n.d.	0.31	0.44	n.d.

Tab. 4: Geographical distribution of *Euprenolepis procera*. Number of mushroom baits (N_{baits}) utilized by *E. procera* (EP), *E. wittei* (EW), and other animals in different regions of peninsular Malaysia.

Region	N_{baits}	Percentage of baits visited by ...		
		EP	EW	Other animals
Ulu Gombak	125	54%	6%	8%
Bukit Rengit	35	11%	6%	49%
Endau Rompin	31	0%	10%	65%
Kuala Lompat	26	15%	4%	77%
Lentang	38	24%	8%	34%

numbers at honey baits (Tab. 2). Ant genera / *Euprenolepis* species also differed in their exploitation duration at honey baits (Kruskal-Wallis test, $\chi^2 = 22.28$, $df = 11$, $p = 0.017$, for sample size see Tab. 1) but most genera stayed for two or more hours (Tab. 2). *Euprenolepis procera* was most dominant at honey baits (*E. procera*: dominant interactions = 10; subordinate interactions = 5; peaceful interactions = 2; Tab. 3), while its first discoverer index and monopolization index showed intermediate values compared with other ants in the community (Tab. 3).

Mushroom baits. *Euprenolepis procera* and *E. wittei* were the only ants utilizing mushroom baits. The present study supports a dominant behaviour of *E. procera* in interactions with *E. wittei*. It recruited higher numbers of ants to mushroom baits (mean number of ants \pm SD: *E. procera* = 74 ± 41 ; *E. wittei* = 30 ± 18 ; Mann Whitney *U* test, $U = 77$, $p = 0.003$, for sample size see Tab. 1; Fig. S1) and dominated interspecific interactions as reflected in the dominance index (*E. procera*: DI = 1, *E. wittei*: DI = 0). Note that the DI is based on only two replacement events and thus no strong conclusion can be drawn on these data alone (but see VON BEEREN & al. 2014 reporting 13 additional replacement events). Both species showed a high

first discoverer index (*E. procera*: FDI = 0.97, *E. wittei*: FDI = 0.86) and *E. procera* (MI = 0.92) showed a higher monopolization index than *E. wittei* (MI = 0.71). The two species did not differ in their exploitation duration (Mann Whitney *U* test, $U = 228$, $p = 0.857$, for sample size see Tab. 1; Tab. 2).

Multi-resource experiment: The presence-absence ratio of *Euprenolepis procera* differed between resources and depended on the presence of competitors (GLMM with binomial distribution: “presence of competitors” x “resource type”: Wald- $\chi^2 = 85.71$, $df = 6$, $N_{total} = 903$, $p < 0.001$; $r^2_{GLMM(m)} = 0.34$, $r^2_{GLMM(c)} = 0.46$; Fig. 2). Yet, in the absence of competitors *E. procera* exploited all three resources equally (for all pairwise comparison of “no competitor at tuna”, “no competitor at honey”, and “no competitor at mushroom”: z-values ≤ 1.399 , $p \geq 0.243$; Fig. 2; for a detailed list, see Tab. S2). While mushrooms were under little to no competition, the presence of *E. procera* at the resources honey and tuna depended on the presence of competitors (Fig. 2). When competitors were present at tuna baits, *E. procera* was less often present at this resource compared to honey and mushroom baits (Fig. 2). Likewise, when competitors were present at honey

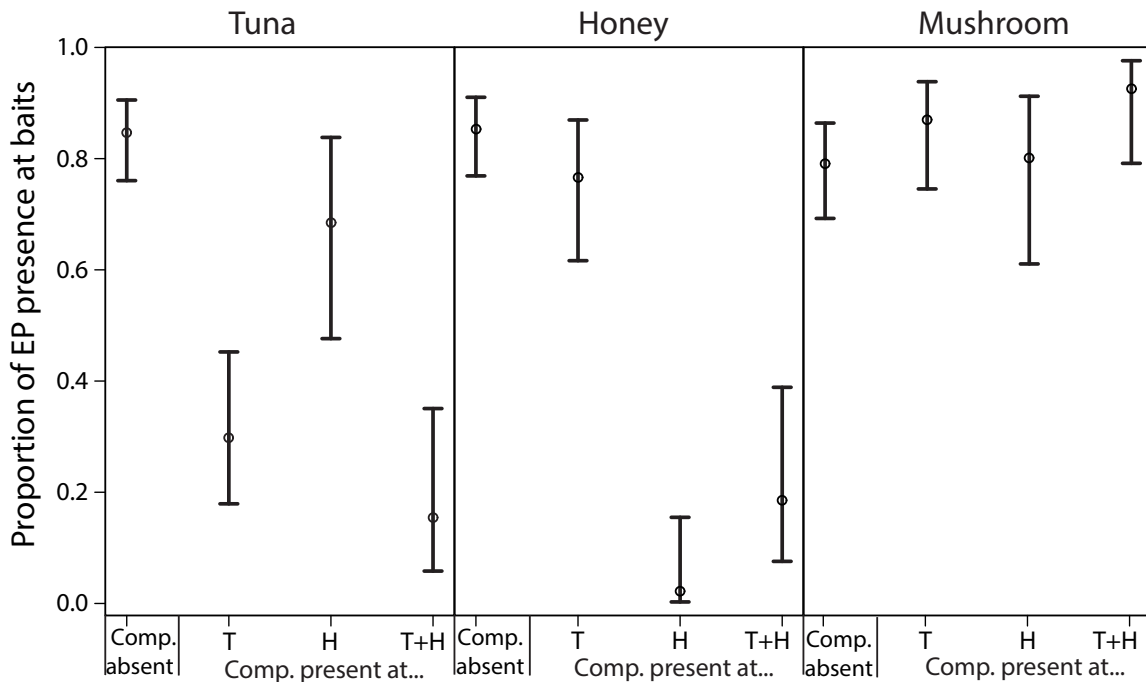


Fig. 2: Generalized linear mixed effect model plot depicting the proportion of tuna, honey and mushroom baits utilized by *Euprenolepis procera* in dependence on competitor presence (multi-resource experiment). Shown are means (circles) and asymmetric standard errors (bars) of the model estimate. Abbreviations: EP = *E. procera*, Comp. = competitor, T = tuna, H = honey, M = mushroom.

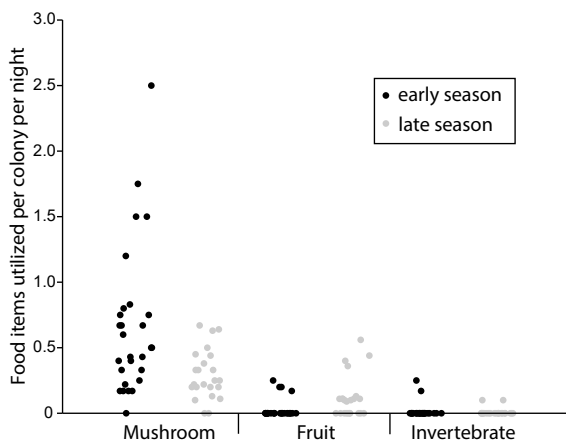


Fig. 3: Food items utilized by *Euprenolepis procera* workers during the early and the late season.

baits, *E. procera* was less often present at this resource compared to tuna and mushroom (Fig. 2). When competitors were present at honey and tuna, *E. procera* almost exclusively exploited mushroom baits (Fig. 2).

Natural history data – seasonal dietary preferences and geographical distribution: Seasonal dietary preferences. We detected slight differences in *Euprenolepis procera*'s resource use between seasons. In total, we detected 99 mushrooms, 4 fruits and 2 invertebrates in the early season and 59 mushrooms, 27 fruits and 2 invertebrates in the late seasons. The resource use per colony per night differed between seasons (MANOVA: Wilk's $\lambda = 0.69$, $F_{1,49} = 6.94$, $p < 0.001$; Fig. 3).

With 94% and 67% of detected food items, mushroom fruiting bodies constituted *E. procera*'s main food in the early and in the late season, respectively (Fig. 3). Yet, the number of harvested mushrooms per colony per night differed significantly between seasons (univariate ANOVA: $F = 10.70$, $p = 0.002$) in that more mushrooms were utilized in the early season (mean \pm SD: early season = 0.67 ± 0.56 mushrooms per colony per night; late season = 0.29 ± 0.19 mushrooms per colony per night). Fruit utilization also differed between seasons (univariate ANOVA: $F = 9.39$, $p = 0.004$) with fruits being more commonly utilized in the late season (early season: mean \pm SD: 0.03 ± 0.07 per colony per night; late season: mean \pm SD: 0.12 ± 0.16 per colony per night). Invertebrate carcasses were virtually not utilized by *E. procera* in both seasons (early season: 2 invertebrates; late season: 2 invertebrates; univariate ANOVA: $F = 0.04$, $p = 0.852$; Fig. 3).

Geographical distribution. Via mushroom baiting, we detected *Euprenolepis procera* in four out of five sampled regions of peninsular Malaysia: Ulu Gombak, Lentang, Bukit Rengit, and Kuala Lompat (Tab. 4). We did not detect *E. procera* in Endau Rompin, while *E. wittei* was detected there on three out of 31 mushroom baits (Tab. 4). The bait discovery of *E. procera*, was highest in Ulu Gombak, while the proportion of other animals at baits such as myriapods and crickets was lowest at this site (Tab. 4).

Discussion

The formicine ant *Euprenolepis procera*, known as a dietary specialist of wild-growing mushrooms, utilized three experimentally offered resources: honey, tuna, and

mushroom (Fig. 1). Hence, more typical ant food was readily accepted, demonstrating that mushroom-harvesting is not a hard-wired foraging strategy in *E. procera* (see also WITTE & MASCHWITZ 2008). However, in the presence of competitors *E. procera* avoided utilization of alternative food resources, indicating that mushroom predominance in *E. procera*'s natural diet can partly be attributed to competition avoidance for more typical ant diets. These results support predictions made by general ecological theory, that is, interspecific competition for food often narrows an organism's theoretical (fundamental) food niche (MITTELBAACH 2012). By using alternative, less-competitive food resources instead, the resulting dietary differentiation among species is expected to facilitate the co-existence of species with otherwise similar dietary demands, i.e., species belonging to the same ecological guild (MITTELBAACH 2012).

A diverse array of nocturnally foraging ants utilized honey and tuna baits, as could be expected in a densely populated rainforest ecosystem like the Ulu Gombak study site (MUSTAFA & al. 2011). Irrespective of this high competition potential, *Euprenolepis procera* was not only abundant at mushroom baits but also one of the most abundant ant species at honey and tuna baits. Besides its high prevalence, *E. procera*'s resource exploitation was also characterized by relatively high numbers of workers at baits, which was achieved through efficient worker recruitment abilities as demonstrated in previous studies (WITTE & MASCHWITZ 2008, VON BEEREN & al. 2014, VON THIENEN & al. 2014, VON THIENEN & al. 2016). This might partly explain its relatively high dominance status in the ant community, because numerical dominance in ants is often positively correlated with behavioral dominance (SAVOLAINEN & VEPSÄLÄINEN 1988, DAVIDSON 1998, MARKÓ & CZECHOWSKI 2004, CERDÁ & al. 2013, POHL & al. 2018). In fact, *E. procera*'s competitive abilities relative to other ants, as measured in first discoverer index (FDI), monopolization index (MI) and dominance index (DI), were intermediate to high. During interactions with other ants, *E. procera* was mostly dominant (in total 37 dominant vs. 13 subordinate interactions), reflected by its relatively high DI for all three resources. As we did not acquire data about direct interactions of ants at baits (e.g., aggressive replacement), we can only assume that *E. procera* was also behaviorally dominant, which would in combination with its numerical dominance define it as an ecological dominant species at the field site (*sensu* DAVIDSON 1998). As expected, competition indices were highest for the resource mushroom, which can be attributed to the lack of competing species for this resource and *E. procera*'s dominance over the mushroom harvesting ant *E. wittei* (VON BEEREN & al. 2014). Interestingly, *E. procera*'s worker counts at baits and its exploitation duration was not affected by resource type, reflecting the fact that *E. procera* mostly stayed at baits, including honey and tuna baits, once they were discovered and exploited. This is in accordance with studies showing that in certain cases dominance at baits can be context-dependent in that ants discovering baits

first behave as dominants ("discovery-defense strategy" *sensu* CAMAROTA & al. 2018), possibly due to an established numerical dominance at these baits (e.g., MARKÓ & CZECHOWSKI 2004, POHL & al. 2018).

Exploitation and interference abilities of ant species are often considered to be a trade-off (WILSON 1971, FELLERS 1987, ADLER & al. 2007, CERDÁ & al. 2013). This so called "dominance-discovery trade-off" often leads to dominance hierarchies in which some species tend to exclude others, while subordinate species are still able to coexist with dominants through more efficient food discovery abilities and opportunistic foraging strategies (FELLERS 1987, SAVOLAINEN & VEPSÄLÄINEN 1988, BLÜTHGEN & STORK 2007). However, the generality of this trade-off has been questioned (LESSARD & al. 2009, PARR & GIBB 2012) and the trade-off has been suggested to be context-dependent (LEBRUN 2005, LEBRUN & FEENER 2007, DRESCHER & al. 2011). Interestingly, *E. procera* do not seem to follow the dominance-discovery trade-off as it showed both relatively high exploitation and high interference abilities for all tested resources compared to other ants in the community. We attribute *E. procera*'s strong competitive abilities for both foraging aspects partly to its high prevalence at the study site (WITTE & MASCHWITZ 2008), because prevalence (e.g., nest density) strongly influences the calculations of competition indices such as discovery and monopolization abilities (e.g., HUMAN & GORDON 1996, DRESCHER & al. 2011, PARR & GIBB 2012, CERDÁ & al. 2013, STUBLE & al. 2017). Hence, we expect *E. procera*'s competitive abilities, as measured in the present study, to vary between ant communities with lower *E. procera* abundance resulting in lower estimates for *E. procera*'s competition abilities.

Euprenolepis procera's high abundance at tuna and honey baits and its strong competitive abilities for these resources at Ulu Gombak prompts the question of why there are so few protein-rich and carbohydrate-rich food items (other than mushrooms) in its natural diet. We suggest that such resources are generally rare on the forest floor of tropical rainforests and that they are quickly consumed by a diversity of ant species. Accessible protein resources for ants in the leaf-litter are mostly living animals, which need to be captured, killed and eventually dismembered for transportation. While ants of the genus *Odontomachus*, for example, show manifold adaptations to a predatory lifestyle (GRONENBERG 1995, CAMARGO & OLIVEIRA 2012, LARABEE & SUAREZ 2014), our yearlong behavioral observations of *E. procera* suggest that hunting abilities are weakly developed in this species. Hence, *E. procera* is likely restrained to forage on easily accessible protein-rich resources (other than mushrooms) on the forest floor such as animal carcasses. These are, however, generally rare and spatio-temporally unpredictable (CARROLL & JANZEN 1973). Furthermore, animal carcasses are expected to be utilized rapidly as supported by the fact that all randomly deployed tuna baits in this study were discovered and exploited by ants within four hours (single-resource experiment). Similarly, honey baits as a carbohydrate-rich

food resource were under strong competition. In particular, ants of the genus *Tapinoma* showed a preference and strong competitive abilities for honey, mostly confirming previous observations about dietary preferences in *Tapinoma* (e.g., BLÜTHGEN & FIEDLER 2004, CHONG & LEE 2006, WETTERER 2009). Compared to the forest floor, canopies in tropical rainforests are expected to offer more and more easily accessible carbohydrate-rich resources to ants, e.g., via honeydew-producing homopterans or the use of extrafloral nectaries (KASPARI & YANOVIK 2001, DEJEAN & al. 2007). However, *Euprenolepis procera* strictly forages on the forest floor (WITTE & MASCHWITZ 2008) and we never observed workers climbing up a tree to forage in the canopy – a habitat in tropical forests where food competition is often strong (BLÜTHGEN & al. 2000, YANOVIK & KASPARI 2000, DEJEAN & al. 2007; but also see CAMAROTA & al. 2015). Neither did we observe *E. procera* exploiting extrafloral nectaries nor tending aphids or coccids in low vegetation or on roots. The only carbohydrate-rich resource in *E. procera*'s diet, other than mushrooms, were the fruits of tropical trees that had fallen to the ground, which were utilized in both studied seasons.

In contrast to tuna and honey, mushroom baits were virtually competition-free, releasing the mushroom-harvesting specialist *Euprenolepis procera* from interspecific competition. Mushroom fruiting bodies have been shown to grow throughout the year in the tropical rainforests of Malaysia (CORNER 1935, LEE & al. 2002) and our survey of *E. procera*'s natural diet indeed confirmed that mushrooms were the primary food source in two different seasons of the year. In fact, *E. procera* appears to be able to derive all vital nutrients from a strict fungal diet as laboratory colonies fed exclusively with oyster mushroom (*Pleurotus* sp.) and champignon mushroom (*Agaricus* sp.) over a period of more than three months thrived (WITTE & MASCHWITZ 2008; personal observation SL and CvB). However, mushrooms need to be intensively processed to acquire vital nutrients (WITTE & MASCHWITZ 2008, VON BEEREN & al. 2014), while nutrients are more readily accessible from animal carcasses and fruits. It thus seems like a good foraging strategy for *E. procera* to opportunistically forage on such easily digestible food in the absence of competitors, but to generally rely on a mushroom diet since it is a virtually competition-free niche space. Noteworthy, *E. procera* was described to visit the reproductive organs of the parasitic flowering plant *Rafflesia* in Western Java (ALI & al. 2016), indicating that opportunistic foraging in *E. procera* includes a greater variety of alternative food resources than shown in the present study.

Lastly, we showed that both mushroom harvesting *Euprenolepis* species were widely distributed in lowland rainforests over peninsular Malaysia. *Euprenolepis procera* was extraordinarily prevalent at the main study site of Ulu Gombak, possibly due to the particularly wet climate compared to other sites which generally facilitates mushroom prevalence (e.g., JOHNSON 1994, LEE & al. 2002, CARRIER 2003; Tab. S1). Yet, the entire geographical distribution of *E. procera* remains unknown. In the most recent

taxonomic revision, workers collected in a few regions of Malaysia (peninsular Malaysia and Borneo) and Indonesia (Sumatra) were identified as *E. procera* (LAPOLLA 2009). Together with some additional records this suggests a wide distribution of *E. procera* (Sumatra: PUTRI & al. 2016, GUSMASRI & al. 2018; peninsular Malaysia: MUSTAFA & al. 2011; Borneo: PFEIFFER & al. 2011, KISHIMOTO-YAMADA & al. 2013, SCHREVEN 2013, ARRYANTO & al. 2018, HUSSON & al. 2018; peninsular Thailand: JAITRONG & NABHITABHATA 2005, PLAPPLUENG 2009; Sulawesi: ASFIYA & al. 2015; Java: ALI & al. 2016). We ask the research community to conduct simple nocturnal baiting experiments throughout Southeast Asia using commercially available oyster or champignon mushrooms to unveil how widespread mushroom harvesting is among ants in the Indomalayan realm (see LAPOLLA & al. 2010 for the known distribution of *Euprenolepis*).

In summary, we confirmed that mushrooms constitute the main part of *Euprenolepis procera*'s natural diet – a virtually competition-free resource at the study sites. Competition was more pronounced for resources mimicking a more typical ant diet (carbohydrate-rich honey and protein-rich tuna) which were heavily utilized by other ants. In the presence of competitors, *E. procera* avoided using these resources suggesting that dietary specialization of the mushroom harvesting ant *E. procera* represents a case of competition-induced niche differentiation.

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