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Consumption of macro-fungi by invertebrates in a Mexican tropical cloud forest: do fruit body characteristics matter?

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ABSTRACT. The emphasis of antagonistic fungus–consumer interactions to date has been on temperate taxa and predominantly zoocentric, neglecting the effects on the fungal component. These interactions are expected to be especially complex and diverse in the tropics, where both components display their greatest diversity. Variability in fungivory (apparent biomass consumed) of understory basidiomycetes in a tropical cloud forest was investigated to test whether this could be explained (at the proximate level) by apparency-related characteristics of the aboveground structures (colour of pileus, stipe and hymenium; size and aggregation), as has been suggested for plant–herbivore relationships. Considerable interspecific variation in fungivory was detected (range 0–50%). Cluster analysis showed that neighbouring clusters had dissimilar levels of fungivory. Such clusters were similar in colour attributes of aboveground structures, but differed in aggregation size and apparent biomass. A quantitative analysis also showed that colour attributes were not strongly associated with the observed variation of consumption levels, whereas apparent biomass and aggregation size did correlate with the observed variation in fungivory. Furthermore, specific identity correlated with fungivory. It was concluded that coloration patterns may not be important for fungivory, whereas genet size and species identity (probably via characteristics unrelated to apparency, such as mycotoxins and nutritional value) seemed to be critical factors.

KEY WORDS: Agaricales, Basidiomycota, Boletales, Cantherellales, El Triunfo, fungivory, evergreen cloud forest, mycophagy, Russulales

INTRODUCTION

Fungi and insects are two highly diverse groups of living organisms (Colwell & Coddington 1994) which have come into trophic contact repeatedly through

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their evolutionary history. Fungus–insect interactions range from complete dependence of strict entomopathogenic fungi on insects as a food resource, to complete dependence of strict fungivorous insects on fungi as a food resource, accommodating a wide spectrum in between (Wilding *et al.* 1989). Only a handful of associations, e.g. mushroom and drosophilids (Hanski 1989), ant fungus gardens (Cherrett *et al.* 1989) and macrotermites and *Termitomyces* fungi (Wood & Thomas 1989) have received recurrent attention. By contrast, a number of other trophic associations such as fungivory on fruit bodies (Guevara 1994, 1998; Lodge 1996) or the assistance in cross-reproduction of phytopathogenic fungi by flies (Bultman 1995; Craigie 1927a, b) have been largely overlooked. Such interactions are expected to be particularly complex and diverse in the tropics in which both insects and fungi display their greatest global diversity (Erwin 1992, Hawksworth 1991, Sutton & Collins 1991).

Among the antagonistic fungus–consumer relationships, the consumption of mushroom-like structures by insects has received considerable attention, but these studies have concentrated on temperate drosophilids, largely with a zoocentric emphasis, dealing with aspects of population structure (Charlesworth & Shorrocks 1980; Jaenike 1977, 1986, 1988; Worthen 1988, 1989a); genetic diversity (Ashe 1984; Jaenike 1986, 1989); competition (Grimaldi 1985, Grimaldi & Jaenike 1984, Shorrocks 1991, Shorrocks & Bingley 1994); predation (Worthen 1989b, Worthen *et al.* 1995, Worthen & Moore 1991) and parasitism (Jaenike 1985, Montague & Jaenike 1985). Complementary studies on the effects of fungivory on fungi have been neglected due to the dominant viewpoint, which considers the fungal partner simply as ‘the resource’. This position is analogous to that observed in the origins of plant–herbivore interactions where plants were only referred to as ‘the food source’ (Dirzo 1984, Harper 1977).

Herbivory and fungivory can be seen as analogous relationships (Bruns 1984, Hanski 1989, Harper 1977) where the trophic activity of consumers may have negative impacts on the reproductive potential of plants and fungi respectively. There is, however, a large disparity in the amount of work carried out with these two interactions. On the one hand, some plant–herbivore relationships have been described and understood since Victorian times. More recently, the last 30 y of empirical and theoretical investigation on plant–herbivore relationships have led to the accumulation of a large body of information that attempts to explain patterns such as the frequency and intensity of herbivory and its variability; the impact of herbivory on the reproductive potential of plants; the distribution and effectiveness of defence mechanisms both chemical and physical; the effect of plant characteristics such as apparency, phenology and life history on herbivory as well as the co-variation, of two or more of these factors (see Crawley 1983, Dirzo 1984, Howe & Westley 1988, Karban & Baldwin 1997, Rosenthal & Janzen 1979, among others). On the other hand, fungus (fruit body)–fungivore interactions have not been described even at the basic

level of patterns of consumption (i.e. frequency and intensity of fungivory and its spatio-temporal variability).

Comparable ecological and evolutionary fungal responses in fungus–fungivore interactions can occur if the trophic activities of fungivores affect the reproductive potential of the host fungus. The fungivory that matters is, therefore, the one that occurs before spores are discharged (Hanski 1989). In other words, from a fungocentric perspective, fungivory matters only while fruit bodies are functional (producing, maturing or discharging spores) rather than when they become dysfunctional and senescent. It has been suggested that fungivory by invertebrates on fruit bodies is unlikely to have any significant effect on the reproductive potential of fungi (Courtney *et al.* 1990, Hanski 1989). This assertion is, however, premature. Given the zoocentric emphasis of studies with fungivorous invertebrates, such studies have concentrated their attention on dysfunctional and senescent fruit bodies (when fungivorous populations are most apparent) rather than assessing consumption while fungi are still functional.

Certain tropical cloud forests provide useful systems to assess fungivory patterns given their high diversity and abundance of macro-fungi (Guevara & Dirzo 1998). Specifically, in this study we quantified the levels of consumption that the fungal community of mushroom-like fruit bodies endure in El Triunfo tropical cloud forest (southern Mexico). We then asked whether variability in the observed consumption levels can be explained (at the proximate level) by fruit body characteristics determining fruit body apparency as has been argued for the case of herbivory on higher plants (Feeny 1976) and whether the observed patterns varied over space or time.

METHODS

The study site is located in core area I (11 000 ha) of the Biosphere Reserve El Triunfo in the state of Chiapas (latitude 15°17'N and longitude 92°48'W) extending between 1000 and 2400 m asl. The dominant vegetation at the plateau, between 1600–2000 m asl, where the present study was carried out, is evergreen cloud forest (Breedlove 1981). The average annual rain fall in the area is 4000 mm (mean of 8 y; El Triunfo Research Station) with a relatively dry season extending from November to May but dense fog is frequent all year round (see García 1987). A detailed account of the physical and biological characteristics of the Reserve is given elsewhere (Gómez-Pompa & Dirzo 1995).

Fruit bodies of macro-fungi were sampled from each of two contrasting habitats in the study area based on randomly established plots covering a total area of 0.1 ha in each habitat. Ten transects, 50-m × 2-m each in closed canopy areas (CCA) and 20 transects 25-m × 2-m each in open canopy areas (OCA) were established. All plots were marked for re-location and sampling in May (dry season) and September (wet season) 1991. We defined the location of each plot by selecting a random number corresponding to the distance in metres

(1 m to 1000 m) from the reserve's field station along either of the two main trails which were also randomly selected. Transects into the forest understorey (CCA) were established perpendicular to the trails whereas transects in OCA were established on the sides (1 m to each side) of trails.

Our sampling units were individual fruit bodies, in the case of a single fungal structure, or locally aggregated groups of fruit bodies of the same species. These are referred to as 'genets', by analogy to the term used in plant ecology (Harper 1977) to describe individual genetic units or clones of modular units belonging to the same genetic individual. Even though we did not verify the physical or genetic continuity of the fruit bodies of each cluster, we used the local aggregation and spatial separation of adjacent fruit bodies or clusters thereof, as criteria by which to name them genets. Individual fruit bodies or clusters were characterized as to the colour of their different structures (pileus, stipe and hymenium), apparent biomass, aggregation size (i.e. number of fruit bodies per genet), habitat (CCA or OCA), season of the year (May or September) and specific identity (morpho-species). For the purpose of this study colours were recorded as substratum-contrasting (bright) and non-contrasting (dull) colours. The former category included yellow, red, blue and white tones whereas brown, grey, green and black tones were assigned to the latter category. Each fruit body in a genet was measured for height and diameter and an estimate of the apparent biomass was calculated as the product of the two measurements. With this procedure we approximated the volumetric mass of fruit bodies rather than attempting to estimate or correlate the measurements with the mass in weight. The apparent biomass of a genet was obtained by adding up the apparent biomass of all fruit bodies in the aggregation. Genets were grouped by the size of the aggregation into two categories: small aggregations (up to four fruit bodies) and large aggregations (five or more fruit bodies). The habitat (CCA or OCA) and consumption level for all sampled macro-fungi were also recorded.

Fungivory, that is the level of apparent biomass consumed (C) of each genet was estimated based on visual categories of percentage of apparent biomass removed from individual fruit bodies. A discrete scale with five levels was used: 0, $C = 0\%$; 1, $0 \leq C \leq 25\%$; 2, $25 \leq C < 50\%$; 3, $50 \leq C < 75\%$ and 4, $75 \leq C < 100\%$ as seen in the field. Consumption was estimated for each of the three aerial structures, pileus, stipe and hymenium of each fruit body, to then calculate a weighted consumption score. To weight the scores we assigned a scalar (1–3) to each of the three structures based on their relative apparent mass contribution, 1 for the structure of least apparent mass and 3 for the structure of greatest apparent mass. The weighted consumption score (WCS) for each genet was then calculated as:

$$WCS = 1/n * \sum_{i=1}^n [(\sum_{j=1}^3 OCL * i)/3]$$

where WCS (with values between 0 and 8) is equal to the average over n fruit bodies (number of fruit bodies in a genet) of the sum of products of the

observed consumption level (OCL) in each structure (0–4) and the i th scalar divided by 3 (number of structures).

We explored gross associations between fungal characteristics and consumption levels by clustering species on the basis of their apparency-related characteristics (i.e. colours, aggregation size, and apparent biomass). We used percentage dissimilarity to measure the distance between species and used the complete linkage procedure to join them (Digby & Kempton 1987). We explored whether average consumption levels for each cluster correlated with some of the characteristics that defined each cluster.

More rigorous analyses were performed by using generalized linear models (Crawley 1993), which are suitable for unbalanced designs and allow for the inclusion of random class variables as opposed to experimental treatments defined a priori. The response variable, WCS, and the predictor, apparent biomass, were transformed to allow for normality of the residuals. WCS was square-root transformed whereas we took the logarithm of apparent biomass divided by the smallest recorded data for that variable. In this way, after transformation, the smallest data were zero. A GLM–ANCOVA (SAS Institute Inc. 1985) model was fitted to investigate whether WCS was related to any of the fungal characteristics recorded or a combination of them. Our initial model included all the main factors (pileus, stipe and hymenium colour; aggregation size; habitat; and season), and all second-level interaction for the colour variables (pileus * stipe, pileus * hymenium and stipe * hymenium) and the spatial–temporal interaction between season and habitat (season * habitat). Apparent biomass was included into the model as a covariate and we also fitted its interactions with all main factors in the initial model. After the initial fitting, simplification was carried out by eliminating, in stepwise fashion, the most insignificant variable in the model. The simplified model was then refitted and again the most insignificant term removed. This procedure was followed until all terms left in the model were significant (see Crawley 1993). A GLM–ANOVA model was fitted for the factor species identity, and the Student–Newman–Keuls test was used to assess *post-hoc* differences in consumption between species.

RESULTS

A total of 234 genets of 63 morpho-species were recorded (Appendix I). One hundred and 37 genets, 38 morpho-species, were recorded in May, whereas 97 genets, 26 morpho-species, were recorded in September. The overall average consumption score was 0.88 (c. 10% of the maximum possible consumption) with a range between 0 to 4 (i.e. 0–50%). The average consumption was lower in May, 0.67 (5.6%), than in September, 1.18 (17.5%). Our observations indicate that most of the consumption was due to invertebrates (tunnels, mines, small bites, radulated tissue, etc. caused mainly by drosophilids, sciarids, staphilinids, slugs and snails), although we can not discount that in the few cases of heavily damaged genets vertebrates may also be involved.

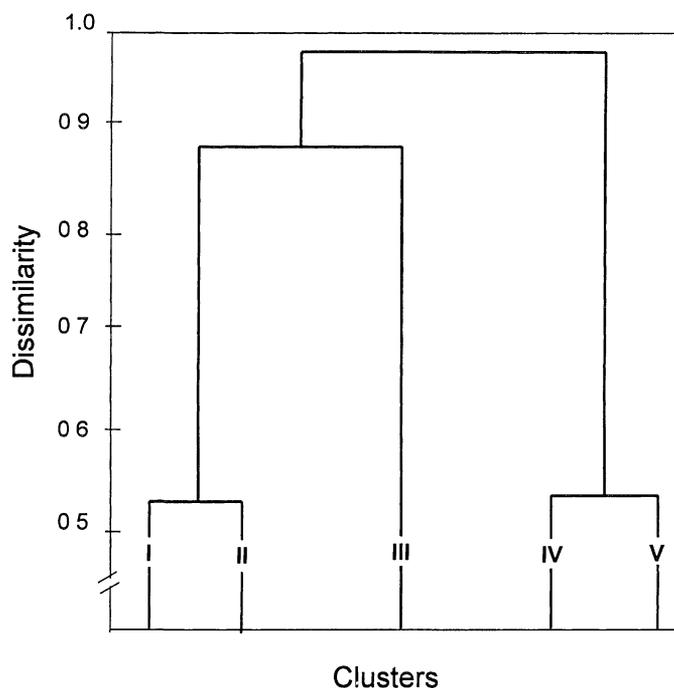


Figure 1. Cluster analysis for the sampled species on the basis of six characteristics (see text for details). The truncated dendrogram reveals five clusters using a 50% dissimilarity threshold. A complete list of all species analysed and their distribution among the five clusters is presented in Appendix I.

Cluster analysis (Statsoft Inc. 1990) grouped species into five distinctive clusters defined at a dissimilarity level of 0.5 (Figure 1). Cluster separation allowed the exploration of variables potentially relevant to the observed patterns of consumption (Table 1). It seems that clusters I and IV had considerably higher levels of consumption than the other three clusters (a 3.1-fold difference on average). The coincidence of level of damage of clusters I and IV disagrees with their position in the dendrogram (Figure 1). This suggests that variables important for the structure of the dendrogram, were not determining factors of the levels of fungivory. Nevertheless, as Table 1 shows, genets in clusters I and IV had large averages of apparent biomass (2457 and 3954 cm³ respectively) and all genets were constituted of small aggregations (<5 fruit bodies), suggesting that these variables may be important for fungivory. By contrast, clusters I and IV differed in coloration patterns (Table 1). Colours of the stipe were predominantly bright in cluster I, whereas they were predominantly dull in cluster IV; colours of the pileus were predominantly dull in cluster I, whereas cluster IV had a similar frequency of genets with both types of coloration. This may indicate that variables related to colour are not relevant for determining fungivory. A similar situation arises when comparing clusters II and III. These had intermediate but similar levels of fungivory (0.44 or 2.4% and 0.41 or 2.1% respectively), yet their coloration patterns were not

Table 1. Descriptive summary of species clusters (a): Frequency of species in each cluster with bright (B) and dull (D) coloured pileus, stipe, and hymenium. (b): Frequency of species in small (<5) and large aggregations (>5) (c) Means and ranges of apparent biomass (cm³) and weighted consumption scores across clusters

	CLUSTERS									
	I		II		III		IV		V	
	B	D	B	D	B	D	B	D	B	D
Colour										
Pileus	4	8	4	8	3	3	11	12	6	5
Stipe	0	12	0	12	4	2	23	0	11	0
Hymenium	12	0	12	0	0	6	23	0	11	0
(b)										
Aggregation	<5	5+	<5	5+	<5	5+	<5	5+	<5	5+
	12	0	0	12	2	4	23	0	0	11
(c)										
Apparent biomass	2457 (436–2062)		2205 (112–3441)		1120 (321–240)		3954 (1084–9765)		1443 (112–7789)	
Consumption	1.12 (0.67–1.72)		0.44 (0–1.65)		0.41 (0–1.01)		1.29 (0.7–1.87)		0.33 (0–1.0)	

coincidental, whereas aggregation size was similar (Table 1). Finally, cluster V, with the lowest level of fungivory (0.33; 1.4%), was positioned next to cluster IV, which had the highest level of consumption. Interestingly, both clusters had the same pattern of coloration, indicating again that these attributes may not be important to fungivory. Nevertheless, their contrasting levels of consumption coincide with their highly contrasting levels of aggregation size and apparent biomass (Table 1), suggesting once more that these attributes may play a significant role in determining consumption. In summary, clusters with species characterized by large individual fruit bodies in small aggregations had higher levels of consumption than clusters composed of genets with individually small fruit bodies. Colour varied in complex ways among clusters and no correlation with consumption was evident in this qualitative analysis.

To explore quantitatively the relative importance of the recorded characteristics in relation to the observed level of consumption we carried out a GLM-ANCOVA model. Due to missing values only 223 out of 234 values were analysed. The full model (see above for details on variables included) was highly significant and explained 83% of the observed variability of consumption levels ($F = 175$; $df = 11, 211$; $P < 0.001$). After simplification, considering only the significant independent variables (see Methods), the model included apparent biomass (the covariate), the main factors stipe colour and aggregation size and the interactions stipe colour*hymenium colour and season*apparent biomass. The simplified model was highly significant and accounted for 80% of the observed variance ($F = 169$; $df = 5, 217$; $P < 0.001$).

There was a significant relationship between genet apparent biomass and consumption, where apparent biomass accounted for 19% of the variability in

Table 2 Statistical summary of the generalised linear analysis of covariance to explore the effect of fruit body characteristics, and their interactions, on consumption

(a) Partitioning of SS type III with df = 217 for the error term

	df	MS	F	R ²
Stipe	1	1.31	26.75***	0.03
Stipe * hymenium	1	0.79	16.08***	0.02
Aggregation	1	11.49	234.27***	0.29
Apparent biomass * season	1	11.03	224.86***	0.27
Apparent biomass	1	7.50	152.89***	0.19

(b) Matrix of estimates

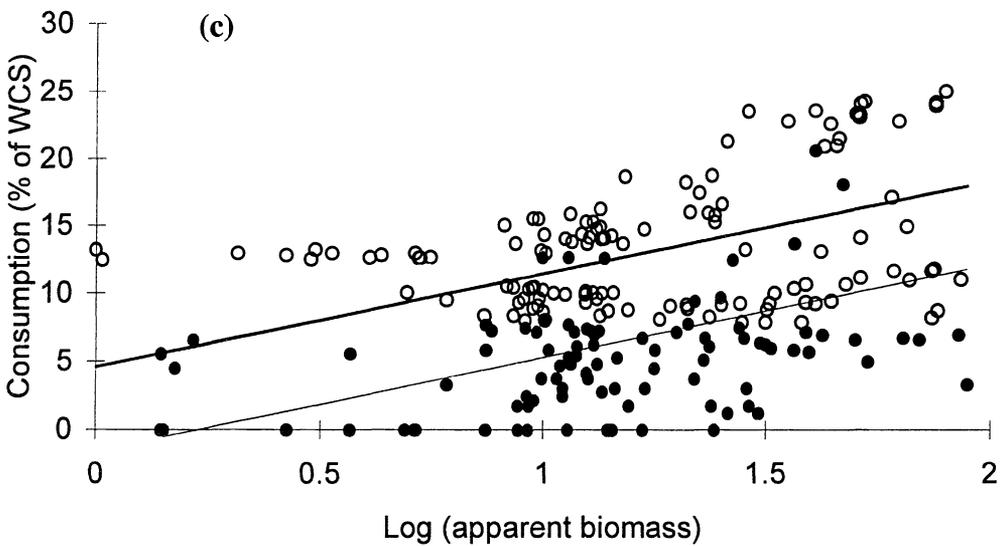
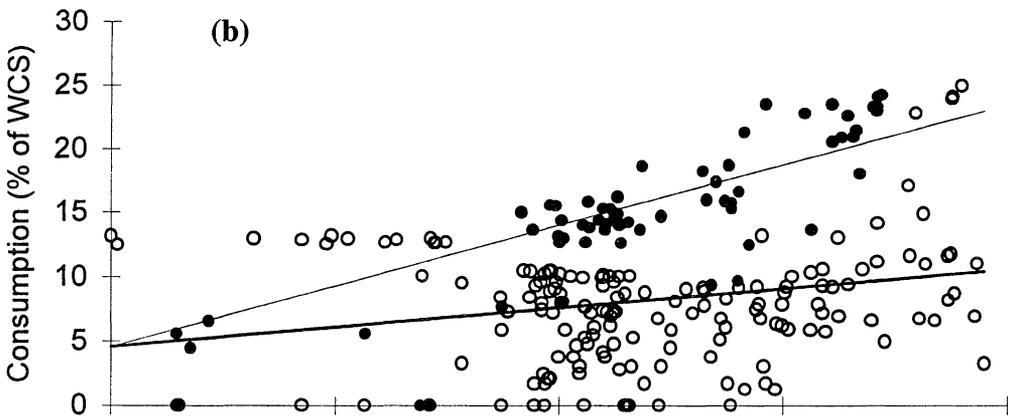
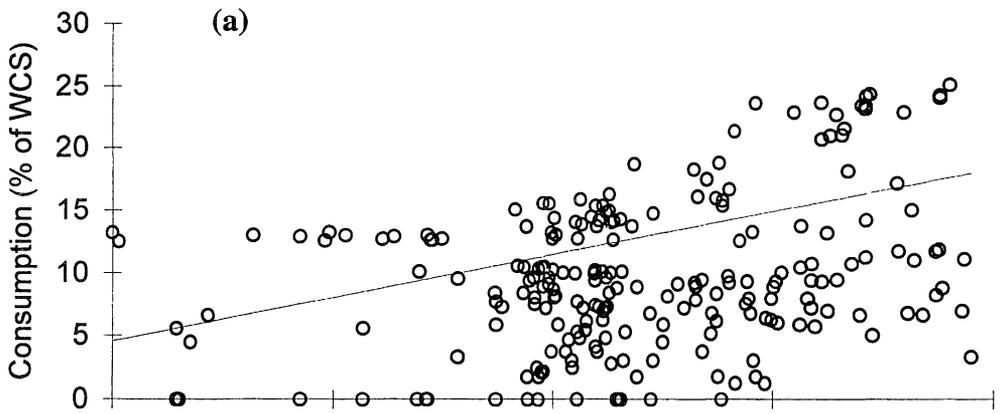
		Estimates	t	SE
Intercept		0.37	5.39***	0.07
Stipe	Bright	0.37	5.17***	0.07
	Dull	0.02		
Stipe*hymenium	Bright	0.12	4.01***	0.06
	Others	0.37		
Aggregation	Small	0.37	15.31***	0.03
	Large	-0.12		
Apparent biomass * season	May	0.24	7.71***	0.04
	Sep	0.76	15.52***	0.05
Apparent biomass		0.55	23.23***	0.05

***, $P < 0.001$

the observed levels of fungivory (Table 2a; Figure 2a). The relationship of apparent biomass with consumption, however, varied significantly over the two seasons (Figure 2b) and accounted for 27% of the observed variability in the observed consumption levels (Table 2a). In September consumption increased at a level over 3-fold the level in May (Table 2b). The factor aggregation size also showed significant effects and accounted for 29% of the observed variance in consumption (Figure 2c). Overall, small aggregations of up to four fruit bodies, were consumed 4 times more, on average, than larger aggregations (Table 2b).

The main factor stipe-colour and the interaction stipe-colour * hymenium colour accounted for a small fraction of the explained variance (3 and 2% respectively, Table 2a), although the relationship across the range of apparent biomass variation was significant. Genets with bright coloured stipes were consumed on average 18 times more than fruit bodies with dull coloured stipes (Table 2b). Genets with bright coloured stipe and hymenium were consumed, on average, 3 times less than fruit bodies with any other combination of colours (Table 2b). Even if the variation in consumption in relation to colour factors

Figure 2 Patterns of consumption by invertebrates in relation to (a) apparent biomass, and (b) the interaction apparent biomass * season; May (open circles and thick line) and September (closed circles and thin line) with consumption, and (c) apparent biomass * genet-size (small aggregations, open circles and thick line, and large aggregations, closed circles and thin line) with consumption. Consumption is expressed in percentage of the weighted consumption score where the maximum score, 8, equals 100%. See text for details.



was significant across the range of apparent biomass, the small amount of explained variance in the model (Table 2a) suggests that these factors were of little relevance for the observed levels of consumption. The lack of apparent patterns related to colour in the cluster analysis supports this statement.

We used a GLM-ANOVA model to explore the relationship between the specific identity of the fungi and the observed levels of consumption. Interspecific variation in consumption levels was considerable and accounted for 61% of the observed variance in consumption ($F = 4.31$; $df = 63, 170$; $P < 0.001$). The Student–Newman–Keuls *post hoc* test revealed the existence of three groups with distinctive levels of consumption. A group of two statistically indistinguishable species, *Hygrophorus* (1) (*sensu stricto*) with score of 1.87 (23.4%), and *Amanita caesarea* (Scop. ex Fr.) Grev. with score of 1.85 (23.2%), presented significantly higher levels of consumption than the rest of the species ($P < 0.01$). A group of six statistically indistinguishable species, *Collybia* (1) (score 1.72; 21.5%), *Tylophilus* (1) (score 1.72; 21.5%), *Cortinarius* (1) (score 1.70; 21.3%), *Russula mexicana* Burlingham (score 1.69; 21%), *Naematoloma* sp (score 1.67; 20.9%) and *Lactarius indigo* (Schw.) Fr. (score 1.65; 20.6%), showed mean levels of consumption significantly higher ($P < 0.01$) than those observed in the 56 remaining species, whose levels of consumption ranged between 0 and 1.44 (18%) (see Appendix I). Thus, specific identity seems to be an important determining factor of consumption levels.

DISCUSSION

One of the most salient aspects of this study was the considerable interspecific variation in fungivory, comparable to that observed in studies on herbivory in tropical plants (Coley 1983, Filip *et al.* 1995), including herbivory in tropical cloud forest plants (Sánchez-Ramos 1999).

Specific identity was significantly related to consumption. Relatively few of the species experienced high or medium levels of consumption (two and six species respectively), whereas 56 species (i.e. 89% of the total) had low levels of consumption. This pattern of consumption suggests the existence of a hierarchy of preferences or palatability, similar to that found in plant–herbivore systems (e.g. Dirzo 1980).

Though colour factors in interaction with apparent biomass showed a significant influence on consumption, the explained variance was negligible, suggesting that there is not a strong association between them and the observed levels of consumption. This is surprising as we expected that the notable coloration of fruit bodies of macro-fungi would affect fruit body apparency to insects either for location of host by specific consumers, or via aposematic avoidance by generalists. Such effects have been observed in plant–herbivore interactions (Crawley 1983, Harper 1977, Howe & Westley 1988). In particular, the known toxicity of many species of mushrooms and toadstools, together with their remarkable coloration, including colour contrasts in taxa such as *Amanita* spp.

and the Boletales and Russulales (Subramanian 1995), could suggest an important coupling that would affect consumption. A counter-argument to this hypothesis is that what is toxic to mammals is not necessarily toxic to invertebrates. However, in several instances, fungi and plant secondary metabolites toxic to vertebrates (e.g. α -amanitin, several alkaloids, cyanogenic glucosides) are also toxic to invertebrates (Jaenike *et al.* 1983, Ehrlich & Raven 1965, Dirzo & Harper 1982, respectively). Finally, we can not discount that perhaps our categorization of colour into bright and dull was too coarse to detect significant patterns. This is clearly an aspect that warrants further work.

Genet apparent biomass and aggregation size had significant effects in the model, with apparently contrasting relationships with the observed levels of consumption. On the one hand, genets of large apparent biomass were more consumed than smaller genets. On the other, genets with small aggregations (<5 fruit bodies) were more consumed than genets with larger aggregations. These results suggest that apparent biomass of individual fruit bodies is a more influential factor than the overall apparent biomass of the genet. Though this pattern was consistent over the two seasons, the rate of consumption was higher in September (rainy season) than in May (dry season). The greater abundance of phytophagous insects during the rainy season in lowland tropical forests (Filip *et al.* 1995, R. Dirzo *pers. obs.*) and cloud tropical forests (Sánchez-Ramos 1999), suggests that this may also be the case in tropical fungus–fungivore interactions. The elucidation of whether such seasonal variation in fungivory is due to an increase of fungivores, or to other reasons, also warrants further investigation.

The importance of apparent biomass and aggregation size was also supported by the cluster analysis. Clusters with high average of consumption levels were characterized by large apparent biomass and small aggregations, whereas clusters with low levels of consumption were characterized by small apparent biomass and large aggregations. It is clear, however, that apparent biomass and aggregation are not the only relevant factors in these interactions.

Though all morpho-species with high and medium levels of consumption were also characterized by possessing large individual fruit bodies in small aggregations, specific identity *per se* appeared to be of overriding importance. Indeed, a number of morpho-species characterized by large individual fruit bodies in small aggregations showed low levels of consumption. Species-intrinsic characteristics unrelated to visual phenotypic apparency are likely to be more critical in determining fungivory. The diversity and widespread occurrence of mycotoxins in mushroom-like fruit bodies (see Konno 1995) suggests that at least part of the unexplained variability of observed consumption levels may be due to chemical defence. Another unaccounted factor is the nutritional value of fruit bodies. Genera such as *Amanita*, *Hygrophorus* and *Hygrocybe* are very oily and may, therefore, be a richer source of energy than other taxa (D. J. Lodge *pers. comm.*).

It has been suggested that chemical defence in macromycete fruit bodies is more likely to have evolved as a defensive mechanism against mammalian consumers rather than invertebrates (Hanski 1989). This study showed, however, that functional fruit bodies are subject to significant levels of consumption by invertebrates (for some genets up to 50% of apparent biomass).

Evaluation of the impact of fungivory on the reproductive potential of fungi was beyond the scope of this study. However, it is likely that at least the highest levels of consumption observed in this study, may have a negative impact on the reproductive potential of fungi, either via reduction in the production of spores, or via disruption of spore dispersal potential and subsequent establishment. To our knowledge no study of fungus–fungivore interactions has addressed these issues.

Overall, this study showed that fungivory by invertebrates in tropical systems is a promising field for observation, experimentation and testing of theories necessary to understand the evolutionary ecology of these important components of biodiversity.

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APPENDIX I List of species according to the defined clusters of Figure 1 The number of genets sampled (N), their average weighed consumption scores (WCS), and their overall rank of consumption (1-47) are included Voucher specimens are deposited in the herbarium XALU of the School of Biology (Facultad de Biología), Universidad Veracruzana (Xalapa, Ver), México

Species	N	WCS	Rank
Cluster I			
<i>Agrocybe</i> (2)	2	0.81	24
<i>Bolbitius vitellinus</i> Fr	2	0.8	25
<i>Cantharellus cibarius</i> Fr.	4	1.33	10
<i>Conocybe</i> (2)	1	1.05	19
<i>Coprinus</i> (1)	2	0.88	22
<i>Hygrophorus</i> (2)	2	1.44	8
<i>Lactarius indigo</i> (Schw) Fr	4	1.65	7
<i>Limacella</i>	2	1.7	4
<i>Macrolepota procera</i> (Scop. ex Fr.) Sing.	3	1.28	12
<i>Marasmius</i> (7)	2	0.67	31
<i>Panaeolus</i> (1)	2	0.74	28
<i>Tricholoma</i> (2)	2	0.83	23
Cluster II			
<i>Agrocybe</i> (1)	2	0	47
<i>Conocybe</i> (1)	1	0	47
<i>Cortinarium</i> (2)	2	0.46	39
<i>Hygrocybe</i> (1)	1	0.77	26

APPENDIX I (cont.)

Species	N	WCS	Rank
<i>Lepiota clypeolaria</i> (Bull ex Fr.) Kumm.	2	0	47
<i>Lepiota rubrotincta</i> Pk	12	0.49	37
<i>Marasmius</i> (3)	4	1.65	7
<i>Marasmius</i> (4)	3	0.53	36
<i>Marasmius</i> (9)	2	0.4	41
<i>Marasmius oreades</i> (Bolt. ex Fr.) Fr.	4	0.58	32
<i>Russula</i> (1)	2	0.24	44
<i>Tricholoma</i> (1)	2	0.14	46
Cluster III.			
<i>Amanita patherina</i> (Fr) Quél.	2	1.01	20
<i>Cortinarius</i> (1)	2	0.54	35
<i>Marasmius</i> (5)	4	0.71	29
<i>Marasmius</i> (6)	3	0.22	45
<i>Panaeolus</i> (1)	7	0	47
<i>Psathyrella smithii</i> Guzman	24	0	47
Cluster IV.			
<i>Amanita caesarea</i> (Scop. ex Fr.) Grev.	8	1.85	2
<i>Boletus griseus</i> Frost in Pk.	3	1.13	16
<i>Clitocybe</i> (1)	2	1.26	13
<i>Clitocybe</i> (2)	2	0.75	27
<i>Collybia</i> (1)	6	1.72	3
<i>Coprinus</i> (2)	3	1.1	18
<i>Cortinarius</i> (1)	5	1.7	4
<i>Crepidotus</i> (1)	6	1.67	6
<i>Crinipellis</i> (1)	1	1.18	15
<i>Hygrophorus</i> (1)	5	1.87	1
<i>Cuphophyllus pratensis</i> Fr.	7	1.22	14
<i>Laccaria</i> (1)	3	0.7	30
<i>Laccaria laccata</i> Scop. ex Fr	8	0.7	30
<i>Leucoagaricus</i> (1)	4	1.22	14
<i>Marasmius chiapensis</i> Sing.	2	0.8	25
<i>Mycena</i> (2)	3	0.81	24
<i>Naematoloma</i> (1)	6	1.67	6
<i>Pluteus</i> (2)	2	1.4	9
<i>Russula mexicana</i> Burlingham	4	1.69	5
<i>Tricholoma</i> (3)	2	1.3	11
<i>Tylopilus</i> (1)	4	1.72	3
<i>Tylopilus balouii</i> (Pk.) Singer	8	1.12	17
<i>Volvariella</i> (1)	3	1.05	19
Cluster V			
<i>Clitocybe</i> (3)	1	1	21
<i>Galerina</i> (1)	1	0.45	40
<i>Hygrocybe</i> (2)	1	0.26	43
<i>Marasmius</i> (1)	2	0.57	33
<i>Marasmius</i> (10)	3	0	47
<i>Marasmius</i> (2)	2	0	47
<i>Marasmius</i> (8)	2	0.3	42
<i>Marasmius cohaerens</i> (Pers ex Fr) Quél	3	0.56	34
<i>Mycena</i> (1)	5	0.47	38
<i>Mycena</i> (3)	4	0	47
<i>Russula virescens</i> Fr.	6	0	47