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ORIGINAL INVESTIGATION

First report of fern (*Culcita macrocarpa*) spore consumption by a small mammal (*Apodemus sylvaticus*)

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Abstract

Few vertebrates are known to consume ferns regularly. Several species of mammals consume leaves to some extent but the consumption of fern spores is much rare. In Galicia (Northwest Spain) we studied the seasonal variation in the consumption of *Culcita macrocarpa* fertile leaves (i.e. with spores) in two populations (Capelada and Eume), assessed whether consumption rate increased with fern population size, and evaluated whether the consumer was a spore predator or a spore disperser. Consumption began in December and finished by mid February, and occurred before spore release, which happened later in Capelada than in Eume, probably influenced by differences in altitude. The consumer was identified as *Apodemus sylvaticus* by DNA analysis of its droppings and by capture of live animals. Throughout Galicia there was a significant increase in fern consumption rate as the population size of *C. macrocarpa* increased. Germination tests from droppings were carried out in 14 dishes but only in two dishes 1% and 0.3% of the spores germinated. Our results suggest that woodmouse can disperse spores of *C. macrocarpa*, although most of the spores were digested.

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Keywords: Apodemus sylvaticus; Culcita macrocarpa; Fern feeding; Spore consumption; Spore dispersion

Introduction

The ingestion of food types by herbivorous-frugivorous animals is mostly influenced by food availability, but also by food size, handling time (Diaz 1994), nutritional value (Schaefer et al. 2003) and secondary compounds such as phenolics. Ferns (Pteridophyta) are often very abundant in forest ecosystems and potentially provide an abundant food resource for consumers (Tryon 1986). In the past, ferns apparently played an important role on the diet of dinosaurs such as Diplodocus (Stevens and Parrish 1999) and Sauropods (Hummel et al. 2008). Nowadays invertebrates such as gastropods and insects consume ferns to some extent but few vertebrate species are known to consume ferns regularly. Several species of mammals ingest leaves of different fern species, for example the red deer (*Cervus elaphus*) feeds on *Osmunda regalis* (Wood 2000), feral goats (*Capra hircus*) on *Blechnum* spp. and *Cyahtea* spp. (Parkes 1984), the Arunachal macaque (*Macaca munzala*), red deer (Wood 2000) and cattle (*Bos taurus*) (Marçal and Campos Neto 1996) on *Pteridium spp.* (Suresh Kumar et al. 2007) and the Japanese macaque (*Macaca fuscata yakui*) on *Dicranopteris linearis* and *Gleichenia japonica* (Hill and Lucas 1996). Also, mountain beavers

(*Aplodontia rufa*) harvest and store a wide variety of plant species, and often cache western sword fern (*Polystichum munitum*) and bracken fern (*Pteridium aquilinum*), plants that most herbivores will not eat (Wall 1990). The consumption of fern spores is much rare; to our knowledge it is only documented for the short-tailed bat (*Mystaina tuberculata*), which feeds on spores of tree ferns such as *Cyathea* spp., *Dicksonia squarrosa*, *Lycopodium* spp. and *Phymatopdes* spp. in New Zealand (Daniel 1976), and for the Azores bullfinch (*Pyrrhula murina*), which takes spores of *Osmunda regalis*, *Pteris incompleta*, *Culcita macrocarpa* and *Woodwardia radicans* (Ramos 1994, 1995; Arosa et al., 2009). Fern phytochemical defences are possibly the explanation for a restricted fern diet (Page 2002). However, and despite the fact that the distribution of chemical toxins in ferns is poorly known (Page 2002) not all fern species seem equally toxic as evidenced by selective browsing of tree ferns (*Dicksonia* spp.) by white-tailed deer (*Odocoileus virginianus*) in New Zealand (Nugent and Challies 1988) and the selection of fern spores and leaves by the Azores bullfinch (Ramos 1994, 1996; Arosa et al., 2009).

In Galicia, northwest Spain, we noticed conspicuous marks of consumption on fertile leaves of *C. macrocarpa* and set out to identify the species, the extent of the herbivory, whether the consumer feeds only in fertile leaves (spores) or also on unfertile leaves (vegetative material), and whether it was a predator or a disperser of spores. The feeding marks left by the consumer were different from those of the Azores bullfinch (Ramos 1994, 1995), with most pinnules and indusia chewed; possibly caused by a small mammal such as a rodent.

Culcita macrocarpa is the only European member of the family Dicksoniaceae. This species typically shows strong clonal growth leading to patch formation and has very large fronds (often over 2 m long), which persist throughout the winter. The maturation of the spores, leading to the accumulation of protein and lipid drops inside the spore, occurs mainly from November to February (Arosa et al., 2009) and after maturation spore release occurs around the spring equinox (authors unpublished data). The main populations of this fern are located in northern coastal regions of Spain, where it is an endangered species, and in the Azores, Madeira and Canary Islands. It is included in several lists of threatened species (Ormonde 1990; Cellinese et al. 1996; Bañares et al. 2003) and in the Annex II of the EU Habitats Directive. The ideal habitat for this species is mature riparian woodland on north-facing slopes of enclosed coastal valleys (Amigo and Norman 1995). Therefore, the identification of the consumer of *C. macrocarpa* in Galicia and the magnitude of interactions between *C. macrocarpa* and its consumer are, therefore, potentially very important for the conservation of the European populations of this rare fern species.

Methods

Study site

We studied two populations 34 km apart, Eume and Capelada, in two river basins in the northwestern Iberian Peninsula. These populations are located in riverine mature forest in narrow north-oriented valleys close to the coast. The tree canopy consists of deciduous tree species such as *Alnus glutinosa*, *Betula alba* and *Corylus avellana* and evergreen species such as *Ilex aquifolium* and *Laurus nobilis* (Amigo and Norman 1995). The climate is markedly oceanic, with narrow annual and daily range of temperatures, large annual rainfall (>1500 mm; Martínez-Cortizas and Pérez-Alberti 1999) and high air humidity (monthly means generally >90%; L.G. Quintanilla unpublished data).

Check and record on fern consumption and spore release

Each population was visited on 1 November 2007 and no marks of consumption on the annual leaves were observed. On 1–2 December 2007 we selected 90 individuals in each population along transects and randomly marked one fertile leave per individual. For each marked leaf we counted the number of sterile and fertile pinnules and noted the pinnules with marks of consumption. Marked leaves were observed every 15 days, until 15 March 2008, to record sterile and fertile pinnules with marks of herbivory. Consumption was evident because fern leaves showed obvious stripping marks (Fig. 1a) and fern fragments from the consumption were visible on the ground beneath individual ferns.

From 15 February to 15 March spore release (= no. of open sori) in marked leaves was also assessed to document the end of spore availability. On each visit, and for each marked pinnule, we counted the number of sori that had released spores. In *C. macrocarpa* this moment can be easily determined because indusium opens. We defined the end of spore release when the individuals had at least 50% of indusia open.

In late March we visited 15 populations in Galicia (Spain) to estimate the degree of sori consumption for each population in relation to population size. In each population we counted the number of mature (i.e. with fertile leaves) individuals in a sample of 90 fertile leaves per population or, in smaller populations, in all available fertile leaves. Only leaves of the previous year cohort were included in the sample. Fern stripping was evaluated as the percentage of sampled leaves with consumption marks.

Consumer identification

On the 1 December 15 pieces of cotton fabric (1 m × 0.5 m) were randomly placed under fertile leaves, on both Capelada and Eume, to collect any droppings from the consumer while feeding. Droppings were either stored in Eppendorfs with 80% alcohol for DNA analysis, i.e. to identify the consumer, or in distilled water, i.e. for germination trials.

Three faecal samples were collected on the 15 December, 1 January and 30 January for DNA analysis. The DNA from these three samples was extracted using the QIAamp® DNA Stool Mini Kit (Qiagen) in accordance with the manufacturer's instructions. Amplification of an 866bp fragment of the mitochondrial cytochrome b gene was achieved using *Apodemus*-specific primers CB-AF and CB-AR2 (Reutter et al. 2003) following a changed PCR protocol and cycle by the authors: 0.1 μg/μL Bovine serum albumin (BSA) was used in place of Q solution; an annealing temperature of 62 °C was used instead of 47 °C; and a final extension of 72 °C for 10 min was added. PCR products were cleaned using ExoSap-IT™ (US Biochemical Corporation), and sequenced using Applied Biosystems Big Dye Terminator Ready Reaction Kit v3.1 with products resolved on an ABI 3100 automated capillary DNA analyzer (ABI Prism model 3100, Beaconsfield, UK). Sequences were aligned using Sequencer™ 4.0 and compared with sequences in NCBI GenBank using the BLAST program to identify DNA matches.

On the 30 January and 1 February 30 Sherman live capture traps (Forestry suppliers, Inc.) were used, respectively on Capelada and Eume to capture small live mammals baited with peanut butter and fertile pinnule pieces, which were used to check whether consumption marks were similar to those observed in the field. Traps were placed in the afternoon and checked the following morning. Droppings from traps were collected and stored in distilled water for germination tests (see below).

Spores in droppings and germination tests

Trials were carried out to assess whether the consumer was a predator or a disperser. This information will help us to know how consumption will affect the conservation status of this endangered fern. In the field each dropping was stored in Eppendorfs with 1.5 ml of distilled water.

Permanent preparations for microscope observations were made with 0.05 ml of the suspension in DePeX (BDH Chemicals, Poole, UK) to quantify the total number of spores per dropping and the % of full spores (unbroken by digestion, i.e. with a protoplast inside).

To estimate the no. of viable spores (i.e. able to germinate) per dropping, 0.5 ml of the suspension was sown on mineral agar, according to Dyer (1979), on plastic Petri dishes subsequently sealed with Parafilm. Fourteen droppings from the two populations were incubated into a growth chamber (20 °C and 16 h light, 8 h dark photoperiod, Quintanilla et al. 2000) for two months. These results were compared with those from the permanent preparations.

(a)   (b)
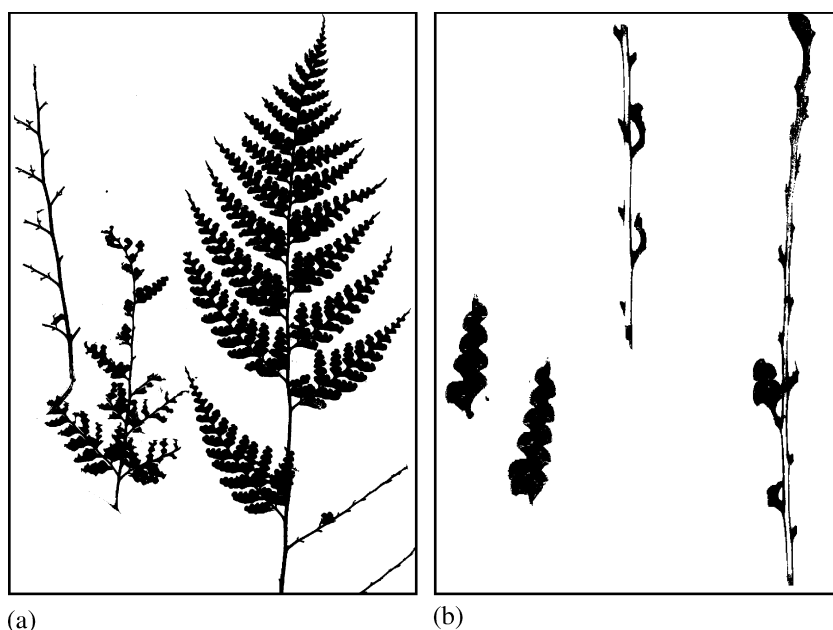
Fig. 1. (a) Consumption pattern of *Culcita macrocarpa* fertile leaves by woodmouse *Apodemus sylvaticus* in the field. (b) Consumption marks from woodmouse on fertile leaves placed inside traps to confirm the observed pattern in the field.

Data analysis

At the end of the period of fern consumption chi-square tests were used to: (1) compare the number of consumed fertile pinnules between Eume and Capelada, and (2) assess differences in the number of leaves that released spores between these two populations.

The relationship between consumption rate (= percentage of fertile leaves with signs of consumption) and *C. macrocarpa* population size was assessed with linear regression. Population size was log $(x + 1)$ transformed and consumption rate was arcsin transformed to normalize the residuals.

Statistical analyses were performed with Statistica 6.0 (StatSoft Inc., 1984–2001).

Results

Check and record on fern consumption and spore release

Fern consumption marks were found exclusively on fertile leaves (leaves with presence of closed sori with mature sporangia inside) indicating that the consumer actively selected the fern spores. The pattern of consumption was very similar between Capelada and Eume (Fig. 2a): fern feeding began with maximum consumption rates in December and virtually finished by mid February (Fig. 2b), when the total number of consumed fertile pinnules at Capelada was significantly higher than that at Eume 56.8% ($n = 1145$) vs. 37.3% ($n = 972$), $\chi_1^2 = 80.4$, $P < 0.001$ with Yates correction).

In mid March only 48% of marked fertile leaves in Capelada had released their spores ($n = 90$), but in Eume this percentage was 96% ($n = 90$). This difference between populations was significant ($\chi_1^2 = 44.7$, $P < 0.001$ with Yates correction).

From the 15 *C. macrocarpa* populations visited in Galicia, all but those with very few individuals showed signs of consumption (Fig. 3). There was a significant increase in fern consumption rate as the population size of *C. macrocarpa* increased: consumption rate (% arcsine transformed) $= -14.4 + 0.9\log$(population size $+ 1$), $r^2 = 0.8$, $F_{1,13} = 52.9$, $P < 0.001$.

Consumer identification

Sequences obtained from DNA extractions of each of the three droppings were identified as woodmouse based on a 98% similarity when compared to sequences in GenBank. A close relative, the yellow-necked mouse (*A. flavicollis*), showed only a 90% match, with other potential small mammals showing even less similarity. On 30 January six woodmouse were captured in Capelada and another six on 1 February in Eume. No injuries from trapping were detected and animals were released after identifying the species. The ferns consumed in the traps showed the same pattern of consumption as those in the field (Fig. 1). Therefore, both methods showed consistency in the determination of the consumer.

Spores in droppings and germination tests

Each permanent preparation had from two to hundred thousands of spores, but only 14%–69% were unbroken by digestion (i.e. full spores with a protoplast inside); i.e. virtually all spores were broken by digestion and had no protoplast inside (Table 1). From the 14 Petri dishes incubated in the growth chamber, germination occurred in only two dishes, with 1% and 0.3% of spores germinating (Table 1). These results suggest that woodmouse can be a potential disperser of spores from *C. macrocarpa*, but that most spores were digested.

Discussion

This study shows, for the first time, consumption of fern spores by a small mammal, the woodmouse. Fossil records show that ferns were important for dinosaurs (Carpenter 2006; Hummel et al. 2008). Despite toxicity of ferns (Page 2002) large herbivorous dinosaurs probably fed on plants whose allelochemical defences were geared more toward reducing digestibility than attacking the herbivore's metabolism directly (Farlow 1987). Presently, there are few records of consumption by mammals and birds; apart from the woodmouse (this study) the only other mammal known to feed on fern spores is the short-tailed bat (*Mystaina tuberculata*), which takes spores from tree ferns such as *Cyathea* spp., *Dicksonia squarrosa*, *Lycopodium* spp. and *Phymatopdes* spp. in New Zealand (Daniel 1976).

Rodents are important seed predators in many habitats, such as tropical and sub-tropical forests (Forget 1992; Hoch and Adler 1997; Brewer and Rejmánek 1999; Zhang et al. 2005), temperate deciduous woodlands (Hulme and Hunt 1999; Zhang et al. 2005), mesic grasslands (Edwards and Crawley 1999), and shortgrass steppes (Hoffmann et al. 1995), but there are no examples of rodents feeding on ferns, neither on leaves nor spores. In our study only fertile leaves showed marks of consumption which means that the consumer selected the sori to feed. Spores of *C. macrocarpa* are rich in calories, lipids and proteins (Arosa et al., 2009) and therefore should provide an energetic food source for woodmouse in winter. The consumption of *C. macrocarpa* by the woodmouse in Galicia occurred when spores were mature and before they were released,

(a)

(b)
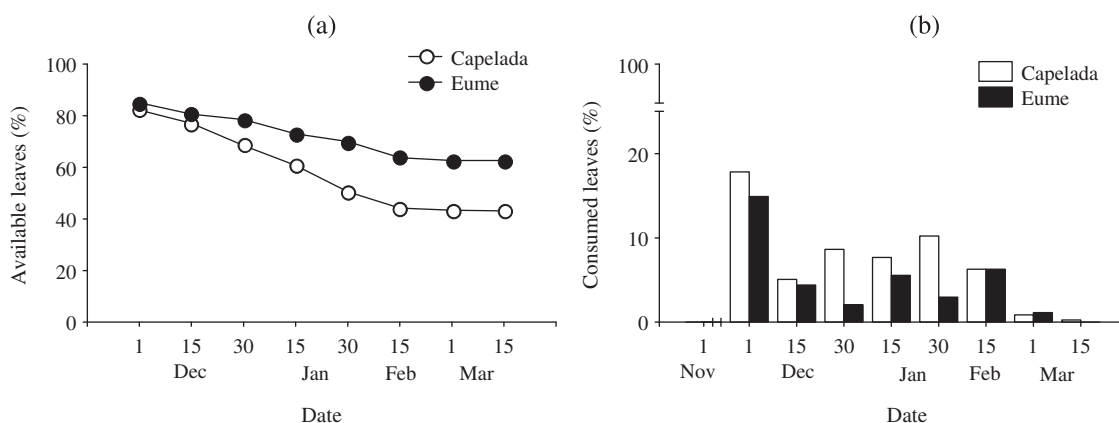
Fig. 2. (a) Seasonal variation in the % of available *C. macrocarpa* fertile leaves without signs of consumption for both populations, and (b) seasonal variation in the % of consumed leaves of *C. macrocarpa* from available fertile leaves at each corresponding date. The two populations, Capelada and Eume, were checked every 15 days from 1 December to 15 March. Note that in b there was no consumption on 1 November, when we checked both populations before marking them.
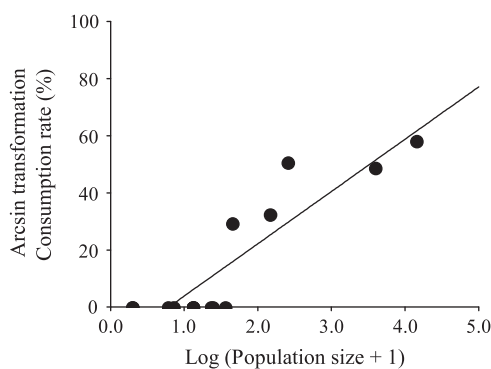
Fig. 3. Linear regression between population size ($\log x + 1$ transformed) and consumption rate (arcsine transformed). To assess consumption rate a sample of 90 leaves was examined in each population.

Table 1. Number of spores in droppings (estimated from preparations) and their viability (estimated from cultures).

Dropping	Total no. spores	Full spores (%)	No. of viable spores	Germination (%)
1	160,085	24	0	0
2	2399	69	0	0
3	45,264	14	0	0
4	92,189	31	0	0
5	69,926	31	0	0
6	103,751	32	0	0
7	23,616	21	0	0
8	169,863	47	0	0
9	22,017	32	0	0
10	10,209	37	0	0
11	36,257	66	0	0
12	67,505	64	0	0
13	76,153	44	740	1.0
14	72,713	36	212	0.3

Spores in preparations were set in two categories: full, i.e. unbroken by digestion, with a protoplast inside; and empty, i.e. broken and lacking most of the protoplast. Viable spores were those able to germinate in culture. Germination percentage was calculated as number of viable spores/total number of spores per dropping.

and the same was observed for the Azores bullfinch (Ramos 1995; Arosa et al., 2009). In Capelada the consumption was higher than in Eume (56.8% vs. 37.3%), which might be associated with the higher abundance and diversity of food sources in Eume. The forest in Eume is characterized by native species such as *Castanea sativa*, *Corylus avellana*, *Q. pyrenaica* and *Quercus robur* with higher availability of winter fruits, whereas in Capelada the forest is fragmented and surrounded by *Eucalyptus globulus* and pastures. The woodmouse is spread through the western Paleartic (Corbet and Southern 1977), where it exploits a wide range of habitats (Montgomery 1989). Its abundance is enhanced by forest fragmentation in such a way that the population size in small forest fragments can be one or two orders of magnitude larger than in large forests (Tellería et al. 1991; Nupp and Swihart 1996; García et al. 1998). Therefore, differences in the density of woodmouse populations between the two areas may

also contribute to explain differences in the consumption, but we did not examine this aspect.

The populations of *C. macrocarpa* appear as an archipelago in the forest and should provide a concentration of food in winter. We showed that *C. macrocarpa* consumption rate increased with fern population size which suggests that larger populations of *C. macrocarpa* can be viewed as stable refuges and safe foraging places for woodmouse in winter (Diaz 1992; Telleria et al. 1992). The percentage of spore release in Capelada was lower than that in Eume, and differences between both

populations were significant. Arosa et al. (2009) studied the influence of altitude and canopy cover on spore release for this fern species in Azores (Portugal) and spore release was significantly influenced by altitude. In our study Capelada populations are situated at 300 m of altitude and Eume populations at 120 m, which may contribute to explain the difference in the timing of spore release between the two populations. It would be interesting to study the population density and movements of woodmouse before and after spore release to assess if the rodents move to *C. macrocarpa* populations to feed when mature spores are available.

This study shows that the spores of the few populations of the endangered fern *C. macrocarpa* in Galicia are highly consumed by woodmouse and that only a very small minority may survive the digestion by the woodmouse. Home range studies of woodmouse showed that small fruits can be dispersed up to 30 m from parent trees (Kiviniemi and Telenius 1998). As populations of *C. macrocarpa* are located in archipelagos inside the forest, this means that new populations of *C. macrocarpa* may appear near deposition sites. In addition, detailed research needs to be done in ecosystems where tree ferns are abundant, because spores of tree ferns seem to be important for rodents.

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