Coprophagy in Lepidoptera: observational and experimental evidence in the pyralid moth *Aglossa pinguinalis*

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Abstract

Larvae of Lepidoptera are mainly herbivores, and only the larval stages of *Bradypodicola* and *Cryptoses* pyralid moths are known to be specialized coprophages. Here, we report coprophagy as a main feeding habit for the larvae of another pyralid moth, *Aglossa pinguinalis*, on the basis of observational and experimental evidence. The larvae of this moth require two years to complete development, and construct silk tubes connecting the food source with a shelter chamber. Larvae of *A. pinguinalis* were mostly found inside caves, where they were about 700 times more abundant than in the open field. Inside the caves, observational results indicate that 98% of the larvae fed mostly on excrement and only 2% were recorded as eating other kinds of detritus (decayed mushrooms). No larvae were recorded eating plant detritus in the censuses nor in experimental detritus patches. The larvae did not show preferences for different types of excrement in the caves. Experimental dog and sheep excrement corroborated this result, showing that the abundance of larvae did not differ between these two excrement types over the entire study. We suggest that habitat selection of *A. pinguinalis* is ecologically similar to the trophic specialization of *Bradypodicola* and *Cryptoses*, in spite of the differences in natural history traits among these moths. Feeding on dry excrement inside caves, or in buried sloth dung, may reflect the constraints for Lepidoptera successfully to colonize excrement: in more exposed excrement, they cannot compete with other coprophagous specialists owing to the lack of parental care (e.g. resource relocation) and slow growth rates. We hypothesize that coprophagous Lepidoptera will be restricted to competition- and predation-free habitats and resources, feeding on excrement inside caves and animal burrows.

Key words: coprophagy, Lepidoptera, larval ecology, *Aglossa pinguinalis*, caves

INTRODUCTION

Most species in the order Lepidoptera are strictly phytophages during their larval stages (Strong, Lawton & Southwood, 1984). However, carnivory, necrophagy, saprophagy, mycophagy, and coprophagy have been reported in some species (Scoble, 1992). Coprophagy was recorded mainly in adults, particularly males who suck fresh dung (Brown, 1977; Schoenly, 1983; A. M. Young, 1984). This behaviour has been explained as a means of supplementing nitrogen (Crawley, 1983) or of taking up sodium (Ray & Andrews, 1980; Adler & Pearson, 1982), which increases male fitness through sodium transfer to the eggs after copulation (Smedley & Eisner, 1995). In larval stages, however, coprophagy is only occasionally reported, usually as exceptional cases and generally without evidence on whether the diet was

strictly based on dung consumption (Leestmans, 1974, 1975; Johnson, 1977; Koryszka, 1989). Although some tineid species have been reported as having coprophagous larvae (e.g. Robinson, 1980; Davis, 1987; Robinson & Nielsen, 1993), their presence in excrement and buccal pellets is more related to their keratophagous diet than to actual coprophagy (Scoble, 1992; Common & Horak, 1994; but see Davis, 1972). Similarly, coprophagy in the larvae of four Australian species of *Telanepsia* oecophorid moths reared on scats of koalas, opossums, and gliders is explained by the specialization of most *Telanepsia* species for feeding on dead myrtaceous (especially eucalyptus) leaves, the main component in scats of koalas and other eucalyptus herbivores (Common & Horak, 1994). Only larvae of Neotropical *Bradypodicola* (one species) and *Cryptoses* (three species) pyralid moths have been shown to be specialized coprophages, feeding exclusively on sloth dung (Waage & Montgomery, 1976; Bradley, 1982; O. P. Young, 1982; Waage & Best, 1985).

Larvae of *Cryptoses* moths develop and pupate in the

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dung pile buried by the sloth (Waage & Montgomery, 1976). The caterpillars construct frass-encrusted tubes which are extended by the larvae as they grow, pupating in a sealed section of their feeding tube. Three to four weeks are required for the development from egg to adult *Cryptoses choloepi* at an ambient temperature on the forest floor (Waage & Montgomery, 1976). The strict specialization of the larvae on sloth dung is linked to permanent residence of the adults in the fur of sloths (Waage & Montgomery, 1976; Waage & Best, 1985). This extreme specialization of *Bradypodicola* and *Cryptoses* moths has been suggested as the way in which adults could have access to and lay eggs in the excrement (Waage & Montgomery, 1976; Waage & Best, 1985). Such extreme specialization is not general in other coprophagous insects (but see Matthews, 1972; Ratcliffe, 1980), and although scarabeid beetles show preferences for some kind of excrement, they do not specialize in a single excrement type (Fincher, Stewart & Davis, 1970; Hanski & Cambefort, 1991*a*; Sanchez-Piñero & Avila, 1991).

We observed larvae of the moth *Aglossa pinguinalis* L. (Pyralidae) feeding on dung inside caves used as stables and dwellings in southern Spain. *Aglossa pinguinalis* is a moth species widely distributed in the Old World (Europe, north Africa up to Cameroon, and the Near East to India; Agenjo, 1952), North America and Australia (see Goater, 1986 and Vives, 1992 for additional information). Larvae are usually found in stables and abandoned human buildings (Buckler, 1901), and although they have been reported as detritivores on plant and animal remains (Buckler, 1901; Spuler, 1910; Báguena, 1952), there is no evidence for strict detritivory and coprophagy in *A. pinguinalis*. We show that these larvae are coprophages, suggesting that habitat selection by *A. pinguinalis* has ecological similarities with the trophic specialization of the dung-feeding larvae of *Bradypodicola* and *Cryptoses* moths. The goals of this study were: (1) to ask if dung is a main food source for *A. pinguinalis* in the south-east of Spain; (2) to test if preferences for the excrement type exist; and (3) to suggest that coprophagy in Lepidoptera is constrained to competition- and predation-free habitats and resources.

STUDY AREA

The study was conducted in three sites (Rambla del Grao, Llanos de Guadix, Barranco del Espartal) in the Guadix-Baza Basin, an arid region located in the Granada province, south-eastern Spain. The climate is mediterranean continental and highly seasonal; temperatures oscillate between zero and $-14°C$ on 60% of the days in winter (October to April) and reach 60°C at ground level in summer (EPYPSA, 1986). Annual rainfall is 250–300 mm, and it occurs mainly during the cold months. Potential evapotranspiration is three times the annual precipitation (Sierra *et al.*, 1990). Vegetation is typical arid open shrub steppe. These traits correspond to a middle arid system (Le Houreou, 1989).

METHODS

Observational evidence of coprophagy

Surveys were conducted over 3 years (1991–1993) both inside caves (constructed as dwellings and stables by people in the area) as well as in the open field. Eighty-nine caves were surveyed in the spring of 1991 and 1992. In each cave, larvae were censused by counting the number of individuals per detritus patch (dung piece or accumulations of detritus other than excrement: plant detritus, decayed mushrooms). Detritus was weighed with 500 g and 100 g Pessola^{TM} scales with a 10 g and 1 g accuracy, respectively. Although plant detritus (mostly dry leaves, straw, and fruit and seed husks of several arid plant species) was very abundant (47% of all the detritus in the caves), only detritus forming a discrete patch was considered, because no larvae were observed feeding on small pieces of excrement or other detritus. To test feeding preferences in the larvae, excrement was differentiated according to type of animal (sheep, dog, human, horse, rabbit, bat, bird) and diet (herbivorous: sheep, horse, rabbit; omnivorous: canid, human; insectivorous: bat, bird) since dung-feeders can show strong preferences for different excrement types (e.g. Hanski & Camberfort, 1991*a*).

In the open field, searches in dung and detritus accumulations were carried out in the study area from 1991 to 1993 with the same protocol as inside the caves. Six hundred sheep droppings, 84 pellet-accumulations of rabbit, 47 canid scats, and 200 plant detritus patches were analysed.

Experimental test of trophic preference

In addition to the observational study, an experiment to test the preferences for plant detritus and different kinds of dung was carried out. We used plant detritus collected in the caves (dry leaves, straw, and fruit and seed husks), omnivore (dog) dung and herbivore (sheep) dung. We used these 2 different types of excrement since strong preferences occur in coprophagous species between omnivore/carnivore dung and herbivore dung (Hanski & Cambefort, 1991*a*; Estrada *et al.*, 1993). In December 1991, 10 caves were cleaned and three 200 g detritus-pads (1 of herbivore dung, 1 of omnivore dung, and 1 of plant detritus) were placed in each cave, separated 1 m from the nearest wall. Each experimental group of detritus-pads had 10 replicates. The experimental pads were monitored for 2 years, being censused once every 3 months from March 1992 to December 1993, until the larvae abandoned the excrement to pupate. Censuses were conducted by counting the number of larvae under and inside the dung until the larvae started to construct silk tubes; then we counted the number of tubes in each excrement to estimate larval abundance. In order to avoid disturbance or tube abandonment by the larvae we did not measure dung consumption by the larvae.

Statistical analysis

We used ANOVA to analyse differences in larval abundance between types of detritus (excrement vs. decaying mushrooms) as well as to test differences of abundance among dung from different types of animal and diet. Data were transformed logarithmically before testing (Zar, 1984).

We tested the influence of detritus and excrement availability on larval feeding preferences using a Pearson correlation, performed after logarithmic transformation of the variables (Sokal & Rohlf, 1995).

Results from the dung preference experiments were analysed using a repeated-measures ANOVA, which tests differences not only in mean abundance between treatments, but also in the trends through time of the different treatments (Gurevitch & Chester, 1986).

RESULTS

Natural history observations

In spring (April, May), adult moths laid eggs. In the laboratory, two females laid eggs in clutches (15–20 eggs) on the sand. After hatching, larvae moved towards the excrement. Larvae started feeding in the bottom part of the excrement, tunnelling into it. Three to six months later, larvae constructed dirt-encrusted silk tubes (34.8 $\pm$ 10.46 cm in length; $n = 20$) inside the caves. The silk tubes were extended on the ground surface inside the caves, and below ground in the open field. Silk tubes, which can be a single tube or form complex ramifications, connected a chamber for shelter (5–10 cm deep in the ground or the cave walls) with the dung. Our observations suggest that larvae required two years to complete development, and different generations could be found at the same time. Pupation occurred inside a silk cocoon on the ground surface, outside the silk tube, and not in the shelter chamber used by the larvae.

Distribution and abundance of larvae

Aglossa pinguinalis showed a strong preference for caves: abundance was 700 times higher inside caves (1.411 $\pm$ 1.770 larvae/detritus patch) than outside (0.002 $\pm$ 0.046 larvae/detritus patch). The two specimens found outside caves were feeding on dry sheep dung.

The presence of larvae was related to the presence of excrement in caves: no larvae were found inside caves with no excrement (21 caves); in contrast, caves with excrement contained 4.68 $\pm$ 4.36 individuals/cave, with 83.8% (57) of the caves with excrement being inhabited by larvae. The abundance of larvae in a cave was significantly correlated with the total amount of resources available (weight of detritus: $r^2 = 0.59$, $P < 0.001$, $n = 89$; number of detritus patches: $r^2 = 0.70$, $P < 0.001$, $n = 89$; Pearson correlation test) inside the cave.

Observational evidence of coprophagy

Larvae of *A. pinguinalis* were found feeding mostly (98%) on excrement, and only three individuals (2% of total individuals censused inside caves) were recorded feeding on other kind of detritus (dead mushrooms) (Table 1); no larvae were recorded associated with or feeding on plant detritus, either in natural or in experimental plant detritus patches (Table 1). These results show the existence of a high degree of coprophagy in the larvae of *A. pinguinalis*, which is significantly more abundant in excrement than in any other detritus in the studied caves (ANOVA: $F = 51.02$, $P = 0.0001$, $d.f. = 1, 95$).

Larvae did not show preferences for a particular kind of excrement, and excrement from different types of animal (Table 1; ANOVA: $F = 1.52$, $P = 0.18$, $d.f. = 6$, 77) and different types of diet (Table 1; ANOVA: $F = 1.26$, $P = 0.29$, $d.f. = 2, 77$) did not differ in larval abundance. Larval abundance was not significantly correlated with the differential availability of excrement (abundance: $r^2 = 0.43$, marginally significant, $n = 7$; weight: $r^2 = 0.001$, not significant, $n = 7$; Pearson correlation test).

Experimental testing

Experimental results agree with observational data: larvae of *A. pinguinalis* only fed on excrement, and no larvae were recorded feeding on plant detritus. In the excrement, larvae of *A. pinguinalis* showed a significant trend of decreasing abundance during their development (Fig. 1; Table 2: Grand mean–linear, quadratic, cubic effects of time). Larval abundance decreased strongly (53.2%) between May and September 1992; although the reduction in the larval population in the excrement continued, the percentage decrease was much smaller than during May–September 1992 (September–December 1992 = 9.4%; December 1992–March 1993 = 18.4%; March–June 1993 = 5.8%), remaining practically

Table 1. Abundance of larvae (mean number of individuals per 100 g of detritus), detritus frequency and total weight in each detritus category inside caves

Type of detritus	Larvae abundance (Mean $\pm$ s.D.)	Detritus frequency	Detritus weight (g)
Excrement:	2.86 $\pm$ 3.34	78	6042
Herbivorous	2.68 $\pm$ 2.23	34	3233
Sheep	2.91 $\pm$ 2.27	30	1998
Horse	0.64 $\pm$ 0.52	2	872
Rabbit	1.31 $\pm$ 0.97	2	363
Omnivorous	2.93 $\pm$ 4.60	33	2076
Canid	4.12 $\pm$ 6.22	17	851
Human	1.66 $\pm$ 0.68	16	1225
Insectivorous	3.21 $\pm$ 1.30	11	733
Bat	3.54 $\pm$ 1.46	6	480
Bird	2.80 $\pm$ 1.10	5	253
Plant detritus	0	11	435
Decayed mushroom	0.42 $\pm$ 0.98	18	632

Table 2. Summary of a repeated measures ANOVA considering the population changes from May 1992 to September 1993 of *A. pinguinalis* in 200 g experimental deposits of dog and sheep dung placed inside caves

Source	d.f.	Linear S.S.	Linear F	Quadratic S.S.	Quadratic F	Cubic S.S.	Cubic F	Total S.S.	Total F
Grand mean	1	6844.50	21.77***	3416.89	21.71***	1922.00	17.63***	–	–
Treatment	1	5.63	0.02[N.S.]	8.71	0.06[N.S.]	10.00	0.09[N.S.]	0.03	0.00[N.S.]
Error	16	5030.88		2158.40		1744.00		1722.28	
Total	17	5036.50		2527.11		1754.00		1722.31	

N.S. = not significant; ***, $P < 0.001$ d.f., degrees of freedom; S.S., sum of squares; F, F-ratio
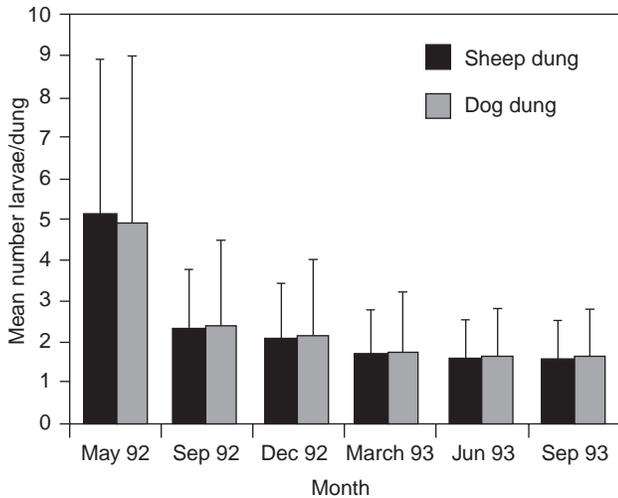
Fig. 1. Mean number of larvae of *A. pinguinalis* in experimental 200 g sheep and dog dung during the study period.

constant during the last months (June–December 1993) of the study (Fig. 1). This trend in time was the same for both kinds of excrement (Treatment: linear, quadratic, cubic and Total effects; Table 2), showing that the types of dung considered had no effects on larval survival of the moth. Therefore, the two kinds of excrement used in the experiment did not differ in larval abundance over the entire study (Fig. 1; Treatment, Table 2). In addition, at the end of the experiment both types of dung had been almost completely consumed, and only the crust or a few crust pieces of excrement remained on the ground.

DISCUSSION

Results show that larvae of *A. pinguinalis* are coprophagous, feeding almost exclusively on dung in the Guadix-Baza Basin. Although three individuals were found eating dead mushrooms, the relative abundance of larvae in the two kinds of remains was substantially different: the mean larval abundance in excrement (1.90 larvae/dung) was more than tenfold the mean abundance in fungi (0.17 larvae/decaying mushroom) (Table 1). Although excrement was much more abundant than fungi in caves (78 excrement vs. 18 mushroom accumulations), larval preference for excrement was not related

to availability of the two types of resources: the presence of larvae on mushrooms was related to the presence of excrement in the same caves (two caves with mushrooms and excrement); caves with mushrooms but without excrement (five caves) contained no larvae. In addition, the use of fungi (and carcasses; see Báguena, 1952) agrees with the fact that many dung-beetles are usually attracted to and feed on fungi (e.g. Howden, 1955; Halffter & Matthews, 1966; Paulian & Baraud, 1982) and carrion (Hanski, 1983; Walter, 1991; Gill, 1991; Sanchez-Piñero, In press). This may be related to the evolution of coprophagous feeding habits from a more generalist detritivorous habit (Cambefort, 1991). This attraction to detritus other than excrement is not unexpected, considering the generalist coprophagous habits of the larvae. The larvae did not show selection for specific dung types. The use of different types of dung was related (at a marginally significant level) to the abundance of these different types and, as suggested by the experimental results from omnivore and herbivore dung, dung type had no effect on larval abundance. Although larval abundance was not significantly correlated with the amount of the different types of dung, it was correlated with total resource availability in the caves. These results could be interpreted as a generalist coprophagous diet in the larvae, due possibly to the fact that larvae have limited ability to disperse and move, and must aggregate or disperse on specific dung patches inside the same cave after hatching.

Are coprophagous moth larvae constrained to habitats and resources that are free of competition and predation?

The generalist coprophagous diet of *A. pinguinalis* larvae contrasts with their restricted habitat, larvae being around 700 times more abundant inside caves (and human constructions, see Buckler, 1901) than in the open field.

Predation and competition are major forces structuring communities that exploit ephemeral resources such as dung (e.g. Hanski, 1987; Hanski & Camberfort, 1991b). Different features of specialized coprophages have evolved as a consequence of the selective pressure of these interactions: Diptera have developed an extraordinarily fast growth rate and the ability to pupate with small larval sizes; dung-beetles relocate resources by burying them in the ground, thus avoiding predation

but increasing competitive pressure (Kuusela & Hanski, 1982; Hanski, 1986; Hanski & Cambefort, 1991*b*). Lepidopteran larvae, however, lack these adaptations. *Aglossa pinguinalis* does not relocate resources, and its slow growth rate, requiring as long as two years to complete development, does not favour larval survival in dung when predators and competitors are present. Although *Cryptoses* larvae have a much faster development (3–4 weeks) than *A. pinguinalis*, adults do not relocate resources for the larvae (Waage & Montgomery, 1976); therefore, these moths could not compete with dung-beetles, which remove most of the available excrement in a few minutes in the tropical rainforest (Estrada & Coates-Estrada, 1991; Estrada *et al.*, 1993).

Aglossa pinguinalis feeds on dry excrement deposited inside caves, with only occasional Tenebrionidae as competitors; during the surveys only one *Blaps waltli* Seidlitz and two *Elenophorus collaris* L. were recorded feeding on dung inside the caves. In contrast, in the open field, high numbers of coprophages such as scarabeids (*c.* 79 individuals/200 g dung) and dipteran larvae, as well as predators (histerid and staphylinid beetles, *c.* 123 individuals/200 g dung) quickly colonize excrement during the short spring (Sánchez-Piñero, 1994), just when *A. pinguinalis* lay their eggs in the Guadix-Baza Basin. Feeding on the excrement deposited inside caves would thus allow *A. pinguinalis* to avoid highly efficient coprophagous competitors and specialized dung-dwelling predators.

This idea is also supported by two facts:

(1) Although the silk tube constructed by *A. pinguinalis* larvae can protect them against predators, as in other Pyralidae (see Vasconcelos, 1991; Stamp & Wilkens, 1993), the tubes were not constructed until several months after hatching. During the first few months, larvae of *A. pinguinalis* inhabited small burrows under or inside the excrement, just when their size was most likely to make them vulnerable to predation by histerid and staphylinid beetles.

(2) Habitat selection by *A. pinguinalis* is ecologically similar to the trophic specialization of *Bradypodicola* and *Cryptoses* larvae on sloth dung which is dry, almost odourless, and buried by the sloth. It has little attraction for dung-beetles (O. P. Young, 1981), so allowing the larvae of *Bradypodicola* and *Cryptoses* moths to develop in it. In the tropical forests of Central and South America, dung beetles are highly abundant, and dung is buried and rolled by the beetles only a few minutes after it appears (Gill, 1991; Estrada & Coates-Estrada, 1991; Estrada *et al.*, 1993).

In conclusion, the fact that coprophagous moth larvae live on dry excrement inside caves (see Davis, 1972; Robinson, 1980) or in buried excrement of sloths could reflect that these larvae are restricted to habitats and resources free of competition and predation. Hence, the evolution of coprophagy in Lepidoptera appears to be constrained by (a) the lack of parental care (i.e. resource relocation for larvae), and (b) the relative inefficiency of lepidopteran larvae, which are very sensitive to low-quality diets (Slansky, 1993), when compared with dung-specialist larvae of Diptera and Coleoptera. Consequently, we hypothesize that coprophagous lepidopteran larvae could have evolved in association with animal burrows (foxes, badgers, rodents) and caves. Coprophagy in Lepidoptera could therefore be more widespread than previously supposed.

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