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Are yellow dung flies domesticated cow dung specialists?

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Abstract

The theory of niche differentiation implies some extent of specialization of species with regard to key resources, notably food. Coprophagous (dung-eating) insect larvae play a critical role in the decomposition of livestock dung in modern and traditional agricultural grasslands. The yellow dung fly (*Scathophaga stercoraria* L.; Diptera: Scathophagidae) is one of the largest, most common and abundant dung decomposers on pastures in cold-temperate regions across the entire northern hemisphere. As this fly is often associated with domesticated cattle or dairy cows, which are commonly kept for human nutrition worldwide (beef, milk, cheese, etc.), it is sometimes suspected to be a cow dung specialist. However, yellow dung flies are regularly active on and around other dung types, and must have reproduced on dung of wild vertebrates before the domestication of cattle. We therefore experimentally studied the performance of yellow dung fly larvae on dung of various large domestic vs. wild mammals (cow, horse, wild boar, red deer) in the laboratory in Switzerland. Larval performance in terms of juvenile survival, egg-to-adult development time, growth rate, and final adult body size, the major life history indicators of individual reproductive success, did not vary greatly among the various dung types tested. Thus, yellow dung flies can successfully reproduce on multiple types of mammal (vertebrate) dung, wild and domestic, and are therefore dung generalists rather than specialists. We conclude that yellow dung flies are common in European low- and highlands because they could plastically shift to dung of common herbivorous livestock after their domestication without losing the ability to reproduce on dung of common wild mammals.

Key Words

Behavioral Ecology, body size, coprophagy, development, Diptera, domestication, dung, food niche, insect, larval food manipulation, livestock dung, *Scathophaga stercoraria*, specialist-generalist, survival

Introduction

According to the theory of niche differentiation, species inhabiting the same ecological niche should not be able to co-exist in the long term (Abrams 1987; Holt 2009). This implies some extent of specialization of species with regard to their key resources, notably food. In the long term, physiological adaptations facilitating efficient nutrient acquisition are expected to evolve, which ultimately drive niche differentiation. Nevertheless, in nature multiple species often live in the same habitat, feeding on roughly the same resource. A prominent example is the coprophagous (i.e. dung-eating) insect community, consisting mainly of beetles and

flies that inhabit and decompose vertebrate, often domesticated livestock dung (Hammer 1941; Holter 1979; Hanski and Cambefort 1991; Skidmore 1991; Lumaret et al. 1992; Rohner et al. 2015; Laux et al. 2019). These species essentially all compete for the same types of resources, although there are consumers, predators and parasitoids, some of which are considered dung specialists, others generalists (Hanski and Cambefort 1991; Skidmore 1991; Pont and Meier 2002; Jochmann and Blanckenhorn 2016). Whereas a generalist of this community can thrive on the dung of various different vertebrates, any specialist may only exploit the dung of a single vertebrate (e.g. cow or human dung). In practice this will be a continuum, however.

Coprophagous insect larvae play a critical role in the decomposition of vertebrate dung, which in turn is crucial for nutrient cycling in managed agricultural grasslands in many parts of the world (Skidmore 1991; Jochmann et al. 2011; Adler et al. 2016; Floate 2023). As a prominent example, the introduction of livestock for farming in many new areas of the world (for instance in Australia) led to the subsequent introduction of dung organisms from other parts of the world (e.g. *Onthophagus* dung beetles from southern Europe) to biocontrol the proliferating excrements, which were not broken down because a co-evolved dung fauna was lacking (Bornemissza 1960, 1976). Nonetheless, to date it is not clear precisely which nutrients are taken up and digested by the various dung feeding insects (plant matter, inorganic components, fungi or bacteria growing on the dung, fluid components, etc.: Lumaret 1995; Holter 2016). Regardless, many of these nutritional components may be alike for particular classes of vertebrate dung depending on the food of the producers, i.e. herbivores vs. carnivores vs. omnivores, so that not only the fibrous content of the dung, but even the microbiome of these animals ending up in their dung might be sufficiently similar (Shukla et al. 2016). One could therefore hypothesize *a priori* that coprophagous insects more likely are generalists rather than extreme dung specialists (Holter 2016; Laux et al. 2019). This, in turn, could facilitate their broader geographic distribution, especially if they can thrive on the dung of common and ubiquitous livestock species such as cattle, sheep, horses, etc.

The yellow dung fly (*Scathophaga stercoraria* L.; Diptera: Scathophagidae) is one of the largest (approaching the size of honey bees) and most abundant dung decomposers on livestock (especially cattle) pastures in cold-temperate regions across the entire northern hemisphere (Hammer 1941; Stone et al. 1965; Gorodkov 1984; Blume 1985; Skidmore 1991; Papp 1992; Bernasconi et al. 2010; Blanckenhorn et al. 2010, 2018). Unlike most insects, which are most common when and where it is warm, this fly actually prefers cooler climates, as it invaded arctic regions in the Old and New Worlds as well as higher altitude habitats in warmer regions, for instance the Alps (Vockeroth 1987; Sigurjónsdóttir and Snorrason 1995; Blanckenhorn 1997; Šifner 2008; Blanckenhorn et al. 2018). In Switzerland this species is omnipresent, likely related to the high density of cows for milk, cheese but also beef production as well as other livestock, which range from low to high altitude pastures in the Alps up to ca. 2000 m beyond the treeline (Kraushaar et al. 2002). Yellow dung flies depend on the availability of fresh vertebrate dung, into which females lay their eggs and which the larvae consume and thereby recycle, eventually pupating in the ground close to a dung pat. Adult flies lick nectar from flowers for energy but additionally require small insect prey to reproduce (nutritional anautogeny: Foster 1967; Gibbons 1980; Blanckenhorn et al. 2007, 2010; Kaufmann et al. 2013). Reproduction consequently also happens around the (fresh) dung pat, and especially the mating behaviour of yellow dung flies has been studied intensively over the past decades (Parker 1970; Parker et al. 2020; Blanckenhorn 2021). Male flies

therefore abound on and around cow dung pats to mate with incoming females. Females only come to the dung when they have eggs ready to be laid, and otherwise spend most of their time foraging for prey and nectar in the vegetation surrounding a pasture to avoid continuous harassment by males (Parker et al. 2020).

From its common link with domesticated cattle worldwide, the yellow dung fly has been implicitly suggested to be a cow dung specialist, but this has not yet been confirmed (Blanckenhorn et al. 2001). Blanckenhorn (2009) further raised the more general hypothesis that this fly's wide range may be a consequence of its documented extensive phenotypic plasticity in various life history and behavioural traits, supposedly mediating dung generalism. Yellow dung flies are regularly active on and around other dung types of common herbivores such as sheep or horses (Cotterell 1920; Hirschberger and Degro 1996), and they must have reproduced on dung of wild vertebrates before the domestication of cattle. Contrary to some other coprophagous insect groups (e.g. dung beetles and sepsid flies: Holter 2016; Laux et al. 2019), the success of yellow dung fly larvae on diverse dung types has so far not been studied systematically in detail. We therefore here provide a comparative assessment in the laboratory of how well the offspring of yellow dung flies perform in dung of various large domestic vs. wild mammals: cow, horse, wild boar, red deer. The precise composition of the dung in terms of bacteria and fungi, its consistency, dryness, particle size and specific nutrients knowingly affects the performance of yellow dung fly larvae in terms of juvenile survival, egg-to-adult development time, growth rate, and final adult body size, the major life history indicators of individual reproductive success (Frank et al. 2017; e.g. Amano 1983). Differentiation along these traits may therefore be used as a surrogate for reproductive fitness, and hence the degree of adaptation and specialisation to any particular dung type of any given coprophagous species, yellow dung flies in particular here (Blanckenhorn 2009).

Thus, if yellow dung flies are indeed herbivore and as such mainly cow dung specialists, then they should perform exclusively, or more likely at least better on that type of dung; that is, they should survive best, develop and grow fastest, and produce largest individuals when raised in cow dung. And if they are secondarily, i.e. evolutionarily recently adapted to and therefore specialized on domesticated livestock, they should perform better on livestock than wild mammal dung. We investigated this by raising yellow dung fly larvae on dung of domesticated cow (herbivore), domesticated horse (herbivore), wild boar (omnivore), and wild red deer (herbivore) in the laboratory.

Material and methods

General rearing methods

We used dung from four large mammals common in Switzerland to raise yellow dung fly larvae from our

existing laboratory stock to adulthood in standard common-garden laboratory conditions (given below). Laboratory flies had been originally caught in Fehraltorf, Switzerland (47°23'N, 8°44'E), and maintained subsequently on defrosted cow dung for several generations in climate chambers. Cow and horse dung was collected from farms near Zürich, wild boar dung from Wildpark Langenberg, and red deer dung from Tierpark Goldau (both in Switzerland). In all cases, freshly collected dung from many individuals was mixed thoroughly and subsequently frozen at -80 °C for at least 2 weeks to kill all arthropods therein. Yellow dung flies had previously been raised already on sheep dung by Hirschberger and Degro (1996), and dung of carnivores was not tested since *S. stercoraria* had not been observed on their faeces.

Larval performance on different dung types

To obtain test individuals for the experiment, single-held yellow dung fly females were allowed to copulate with a random male in a 100 ml glass vial containing water, sugar and *Drosophila* prey as nutrients, at room temperature of roughly 22 °C. The females (total N = 26) could lay a clutch of eggs into a smear of cow dung on a filter paper. Using a split-brood design, typically n = 10 of these eggs were then transferred with a small layer of the original dung smear into a small plastic container with overabundant (>2 g/egg; Amano 1983) dung of any of the 4 dung types, in which the larvae could subsequently develop and eventually emerge as adult flies in a climate chamber set at 19 °C, 60% relative humidity, and 13 h light period.

We scored survivorship as the proportion of individuals (of both sexes) that emerged from the typically 10 eggs transferred, their sex-specific egg-to-adult development time, and measured the length of their hind tibia as a reliable index of final structural adult body size (size data unfortunately missing for red deer dung). Linearized growth rate was crudely calculated as hind tibia length (in mm) divided by development time (in days; Blanckenhorn 2009). All life history variables were analyzed separately in SPSS V29 with generalized linear models (survival with binomial errors, all others with normal errors), entering dung type and fly sex (plus their interaction) as fixed factors and the mother's identity (i.e. family) as random factor because related sibling individuals of both sexes emerged from each clutch.

Table 1. Analysis of variance tables for the effects of 4 (3) dung types, sex, and their interaction on egg-to-adult development time, tibia length (body size), and linearized calculated growth rate, with family variation (i.e. clutch) removed as random effect (no size data for deer dung).

	development time				hind tibia length				growth rate		
	df	MS	F	P	df	MS	F	P	MS	F	P
dung type	3	359.66	437.84	<0.001	2	4.89	331.41	<0.001	0.008	200.68	<0.001
sex	1	231.01	281.22	<0.001	1	48.38	3281.17	<0.001	0.036	894.51	<0.001
sex * dung type	3	13.29	16.18	<0.001	2	0.59	40.38	<0.001	0.001	12.96	<0.001
family	25	5.82	7.09	<0.001	16	0.11	7.32	<0.001	0.00001	4.84	<0.001
error	407	0.821			342	0.015			0.00004		

Results

Larval performance on different dung

Larva-to-adult survival did not vary significantly among the 4 different dung types ($\chi^2 = 5.58$; $P > 0.15$), hovering around an overall mean of 80% ($\pm 2.4\%$ (SE), $\pm 11.2\%$ (SD)), a typical value for cow dung (Table 1; Fig. 1). Survival was a little lower in boar dung ($72.6 \pm 4.1\%$ SE) and a bit higher in red deer dung ($92.5 \pm 11.1\%$ SE; Fig. 1); consequently there was also no overall difference between domestic (cow, horse) and wild mammals (boar, deer; planned comparison; $P > 0.3$). Juvenile survival in dung of the only omnivore tested (boar) appeared lower than overall survival in dung of herbivores (cow, horse, deer; planned comparison: $P < 0.1$), but omnivore dung remains unreplicated here.

Juvenile performance as measured by all other life history traits assessed varied significantly among the dung

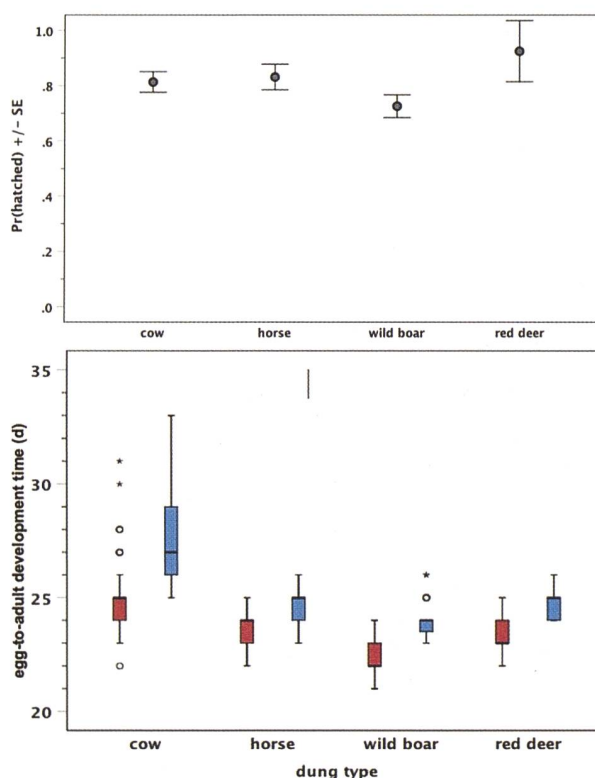


Figure 1. Mean proportion of emerged adults (\pm SE) on 4 types of mammal dung (top), and corresponding egg-to-adult development times of male (blue) and female (red) flies.

types (Table 1). Egg-to-adult development time at 19 °C was longer in cow dung than all other dung types, and longer for the larger males than the females (the latter is well known in this species: Blanckenhorn 2009; Blanckenhorn et al. 2010; Fig. 1; Table 1). Body size varied somewhat among the dung types, being largest in cow dung, while growth rate was highest in boar dung (Fig. 2; missing data for red deer dung). The sex-by-dung type interaction was also highly significant for all performance variables assessed (Table 1; Figs 1, 2), which is typical in this species with strong sexual dimorphism (males larger) (Blanckenhorn 1998a, 2009; Blanckenhorn et al. 2010).

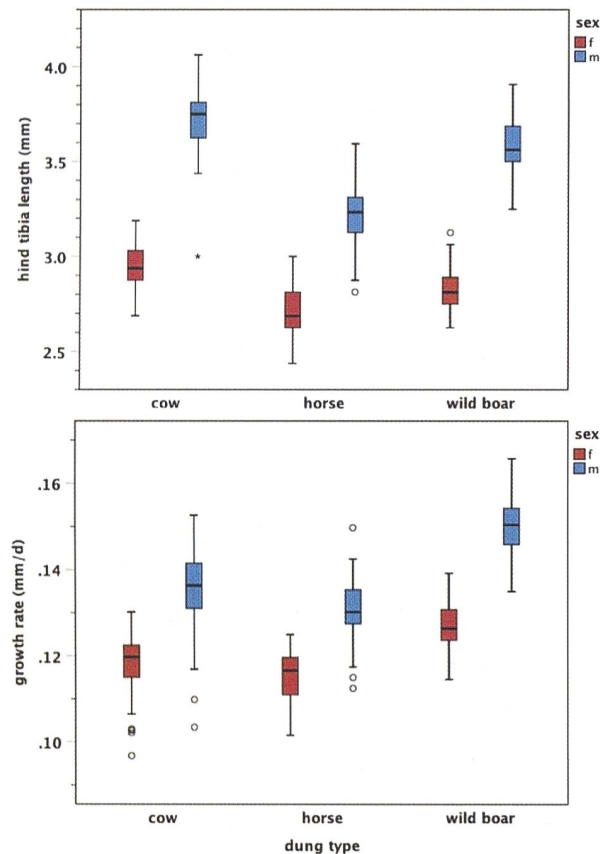


Figure 2. Box plots for hind tibia length (top) and linearized growth rate (tibia length/day) of yellow dung fly females (red) and males (blue) raised on three types of mammal dung.

Discussion

We here compared the life history performance of yellow dung fly larvae in overabundant dung of various large mammals, wild or domestic, in the laboratory to investigate presumed domestic cattle dung specialization of this species. In essence, we found some variation in juvenile survival, roughly between 73% and 93%, among the various dung types tested (cow, horse, wild boar, red deer). Nevertheless, the overall survival average of $80\% \pm 2.4\%$ (SE) found here corresponds to the long-term average and range typically observed in the laboratory in unmanipulated cow dung (Blanckenhorn et al. 2010; Fig. 1).

Although power analysis indicates that an increase in sample size by ca. 50% (from 65 to 100) would render the overall dung type variation in juvenile mortality obtained significant, with some pairwise comparisons also differing significantly (e.g. boar vs. red deer dung; Fig. 1), we judge this variation minor relative to that typically induced by other environmental stressors (dung limitation, heat, drought, etc.; Blanckenhorn 1998a, 2009) and, importantly, not in accordance with our tested main hypotheses specified in the Introduction.

The body size of emerged flies also varied somewhat among the various dung types (Table 1; Fig. 2), but again was well within the range of what is typically observed in the field or the laboratory at overabundant cow dung, and large in comparison to situations when dung (i.e. food) is limited (Amano 1983; Blanckenhorn 1998a; Blanckenhorn et al. 2010). Somewhat unexpectedly, juvenile development was longest in cow dung to however result in the largest adult flies, while flies emerged smallest in horse dung (Figs 1, 2). Probably the best indicator of success, growth rate – calculated crudely as tibia length increment per day of juvenile development – was fastest in wild boar dung, nevertheless resulting in relatively small adults (Fig. 2). That is, as observed before in cattle dung, growth and development varied flexibly in response to environmental factors, here dung type, so as to affect the life history of the species presumably in an adaptive manner, with recognized consequences for survival and reproduction (Blanckenhorn 1998a, 1999, 2009; Jann et al. 2000; D'Amico et al. 2001; Rohner et al. 2017). We therefore conclude that yellow dung fly juveniles grow and survive reasonably well in the dung of all vertebrates tested here.

As the amount of dung available was more than sufficient in all cases, i.e. not limited in terms of quantity, we here tested for physiological (digestive) responses of yellow dung fly larvae to presumed variation in dung quality mainly depending on the food and/or digestive system of the various mammals considered (in consistency, dryness, particle size, bacteria or fungi content, specific nutrients, etc.; Frank et al. 2017). For instance, the proportion of water (\pm SE) of the different dung types used was previously estimated as $0.81 (\pm 0.001)$ for typical cow, $0.77 (\pm 0.013)$ for horse, $0.69 (\pm 0.007)$ for red deer, and $0.71 (\pm 0.003)$ for wild boar dung ($P < 0.01$; Laux et al. 2019), which likely differentially affects the ability of dung fly larvae to move in and digest their food. We judge the typical variation between the sexes in growth trajectories (significant sex-by-dung type interactions in all performance variables in Table 1) of this species with strong sexual dimorphism (males larger) as mainly reflecting size scaling rather than differential physiological responses to the food source (Blanckenhorn 1998a, 2009; Rohner et al. 2017). It was already previously well documented for yellow dung flies that (cow) dung limitation, typically mediated by high intra- or inter-specific competition of larvae in the food resource, strongly reduces larval survival and final body size of the emerging adults (Amano 1983; Blanckenhorn 1998a, 1999, 2009; Jann et

al. 2000; Blanckenhorn et al. 2010). The finer-scale variation in survival, growth, development and final body size obtained here (Figs 1, 2; Table 1) most likely reflects differences in dung consistency and the nutritional value of the dung microbiome of the various mammals tested, but this remains to be investigated further in detail.

At least in species whose immatures are poor dispersers, choice of oviposition site by the mothers plays an additional major role. A female's choice of oviposition site may be innate (Barron 2001; Dormont et al. 2010), but should generally evolve to maximize juvenile performance (Wiklund 1975; Fox and Czesak 2000; Forister 2004; Gómez Jiménez et al. 2014; König et al. 2016). In addition to dispersal ability, other factors, such as optimal foraging of gravid females (Forister et al. 2009), may lead to suboptimal outcomes. A next investigatory step would therefore be testing oviposition preferences of gravid females in choice experiments, which we would expect to correlate with the performance ranking indicated by the various life history traits tested here (Figs 1, 2; see e.g. Laux et al. 2019).

Most likely, our study signifies that yellow dung flies are opportunistic in their choice of dung depending on availability in their environment, given their good performance on many different types (qualities) of dung/food documented here (Holter 2016; Laux et al. 2019). Thus, flies may reproduce on deer or boar dung when in the forest, or alternatively on cow, horse or sheep (Hirschberger and Degro 1996) dung when in grasslands, readily switching between these habitats depending on site and weather (Blanckenhorn et al. 2001). In Swiss lowland pastures interspersed with agricultural areas and forests there may be more alternative livestock substrates available than in highland grasslands. While in the Alps cows and sheep abound up to the treeline at roughly 2000 m, wild animal dung (deer, ibex, mountain goat, some carnivores, etc.) should be relatively more abundant there, again permitting easy switching between various dung types. Longer winters shorten the growing season and extend winter diapause of dung fly pupae in the Alps, but should not strongly reduce fly mortality and population density (see Blanckenhorn 1998a, b). As yellow dung flies are cold-adapted in general (see Introduction), flexible oviposition substrate can explain the ubiquity of this species in low- and highland Europe unless temperatures become excessive (e.g. in the Mediterranean; Blanckenhorn et al. 2001, 2018; Scharf et al. 2010).

Even though we here tested merely a small subset of all dung types available in nature, we conclude that yellow dung flies can reproduce successfully on multiple types of mammal (vertebrate) dung, wild or domestic, herbivore or omnivore (and likely also carnivore). At least their reproductive fitness does not strongly deviate from that observed in cattle dung (summarized in Blanckenhorn 2009). Yellow dung flies are therefore probably rather dung generalists than specialists. This dung fly species is widespread presumably because they could plastically shift to dung of common herbivorous livestock species after their domestication, without losing the ability

to reproduce on dung of common wild mammals (cf. Blanckenhorn et al. 2018). The yellow dung fly *Scathophaga stercoraria* thus definitely belongs to the minority of insect taxa that benefit from humanity's agricultural activities (e.g. Loboda et al. 2018), and which therefore are not of special conservation concern.

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Supplementary material 1

Data file corresponding to the submitted paper

Authors: Wolf U. Blanckenhorn, Dieter Burkhard

Data type: xlsx

Explanation note: Individual trait values for male and female yellow dung flies: developmental duration, tibia length, growth rate.

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