There is no such thing as an herbivore: incidental and intentional ingestion profoundly affects both herbivores and plant-dwelling invertebrates.

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Abstract:

Real-life ‘herbivores’ are not the herbivores of our simplistic ecological and behavioral models – real-life herbivores constantly consume other organisms both incidentally and intentionally, with the ‘prey’ usually consisting of plant-dwelling arthropods, smaller invertebrates, and carrion. A remarkable amount of disparate literature has amassed on these phenomena, yet the implications of these interactions are rarely considered, despite their potential importance. Here I argue that to fully understand behavior, morphology, and coloration of insect-dwelling arthropods, as well as of that of ‘large’ herbivores (whether arthropod or vertebrate), these important interactions must be considered. This perspective has two aims. The most important is to encourage researchers working on herbivores and plant-dwelling invertebrates to think more broadly about what is ingested, and what is not ingested, and why. The second is to propose several hypotheses about these interactions shape the morphology, behavior, and chemistry of these organisms. Specifically, I propose that aposematic and masquerade phenotypes, escape behaviors, feeding and pupation location, survival of gut passage, and aggregative behaviors, most of which are thought to be driven by predators, may be also driven by incidental ingestion. Lastly, to draw attention to the role that inclusion of animal food into a phytophagous diet may play in niche space, competitive interactions, and organismal nutrition. I ultimately hope this perspective encourages many creative new lines of research on the broadened phenomenon of ‘herbivory’.

Keywords: Herbivory, omnivory, aposematism, insects, ungulates, parasites, intraguild predation, mimicry

Introduction:

Much of community ecology and organismal evolution is built on the intuitive idea of discrete trophic levels – producers, primary consumers, secondary consumers, and so on – despite long-time recognition that further complexity, including omnivory at many scales, is the rule, not the exception (Clausen 1940; Elton 1953; Polis et al. 1989; Richardson et al 2010; Gish et al. 2017). Certain types of trophic omnivory, such as intraguild predation among predators (Polis et al. 1989), are well-studied and have accrued solid theory in order to make predictions. However, trophic omnivory by 'herbivores' has not attracted the same attention and yet, it has far-reaching implications. Herbivores are an integral link in terrestrial, aquatic, and marine communities and rightfully the subject of much work in ecology and evolution. The simplistic view that herbivores eat only plants is fundamentally incomplete for four ecologically- and evolutionarily- important reasons:

(1) Incidental ingestion of non-plant material. Herbivores, both large and small, constantly consume smaller organisms during feeding. The consumer is usually unaffected (an amensalism), but may be affected negatively when the consumed organism is toxic or a parasite. More profoundly impacted are usually the ingested organisms; many of which have highly specialized behaviors and morphologies which reduce the chance of consumption.

(2) Behavioral avoidance of incidental ingestion of non-plant material. Certain herbivores have remarkable behaviors that pre-empt ingestion of smaller organisms. These behaviors prolong handling time, reduce consumption rate, and are even expressed in naïve young herbivores, which are strongly suggestive of past selection against incidental ingestion of toxic, irritating, nonnutritive, or distasteful organisms.

(3) Intentional ingestion of non-plant material. From deer, cattle, and beavers to caterpillars and caddisflies, normally herbivorous animals commonly seek out animal tissue through opportunistic scavenging and direct predation. These consumptive behaviors have important implications, such as survival in nutrient-limited environments, elimination of competitors, potential niche expansion, and macroevolutionary shifts in diet. While scavenging cannot affect prey populations, intentional predation by 'herbivores' may have broader population and community-wide consequences, as well as inform our understanding of large-scale macroevolutionary diet switches.

(4) The existence, ubiquity, and importance of micro-organisms. With every bite of a plant, an herbivore takes in untold numbers of microbes, each of which may be beneficial, pathogenic, or neutral; Janzen (1977) persuasively suggests that incidental ingestion selects for nutrient degredation, toxicity, or in those organisms – an analogous argument to those made here. However, the inclusion of micro-organisms is a topic is far is too broad for this review, though it has myriad effects on herbivory and life-history of those microbes.

These four often-ignored interactions lead to interesting short- and long-term implications for both the herbivorous consumer and the potentially-consumed that would not be predicted by our currently trophic position centered paradigms. Table 1 lists several examples of our current paradigm and hypotheses informed by a more accurate consideration of herbivory that would add to – not replace – our knowledge of those phenomena.

I do not mean to overturn well-established ideas about predation, coloration, and more, instead, just to broaden the discussion around these topics. The current paradigmatic thinking is extremely useful – herbivores do primarily eat plants and have driven the evolution of both direct and indirect plant defenses; predators are a larger source of mortality for plant-dwelling arthropods than herbivores are, etc. – yet, there is much to be gained from a broader perspective. However, recognition of non-plant food is necessary for a fuller understanding of the ecology and evolution of both 'herbivores' as well as plant-dwelling arthropods and propose testable hypotheses where this broader consideration could enrich our current knowledge.

Incidental ingestion of non-plant material

Incidental ingestion of plant dwelling arthropods and other invertebrates (including nematodes, mollusks, annelids, and platyhelminths) by other herbivores is ubiquitous. Most studies on the topic have noted, and even occasionally quantified, large mammalian herbivores eating insect herbivores while ingesting plant material. Gish et al. (2017) provide an excellent review of ungulate ingestion of plant-dwelling arthropods. They call for increased quantification of the frequency and factors that affect incidental ingestion (Gish et al.'s Figure 1). Yet, incidental ingestion includes much more than just the ungulate herbivores discussed by Gish et al; arthropod and molluscan herbivores are consuming smaller invertebrates still, especially when size discrepancies are quite large (e.g. nymphal mites consumed by relatively 'gigantic' caterpillars: Shirotsuka and Yano 2012; caterpillars of all sizes commonly consume insect eggs, small leaf miners, and other immobile insects while feeding; pers. obs.). This phenomenon also extends far beyond the terrestrial environment; both marine and freshwater manatees ingest many invertebrates while feeding on plant-material, though they likely do not gain nutritionally from it (Guterres-Pazin et al. 2018; Allen et al. 2018). Waterfowl ingest large numbers of invertebrates incidentally with aquatic vegetation (Conde-Porcuna et al. 2018; Barboza et al. 2022). Herbivorous fish commonly ingest large amounts of detritus and animal material; Clements et al. (2009) argue that because of this phenomenon, these fish, "commonly categorized as herbivores… are functionally distinct from herbivores". I strongly encourage reading Gish et al.'s review with an expanded view of its relevance (both to the micro-scale and into aquatic realms). Here I will conceptually build upon Gish et al.'s persuasive argument of the ubiquity of incidental ingestion by making broad, testable, ecological and evolutionary hypotheses about the impact of this consumption on different guilds and bringing further attention to its ubiquity and impact.

Incidental ingestion as an evolutionary driver of arthropod behavior, morphology, and populations

Whether consumed by a predator or herbivore, the eaten organism is equally dead. Any traits – morphological, physiological, or behavioral – that lessen consumption by either these 'true' or incidental predators are likely to be selected on. Therefore, it is unsurprising that we have several strong examples that incidental ingestion shapes plant-dwelling arthropod behavior (i.e. Ben-Ari et al. 2019), though much more work is necessary to capture the true importance of these interactions.

Below, I discuss how incidental ingestion could contribute to patterns of herbivore behavior and morphology that are usually ascribed to completely to selection by predators (see also Table 1). Incidental ingestion is probably rarely more important than predation in determining some of the below patterns, but the few examples known do show its potential importance. Additionally, many of the same defensive traits could protect against both predators and herbivores, and overall, both factors likely contribute to the selective environment shaping the behavior and morphology of plant-dwelling arthropods.

The effect of incidental ingestion on populations of plant-dwelling arthropods

Although the effects of predation and intra- and interspecific competition on plant-dwelling arthropod populations have been long-studied, incidental ingestion is rarely considered as a factor contributing to population dynamics. However, it may cause large amounts of mortality for some species (e.g. Van Noordwijk et al. 2012) and even when the herbivores do not incidentally consume plant-dwelling arthropods, they may incidentally kill them (Berman et al. 2018) or cause them to move away from host plants (Gish et al 2010). Large mammalian herbivores generally cause declines in herbivorous arthropod populations (Takagi and Miyashita 2014; Foster et al. 2014). These declines could be driven by several processes, usually invoked are resource competition, alterations of habitat, and induced changes in host plant chemistry, though the relative contributions of these processes and incidental consumption cannot be determined with standard experimental designs (i.e. herbivore exclosures). Herrera (1989) argued that incidental consumption drove lower populations of seed-predator beetles in areas with ungulates, which functioned more as incidental predators than competitors in his system. Tellingly, it is not only herbivorous arthropods that suffer. Other plant-dwelling arthropods (i.e. spiders; Foster et al. 2014), decline, too – possibly due to habitat or prey reduction, but these too are incidentally consumed by large herbivores. While totally unstudied, there is no reason that insect herbivores would have a different effect; indeed, total defoliation, such as occurs regularly from the caterpillar *Lymantria dispar* in the Northeastern United States (Davidson et al 1999) is of a greater magnitude than ungulates could do, further, it may extend from ground to canopy in forests; those caterpillars surely consume nearly every leaf miner, arthropod egg, or small immobile stage during that defoliation.

Any effects are almost certainly mobility, stage- and size-specific. For example, flying adult Lepidoptera, flies or beetles are less likely to be consumed than larvae, which are less likely still than eggs. I can find no quantification of incidental mortality on insect eggs, but it has been repeatedly noted and suggested as important (Lu and Samways 2002; Armstrong and Louw 2013; Robertson and Baltosser 2018). Nordkvist (2020, 2023) modelled that moose incidentally consuming sawfly eggs during browsing had the potential to alter population dynamics of the sawfly. While it seems likely that this incidental mortality would largely be non-targeted – truly incidental - especially of tiny insect eggs, outbreak situations where little or no host plant material remains and eggs or larvae are concentrated on that which remains (e.g. for checkerspot butterfly caterpillars: Bowers and Schmitt 2013) could very produce strong density-dependent mortality. Furthermore, consumption could affect female oviposition decisions when consumption is predictable and obvious, though we can find no studies examining it. Testing the importance of mortality could employ sentinel egg masses or clay caterpillars integrated into a population model parameterized with stage-specific mortality from other sources.

Location of feeding may determine relative importance of incidental ingestion

Where an arthropod herbivore feeds has long been known to determine its susceptibility to different guilds of mortality (Hawkins et al. 1997), though incidental ingestion is rarely considered. It is likely that these effects are especially acute for internally-feeding herbivores, which cannot escape. Herrera (1984) found that insects which fed on the surface of fruits avoided ripe fruits in areas of high frugivory; yet internally-feeding insects, as many seed and fruit feeders are, are particularly susceptible to consumption by frugivorous organisms, many of which are birds and non-ungulate mammals. A majority of fruit fly larvae (up to 77%) were ingested by vertebrate frugivores consuming the host fruit (Drew 1987; Wilson et al. 2012; for fruit-feeding beetles: Or and Ward 2003; Bonal & Muñoz 2007). Indeed, decaying flower-feeding *Drosophila* lay only 13% of the eggs of their closely-related fruit-feeding kin; assuming relatively constant populations, a higher survival rate of larvae must occur on this non-frugivore consumed source (Ishikawa et al. 2022). Ungulates consumed ~20% of gall makers and 17% of seed predators of a wallflower (Gómez and González-Megías 2007). Indeed, squirrels may even target acorns with weevils in them, and both avian and mammalian frugivores may target insects in fruit (Davis 1907; Drew 1987; Or and Ward 2003). Because of the risk of incidental ingestion, it seems likely that internally-feeding herbivores would evolve strategies to avoid this source of mortality.

The simplest anti-predation strategy, if one may call it that, is passively altering the nutritional content, or ripeness, of the host and advertising that change (Janzen 1977; opposite of the leaf apparency hypothesis of Smith 1986). Delayed ripening, obvious feeding damage, or premature abscission before ripening, may deter frugivores (see Janzen 1977 for a review). Traveset et al (1995) found that birds avoided irregularly shaped blueberries; that deformation, due to moth and sawfly feeding, acted as a visual signal to pre-empt incidental ingestion and increased the survival a results consistent with the negative correlation between insect infestation of fruit and bird fruit removal found by Jordano (1987). Leaf miners, leaf suckers, and gall makers usually strongly change the appearance of the tissue on or in which they feed, again creating a strong visual signal (see Lev-Yadun and Inbar 2023). The white or brown blotch of a leaf mine is highly apparent and this apparency may account for the avoidance of leaf mine tissue by herbivorous insects (Figure 1; C. Eiseman, pers. comm.). I can find no studies which test whether mined leaves are consumed less frequently by browsers; experimental approaches of making false mines or masking the color of a real mine would be powerful ways to determine whether discoloration reduces incidental ingestion (also suggested by Yamazaki 2010).

Other behaviors or life-history strategies that prevent incidental ingestion occur as well. Insects feeding on ripe fruit are limited both by the lifespan of the fruit, as well as the risk that it will be consumed by a larger frugivore and they will be ingested. A well-established hypothesis for trade-offs in insect life-history – the "slow growth high mortality hypothesis" (Feeny 1976) – posits that slower growing organisms are more likely to be consumed and that increased consumption should select for faster development (Benrey and Denno 1997, Singer et al. 2012). For ripe fruit-feeding insects, we can reasonably expect that if ripe fruit are consumed at a faster rate than other resources (and those insects slow or stop the process), those species will both (1) speed up their development compared to species feeding on immature fruit or other resources (i.e. mushrooms) less likely to be consumed by incidental consumers, and (2) conduct no other life-stage (i.e. pre-pupal or pupal period) in the fruit. While the ephemeral, and occasionally-consumed, nature of non-fruit feeding *Drosophila* substrates (mushrooms, rotting flower tissue) makes larval period comparisons difficult, three unrelated *Drosophila* species which feed on microorganisms on land crabs have particularly prolonged larval periods (Carson 1974). Also consistent with a minimization of time in the fruit, larvae of ripe-fruit feeders (i.e. *Anastrepha, Ceratitis*, *Drosophila*, *Rhagoletis*) leave the fruit immediately upon cessation of feeding and pupate elsewhere, often in the soil (Guillén et al. 2002, Ajula et al. 2005, Renkema et al. 2012; Woltz and Lee 2017). This behavior occurs despite heavy risk of predation by ants and beetles after leaving the fruit, yet little risk of predation inside the fruit, a decision Ajula et al. (2005) is driven by vertebrate fruit consumption. Many non-frugivorous, externally-feeding caterpillars, fly, and beetle larvae also leave host plants to pupate in the soil or other protected places, including prickly nonhost plants (Grof-Tisza et al 2015), behaviors which also could reduce consumption by herbivores, though also surely ameliorates environmental stressors and risk of parasitism and predation.

Additional life-history strategies can reduce the chance of incidental ingestion. Galls may also cause unpalatability of the plant to other herbivores, probably protecting the gallmaker from incidental ingestion (Kurzfeld-Zexer and Inbar 2021). This unpalatability is probably due to upregulation of chemical defenses, famously tannins in many galls on willows and oaks (Nyman and Julkunen-Tiitto 2000; Foss and Rieske 2004), which may also affect the color, signaling the unpalatability (Lev-Yadun and Inbar 2023). The concentrations of putative defensive compounds in plant tissue are unlikely to affect predators or parasitoids, at least directly, suggesting that these do not reduce chances of more traditional predation (and indeed, a conspicuous color could increase that risk). While increased concentrations of defensive compounds in gall tissue (especially outer gall tissue) have been suggested to protect against fungi (Taper and Case 1987), it also seems likely that it would minimize the chance of incidental ingestion because of its unpalatability, after all "defensive" in this case usually refers to reducing herbivory on the plant (Lev-Yadun and Inbar 2023). Many skippers in the subfamily Hesperiinae, especially in prairies, form nests on the base of culms of graminoids. These nests are often virtually underground and this location presumably protects them from grazer ingestion, even when the plant is clipped near to the ground. Examining distributions of patterns of herbivores or plant tissue removal patterns (galls, mines, nests, fruits, seeds) in areas without herbivore pressure (e.g. deer exclosures, or more powerfully: ungulate-free islands), versus areas with herbivore pressure allows a test of whether the distribution minimizes potential for incidental ingestion and can be easily accomplished.

Evolution of avoidance or escape abilities to prevent incidental ingestion.

If incidental ingestion were an important selective force, one could reasonably expect to find arthropods with behaviors that pre-empt this ingestion. Organisms may perceive other herbivore cues and avoid areas that would subject them to incidental ingestion. Gall makers may avoid ovipositing in areas on plants more likely to be eaten by goats (Zamora and Gómez 1993). Large caterpillars indiscriminately consume leaves with or without spider mites, leading to much incidental ingestion of immobile and less mobile stages (Shirotsuka and Yano 2012). Yet, more mobile mites detect and avoid chemicals left by large silk moths, an incidental consumer of the mites (Kinto et al, preprint). Even the best avoidance behaviors do not guarantee success and therefore, escape behaviors – also useful against predators – could evolve to deal with incidental ingestion. Though spider mites have previously been shown to use predator odors to trigger escape behaviors, mobile stages also used escape behaviors when large caterpillars began consuming the leaves they were inhabiting (Shirotsuka and Yano 2012). Gish et al. (2010) found that the humidity and warmth of sheep breath caused dropping of >50% of aphid individuals from food plants. This behavior is not confined to a single species. Over 75% of individuals across different aphid species were able to escape consumption of their host plant by dropping off (Gish et al. 2011). Further research showed that aphid biotypes locally adapted to legumes that are more palatable to ungulates the dropping escape response was more pronounced than from biotypes adapted to less-palatable legumes (Ben-Ari et al. 2019). Nor is it confined to aphids, predatory ladybird beetles respond to mammalian breath in the same way (Ben-Ari and Inbar 2013). While predation and incidental ingestion are different from our perspective, they are the same for the consumed. Nonetheless, the cues differ greatly – the aphid dropping behavior detailed above would not be triggered by a predatory beetle or lacewing larva; a large caterpillar about to incidentally consume a mite would give different cues entirely (visual, chemical, or vibrational). How prevalent these specialized escape and avoidance behaviors to avoid incidental ingestion, and how they differ or do not differ from those employed to avoid predators, are would greatly inform our understanding of the selective pressure that ‘herbivores’ exert on their unlucky prey.

The finding that aphids on less-palatable legume species had a reduced escape response (Ben-Ari et al. 2019) suggests the intriguing possibility that absence of incidental ingestion – not just predation – could also cause an evolutionary loss of escape behavior and, perhaps, mobility more generally. Insects have repeatedly evolved loss of flight and reductions in movement, especially on islands. Suggested drivers of this loss include diverse biotic and abiotic factors including predator release, wind speed, temperature, habitat stability, competitor release and more (Wagner and Liebherr 1992, Leihy and Chown 2020). In a remarkably comprehensive analysis of flightlessness across insects Leihy and Chown (2020) found that flightlessness is more prevalent in subantarctic islands than arctic islands. They tested predator release by analyzing insectivore richness as a predictor. However, all but one of the arctic islands they analyzed – Bathurst, Ellef Ringes, St. Matthew, Svalbard & Jan Mayan - have native mammalian grazers, whereas none of their subantarctic islands, with higher rates of flightlessness, do. Wagner and Liebherr (1992) further note that in non-island environments flightlessness of insects is common in inland and coastal dunes, salt marshes, and high montane environments, all of which also may have low densities of large herbivores. While it is unlikely that mammalian grazers would be the primary driver for a great many losses of flight, the aphid examples demonstrate the remarkable effects that incidental ingestion can have on intrinsic escape behaviors and make this hypothesis worthy of greater exploration.

Aposematism as a defense against herbivores

Aposematism – warning coloration advertising unpalatability – is well-studied empirically and theoretically and is usually considered solely in the context of predators (i.e. Stevens and Ruxton's [2012] excellent review). However, I suggest here that a broader consideration of the effect of aposematic coloration on incidental ingestion may have value in considering behavior of aposematic animals. Further, it could help resolve the long-standing evolutionary paradox of how aposematism increases when rare. When aposematic coloration is rare in populations and only driven by predation, there should be selection against it due to the inability of predators to associate the cue with unpalatability (Grabovskii 2012). However, if aposematism deters herbivores, especially naïve ones (e.g. Berman et al. 2018), from consuming the aposematic prey, it present a solution to how this trait is initially selected for.

Of note is that despite large numbers of plant-dwelling invertebrates are consumed incidentally by large herbivores, yet, as will be discussed later, those large herbivores will occasionally go to great lengths to avoid consuming certain insects on foodplants (Berman et al. 2017, 2018). This behavior is probably driven by unpalatability or toxicity. Unpalatability is relative and herbivores may be less tolerant of animal toxins than predators are. Predators and prey may be involved in arms-race dynamics, but it is highly unlikely that herbivores are. Even highly toxic chemicals, like cantharidin found in blister beetles (Meloidae), does not stop their consumption by diverse insectivores – lizards (Cohen and Cohen 1990), birds (Heneberg 2016), frogs (Eisener et al. 1990) and many predatory and parasitic insects (Young 1984). However, cantharidin poisoning from consumption of blister beetles in hay fed to domestic cattle and horses can cause mortality and morbidity (Capinera et al. 1985; Ray et al. 1990). For this reason, aposematism may be a universally honest signal to pre-empt incidental ingestion by herbivores. Therefore, the initial benefit of apparency to herbivores may allow aposematism to reach a threshold where the effect on predation could allow it to more likely to go to fixation in populations.

Furthermore, incidental ingestion might select for different behaviors in aposematic prey than predators would. Many toxic, aposematic caterpillars perch conspicuously on host plants; conspicuousness, either both color or location, may be costly because of increased predation from specialists or naïve predators (Barnett et al 2016). Other factors – such as temperature and availability of resources – may also play into this calculation, and conspicuousness may allow better recognition by predators as well (Nielsen and Mappes 2020). A conspicuous location would also make them more apparent to herbivores. Since many aposematic insects aggregate in conspicuous locations, this detectability would be compounded to either predator or herbivore (Mappes et al 2005, many examples in Cott 1940). Examining effects of coloration, conspicuousness, and aggregation on herbivore foraging decisions would again be possible using clay caterpillar models.

Aposematism need not be coloration of the organism itself; many internally-feeding herbivores create highly conspicuous markings. Galls are formed of plant tissue through a complex interplay of insect and plant physiology, but often have higher concentrations of toxic chemicals. Many are brightly colored, conspicuous and avoided by insect herbivores (Kurzfeld-Zexer and Inbar 2021). In fact, Inbar et al. (2010) and Lev-Yadun and Inbar (2023) suggest this coloration is aposematism not only against predators but also against incidental ingestion by herbivores. This possibility, including quantitative comparisons of the contrast between the gall and the background using realistic animal visual system models, ought to be investigated in more detail, as the diversity and conspicuousness of gall and mine forms is astounding.

Interestingly, specific types of herbivory could be a path to consumption of toxic, aposematic insects in very specific cases. Frugivorous birds which more commonly feed on toxic fruit include toxic insects in their diet more often than species which consume fewer – or no – toxic fruit (Herrera 1985). If Herrera's finding is broadly true, it may permit a very clever test of the selective pressure exerted by predators and herbivores. Herbivorous insects may be toxic due to consumption of plant toxins (sequestration) or synthesis of unique toxins. Any herbivore eating the toxic plant would likely have some degree of tolerance of sequestered toxins; however, a generalist predator would not. Therefore, if aposematism is found to have an equal or greater prevalence or more pronounced visual contrast with vegetation in toxin-sequestering species than in toxin-synthesizing species, it is more likely that predatory pressure drives the phenomenon. Conversely, if toxin-synthesizing species are more likely to be aposematic or have a greater visual apparency, this would be consistent with incidental ingestion driving the pattern. Large-scale comparative investigations of coloration such as Robinson et al. (2023) could be integrated with the detailed chemical data available for certain lepidopteran groups (i.e. the Arctiinae) in order to answer to test these predictions.

Masquerade as a defense against herbivores:

Mimicking the appearance of something else, masquerade, allows many arthropods to avoid consumption by predators (e.g. Liu et al. 2014). It is also possible that certain instances of masquerade are also effective at preventing incidental ingestion. One particular, repeatedly evolved, instance of masquerade on foliage inhabiting arthropods is mimicry of bird feces (suggested as antiherbivory for leaf mines by Yamazaki 2009; also see Cott 1940). This has evolved many times, including in spiders, beetles, moths, leaf-mining fly larvae, wasps, treehoppers, and caterpillars (e.g. Minno and Emmel 1992, Auko et al. 2015, Suzuki and Sakuria

2015; also see Cott 1940). These mimics do not smell like feces (but see Auko et al. 2015) and therefore, this masquerade is likely not particularly convincing against parasitoids, ants, and other chemosensory predators. However, it has the potential to be be highly effective deterrence against incidental ingestion by larger herbivores. While no research has explicitly examined this question, fecal recognition and avoidance occurs in vertebrates and invertebrates. Mammalian herbivores have strong fecal avoidance, probably driven by the risk of acquiring parasites, though this has been tested mostly for mammalian feces (Cooper et al. 2000; Ezenwa 2004; Chubb et al. 2020). Insects, too, may avoid conspecific and heterospecific predator feces (e.g. Agarwala et al 2003; Zhang et al 2019). Results demonstrating avoidance of both bird poop and bird-feces-mimicking caterpillars (or artificial bird feces) by herbivores would be consistent with avoidance of ingestion contributing to these masquerade phenotypes. Other instances of masquerade may also be effective, mimicking stem or midvein prickles is common in treehoppers. Prickle-mimicking could visually deter herbivores as the mimicked plant prickles do successfully (Cooper and Owen-Smith 1986, Gontijo et al. 2019). Many prickle-mimicking treehoppers aggregate, which makes unoccupied branches of the same plant appear less defended and possibly direct herbivore feeding towards them, minimizing risk to the aggregating treehoppers. Again, model treehoppers could be employed to test whether these aggregations function to minimize incidental ingestion.

It is worthwhile to consider that both aposematism and masquerade rely on apparency; in contrast, crypsis of plant-dwelling arthropods could increase the risk of incidental consumption, especially when not coupled with other either avoidance or escape behaviors.

Aggregations to increase signal to herbivores

Many plant-dwelling insects, including both herbivores and predators, have conspicuously clumped distributions at plant or within-plant scales (Cornelisson and Stiling 2008, Miñarro and Jacas 2011, Aparicio et al. 2015). Aggregation can decrease per capita predation on plant-feeding insects (Turchin and Karieva 1989; Dittman and Schausberger 2017), though predators may also concentrate at aggregations, leading to higher per capita predation at higher density (Kareiva and Odell 1987; Losey and Denno 1998, Evans 2003, Singer et al. 2012) and aggregations may lead to nutritional benefits or costs (Karban and Agrawal 2002). As mentioned above, aposematic or masquerade phenotypes (morphology or behavior) may be more effective at preventing incidental ingestion when the individuals are aggregated by increasing signal intensity. We do not have a full understanding of the cues that herbivores – large and small – use to avoid ingesting smaller arthropods when they avoid them. However, whatever the cues are – some combination of visual, tactile, chemical/olfactory, or auditory – they will be amplified by associations with conspecifics. The benefit, however, may not be solely from the amplification, it may also be a sampling effect. Goats that reject leaves after contacting webworm caterpillars (Berman et al. 2018) could be reasonably expected to switch host plants if contact rate becomes too high. This increased contact rate would be different in mechanism from signal amplification, but both could operate and reduce incidental ingestion, and both would favor aggregation over dispersion. Manipulating densities of incidental prey is a straightforward way of testing this hypothesis.

Direct defense against incidental ingestion: survival of it and dispersal implications

The preceding sections all assume that incidental ingestion is fatal to the ingested organism, and this mortality provides a selective pressure to pre-empt it. In stark contrast to that, some plant-dwelling organisms have evolved morphologies or behaviors that simply allow them to pass through the guts of herbivores unharmed. This phenomenon is well-reviewed by Hernández (2011) for fruit- and seed-feeding insects, as well as their parasitoids, which sometimes make a successful journey as well. Many of these feed or shelter within the seeds of fleshy fruit and use the seed coat as the protective layer, as seeds of fleshy fruit are themselves often adapted to gut passage (Hernández 2011). However, gut passage survival is not confined to organisms inhabiting seeds or fruit: aquatic mollusks can survive gut passage through waterfowl (van Leeuwen et al 2012) and fish (Brown 2007), and many foliage-dwelling arthropods can survive an avian or mammalian gut passage (e.g. Guix and Ruiz 1997; Laux and Kolsch 2014), and indeed, may be a mechanism for dispersal.

After successful gut passage, it is likely that the incidentally-consumed organism is in a different place than when it began. I can find no exact estimates of distance moved, but Guix and Ruiz (1997) suggest that guans (frugivorous birds) move around 3-7 hectares each day, and over 15% of weevil-containing-seeds (with 100% survival of gut passage) spent more than 10 hours in the gut. Laux and Kolsch (2014) argued that the widespread distribution of an aquatic leaf beetle is due to dispersal by ducks (also suggested for snails: van Leeuwen et al 2012). Though survival rates of the eggs were low, the ducks may ingest hundreds of eggs per feeding bout and a small percentage of them survived 8 hours in the gut. Lin et al. (2021) demonstrated that the eggs of island-dwelling flightless weevils survived gut passage at high rates (83-100%) and conclude this is the most likely method for repeated colonization of islands by this group. These studies suggest that incidental ingestion has the potential to profoundly shape both landscape- and large-scale distribution patterns. There are a great many systematic studies of endozoochory of plants, usually by germinating mammalian or bird scat; determining the invertebrate composition would be both logistically feasible and extremely informative.

Avoidance as an evolutionary driver of herbivore behavior

If there is a large enough cost to incidental ingestion (be it toxins, irritants, low nutritional value, parasites, etc.), selection should alter behaviors or morphology of the herbivore to minimize this cost. Herbivores, especially folivores, need to consume relatively amounts of food. At optimal temperatures *Manduca* caterpillars consume more than their body weight per day (Kingsolver and Woods 1997). Unsurprisingly herbivores ingest a great diversity of animal material in the process (for ungulates: Berman and Inbar 2021). Incidental ingestion of various small arthropods can be costly, or even fatal, to larger herbivores directly, through toxicity or indirectly, as intermediate hosts of parasites (Capinera et al. 1985; Ray et al. 1990; Webb et al. 2004). Therefore it is unsurprising that large mammals, including both goats and cattle have evolved remarkable avoidance behaviors, and their presence in naïve young indicates that these behaviors are intrinsic (Berman et al.. 2017, 2018, 2019a,b). Berman (2019a) demonstrated that the presence of unpalatable caterpillars on plants – and the threat of incidental ingestion – altered preferences of goats away from plants with these the caterpillars. These studies show that detriment from incidental ingestion can cause evolved behaviors of non-consumption in large herbivores.

Furthermore, while strongly implied by the existence of these remarkable behaviors, the costs of accidental ingestion have not been explored. Therefore, understanding foraging decisions requires understanding the balance of these time-consuming avoidance behaviors with the costs of accidental ingestion of potentially harmful prey. This would give us great insight into a new, and important aspect, of herbivore foraging behavior that is exhibited not just by ungulates, but also by insect herbivores (Figure 1). The avoidance, however, may not be due solely to a risk, as suggested earlier, a correct perception of lowered nutritional quality could drive avoidance behavior as well. These avoidance behaviors may have broader consequences, as well, perhaps affecting intra-plant patterns of herbivory or competitive outcomes between herbivores of different sizes.

Avoidance of incidental ingestions as a community structuring force

If herbivorous animals can recognize plant-dwelling arthropods directly or indirectly (i.e. through damaged leaves; Heinrich and Collins 1983), their presence may alter foraging decisions and have cascading indirect effects. Berman et al. (2018) found that goats strongly preferred foliage without caterpillars on it; they initiated feeding more slowly and dropped leaves which had webworms on them. These potential effects could take myriad forms, altering competitive outcomes between plants, changing population growth rates, altering higher trophic levels (predators or parasitoids of the arthropods on any of the plants) and more. Whether any of these effects occur, and whether commonly or rarely is unknown, but if suspected can be tested, using simple methods. Many recent studies have employed a clever method to look for predation on caterpillars: using clay caterpillars that can be analyzed for bite marks, ovipositor signs, or other evidence of attempted predation (methodology outlined in Low et al 2014; but see Zvereva and Kozlov 2022). These studies have given us extensive insight into predation pressure across large- and small-scale gradients or experimental treatments. Examining the effect of clay caterpillars on browsing or grazing patterns by larger herbivores would be a simple, low cost, and strong way to test any plant community effects of avoidance behavior (though driven only by a direct visual, not chemical, signal of caterpillar presence). An alternative method would be to remove herbivores manually in the presence and absence of larger herbivores and examine appropriate response variables, though indirect cues (i.e. damage to plants or volatile evidence) would remain. The indirect effects of host plant or patch avoidance, or attraction for the purposes of intentional consumption (see below), are a plausible and potentially important implication of ‘herbivory’ (also see Gish et al 2017).

The effect of incidentally consumed parasites on populations of herbivores

Individual and population consequences of incidental ingestion of parasites are well-known (Roy and St-Louis 2017; Chubb et al. 2020). The vast majority of helminth infections of ungulates occur via two distinct incidental ingestion pathways: eggs or larvae ingested on vegetation or ingestion of an intermediate host, usually an invertebrate (Chubb et al. 2020). Each of these pathways has evolved many times, and thousands of species and hundreds of genera of parasites require this incidental ingestion to complete their life-cycles, not just in ungulates, but across herbivorous mammals, birds, fish, and even reptiles (Leung and Koprivnikar 2018; Chubb et al. 2020). In a marked contrast from the previous examples, parasites seek to be incidentally ingested and their life-histories, morphologies, and behaviors reflect this constraint; they are largely inconspicuous, non-gregarious, and place themselves in locations likely to be foraged. Mortality or morbidity due to successful parasite infections, in turn, may have effects on populations and even have conservation implications (Mathieu et al. 2022). The most striking, and most well-documented are severe mortality events. Trematodiasis may cause mass die-offs of waterfowl. Although these are usually of molluscivorous waterfowl, herbivorous species also become infected, via incidental ingestion of snails on consumed vegetation (Griffiths et al. 1976, Roy and St-Louis 2017). However, even in the absence of a die-off, incidentally-ingested parasites can have profound morbidity effects. Incidentally-consumed helminths regulate populations of reindeer via lessening reproductive rates in Svalbard (Albon et al. 2002). Helminth ecologists are among the most cognizant of the profound effects of incidental ingestion, and much excellent work has been on the evolution and ecology of both trophic levels.

Intentional consumption of non-plant material

Diverse ‘herbivores’, from tiny insects to large mammals, intentionally seek out and consume animal matter regularly. This consumption has not been the subject of very much directed study, with the exception of cannibalism in herbivores, a particularly interesting and ecologically-important case of this more general pattern (e.g. Fox 1975; Polis et al 1989; Richardson et al 2010; Orrock et al 2017, 2022). However, the overall phenomenon is becoming much better-documented; reports on consumption of animal matter by phytophagous organisms have piled up, with the pace greatly accelerating in recent years with the advent of modern technology (especially camera-trapping, though this likely biases the data towards larger animals).

Mammalian ‘herbivores’ often seek out non-plant foods. Deer are important predators of nestling songbirds and they consume mammalian and bird carrion (Allan 1978, Pietz and Granfors 2000, Estellés-Domingo et al 2022), cows and elk eat eggs from birds’ nests (Holloran and Anderson 2003, Nack and Ribic 2005), caribou eat baby geese in the tundra (Abraham, Mineu, and Cooke 1977), sheep seek out and eat nestling seabirds on islands (Furness 1988), and even hippopotamuses will eat birds (as well as live and dead mammals: Dudley et al. 2016). Rabbits scavenge dead animals (Clauss et al. 2016, Peers 2018) and they themselves, as young, are occasionally heavily preyed on by squirrels (O’Donoghue 1994). Porcupines consume dead birds and also chew on bones (Coppola et al. 2020). Fish carcasses become a sashimi buffet for beavers and deer (Gleason et al. 2005, Case and McCullough 1987); manatees in Jamaica have learned to scavenge fish out of gill nets (Powell 1978). Herbivorous marsupials, such as kangaroos and wallabies, scavenge carcasses as well (Fitzsimons 2016; Leggett et al.. 2019).

While the vast majority of documented cases are of mammals, this likely represents observation or publication bias. Ectothermic herbivores – vertebrates and invertebrates - are certainly not excepted from opportunistic carnivory or scavenging. American toad tadpoles, usually algal feeders, grow better when scavenging on carcasses of other toadpoles (Heinen and Abdella 2005). Tortoises scavenge on dead conspecifics and remains of mammals (Naish 2014), as do herbivorous lizards, which may pick dead insects out of spider webs (Castilla et al. 2011). Insect 'herbivores' seek out animal flesh to eat, as well. Dozens of species of normally herbivorous caterpillars scavenge on dead insects and on conspecifics, even in the presence of excess food (Clausen 1940, LoPresti 2018; Fox 1975; Richarson et al 2010). In a particularly noteworthy case, lacewing larvae introduced as biocontrol for tobacco budworm caterpillars were preyed upon by the budworms themselves (Davidson et al 1992). Aquatic invertebrates are not excepted. Many herbivorous or detritivorous caddisflies will graze on dead fish (Fenoglio et al 2010; Carlson et al. 2020); Fenoglio et al (2014) suggest that most aquatic invertebrates have high trophic plasticity. These disparate examples all demonstrate that many herbivores have the capacity to recognize, consume, and process animal matter, though most examples do not demonstrate a benefit (but see LoPresti 2018).

Altered interactions and niche space due to intentional ingestion of non-plant material

Omnivory in phytophagous insects has many potential benefits, including obtaining limiting nutrients, faster development, reduced competition, and greater protection from predators or the environment (Richardson et al 2010). Herbivores often obtain limiting nutrients by switching from plant to animal material; this behavior and its consequences are a somewhat well-studied aspect of animal consumption by herbivores. Ingestion of bone and marine mollusk shells by tortoises provides extra calcium during egg maturation, a fitness boost, though not a niche expansion, *per se* (Moore and Dornberg 2014), sheep and deer feeding on limited island vegetation prey upon tern and skua chicks to obtain phosphorous and magnesium, probably allowing a higher population carrying capacity (Furness 1988; Bazely 1989). See White (2011) for additional examples. These occasional forays, or even seasonal shifts in diet, are certainly important for understanding individual movement, foraging strategies, and even mating interactions (i.e. Heneberg 2016). Another mechanism for a fitness benefit is that omnivory permits faster growth and escape from natural enemies on more risky hosts (e.g. Benrey and Denno 2012, Singer et al.. 2012; consistent with growth rates found in LoPresti 2018). Clausen (1940) details a crambid caterpillar that consumes the eggs contained in a bagworm's (Lepidoptera: Psychidae) shelter, before hibernating in the psychid's bag; this may represent a behavior allowing it protection both from abiotic stressors and from predators in addition to any nutritional benefits of that consumption.

Competition for limiting resources, too, is commonly suggested as a driver of omnivory in herbivorous insects, either as cannibalism or consumption of other species on the same plant (Richardson 2010). These two behaviors subtly differ; recognizing conspecifics as food may be different than recognizing non-conspecifics as food. Wagner (2005) hypothesizes that cannibalism in longwing butterflies occurs because of the scarcity of palatable new growth on their host plants. Despite the longwing *Agraulis vanillae* consuming conspecific pupae readily (Sencio 2017), my lab has found they refuse to scavenge on dead fruit flies, acceptable food to most omnivorous Lepidoptera (LoPresti, unpublished data), suggesting that they are not recognizing all animal matter as food. This striking result could be suggestive of competition, though it may also be a limitation of some phagostimulant from the host plant that is present in the pupae causing misplaced recognition of them as food.

Occasional bouts of predation or scavenging by herbivores may also allow expansion into new niche space. This rationale should not be used to suggest that the life histories of all 'herbivores' have been shaped by their occasional bouts in the carnivore or scavenger guild (though that assertion probably holds for select species, see White 2011). Instead, occasional or small amounts of animal material in an otherwise herbivorous diet may permit a temporarily broader niche and, over evolutionary time, possibly profound changes in the ecological characters of that lineage. The intentional consumption of small amounts of insect material allowed generalist caterpillars to perform better on marginal host plant species (LoPresti 2018). The niche space, in this case host plant range, available to these caterpillars was therefore larger when they scavenged ('polyphagy by omnivory'). Does this scavenging, affect what they feed on in nature and what we know to be the host range of acceptable plants in the field? The follow-up experiment needs to be done; however, macroevolutionary evidence suggests that insect lineages that have included animal matter in their diet have broader host ranges (Eubanks et al. 2003) and diversify into new niche space (Montgomery 1983).

Indeed, switches away from phytophagy are quite common across insects. Clausen (1940) listed myriad examples of predatory insects in otherwise herbivorous lineages of flies, beetles, hymenopterans, heteropterans, stoneflies, grasshopper, and lepidopterans. Pierce (1995) expanded on this list for strictly carnivorous Lepidoptera, though explicitly excluded cannibalism or occasional predators and scavengers; nonetheless, several dozen genera are included, representing many independet evolutionary origins. While omnivory need not be a main selective force behind each of these dietary switches, it is a necessary step in each origin of carnivory in any phytophagous lineage and therefore, the mechanisms driving switches to omnivory are necessary for understanding the derived condition of carnivory.

Final Remarks

Our paradigm of herbivores being solely plant-feeders is directly contradicted by an immense number of anecdotes and a handful of directed studies demonstrating incidental and intentional consumption. Broadening our treatment of herbivores will allow us to more accurately describe many phenomena, for both the consumer and the consumed, that we have long studied from a with a narrow perspective. Furthermore, it will allow us to make and test new and exciting large-scale hypotheses about the broader ecological and evolutionary implications.

The conception of the herbivore in trophic and ecosystem ecology is still extremely useful, if reductionist at times. For this reason, some scholars of omnivory have advocated for abandoning the trophic position paradigm (e.g. Polis et al 1989). In coastal and marine ecology, many ecologists also have moved away from the term herbivore, specifically referring to grass and algal-feeders as “grazers” rather than herbivores, given that large ones ingest invertebrates and small ones ingest microorganisms (e.g. Silliman and Zieman 2001; Clements et al. 2009). In copepod communities, Benedetti et al. (2016) defines the most highly herbivorous trophic position as “herbivore – omnivore”. The title of this work nonwithstanding, I do not advocating abandoning the term herbivore completely; instead, like the excellent aquatic work cited, to examine closely the diet and think of the potential importance of even small amounts of consumed non-plant material. My sincerest hope is that this piece further encourages study on the fascinating complexities that occur in every system involving herbivores and plants.

References

Abraham, K., Mineau, P. & Cooke, F. (1977). Unusual predators of snow goose eggs. Canadian Field-Naturalist, 91, 317–318.

Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E. & Halvorsen, O. (2002). The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society B: Biological Sciences*, 269, 1625–1632.

Allen, A.C., Beck, C.A., Bonde, R.K., Powell, J.A. & Gomez, N.A. (2018). Diet of the Antillean manatee (Trichechus manatus manatus) in Belize, Central America. *Journal of the Marine Biological Association of the United Kingdom*, 98, 1831–1840.

Aluja, M., Sivinski, J., Rull, J. & Hodgson, P.J. (2005). Behavior and Predation of Fruit Fly Larvae (Anastrepha spp.) (Diptera: Tephritidae) After Exiting Fruit in Four Types of Habitats in Tropical Veracruz, Mexico. *Environ Entomol*, 34, 1507–1516.

Aparicio, M.L., Fenoglio, M.S. & Videla, M. (2015). Leafminer egg distribution at decreasing leaf availability levels: Do females avoid intraspecific competition? *Entomol Exp Appl*, 156, 170–177.

Armstrong, A.J. & Louw, S.L. (2013). Monitoring of the eggs of the Karkloof blue butterfly, Orachrysops ariadne, for its conservation management. *Koedoe*, 55.

Auko, T.H., Trad, B.M. & Silvestre, R. (2015). Bird dropping masquerading of the nest by the potter wasp Minixi suffusum (Fox, 1899) (Hymenoptera: Vespidae: Eumeninae). *Tropical Zoology*, 28, 56–65.

Barboza, L.C., Silva, G.G., Green, A.J., Maltchik, L. & Stenert, C. (2022). Potential dispersal of aquatic snails by waterbird endozoochory in neotropical wetlands. *Biota Neotrop*, 22.

Bazely, D.R. & Garcia, A. (1989). Carnivorous herbivores: mineral nutrition and the balanced diet. Trends Ecol Evol, 4, 155–156.

Ben-Ari, M. & Inbar, M. (2013). When Herbivores Eat Predators: Predatory Insects Effectively Avoid Incidental Ingestion by Mammalian Herbivores. *PLoS One*, 8.

Ben-Ari, M., Outreman, Y., Denis, G., le Gallic, J.F., Inbar, M. & Simon, J.C. (2019). Differences in escape behavior between pea aphid biotypes reflect their host plants' palatability to mammalian herbivores. *Basic Appl Ecol*, 34, 108–117.

Benrey, B. & Denno, R.F. (1997). The Slow-Growth--High-Mortality Hypothesis : A Test Using the Cabbage Butterfly, 78, 987–999.

Berman, T., Glasser, T. & Inbar, M. (2019a). Goats adjust their feeding behaviour to avoid the ingestion of different insect species. *Can J Zool*, 97, 805–811.

Berman, T.S., Ben-Ari, M., Glasser, T.A., Gish, M. & Inbar, M. (2017). How goats avoid ingesting noxious insects while feeding. *Sci Rep*, 7.

Berman, T.S., Ben-Ari, M., Henkin, Z. & Inbar, M. (2018). Immediate and long-term facilitative effects of cattle grazing on a polyphagous caterpillar. *Agric Ecosyst Environ*, 261, 45–53.

Berman, T.S., Messeri, N., Glasser, T.A. & Inbar, M. (2019b). Innate ability of goats to sense and avoid ingestion of noxious insects while feeding. *R Soc Open Sci*, 6.

Bodmer, R.E. (1990). Ungulate Frugivores and the Browser-Grazer Continuum. *Oikos*, 57, 319–325.

Bonal, R. & Muñoz, A. (2007). Multi-trophic effects of ungulate intraguild predation on acorn weevils. *Oecologia*, 152, 533–540.

Bowers, M. D., & Schmitt, J. (2013). Overcrowding leads to lethal oviposition mistakes in the Baltimore checkerspot, Euphydryas phaeton Drury (Nymphalidae). *The Journal of the Lepidopterists' Society*, 67: 227-229.

Brown, R.J. 2007. Freshwater mollusks survive fish gut passage. *Arctic* 60: 124-128.

Capinera, J.L., Gardner, D.R. & Stermitz, F.R. (1985). Cantharidin Levels in Blister Beetles (Coleoptera: Meloidae) Associated with Alfalfa in Colorado. *J Econ Entomol*, 78, 1052–1055.

Carson, H.L. (1974). Three Flies and Three Islands: Parallel Evolution in Drosophila (Caribbean Sea/Indian Qcean/ecology/land crabs). *Proceedings of the National Academy of Sciences*, 71, 3517–3521.

Case, D.J. & Mccullough, D.R. (1987). White-Tailed Deer Forage on Alewives. J Mammal, 68, 195–198.

Castilla, A.M., Richer, R., Herrel, A., Conkey, A.A.T., Tribuna, J. & Al-Thani, M. (2011). First evidence of scavenging behaviour in the herbivorous lizard Uromastyx aegyptia microlepis. *J Arid Environ*, 75, 671–673.

Chubb, J.C., Benesh, D. & Parker, G.A. (2020). Ungulate Helminth Transmission and Two Evolutionary Puzzles. *Trends Parasitol*.

Clausen, C.P. (1940). *Entomophagous Insects*. 1st edn. McGraw-Hill , New York.

Clauss, M., Lischke, A., Botha, H. & Hatt, J.-M. (2016). Carcass consumption by domestic rabbits (Oryctolagus cuniculus). Eur J Wildl Res, 62, 143–145.

Clements, K.D., Raubenheimer, D. & Choat, J.H. (2009). Nutritional ecology of marine herbivorous fishes: Ten years on. *Funct Ecol*.

Cohen, A.C. & Cohen, J.L. (1990). Ingestion of Blister Beetles by a Texas Horned Lizard. *Southwest Nat*, 35, 369.

Conde-Porcuna, J.M., Pérez-Martínez, C. & Moreno, E. (2018). Variations in the hatching response of rotifers to salinity and waterbird ingestion. *J Plankton Res*, 40, 326–341.

Cooper, J., Gordon, I.J. & Pike, A.W. (2000). Strategies for the avoidance of faeces by grazing sheep. *Appl Anim Behav Sci*, 69, 15–33.

Cooper, S.M. & Owen-Smith, N. (1986). Effects of plant spinescence on large mammalian herbivores. *Oecologia*, 68, 446–455.

Coppola, F., Guerrieri, D., Simoncini, A., Varuzza, P., Vecchio, G. & Felicioli, A. (2020). Evidence of scavenging behaviour in crested porcupine. Sci Rep, 10.

Cornelissen, T. & Stiling, P. (2008). Clumped distribution of oak leaf miners between and within plants. *Basic Appl Ecol*, 9, 67–77.

Davidson, C.B., Gottschalk, K.W. & Johnson, J. E. (1999). Tree mortality following defoliation by the European Gypsy Moth (*Lymantria dispar* L.) in the United States: a review. *Forest Science* 45: 74-84

Davis, W. (1907). Insects as the Food of Squirrels. *Can Entomol*, 4, 16–16.

Dittmann, L. & Schausberger, P. (2017). Adaptive aggregation by spider mites under predation risk. *Sci Rep*, 7.

Drew, R.A.I. (1987). Reduction in Fruit Fly (Tephritidae : Dacinae) Populations in their Endemic Rainforest Habitat by Frugivorous Vertebrates. *Aust J Zool*, 35, 283–288.

Dudley, J.P., Hang'Ombe, B.M., Leendertz, F.H., Dorward, L.J., de Castro, J., Subalusky, A.L., *et al.*. (2016). Carnivory in the common hippopotamus Hippopotamus amphibius : implications for the ecology and epidemiology of anthrax in African landscapes. *Mamm Rev*, 46, n/a-n/a.

Eisner, T., Conner, J., Carrel, J.E., Mccormick, J.P., J° Siagle, A., Gans, C., *et al.*. (1990). Systemic retention of ingested cantharidin by frogs*. *Chemoecology*, 1, 57–62.

Elton, C. (1927). *Animal Ecology*. 1st edn. MacMillan Company, New York.

Eubanks, M.D., Styrsky, J.D. & Denno, R.F. (2003). The evolution of omnivory in heteropteran insects. Ecology, 84, 2549–2556.

Evans, E.W. (2003). Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): A review. *Eur J Entomol*, 100, 1–10.

Ezenwa, V.O. (2004). Selective Defecation and Selective Foraging: Antiparasite Behavior in Wild Ungulates? *Ethology*, 110, 851–862.

Feeny, P. (1976). Plant apparency and chemical defense. *Recent Adv Phytochem*, 10, 1–40.

Fenoglio, S., T. Bo, M. Cammarata, G. Malacarne, and G. del Frate. 2010a. Contribution of macro- and micro-consumers to the decomposition of fish carcasses in low-order streams: an experimental study. Hydrobiologia 637:219–228

Fitzsimons, J.A. (2017). Carrion consumption by the swamp wallaby (Wallabia bicolor). Aust Mammal, 39, 105–107.

Foss, L. & Rieske, L. (2004). Stem galls affect oak foliage with potential consequences for herbivory. *Ecol Entomol*, 29, 273–280.

Foster, C.N., Barton, P.S. & Lindenmayer, D.B. (2014). Effects of large native herbivores on other animals. *Journal of Applied Ecology*.

Furness, R.W. (1988). Predation on ground-nesting seabirds by island populations of red deer Cervus eluphus and sheep Ovis. The Zoological Society of London, 216, 565–573.

Gish, M., Ben-Ari, M. & Inbar, M. (2017). Direct consumptive interactions between mammalian herbivores and plant-dwelling invertebrates: prevalence, significance, and prospectus. *Oecologia*.

Gish, M., Dafni, A. & Inbar, M. (2010). Mammalian herbivore breath alerts aphids to flee host plant. *Current Biology*.

Gish, M., Dafni, A. & Inbar, M. (2011). Avoiding incidental predation by mammalian herbivores: Accurate detection and efficient response in aphids. *Naturwissenschaften*, 98, 731–738.

Gleason, J.S., Hoffman, R.A. & Wendland, J.M. (2005). Beavers, Castor canadensis, feeding on salmon carcasses: Opportunistic use of a seasonally superabundant food source. Canadian Field-Naturalist, 119, 591–593.

Gómez, J.M. & González-Megías, A. (2007). Long-term effects of ungulates on phytophagous insects. *Ecol Entomol*, 32, 229–234.

Gontijo, L.M. (2019). Female treehoppers camouflage behaviour is evidenced during oviposition on wild shrubs. *J Nat Hist*, 53, 1061–1069.

Grabovskiĭ, V.I. (2012). Model of early evolution of aposematic coloration. *Zh Obshch Biol*, 73, 37–48.

Griffiths, H.J., Gonder, E. & Pomeroy, B.S. (n.d.). An Outbreak of Trematodiasis in Domestic Geese. *Source: Avian Diseases*, 20, 604–606.

Grof-Tisza, P., Holyoak, M., Antell., E. & Karban, R. (2015) Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar. *Ecology* 96: 80-89.

Guillén, L., Aluja, M., Equihua, M. & Sivinski, J. (2002). Performance of two fruit fly (Diptera: Tephritidae) pupal parasitoids (Coptera haywardi [Hymenoptera: Diapriidae] and Pachycrepoideus vindemiae [Hymenoptera: Pteromalidae]) under different environmental soil conditions. *Biological Control*, 23, 219–227.

Guix, J.C. & Ruiz, X. (1997). Weevil Larvae Dispersal by Guans in Southeastern Brazil. *Biotropica* , 29, 522–525.

Guterres-Pazin, M.G., Rosas, F.C.W. & Marmontel, M. (2012). Ingestion of invertebrates, seeds, and plastic by the amazonian manatee (Trichechus inunguis) (Mammalia, Sirenia). *Aquat Mamm*.

Hawkins, B. a., Cornell, H. v. & Hochberg, M.E. (1997). Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology*, 78, 2145–2152.

Heneberg, P. (2016). On Otis tarda and Marquis de Sade: what motivates male Great Bustards to consume Blister Beetles (Meloidae)? *J Ornithol*, 157, 1123–1125.

Hernández, Á. (2011). Internal dispersal of seed-inhabiting insects by vertebrate frugivores: A review and prospects. *Integr Zool*.

Herrera, C. (1985). Aposematic insects as six-legged fruit: incidental short-circuiting of their defense by frugivorous birds. *Am Nat*, 126, 286–293.

Herrera, C.M. (1989). Vertebrate Frugivores and Their Interaction with Invertebrate Fruit Predators: Supporting Evidence from a Costa. *Source: Oikos*, 54, 185–188.

Holloran, M.J. & Anderson, S.H. (2003). Direct Identification of Northern Sage-grouse, Centrocercus urophasianus, Nest Predators Using Remote Sensing Cameras. Can Field Nat, 117, 308–310.

Inbar, M., Izhaki, I., Koplovich, A., Lupo, I., Silanikove, N., Glasser, T., *et al.*. (2010). Why do many galls have conspicuous colors? A new hypothesis. *Arthropod Plant Interact*, 4, 1–6.

Ishikawa, Y., Kimura, M.T. & Toda, M.J. (2022). Biology and ecology of the Oriental flower-breeding Drosophila elegans and related species. *Fly (Austin)*, 16, 207–220.

Janzen, D.H. (1977). Why fruits rot, seeds mold, and meat spoils. American Naturalist 111:691-713

Jordano, P. (1987). Avian fruit removal: effects of fruit variation, crop size, and insect damage. Ecology 68:1711-1723.

Karban, R. & Agrawal, A.A. (2002). Herbivore offense. *Annual Review of Ecology and Systematics*. 33: 641-664

Kareiva, P. & Odell, G. (1987). Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *Am Nat*, 130, 233–270.

Kinto, S., Akino, T. & Yano, S. (2022). Spider mites avoid caterpillar traces to prevent intraguild predation. *Research Square Preprint*.

Kurzfeld-Zexer, L. & Inbar, M. (2021). Gall-forming aphids are protected (and benefit) from defoliating caterpillars: the role of plant-mediated mechanisms. *BMC Ecol Evol*, 21.

Laux, J.J. & Kölsch, G. (2014). Potential for passive internal dispersal: Eggs of an aquatic leaf beetle survive passage through the digestive system of mallards. *Ecol Entomol*, 39, 391–394.

Leggett, K.E.A., Stubbs-Oliver, A., Brun, M.L. & Dawson, T.J. (2019). Carnivory in euros, inland wallaroos (Macropus robustus erubescens). Aust Mammal, 42, 357–358.

Leihy, R.I. & Chown, S.L. (2020). Wind plays a major but not exclusive role in the prevalence of insect flight loss on remote islands: Insect flight loss on islands. *Proceedings of the Royal Society B: Biological Sciences*, 287.

Leung, T.L.F. & Koprivnikar, J. (2019). Your infections are what you eat: How host ecology shapes the helminth parasite communities of lizards. *Journal of Animal Ecology*, 88, 416–426.

Lin, S.M., Li, T.W., Liou, C.H., Amarga, A.K.S., Cabras, A. & Tseng, H.Y. (2021). Eggs survive through avian guts—A possible mechanism for transoceanic dispersal of flightless weevils. *Ecol Evol*, 11, 7132–7137.

Liu, M.H., Blamires, S.J., Liao, C.P. & Tso, I.M. (2014). Evidence of bird dropping masquerading by a spider to avoid predators. *Sci Rep*, 4.

LoPresti, E.F. (2018). Polyphagy by omnivory: scavenging improves performance of a polyphagous caterpillar on marginal hosts. Oecologia, 186, 1–9.

Losey, J.E. & Denno, R.F. (1998). Positive predator-predator interactions: Enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, 2143–2152.

Low, P.A., Sam, K., McArthur, C., Posa, M.R.C & Hochuli, D.F. 2014. Determining predator identity from attack marks left in model caterpillars: guidelines for best practices. *Entomologia Experimentalis et Applicata* 152: 120-126.

Lu, S.-S. & Samways, M.J. (2002). Behavioural ecology of the Karkloof blue butterfly Orachrysops ariadne (Lepidoptera : Lycaenidae) relevant to its conservation Terrestrial Sensor Networks View project Developing and testing a new environmental management checking tool (MATCH) for timber production landscapes *African Entomology*.

Miñarro, M. & Jacas, J.A. (2011). Pest status of leafminers in cider-apples: The case of orchards in Asturias (NW Spain). *Crop Protection*, 30, 1485–1491.

Minno, M.C. & Emmel, T.C. (1992). Larval protective coloration in swallowtails from the Florida Keys. *Tropical Lepidoptera*, 3, 47–49.

Montgomery, S. (1983). Carnivorous caterpillars: the behavior, biogeography and conservation of Eupithecia (Lepidoptera: Geometridae) in the Hawaiin Islands. *GeoJournal*, 7, 549–556.

Nack, J.L. & Ribic, C.A. (2005). Apparent Predation by Cattle at Grassland Bird Nests. Wilson Bull, 117, 56–62.

van Noordwijk, C.G.E., Flierman, D.E., Remke, E., WallisDeVries, M.F. & Berg, M.P. (2012). Impact of grazing management on hibernating caterpillars of the butterfly Melitaea cinxia in calcareous grasslands. *J Insect Conserv*, 16, 909–920.

Nordkvist, M. (2020). Interactions between ungulates and forest insects. Swedish University of Agricultural Sciences, Uppsala.

Nyman, T. & Julkunen-Tiitto, R. (2000). Manipulation of the phenolic chemistry of willows by gall-inducing sawflies. *Proceedings of the National Academy of Science*, 97, 13184–13187.

O'Donoghue, M. (1994). Early survival of juvenile snowshoe hares. Ecology, 75, 1582–1592.

Or, K. & Ward, D. (2003). Three-way interactions between Acacia, large mammalian herbivores and bruchid beetles - A review. *African Journal of Ecology*, 41, 257–265.

Orrock, J.L., Guiden, P.W., Pan, V.S. & Karban R. (2022) Plant induced defenses that promote cannibalism reduce herbivory as effectively as highly pathogenic herbivore pathogens. Oecologia 199: 397-405

Orrock, J.L. (2017) Induced defences in plants reduce herbivory by increasing cannibalism. *Nature Ecology and Evolution* 1: 1205-1207

Peers, M.J., Majchrzak, Y.N., Konkolics, S.M., Boonstra, R. & Boutin, S. (2018). Scavenging by snowshoe hares (Lepus americanus) in Yukon, Canada. Northwestern Naturalist, 99, 232–235.

Pietz, P.J. & Granfors, D.A. (2000). White-tailed deer (Odocoileus virginianus) predation on grassland songbird nestlings. Am Midl Nat, 144, 419–422.

Polis, G. A., Myers, C. A. & Holt, R.D. (1989). The ecology and evolution of intraguild predation. *Annu Rev Ecol Syst*, 20, 297–330.

Powell, J.A. (1978). Evidence of Carnivory in Manatees (Trichechus manatus). Source: Journal of Mammalogy, 59, 442.

Ray, A., Post, L. & Reagor, J. (1980). GC/MS confirmation of cantharidin toxicosis due to ingestion of blister beetles. *Veterinary Human Toxicology*, 22, 398–399.

Renkema, J.M., Lynch, D.H., Cutler, G.C., MacKenzie, K. & Walde, S.J. (2012). Emergence of blueberry maggot flies (Diptera: Tephritidae) from mulches and soil at various depths. *Environ Entomol*, 41, 370–376.

Robertson, S.M. & Baltosser, W.H. (2018). Deer Browsing Influences Population Dynamics of the Ozark Baltimore Checkerspot (Euphydryas Phaeton Ozarkae: Nymphalidae). *J Lepid Soc*, 72, 270–275.

Robinson, M., Weber, M., Feedman, M., Jordan E, Ashlock, S., Yonenaga, J., *et al.*. (n.d.). IN PRESS Broadscale evolution of coloration in caterpillars reflects their interactions with plants. *Proceedings of the Royal Society: B*.

Roy, C.L. & St-Louis, V. (2017). Spatio-temporal variation in prevalence and intensity of trematodes responsible for waterfowl die-offs in faucet snail-infested waterbodies of Minnesota, USA. *Int J Parasitol Parasites Wildl*, 6, 162–176.

Shirotsuka, K. & Yano, S. (2012). Coincidental intraguild predation by caterpillars on spider mites. *Exp Appl Acarol*, 56, 355–364.

Silliman, B.R. & Zieman, J.C. (2001). Top-down control of Spartina Alterniflora production by periwinkle grazing in a Virginia salt marsh. *Ecology*, 82, 2830–2845.

Singer, M.S., Farkas, T.E., Skorik, C.M. & Mooney, K.A. (2012). Tritrophic interactions at a community level: Effects of host plant species quality on bird predation of caterpillars. *American Naturalist*, 179, 363–374.

Smith, A.P. (1986) Ecology of a leaf color polymorphism in a tropical forest species: habitat segregation and herbivory. Oecologia 69:283-287

Stevens, M. & Ruxton, G.D. (2012). Linking the evolution and form of warning coloration in nature. *Proceedings of the Royal Society B: Biological Sciences*.

Suzuki, T.N. & Sakurai, R. (2015). Bent posture improves the protective value of bird dropping masquerading by caterpillars. *Anim Behav*, 105, 79–84.

Takagi, S. & Miyashita, T. (2014). Scale and system dependencies of indirect effects of large herbivores on phytophagous insects: A meta-analysis. *Popul Ecol*.

Taper, M.L. & Case, T.J. (1987). Interactions between oak tannins and parasite community structure: Unexpected benefits of tannins to cynipid gall-wasps. *Oecologia*, 71, 254–261.

Triad, E. & Herrera, C.M. (1984). Avian Interference of Insect Frugivory: An Exploration into the Plant-Bird-Fruit Pest Evolutionary Triad. *Source: Oikos*, 42, 203–210.

Turchin, P. & Kareiva, P. (1989). *Aggregation in Aphis Varians: An Effective Strategy for Reducing Predation Risk*. *Source: Ecology*.

van Leeuwen C.H.A. van der Velde, G., van Lith, B. & Klaasen M. (2012) Experimental quantification of long distance dispersal potential of aquatic snails in the gut of migratory birds. PLOS One: e32292

Wagner, D. & Liebherr, J. (1992). Flightlessness in Insects. *Trends Ecol Evol*, 7, 216–220.

Webb, B.A., Barney, W.E., Dahlman, D.L., DeBorde, S.N., Weer, C., Williams, N.M., *et al.*. (2004). Eastern tent caterpillars (Malacosoma americanum) cause mare reproductive loss syndrome. *J Insect Physiol*, 50, 185–193.

White, T.C.R. (2011). The significance of unripe seeds and animal tissues in the protein nutrition of herbivores. *Biological Reviews*, 86, 217–224.

Wilson, A.J., Schutze, M., Elmouttie, D. & Clarke, A.R. (2012). Are insect frugivores always plant pests? The impact of fruit fly (Diptera: Tephritidae) larvae on host plant fitness. *Arthropod Plant Interact*, 6, 635–647.

Woltz, J.M. & Lee, J.C. (2017). Pupation behavior and larval and pupal biocontrol of Drosophila suzukii in the field. *Biological Control*, 110, 62–69.

Young, D.K. (1984). Cantharidin and insects: an historical review. *Great Lakes Entomol*, 17, 187–194.

Zamora, R. & Gómez, J.M. (1993). Vertebrate Herbivores as Predators of Insect Herbivores: An Asymmetrical Interaction Mediated by Size Differences. *Oikos*, 66, 223–228.

Zhang, J., Bisch-Knaden, S., Fandino, R.A., Yan, S., Obiero, G.F., Grosse-Wilde, E., Hansson, B.S. & Knaden, M. (2019) The olfactory coreceptor IR8a governs larval feces-mediated competition avoidance in a hawkmoth. *Proceedings of the National Academy of Sciences*, 116: 21828-21833.

Zvereva, E.L. & Kozlov M.V. (2023) Predation risk estimated on live and artificial insect prey follows different patterns. *Ecology*, ecy3943.

Figure 1:

The leaf mine (above) of a caterpillar, *Coptotriche citrinipennella*, and vein-fold galls (lower) of a fly, *Contarinia* sp., were arduously avoided by feeding sawfly larvae (inset right, *Arge quidia*: Argidae). Photos: Charley Eiseman, used with permission.