Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Insect Science

Mass mortality events and the role of necrophagous invertebrates

Jeffery K Tomberlin[1], Brandon T Barton[2], Marcus A Lashley[3] and Heather R Jordan[2]

Scale is important in understanding and applying concepts in ecology. Historically, the mechanisms regulating necrophagous arthropod community structure have been well explored on a single vertebrate carcass. However, practically nothing is known of whether such findings can be extrapolated to cases where large numbers of carcasses have been introduced into an ecosystem at a single time point. With the increasing incidences of mass mortality events (MMEs), understanding how scale effects community assembly of necrophagous insects and the resulting bottom-up or top-down effects on the impacted ecosystem are of utmost importance. Unfortunately, MMEs are unpredictable, making their study nearly impossible within a robust experimental framework. The objectives of this paper are to provide a brief overview of what is known with regards to ecological responses to carrion, opine on the ramifications of MMEs on local communities, and provide a brief overview of knowledge gaps, avenues for future research, and a potential study systems for rigorous MME experiments.

Addresses
[1] Department of Entomology, Texas A&M University, United States
[2] Department of Biology, Mississippi State University, United States
[3] Department of Wildlife, Fisheries, and Aquaculture, United States

Corresponding author: Tomberlin, Jeffery K (jktomberlin@tamu.edu)

Current Opinion in Insect Science 2017, **23**:xx–yy

This review comes from a themed issue on **Global change biology**

Edited by **Brandon Barton** and **Jason Harmon**

doi:10.1016/j.cois.2017.06.006

Introduction

Even after death, an animal continues to affect an ecosystem. A tremendous amount of research has explored decomposition processes of vertebrate carrion across terrestrial and aquatic ecosystems. Seminal works in the 1960s and 1970s [1••,2,3,4••] revealed that a suite of specialist and generalist invertebrates played crucial roles in recycling carrion nutrients and making those resources available to other organisms. Hence, decomposing carrion effects soil nutrients [5,6], and tissue chemistry [7], and have direct and indirect effects on invertebrate [8,9] and vertebrate communities [10,11,12••,13]. Indeed, vertebrate carrion is not just a dead animal; it is a basal resource that supports diverse communities, which in turn influences ecosystems [22••].

Competition and adaptation for finding unpredictable carrion

Except in special cases, such as phenology-driven resource pulse events (e.g. cicadas [14]; salmon runs [15]) or industrial activity (e.g. confined animal facilities [16]), vertebrate carrion availability is generally unpredictable. The unpredictable, ephemeral nature of this resource generates intense competition between organisms and strong selection for rapid detection, location, and utilization of carrion, as well as the evolution of elaborate strategies to exclude competitors (e.g. carrion beetles bury carrion and invest in parental care [17,18]; blow flies release antimicrobials to reduce competing bacteria [19•]). Early research considered invertebrates as the primary decomposers of vertebrate carrion [1••,20,21•]. But, more recent work has illuminated the important role of vertebrates in carrion decomposition, especially in terms of efficiently recycling nutrients back into the ecosystem [10,22••].

In addition to animal consumers, microbes are now recognized as playing important roles in the decomposition process. Microbial decomposition begins immediately after an animal's death, where microbial community, activity, and chemical ecology greatly influences the direction, magnitude, and spatial and temporal dynamics of higher organism decomposition involvement (e.g. recruitment of invertebrate or vertebrate scavengers), through cooperative or exclusionary microbe–invertebrate–vertebrate interactions [7,23,24]. While invertebrates (Figure 1), vertebrates (Figure 2), and microbes all compete for the same carrion resources, they generally fill different niches, using the resource in different ways, and generating different effects on nutrient recycling and ecosystem processes [23].

Decomposition across scales

The range of sizes of vertebrate carrion spans several orders of magnitudes, from 7 mm and ∼20 mg (e.g. *Paedophryne* tree frog in New Guinea) to 25 m and over one hundred metric tons (blue whale *Balenoptera musculus*) [25]. Based solely on the shear difference in size, one

Please cite this article in press as: Tomberlin JK, et al.: Mass mortality events and the role of necrophagous invertebrates, Curr Opin Insect Sci (2017), http://dx.doi.org/10.1016/j.cois.2017.06.006

Figure 1

Current Opinion in Insect Science

A typical blow fly adult associated with vertebrate carrion.

can imagine the use of these resources and their ecological effects would differ dramatically. For example, decomposition time increases with carcass size [26], whereas carcass detection time by scavengers and the percentage of carrion biomass consumed negatively relates to carcass size [27]. Furthermore, carcass size has significant effects on the soil and microbial communities [7], as well as vertebrate scavenger assemblages [27]. Just as carcass size can have ecological effects, so too can different numbers of carcasses. For example, Evelsizer *et al.* [28] demonstrated that increasing the number of duck carcasses had a nonlinear effect on disease outbreaks in the remaining population.

Most interestingly, a meta-analysis of studies examining the mechanisms regulating carrion decomposition determined invertebrates had the greatest effect on decomposition rate regardless of environment; however, size of the carcass in conjunction with invertebrate activity co-varied, indicating size was a major factor impacting the ability of invertebrates to recycle carrion [29] (Figure 3). Furthermore, microbial-mediated decomposition is generally unaffected by carrion biomass. These results are consistent with recent work showing that important microbial decomposers are ubiquitous throughout the environment [30] and can quickly colonize, replicate, and decompose carcasses of virtually any size at virtually any location.

In many cases, detection time of carcasses by vertebrate scavengers is negatively related to biomass [27] and larger carcasses are often consumed more quickly than smaller ones [31]. Linz *et al.* [32] reported that vertebrate scavengers were more important in the decomposition process when carcass density was high (75 bird carcasses) rather than low (15 bird carcasses). They concluded the

Figure 2

Current Opinion in Insect Science

Examples of various vertebrate scavengers frequenting vertebrate carrion, **(a)** bobcat (*Lynx rufus*), **(b)** raccoon (*Procyon lotor*), **(c)** golden eagle (*Aquila chrysaetos*), and **(d)** black vultures (*Coragyps atratus*).
Photographs courtesy of J. Beasley and K. Turner.

Please cite this article in press as: Tomberlin JK, et al.: Mass mortality events and the role of necrophagous invertebrates, Curr Opin Insect Sci (2017), http://dx.doi.org/10.1016/j.cois.2017.06.006