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TESTING MULTIGENERATIONAL COLONIZATION OF CARRION BY BLOW FLIES IN THE GREAT PLAINS

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ABSTRACT—The relationship between carrion and blow flies is well understood, but in situations where fresh carrion sources are unavailable, as may occur on the Great Plains, the potential for multigenerational colonization of a single carcass exists. By testing this possibility through a replicated choice/no-choice experiment using pig carcasses, we were able to demonstrate that multigenerational colonization of carrion by blow flies does not occur. Fresh pig carcasses were exposed to blow fly infestation, then placed in insect exclusion cages. After the emergence of this first generation of blow fly adults, “choice” cages were supplied with a fresh pig cadaver. No multigenerational colonization of the parent carcass took place in any of the choice or no-choice replicates. This demonstrates that carcasses act as temporary resource islands, with a “window of opportunity” of colonization in the ecosystem, and are vital for the biodiversity of the Great Plains.

Key Words: cadaver, Calliphoridae, carcass, decomposition, Diptera, entomology, forensic resource island, taphonomy

INTRODUCTION

The decomposition of carcasses is a vital process in every terrestrial ecosystem. Carcasses release water, energy, and nutrients that are largely unavailable to the wider ecosystem during the life of an animal. This process might have particular importance in grassland ecosystems, such as the Great Plains, where carcasses act as islands of fertility within an ecosystem where resources are generally evenly distributed (e.g., Garcia-Moya and McKell 1970; Camargo-Ricalde and Dhillon 2002; Mummey and Stahl 2003). The formation of these resource islands are of great importance to grassland ecosystems, as they support niche provisioning and act as corridors for the dispersal of biota within and across ecosystems (e.g., Finn 2001; Carter et al. 2007). However, the relative lack of carcass decomposition studies has resulted in a generally poor understanding of the fundamental processes associated with carcass breakdown. Much of what is currently understood is entomological. For example, when insects are active they can successfully compete with vertebrate scavengers for available carcasses (DeVault et al. 2003, 2004). Critical to this competition, and ultimately carcass decomposition, is the activity of dipterans.

The role of flies in the decomposition of animal carrion has been recognized by playwrights and studied by naturalists and scientists for thousands of years (Greenberg and Kunich 2002), yet there are many aspects of this process that scientists do not understand. One clear example of our lack of understanding lies in the attraction of carrion flies (primarily blow flies [Diptera: Calliphoridae (Fig. 1)] and, to a lesser extent, flesh flies [Diptera: Sarcophagidae]) to decomposing animals. A variety of studies have shown that blow flies will alight on a dead animal within a very short time after death, often within minutes, and will begin to oviposit shortly thereafter (Payne 1965; Johnson 1975; Lane 1975; Goddard and Lago 1985; Tullis and Goff 1987; Anderson and VanLaerhoven 1996; Tabor et al. 2004), and the succession of various species of blow flies associated with the decomposition of carrion has also been studied (Denno and Cothran 1975). These studies form the foundation upon which medicocriminal, or forensic, entomology is based (Catts and Goff 1992). What goes largely ignored in these studies, however, is the fact that the same species of blow flies that colonize shortly after death continue to be attracted to the carrion long into the process of decomposition.

Carrion flies are attracted by volatile chemicals, particularly sulfurous compounds that are released from



Figure 1. The blue bottle fly (*Calliphora vicina*) is a blow fly most frequently seen in urban areas during the fall and spring. Here it is seen feeding on liver that also serves as an egg-laying substrate in a laboratory colony. Photo by Tim Huntington.

carcasses during decomposition (Ashworth and Wall 1994). Hydrogen sulfide originates from the metabolism of the sulfur-containing amino acids (methionine, homocysteine) by anaerobic bacteria, which occurs primarily during putrefaction, while the flesh of the body still remains intact and relatively unchanged (Gill-King 1997). While there might be other chemicals (Jürgens et al. 2006) which hold some level of attraction in the mélange of chemical compounds released from a decomposing corpse (Vass et al. 2004), it is likely that flies can discriminate between a fresh corpse and a decomposed corpse.

Archer and Elgar (2003) examined this theory by successively trapping the flies attracted to carrion over the course of decomposition. They found that there are clear interactions between the gender of the flies and the stage of decomposition (early or late). Additionally, interactions between the ovarian status of the females (gravid, nongravid, early egg development, or late egg development) and the stage of decomposition were observed. Those flies that were ready to oviposit were attracted immediately after death, and those with undeveloped

ovaries comprised higher proportions of the populations later in the decompositional stages.

This behavior is not unexpected, as Hayes et al. (1999) showed that flies of different genders and reproductive statuses had different resource requirements that attracted them to the carrion. Aside from the obvious attraction to carrion as an oviposition medium (Norris 1965), males are apparently attracted to the carrion as a place to find virgin females (Erzinclioglu 1996), and virgin female blow flies are attracted to carrion as a protein source to complete egg development (vitellogenesis) (Belzer 1978; Barton Browne and Van Gerwen 1992; Barton Browne 1993). This protein requirement does not appear to be “source dependent,” and presumably females can obtain their protein from fresh carcasses and carcasses in latter stages of decomposition (Archer and Elgar 2003).

While these blow flies continue to be attracted to the carrion well into the later stages of decomposition, the carcass is no longer attractive as an oviposition medium after some point, and it is widely held that the maggots that fed on a corpse will not normally eclose as adults

and oviposit on the same corpse (Nuorteva 1977). Flies in abnormal conditions, however, have been known to alter their behavior as a response to their circumstances (Greenberg and Kunich 2002).

If adult blow flies experience a situation where there is no carrion source other than their larval host, will they oviposit on this carcass or die without reproducing? Carrion is typically an ephemeral nutrient source for insects and other scavengers (DeVault et al. 2003; Carter et al. 2007), and in a grassland ecosystem like the Great Plains, carrion may be geographically, as well as temporally, sparse. Behavioral and physiological adaptations allow blow flies to detect and exploit this transient carcass resource from hundreds or thousands of meters away (Braack 1981; MacLeod and Donnelly 1963) and in intervals as short as seconds to minutes after death. Given the obvious adaptive benefit of locating carrion and maximizing cadaveric resources, the failure of blow flies to complete multiple generations on a carcass has important evolutionary and forensic implications. In particular, given the strong evidence of insect succession on carrion, the lack of multigenerational exploitation of carrion by blow fly species would support the notion that interspecific competition for carrion has been a primary force for selection leading to temporal specialization by carrion-feeding insects. As an issue in criminal investigations, the absence of multigenerational development by some blow flies would narrow the potential postmortem window during which their development might occur, thus increasing the potential accuracy when estimating the time of death.

METHODS

On July 12, 2006, six pig (*Sus scrofa* L.) cadavers, ranging from 48 to 58 kg, were obtained from the Veterinary Diagnostic Center in Lincoln, NE. These pigs were killed via electrocution, and had their tonsils removed as part of another investigation. The pigs were received approximately 1 hour after death, and were immediately transported to the Carter-Huntington taphonomy research site at the University of Nebraska Agricultural Research and Developmental Center near Mead, NE. This location is an open pasture, primarily composed of smooth brome (*Bromus inermis* Leyss) and white clover (*Trifolium repens* L.), and the site is fenced to restrict the access of large vertebrate scavengers. The cadavers were placed directly on top of the existing vegetation 10 m apart to allow for insect colonization.

After being exposed for approximately 45 hours, a 2 m³ outdoor insect exclusion cage (BioQuip Products,

Inc., Rancho Dominguez, CA) was erected over each pig to contain the insects already associated with the cadaver and exclude further colonization by other insects. Sand was poured around the bottom edge of each cage to better seal the cage bottoms. Adult flies trapped inside each cage were collected and removed with an aerial insect net, and several strips of flypaper were placed in each cage to help trap any adult flies that remained in the cage after the use of the net.

After the placement of the cages, carcasses remained undisturbed for one week. After this time, sticky traps were removed from the cages, and observations of maggot activity were made to ensure that maggots migrating away from the carcasses pupated within the cage, and to identify fly emergence.

Eclosion of adult flies within the cages occurred 13 days after the placement of the pigs. Each cage was provisioned with sucrose and water ad libitum to maintain healthy adult flies. These adult flies represented the first generation of insects to use the cadavers as a resource.

To test for multigenerational colonization, a choice/no-choice observational study was conducted. Three freshly killed pigs were again obtained from the Veterinary Diagnostic Center in Lincoln, NE. These pigs were prepared in the same manner as those of the first portion of this study, and weighed between 45 and 49 kg each. Three of the previously caged carcasses were chosen at random, and a fresh pig carcass was placed approximately 0.5 m from the decomposed remains in these cages. Thus, in three cages (the choice treatments) flies from the first generation could oviposit on either the decayed carcass or the fresh carcass. In the three cages without fresh carcasses (the “no choice” treatments) the only ovipositional choice was the decayed carcass.

Scoring of the pigs took place after three days. Each cadaver was observed for colonization by the adult flies, indicated by eggs or maggots on the carcass. Because of the insect exclusion cages, any further insect activity on the “no choice” carcasses at this stage would be limited to those adult flies that have developed on the corpse (first generation), and eggs which may have been deposited on the remains at that time would represent the second generation of flies.

RESULTS

Weather conditions during the experiment were hot and humid, with daily high temperatures ranging from 39° to 27°C and daily low temperatures from 24° to 14°C. The rainfall total during the experimental period

measured 6.35 cm, and the average relative humidity was 69%.

Initial blow fly colonization of the remains occurred rapidly by *Phormia regina* (Meigen) and *Cochliomyia macellaria* (Fabricius). Both of these species are extremely common during the summer in Nebraska and throughout much of the Great Plains (Hall 1948; Huntington 2005). No other calliphorid species colonized the carcasses, although sepsids (Diptera: Sepsidae) and piophilids (Diptera: Piophilidae) did occur after initial colonization by calliphorids. No sepsid or piophilid adults were observed when cages were established, but adults in both families are sufficiently small that they may have entered the cages through the mesh. Other carrion insects colonizing the carcasses were limited to beetles, and included *Creophilus maxillosus* (Gravenhorst) (Coleoptera: Staphylinidae), *Necrobia rufipes* (DeGeer), *N. violacea* (L.), *N. ruficollis* (Fabricius) (Coleoptera: Cleridae), and *Dermestes maculatus* (DeGeer) (Coleoptera: Dermestidae). Although some of these beetles are predacious on fly maggots, there was no appreciable affect on the numbers of maggots or their development.

In each of the six trials several kilograms of moist skeletal muscle remained on the decomposed pigs at the time of scoring. In each of the "choice" replicates, blow flies colonized the fresh carcass rapidly, and no fly eggs or maggots were observed on the decomposed carcass after three days of observation. Adult populations in each of these cages appeared to remain healthy and stable in numbers.

In the cages containing the "no choice" replicates, no additional fly colonization took place. Adult flies continued to feed on the carcasses and sucrose, but after three days of observation there was noticeable fly mortality (>50%) occurring in each of the "no choice" cages, despite the availability of both food and water. Continued observation of the "no choice" cages showed total fly mortality and no recolonization of the carcass.

CONCLUSIONS

The failure of *P. regina* or *C. macellaria* to produce a second generation on decomposed cadavers supports the conventional understanding that only a single generation of blow flies will result from a carcass. Although only two species of blow flies were represented in this study, both belong to the subfamily Chrysomyinae, a group of blow flies known to delay oviposition by a day or more after an animal's death, as opposed to the subfamilies Calliphorinae and Luciliinae, which are comprised of

blow flies that generally prefer to oviposit immediately following death of the host (Hall and Doisy 1993). This leads us to conclude that other species of carrion-feeding blow flies will also fail to produce multiple generations on a single carrion source. It seems most likely that this lack of recolonization (specifically, oviposition) is a consequence of insufficient or inappropriate ovipositional cues (given the more advanced stage of decomposition), but other explanations, such as a nutritional or physiological barrier to oviposition, cannot be excluded.

The current study demonstrates the importance of the spatial and temporal distribution of resources in terrestrial ecosystems. It is well established that carcasses act as specialized resource islands for several insect taxa and a corridor for the dispersal of biota throughout an ecosystem (see Carter et al. 2007). That the observed flies did not use decomposed remains as an oviposition site demonstrates that these insects must move from fresh resource to fresh resource. This apparent "window" of opportunity demonstrates the effect that a carcass can have on spatial and temporal patterns of biodiversity and reinforces the idea that carcasses may play a critical role in maintaining life in an ecosystem (Carter et al. 2007).

From an evolutionary perspective, failing to produce multiple generations on a single resource base is surprising. This type of behavior would be expected if the resource base were small, and there was a risk of a second generation failing to complete development. In fact, in another group of dipterans, fruit flies (Diptera: Tephritidae) in the genus *Rhagoletis*, females use spacing, or epideictic pheromones, to avoid repeated oviposition into fruit that cannot support development of more than one larva (Averill and Prokopy 1987). However, given the size of the carrion used, insufficient resources for a second generation was not an issue with our experiments.

A second explanation is that some other limitation prevents use of the carrion through multigenerational development. Changes in the biochemistry and microbiology of decomposition of the carrion might seem to represent such a limitation, but with a large carcass, like the pigs used in this experiment, decomposition is not a single process: portions of the carcass will be simultaneously at more and less advanced stages of decomposition. So while some physiological limitation in the nutritional suitability of a carcass would certainly lead to selection against multigenerational use, such a limitation seems unlikely in a carcass that still has relatively fresh tissues available even after the first generation of blow flies have completed development.

To us, a more likely explanation for single-generation use of carrion by blow flies is competition between carrion-using insects. Existing evidence of competition exists in some species of carrion-feeding beetles where the beetles kill maggots on carrion, without eating these maggots (Trumbo and Fiore 1994). Similarly, the removal and burying of carrion by some silphid beetles points to an evolutionary strategy of removing the resource to avoid competition (Trumbo 1990). In the *Rhagoletis* example, the strong selection pressure of insufficient larval resources leads to the evolution of a spacing pheromone. Among blow flies, the evolution of highly sensitive chemoreceptors was essential for flies to find and exploit a spatially and temporally scarce resource. Possibly this host detection system also represents a pre-adaptive trait that has allowed blow flies to discriminate between different initial stages of decay (when sufficient time exists for complete larval development) versus later stages of decay (when predation or competition from other carrion feeders might prevent successful reproduction).

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