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Review Article

Heat Production by Necrophagous Fly Larvae: Implications for Forensic Entomology

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Abstract

Necrophagous fly larvae are the most useful insects for forensic investigations. The development of such larvae can be linked to the ambient conditions associated with a crime scene, and thus are important tools for estimating a portion of the Post Mortem Interval (PMI). However, one major complicating factor is that these flies display short-term heterothermy. In other words, heat is generated within the large feeding masses created by fly larvae. In fact, the internal heat of this microhabitat has been shown to exceed ambient environmental temperatures by as much as 30°-50° C. The resulting heat production alters several aspects of fly development that cannot be discerned from a record of ambient air temperatures. Thus subsequent estimations of the time of death based on fly evidence have inherent error since the true conditions of the microhabitat (i.e., maggot mass) have not been used. Current models using insect data to estimate portions of the PMI rely on ambient temperatures rather than maggot mass temperatures. This review examines what is known about maggot mass internal temperatures and examines how the maggot mass complicates estimations of the PMI.

ABBREVIATIONS

HSPs: Heat Shock Proteins; PMI: Post Mortem Interval

INTRODUCTION

Faunal succession of insects on human and other animal carcasses often results in larvae from several species of necrophagous flies forming dense feeding aggregations that can generate internal heat [1,2]. Heat production is not only unique for insects, but within the context of fly maggot masses, can yield temperatures that exceed ambient air temperatures by more than 30°C. The source of heat production is not known. Heat generation has been attributed to microbial activity [3,4] and/or as a byproduct of aerobic metabolism by fly larvae, principally linked to digestive processes [5,6]. The latter is predicted to be associated with rapid rates of food consumption and muscle movement along the fore- and mid gut regions of the digestive tract [7,8]. None of these predications have been experimentally tested. Slone and Gruner [6] found that the volume of a maggot mass developing on pig carcasses and how 'tight' the mass was packed together profoundly influenced internal mass temperatures. Larval age and fly species were not found to be important contributing factors to maggot mass temperatures. These observations were made under field conditions in which flies used pig carcasses during natural succession and hence, no variables were controlled.

By contrast, investigations [9] performed under laboratory conditions using both calliphorids and sarcophagids have shown that age of the fly larvae and species did result in differences in mass temperatures when flies were reared on bovine liver. However, the actual temperatures recorded in laboratory generated maggot masses do not achieve the maximum temperature elevations observed from larval aggregations formed during natural faunal succession [1,2,10]. Collectively, these observations suggest that multiple factors, including both abiotic and biotic, contribute to heat generation in larval aggregations [4,6,9-11]. At this time, no study has yet to decipher the exact contribution of these potential heat sources to the internal mass temperatures, leaving several questions related to heat production and development of fly larvae unanswered. Such information is important not only for basic physiological understanding of how the microhabitat of the maggot mass contributes to the overall development of necrophagous flies residing in carrion communities, but also to the development of mathematical models based on fly development. It is the latter information that is used in the estimation of the Post Mortem Interval (PMI) based on fly evidence during legal investigations. Consequently, there is an absolute need for further study into deciphering the mechanisms of internal heat production associated with fly aggregations that form on various forms of vertebrate carrion, specifically human remains.

ROLE OF INSECTS IN ESTIMATING THE POST MORTEM INTERVAL

Insects can aid in several types of medico criminal investigations, but perhaps the capstone lies with death, most typically homicides. It is human death that draws the most attention of criminal and forensic investigators, the lay public, and insects. Necrophagous flies are particularly useful in helping to decipher when the deceased actually died. The patterns of faunal succession during physical decomposition of a corpse coupled with the unique growth of certain species of flies (Families Calliphoridae and Sarcophagidae) that feed nearly exclusively on tissues of the deceased and having their development linked to ambient temperatures, permits the use of these insects to uncover the PMI [12]. Actually it is more correct to say that the information revealed is the time since colonization, since the flies do not colonize the body exactly at the moment of death. Insects as poikilotherms; that is, animals in which body temperature fluctuates with ambient conditions, are powerful tools for relating development with the temperatures experienced by and on the corpse, which in turn can be linked to time estimates. Using insects to estimate the PMI is relatively straightforward in terms of calculation but relies on complex ecological and biological principles, complicated by numerous contributing factors, many of which are not fully understood.

Insects are the most useful of all ecological evidence that can aid in a death investigation, especially when the time of death is unknown. What makes them so useful? For one, several species of insects are attracted to carrion within a few minutes of death, so faunal succession is relatively predictable for specific stages of physical decomposition of the corpse. The second reason is that some species produce larvae whose development is tied to feeding on the corpse [13]. These traits allow necrophagous insects to contribute to a portion of the PMI in at least two ways. The first relies on the relative predictability of species that arrive and use carrion in waves during physical decomposition. The presence or absence of particular species can convey qualitative information about the length of time the body has been available for insect colonization as well as ambient conditions. For example, the absence of first wave colonizers, namely flies in the Family Calliphoridae, signifies that the remains were not assessable for a set period of time, or that environmental conditions did not favor fly activity until later in decomposition. There are other possible explanations but the examples serve to illustrate how the PMI can be influenced by the mere presence or absence of insects. In the second approach, a portion of the PMI can be estimated based on necrophagous fly larval development. More specifically, the age of the oldest larva found on the body can be used for making a time estimate of the association between the fly and body. This approach relies on working backward from the developmental stage discovered to oviposition/larviposition. A time can then be estimated for how long development would have taken under the environmental conditions associated with the crime scene. If this range of time is then coupled with an estimate of body placement (death) to oviposition, an overall PMI can be predicated [14]. Actually, only a portion of the PMI can be estimated in this fashion, known as the minimum PMI. The minimum PMI is an indication of the minimum length of time that the insect had access to the body for colonization and development up to the point of discovery; a period of time exists between insect colonization and the agonal period, or moment of death [15,16]. Thus, insect data generally can reveal aspects of a portion, but not all, of the PMI.

THE PROBLEM WITH MAGGOT MASSES AND HEAT PRODUCTION

For many of the fly species attracted to a corpse, following egg hatch or after larviposition, the larvae establish a unique microhabitat on the corpse referred to as maggot masses. A hallmark feature of maggot masses is the generation of internal heat that elevates the local temperature to several degrees above ambient temperatures [4]. The extent of heat production is dependent on an array of factors, including but not limited to the size, density and/or volume of the feeding aggregation, species composition, food source which may have varying influences dependent on where the mass forms on a corpse, microbiota present in the mass, and influence of ambient conditions [2,6,9,17-19]. Heat production generally changes over time, reaching peak elevations early during the third stage of larval development, and then dropping sharply once post feeding begins [5,9]. Higley and Haskell [14] have argued that if known, maggot mass temperatures should be used as the ambient temperatures for calculations of the PMI. Unfortunately, rarely are these temperatures known, and they are very difficult to model since so many factors influence the hourly internal mass temperatures. There currently is no means for determining what the maggot mass temperatures actually were during larval development prior to the time of body discovery. Here lies an important area of further investigation: to develop tools that permit understanding the true ambient temperatures experienced by flies during development on a corpse. One approach is to determine if the thermal history of the flies can be deciphered from molecular markers associated with the stages of development discovered at the crime scene. For example, it may be possible to examine heat shock protein (hsps) expression in fly larvae and puparial stages to gain a snapshot of the thermal history of the flies while feeding on the corpse [20]. The presence of certain hsps (i.e., temperature and/or stage specific), quantity (dependent on duration of exposure or maximum temperature experienced), level of hsp decay (revealing time since exposure), as well as gene expression in later stages of development may provide valuable insights into temperatures experienced at an earlier stage of development. However, only one such study [11] is known to have tackled this topic in the context of maggot masses, so more definitive work is needed before this approach can be validated. With a lack of alternative data, ambient air temperatures are used to estimate the conditions that were experienced during larval development. This introduces inherent error into PMI calculations since 1) maggot masses ordinarily will form on a corpse, 2) internal temperatures of the aggregations will far surpass ambient conditions under most conditions, and 3) maggot temperatures also influence later colonizers and species-species interactions within the same maggot mass. The combination of these maggot mass influences strongly argues that ambient air temperatures do not accurately portray the actual developmental conditions of many species of necrophagous flies. Focused research on the basic physiology of maggot mass heat production is needed to help elucidate the mechanisms behind the generation of heat, which in turn may lead to new approaches to monitoring and predicting the thermal history of flies developing on a corpse. Such studies include determination of maggot masses temperatures during developmental progression under a variety of conditions (static and variable ambient conditions, including temperature, relative humidity and photoperiod), examination of whether fly larvae rely on 'cooling' mechanisms that permit avoidance of overheating in maggot masses [21], which may include maintenance of individual body temperatures that differs from internal maggot mass temperatures, and deciphering whether the location on a corpse influences developmental temperatures achieved by the maggot mass. The later necessarily implies nutritional differences in corpse tissues, which undoubtedly impacts internal heat production and rate of development.

DISCUSSION AND CONCLUSION

The reality is that many factors remain poorly understood in terms of heat production in maggot masses. No study has attempted to decipher the physiological bases of heat production by necrophagous fly larvae. Consequently, use of PMI estimates based on fly development in legal matters remains precariously challengeable either because the ambient temperatures used for developmental calculations ignore the microhabitat of maggot masses, or such temperatures have been incorporated but cannot be discussed with certainty or accuracy as to how long they represent the true ambient temperatures experienced by the insects. New research is needed to address this deficit in our understanding and to help improve the precision of models based on fly development data for estimating portions of the PMI.

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