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ABSTRACT

This paper deals with an important issue of forensic entomology: the estimation of the temperature in a "maggot mass". An agent-based model of the thermoregulation behaviour of fly (*Protophormia terraenovae*) larvae is described. Simulation results show that the model reproduces an important observed pattern and thus, might be used in entomological expertises.

INTRODUCTION

Forensic entomology is widely used in criminal investigations to determine post-mortem interval (PMI) and possibly information about the crime such as death location (Marchenko 2001). This is done studying the entomofauna, *i.e.*, the insects, mainly maggots (fly larvae), found on the corpse. A PMI is usually estimated by experts using analytic models of insect development. These models can be easily employed to perform retrodictive reasoning but do not take into account the ecosystemic context. Thus, datings performed using these methods are sometimes overestimated and not as precise as they could be. An important cause of inaccuracy is the thermoregulation behaviour of larvae. This phenomenon, known as the "maggot mass effect" has been described in numerous publications. However, no model has been proposed to handle this issue. In this article, an agent-based model of the thermal behaviour of fly larvae is introduced. A species of forensic interest, *Protophormia terraenovae*, is considered. First, forensic entomology methods and issues are introduced, then, the thermoregulation model is described, as well as its implementation. Finally, simulation results are detailed.

INTRODUCTION TO FORENSIC ENTOMOLOGY

Overview of the colonization process of a corpse

A cadaver is an important source of nutriments for insects, especially for necrophagous species. Many species will succeed on the body, each one of them being interested by a particular stage of decomposition. The first necrophagous species to colonize a cadaver are Diptera but in advanced stages it is common to find Coleoptera species. A few hours after the death, the first Diptera females are attracted by the body and lay eggs on it, mainly on natural orifices. Once the eggs hatch, Diptera larvae colonize the body to feed. Three larval stages, or instars, named L1, L2 and L3 will succeed. When a larva ends its development cycle, it leaves the corpse to find a suitable place for pupariation, an inactive stage at the end of which the larva eventually turns into an adult fly (figure 1).

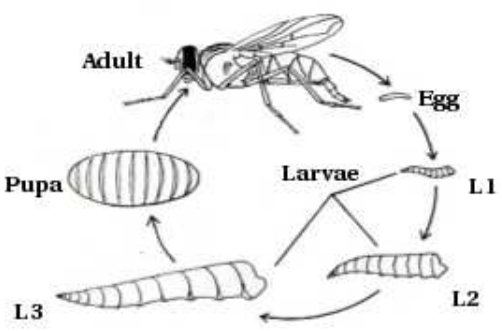

Figure 1: Development cycle of a Diptera.

As many living organisms, the development of Diptera is temperature-dependent (Stinner et al. 1974). Thus, the development speed $\frac{da}{dt}$ of an individual is given as a function f of the temperature T varying in the time t

$$\frac{da}{dt} = f(T(t)). \quad (1)$$

On this basis, various models have been developed, some

assuming a linear relation between development speed and temperature, some a more complex relation. A review of development models can be found in Wagner et al. (1984). The validity of those models will not be discussed in this paper.

Methodology of entomological expertises

When a cadaver is discovered, investigators take samples of eggs, larvae or pupae from the body. Entomologists determine the species and the accumulated rates of development (denoted Δa) of the oldest individuals. Then, for each one of them, the laying time t_1 (generally close to the time of death) can be calculated from the equation

$$\Delta a = \int_{t_1}^{t_2} f(T(t))dt, \qquad (2)$$

where t_2 represents the time of the cadaver discovery.
Data from the nearest meteorological station are used in order to estimate the temperature. However, considering that the temperature at any point of the body is equal to the temperature recorded by the nearest meteorological station is not exact for three reasons. Firstly, ecosystem specificities can radically influence the temperature around the body as shown in Gosselin et al. (2006). Secondly, the thermal inertia of a corpse is important, especially in the first hours after death (Henssge 2004). Thirdly, the heat generated by larval aggregations can raise the temperature locally up to 20°C. This phenomenon, known in the literature as the "maggot mass effect" and its consequences on PMI estimation have been discussed by many authors (Marchenko 2001, Slone and Gruner 2007). Thus in many cases, entomological expertise results are inaccurate and given with an important margin of error.
The agent-based model presented in the next section focuses on the third cause of inaccuracy. Indeed, this model allows to simulate the thermoregulation behaviour of large masses of Diptera larvae.

Behaviour of Diptera larvae

The behaviour of Diptera larvae remains mostly unknown. The present study is based on observations performed by the authors and found in the literature, *e.g.,* in Hobson (1931). It is well known that Diptera larvae have a gregarious behaviour that favours the formation of huge aggregations. This behaviour is not species or instar specific. Moreover, there is no discrimination between instars or species in aggregations. It has been shown that larvae are attracted by a stimulus emitted by conspecifics. Though the nature of the stimulus (vibrations, ammonium hydroxide, etc.) has not been cleary idenfied, we assume that this stimulus can be represented by a pheromone-like variable. The dynamics of larvae inside an aggregation is very complex. However, the observation of larva masses revealed a precise repartition of individuals, depending on their physiologic state. Thus, it is possible to distinguish between three main behaviours:

- **feeding**: larvae are immobile, vertically aggregated and in direct contact with the nutritive substrate;
- **looking for food**: larvae which the crop is empty try to reach the centre of the aggregation, *i.e.*, to access to the food;
- **digestion**: larvae which the crop is full move around the aggregation, looking for optimal temperature.

The structure of a maggot mass can be explained from these three simple behaviours. While there is no collective decision or space optimisation, a coherent and self-organised behaviour emerges from local interactions between larvae. This gregarious behaviour can be regarded as a primitive, though very efficient, form of collaboration. Indeed, it allows larvae to share digestive fluids and optimise the temperature in the aggregation. Each larva emitting heat, due to its metabolism and rubbings, it can result an important, quick and local increase of the temperature. Thus, larvae in an aggregation speed up their development period and maximise their chance of surviving.

DESCRIPTION OF THE MODEL

Model structure

The model has been implemented on TurtleKit (Michel 2002, Michel et al. 2005), a logo-like simulation platform built on the generic multi-agent platform MadKit[1] (Ferber and Gutknecht 1998). In TurtleKit, simulation agents act in a two-dimensional environment discretized into "patches". A patch is then an homogeneous environment portion to which "patch variables" are attached. Simulation agents can perceive and act in the environment by manipulating patch variables. However, patch variables can have their own dynamics. The behaviour of a simulation agent is defined as a finite state automaton, each state representing an atomic behaviour. Moreover, the TurtleKit platform provides graphical monitoring tools.
Our model environment has been designed to imitate the environment used in the experiments performed at the entomology laboratory of the medico-legal institute of Lille. Three variables are attached to patches : the amount of food available, the concentration of a pheromone-like substance emitted by larvae and the temperature. The thermal dynamics of the environment has been modelled using a cellular automaton approach presented in Veremme et al. (2008). Simulation agents represent *P. terraenovae* individuals during

[1] `http://www.madkit.org`

their preimagal life, *i.e.*, until they become adult flies. The development model implemented in the simulation agents is described in Stinner et al. (1974). A model of development variability inside the larva population based on Régnière (1984) is also used. The crawling speed of larvae has been estimated using the model presented in Charabidze et al. (2008). In the next section, the architecture of simulation agents is presented. These agents are purely reactive, *i.e.*, they do not have any symbolic representation of their environment or the other agents. Their behaviour depends on environmental stimuli and their internal state. Thus, they can be characterised as "drive-based agents" (Ferber 1999).

Architecture of the agents

The main idea behind this model is that the behaviour of a larva is different whereas it is in viable or non-viable conditions and that its behaviour in non-viable conditions regulates the temperature of the aggregation by optimising its density. The architecture of the simulation agents can then be represented as a 2-state automaton (figure 2). The state b_1 represents the behaviour of the agent in viable conditions whereas the state b_2 represents the behaviour of the agent in non-standard, *i.e.*, non-viable or "stress" conditions. The transition between these two states depends on a condition c_p. Here, c_p is defined as follows :

$$c_p : T > T_{max}, \tag{3}$$

where T is the temperature felt by the agent and T_{max} is the maximal temperature supported by a larva.

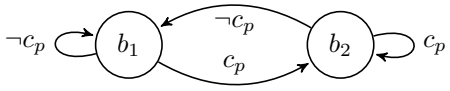

Figure 2: Behavioural model overview. b_1: "normal" behaviour, b_2: "panic" behaviour.

In the state b_2, the agent moves randomly in the environment. The "normal" behaviour is a little more complicated and can be defined as a 3-state automaton representing the three standard atomic behaviours of a larva (figure 3).
A variable j, proper to each agent, is introduced to represent the state of the crop of the larva ($j = 0$ if the crop is empty, $j = 1$ if the crop is full). Moreover, we assume that the feeding speed is a function of the temperature T, *i.e.*,

$$\frac{dj}{dt} = \begin{cases} 0 & \text{if } T \leq T_{min} \\ 1 & \text{if } T \geq 25 + T_{min} \\ \frac{T - T_{min}}{25} & \text{otherwise,} \end{cases} \tag{4}$$

where T_{min} is the minimal temperature at which a larva is active.
Each state of the automaton represents a specific behaviour. The state $b_{1,1}$ represents the feeding behaviour: the agent does not move and consumes environment resources. An agent feeds on a given patch *iff* its crop is not full (*i.e.*, $j < 1$) and a condition c_e is true. c_e can be intuitively defined as follows: *the patch where the agent is located is a local maximum for the maggot signal and the nutritional capacity of the patch is superior to a threshold,* n_{min}.
The state $b_{1,2}$ represents a temperature optimisation behaviour. After feeding, the larva looks for the patch that optimises its development speed $f(T(t))$. The algorithm that underlies that behaviour is a simple gradient descent. The agent keeps on that state until its crop is below a given value, *i.e.*, $j < \gamma$.

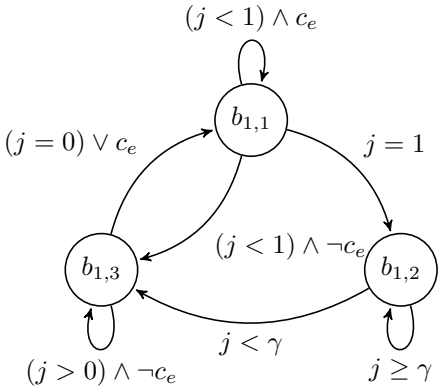

Figure 3: Behavioural model of a larva in standard conditions. $b_{1,1}$: feeding behaviour, $b_{1,2}$: temperature optimisation behaviour, $b_{1,3}$: food searching behaviour

Then, the agent switches to the state $b_{1,3}$ which represents a food searching behaviour. In this state, we assume that larvae try to aggregate with conspecifics. Similarly to the state $b_{1,2}$, the algorithm that underlies that behaviour is a gradient-descent.
The perception accuracy of the agents is not optimal. Thus, perception levels are determined for the patch variables used in the gradient-descent algorithm. *E.g.*, for a given patch variable, let v be the patch variable value, and l its perception level; it means that the agent is not able to differentiate between v and $v \pm l$. Let l_t and l_a be the perception levels for the temperature and aggregation stimuli.
The temperature elevation T_e, resulting from the activity of a larva on a patch during a simulation step s (one minute in the simulations presented in the next section), is defined as follows:

$$T_e(s) = \lambda \cdot \Delta a(s), \tag{5}$$

where $\Delta a(s)$ is the accumulated rate of development of the larva at the step s, and λ a parameter of the model. The parameters of the model in "normal" conditions (state b_1) have been identified through a qualitative calibration process. The table 1 gives the values determined for these parameters. Perception levels had already been identified in Hafez (1948). However, slightly different values have been determined here.

parameter	value	unit
γ	0.95	–
T_{min}	10	°C
l_t	0.5	°C
l_a	10^{-7}	–
n_{min}	$9 \cdot 10^{-3}$	kg

Table 1: Parameters identified in normal conditions

Thus, only two parameters remain to be identified: the maximal temperature supported by a larva, T_{max}, and λ.

RESULTS

Model exploration and calibration

A brute-force exploration of the model predictions has been performed to determine the best values for λ and T_{max}. The root mean square deviation (RMSD) is used to measure the difference between predicted and measured values.

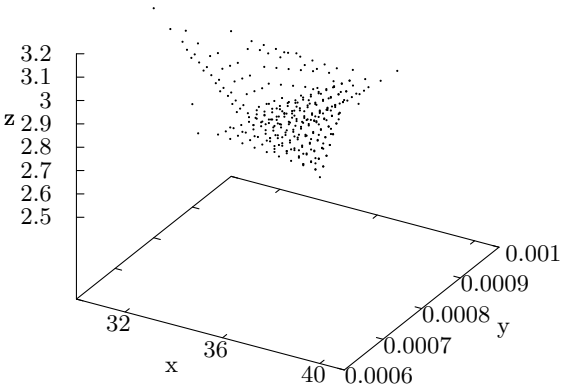

Figure 4: Exploration of model predictions (axis x: value of T_{max}, axis y: value of λ, axis z: RMSD).

Measured values have been obtained from experiments conducted at the Medicolegal Institute of Lille. *P. terraenovae* larvae were placed without food at the experimental temperature during five hours in order to synchronise their metabolism. Larvae were weighted and placed in a box with sawdust and a piece of beef heart of the same weight than the larva batch. The box was then placed in a thermostatic area programmed at constant temperature. Two temperature probes (precision: ±0.5°C) recorded the temperature inside and outside the box every minute. The maximal temperature increase in function of the number of individuals in the aggregation and the temperature of the environment has been identified as stable pattern that simulations should reproduce. Simulations have been repeated ten times to guarantee the robustness of the results. The mean is used to merge the results of the simulations. The values of the patch variable properties used to simulate the nutritive substrate can be found in Veremme et al. (2008). The figure 4 gives the shape of the two parameter space that has been explored. The table 2 gives the best values found for λ and T_{max}.

parameter	value	unit
T_{max}	35	°C
λ	$9 \cdot 10^{-4}$	–

Table 2: Values of the parameters of the thermoregulation model identified by simulation

Simulation results and discussion

The figure 5 compares maximal temperature increases observed *in vitro* and predicted *in silico*. As a few replicates have been done, experimental results exhibit an important variability. More experiments should be carried to "smooth" the results. Thus, the difference between experimental and simulation results is sometimes important. On the contrary, the dispersion of simulation results is small, but not constant, as shown in figure 6.

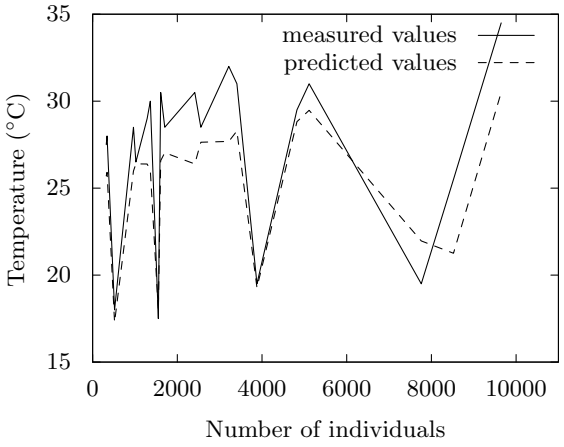

Figure 5: Simulation and experiment results of temperature in *P. terraenovae* masses in various cases.

Though the results are promising, in "huge aggregation" cases the model tends to underestimate the temperature in the aggregation. The existence of such a bias in predictions could be caused by two phenomena that have been neglected in the model.

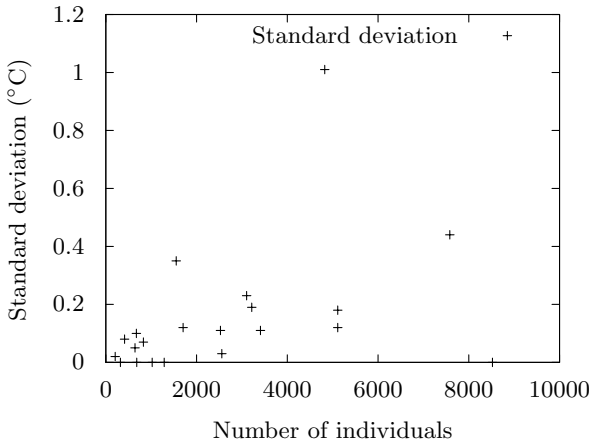

Figure 6: Standard deviation (°C) of model predictions in function of the number of individuals in the aggregation.

First, this model is based on the generally accepted assumption that temperature increases in aggregations are caused by the metabolic activity of larvae during the digestion process as shown in Slone et al. (2005) and Slone and Gruner (2007). But rubbings between individuals could be responsible, for a part, of the temperature increase especially when many individuals are involved: the competition to reach the food is then harder and larvae are more active. Though this hypothesis has to be validated, experiments carried with starving larvae seem to confirm it: in large aggregations, a temperature increase can be observed, even if there is no digestive activity as shown in figure 7. Nevertheless, this effect has to be precisely quantified before it can be included in the model.

Second, in small aggregations, heat transfers with the environment are important, which is not the case in bigger aggregations. Indeed, the main heat source, the feeding larvae, is isolated from the environment by larvae that are trying to reach the food. Thus, the density of larvae should be taken into account to estimate heat transfers between an aggregation and its environment.

However, as the figure 8 shows, using this model in entomological expertises should increase the accuracy of the results. Indeed, in all tested cases, the difference between simulated and measured temperatures is less than the difference between environment and measured temperatures, *i.e.*, less than the difference between the temperature used to perform expertises and the temperature felt by larvae.

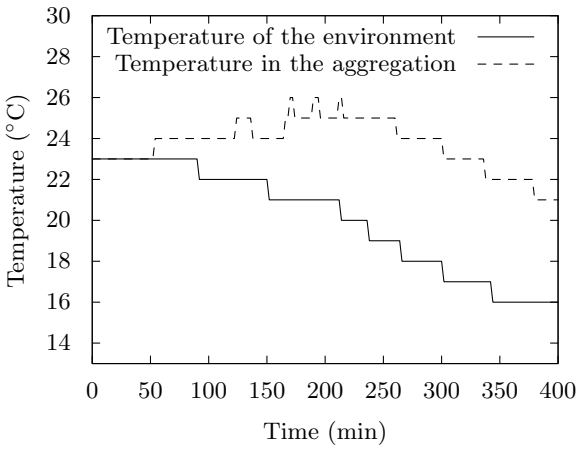

Figure 7: Temperature (°C) recorded in an aggregation of starving larvae.

CONCLUSION

In this article, an agent-based model of thermoregulation in *P. terraenovae* masses has been presented. Though the model has been validated for this particular species, it might be used to predict the temperature increase in other/mixed species aggregations as their thermoregulation behaviours are similar. Thus, this model should increase the accuracy of entomological expertises in complex cases.

To use this thermoregulation model in real world cases, a model of human body has been developed (Veremme et al. 2008). However, as the legislation on human cadaver experiments is very strict in France, experimentations are conducted on cow carrions to validate the model in real world conditions. This model has already been included in ForenSeek, a decision support system for forensic entomology[2]. Moreover, this simulator can be used as a virtual laboratory to test hypotheses about necrophagous Diptera larvae and especially the behavioural and physiological causes of the maggot mass effect.

Beyond the application to forensic entomology, these results show that a complex thermoregulation behaviour can be produced using simple reactive agents, that do not have any knowledge of the global structure of the system. In this perspective, self-organisation and non-intentional cooperation in Diptera larva masses could be studied from a more theoretical point of vue. The simplicity and efficiency of such simple organisms is interesting to understand the formal characteristics of col-

[2] `http://www.forenseek.org`

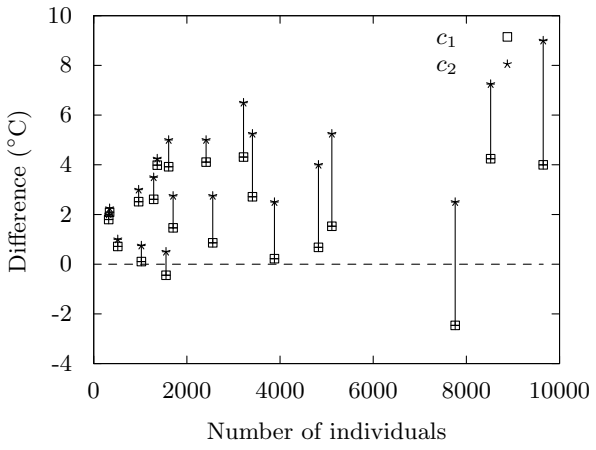

Figure 8: Difference (°C) between the temperatures measured in the aggregation and predicted by the model (c_1) and between the temperature measured in the aggregation and the temperature of the environment (c_2) in function of the number of individuals in the aggregation.

laboration in systems composed of numerous reactive agents (Deneubourg and Goss 1989).

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