Modeling population dynamics of two cockroach species: Effects of the circadian clock, interspecific competition and pest control

Hsin-Hue Wu\textsuperscript{a}, How-Jing Lee\textsuperscript{a}, Shwu-Bin Horng\textsuperscript{a,†}, Luděk Berec\textsuperscript{b,*}

\textsuperscript{a}Department of Entomology, National Taiwan University, 27, Lane 113, Section 4, Roosevelt Road, Taipei 106, Taiwan
\textsuperscript{b}Department of Theoretical Ecology, Institute of Entomology, Biology Centre ASCR, Braníčkova 31, 37005 České Budějovice, Czech Republic

Received 9 March 2007; received in revised form 27 July 2007; accepted 14 August 2007
Available online 25 August 2007

Abstract

The German cockroach \textit{Blattella germanica} is obviously one of the most spread household pests in the world, and is now virtually impossible to sustain outside human constructions. The double-striped cockroach \textit{B. bisignata}, on the other hand, is limited to Southeast Asia and mostly living in the open space, yet is able to establish in cockroach-free households, too. In this article, we develop a stage-structured population model of these two species to explore (i) whether their circadian clocks impact their long-term population dynamics, (ii) which of these species is a superior competitor, and (iii) how stringent potential pest control strategies have to be to significantly impact established populations of the German cockroach. The results of the model are as follows. Firstly, phase shifts in the light-to-dark cycle did not affect cockroach population dynamics unless males and females were out of phase and their mate finding abilities rather limited. In addition, for the hypothesized circadian clock genotypes, the shorter is the inactivity period relative to the activity one or the less arrhythmic is the population, the more viable the population is and the quicker it grows to large numbers. Secondly, the German cockroach was the superior competitor: it was able to invade and drive out established populations of the double-striped cockroach and prevent any invasion of the latter. Finally, only a significant and simultaneous reduction in a number of most sensitive German cockroach parameters resulted in species extirpation. Only carefully designed and data-based models of German (and double-striped) cockroach population dynamics can be helpful in our quest to win the fight over this unwelcome but very sturdy species.

Keywords: German cockroach; \textit{Blattella germanica}; \textit{Blattella bisignata}; Sensitivity and elasticity analysis; Pest control

1. Introduction

The German cockroach \textit{Blattella germanica} (L.) (BG) is a cosmopolitan species that lives gregariously in a close association with humans where it can find food, water and shelter—there is hardly any viable population off the actively used human constructions (Cornwell, 1968; Rust et al., 1995). Negative impacts of this association (e.g. adulteration of food with feces and defensive secretions, transport and harboring of pathogenic organisms, or initiation of severe allergic reactions) and its fruitful way of life (gregariousness coupled with vigorous female fecundity) make this species one of the most troublesome nuisance pests of the world (Fan et al., 2004; Zurek and Schal, 2004). Unfortunately, this does not appear to change in a due time, as there is currently no efficient and widely applicable strategy that would securely eliminate populations of this species (Kinscherf et al., 1996; Nalyanya et al., 2001; Schal, 1988; Zurek et al., 2002).

The double-striped cockroach \textit{Blattella bisignata} (Brunner) (BB), on the other hand, is a feral species that lives outdoors in a solitary manner and is distributed only in Southeast Asia (Roth, 1985), yet it is able to establish in cockroach-free households, too. The question has been recently raised whether BG, invading growing or established populations of BB, is vital enough to replace BB in such places, or vice versa. Available empirical evidence on competition between these two species is rare (Tsai and Lee, 2001; see also Section 4).
Both BG and BB demonstrate strong circadian rhythms in their locomotion activity (Tsai and Lee, 2000; Wei and Lee, 2001). The endogenous biological clocks controlling circadian rhythms are among important mechanisms expressed in animals. They synchronize animal activity within the day and night cycle, persist even in the absence of any environmental time cues (such as constant darkness or constant illumination), and provide animals with means for coordination of their fundamental life processes, such as feeding, predator avoidance, and mating (Bloch et al., 2004; Funk and Amir, 2000; Yang et al., 2005). Impacts of the circadian clock and animal synchronization on long-term population dynamics are, however, unknown.

In this article, we develop a stage-structured population model of the BG and its closely related species, BB, to explore impacts of the circadian clock and interspecific competition on dynamics of their populations. Models of this kind can complement short-term empirical evidence and set our understanding of biological processes on. We also suggest directions in which further experimentation is needed to make the model more reliable and to verify its predictions.

The population model we develop in this paper provides currently the most detailed description of the adult phase of the cockroach life cycle; we also provide values for its parameters that have so far been scattered throughout the literature. Alternative population models of BG were developed by Müller-Graf et al. (2001), considering just two animal stages—juveniles and adults, and by Zeman (1993) who focused in detail on the structure of the juvenile stage. As an extension of our modeling exercise, we carry out sensitivity and elasticity analysis of a density-independent, discrete-time (matrix) version of the BG model with respect to its parameters, showing how is the population growth rate sensitive to small parameter changes and where possibly control efforts could primarily be directed. Also, we perform a couple of perturbation experiments to see how BG populations might respond to some pest control strategies.

### 2. Methods

#### 2.1. Brief description of cockroach life cycle

Both German and double-striped cockroaches share a similar life cycle that consists of three developmental stages typical of insects with incomplete metamorphosis: eggs, nymphs, and adults. Eggs develop in an ootheca, protruding from the posterior end of a female and carried by the female before nymphs hatch. The number of molts required to reach adulthood varies and the most frequently reported number of molts is six. Adult males and females need a couple of days to become receptive. Males then stay virtually continuously receptive until they die (actually, male cockroaches make spermatophore during the ~90-min-long copulation; although an immediate re-copulation is rare, we observed two subsequent copulations within 2h). On the other hand, females go through a number of reproductive cycles—they have to find a receptive male, mate during a short mating window, spend some time pregnant (carrying ootheca), and finally recover to become receptive again. Even females that do not succeed to mate within the mating window become pseudo-pregnant and need to recover after that. Once mated, females store sperm and hence need not mate again in order to develop another fertile ootheca. However, not all matings result in a fertile ootheca and one mating is often not sufficient to supply enough sperm to avoid a need of new mating (and hence another mate search) later in life. Fig. 1 is a flowchart of this life cycle. Both cockroach species mate and reproduce continuously, with many overlapping generations present at any time.

#### 2.2. Mating activity data

To examine impacts the circadian clock might have on long-term population dynamics, we consider both the empirically determined mating activity of males and females adapted to different light-dark (LD) conditions.

---

**Fig. 1.** A flowchart of key components in the life cycle of *Blattella germanica* and *B. bisignata.*
2.3. Biological clock mutants

Since it is likely that any short-term acclimation for lighting will not persist for generations, long-term effects of the circadian clock on population dynamics would best be studied using organisms with genetically distinct clocks. Unfortunately, no clock mutants of either BG or BB have been available to us so that we resorted to a kind of thought experiment regarding the effects on population dynamics of such hypothesized circadian clock mutants. This exercise was inspired by the observation of three clock mutants of the fruit fly Drosophila melanogaster which were either arrhythmic in their locomotion activity or possessed short- and long-period clocks (Konopka and Benzer, 1971). Short- and long-period clock mutants of D. melanogaster had roughly the same 12 h period of inactivity and a short (~7 h) or long (~16 h) period of activity. We assume here that we have a ‘normal’ genotype of BG or BB characterized by 12 h of inactivity and 12 h of activity, and three mutant genotypes: (i) ‘long’ (9 h of inactivity and 15 h of activity), (ii) ‘short’ (15 h of inactivity and 9 h of activity), and (iii) ‘arrhythmic’, characterized by 12 h of inactivity and 12 h of activity which are nevertheless randomly distributed over the 24 h cycle. We also assume that mating activity of all these mutants corresponds to the 10 L ~10 L ～ scenario described above.

2.4. Cockroach population model

Since both cockroach species mate and reproduce continuously, with many overlapping generations present at any time, we have developed two comparable models: a stage-structured matrix model that runs in discrete time steps (1 day in our application) and a stage-structured continuous-time model defined by a system of ordinary differential equations. In both cases, the stage structure of the model accounts for the nine compartments displayed in Fig. 1. In addition, to utilize the information provided by

---

**Table 1**
The mating probability or acceptability of a male to a female upon encounter as a function of the day within the mating window and the male and female phase-related scenario, conditioned by the fact that the pair has not mated so far.

<table>
<thead>
<tr>
<th>Phase-related scenario</th>
<th>Blattella germanica</th>
<th>Blattella bisignata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10 L ~10 L ～</td>
<td>10 L ~22 L ～</td>
</tr>
<tr>
<td>Number of replicates</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td>Number of matings</td>
<td>9</td>
<td>24</td>
</tr>
</tbody>
</table>

| Day 1 | 0.0625 | 0.0357 | 0.0833 | 0.1563 | 0.1250 | 0.0556 | 0.0313 |
| Day 2 | 0.4000 | 0.2778 | 0.2045 | 0.4445 | 0.2501 | 0.0862 | 0.0968 |
| Day 3 | 0.1067 | 0.2782 | 0.1958 | 0.0594 | 0.1829 | 0.1509 | 0.1580 |
| Day 4 | 0.1138 | 0.1574 | 0.2947 | 0.1836 | 0.2613 | 0.3502 | 0.2386 |
| Day 5 | 0.0000 | 0.0691 | 0.0807 | 0.0000 | 0.1239 | 0.1813 | 0.1576 |
| Day 6 | 0.1321 | 0.1349 | 0.0745 | 0.1656 | 0.1321 | 0.1349 | 0.0745 |
| Day 7 | 0.0000 | 0.1086 | 0.0259 | 0.1218 | 0.0000 | 0.1086 | 0.0259 |
| Day 8 | 0.0000 | 0.0263 | 0.0651 | 0.0651 | 0.0000 | 0.0263 | 0.0651 |

It was estimated by placing one 2-day-old female and one 2-day-old male together. As we give probabilities calculated based on a number of experimental replicates, there is no mean and standard deviation.
the mating activity data, the \( F_a \) class (receptive females) is divided into an data of 1-day-long classes, five for BG and eight for BB (see also Table 1). We sketch the matrix population model here and leave description of the continuous-time model for Appendix A.

For BG, the full matrix model has the form \( x_{t+1} = A x_t \) where \( x = (N, M_N, M_{N0}, F_a, F_{a0}, F_a^2, F_a^3, F_a^4, F_a^5, F_{a0}, F_{a00}, F_{a000}) \) is the vector of system states (see Fig. 1 for the explanation of state variables), \( t \) counts discrete time steps (\( t = 1, 2, \ldots \)) and the transition matrix \( A \) looks as follows (the corresponding model for BB differs only by having eight \( F_a \) classes instead of five):

\[
\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \frac{s_N(1-r_N)}{s_N} & \frac{s_M(1-r_M)}{s_M} & 0 & 0 & 0 & 0 \\
0 & 0 & \frac{s_M}{s_M} & \frac{s_N}{s_N} & 0 & 0 & 0 \\
0 & 0 & 0 & \frac{s_Y(1-r_F)}{s_Y} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{s_Y(1-\phi_1)}{s_Y} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \frac{s_Y(1-\phi_2)}{s_Y} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{s_Y(1-\phi_3)}{s_Y} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{pmatrix}
\]

Each model equation (row of the transition matrix) describes temporal evolution of the size of subpopulation corresponding to a given stage, with non-zero elements of the interaction matrix representing stage transitions or arrows of Fig. 1. For example, nympha become adults (and thus leave the nymphal stage) with probability \( s_N(1-r_N) \), where \( s_N \) is the fraction of nymphs surviving one time step and \( 1/r_N \) is the length of the nymphal stage, and stay as nymphs with probability \( s_M(1-r_M) \), while \( b \) new nymphs recruit each time a mated pregnant female enters the recovery stage, an event that happens with probability \( s_M r_M \), where \( b \) is the number of eggs per fertilized ootheca, \( s_F \) is the fraction of adult females surviving one time step and \( 1/r_{MP} \) is the length of pregnancy period for mated females. Following the life cycle flowchart, analogous reasoning can be made to advocate the other model equations.

The precise meaning of all model parameters and their values used in our simulations are summarized in Table 2. There is apparently no unique source of life-history data for BG and BB, and the available data is quite heterogeneous among the different sources. The only information on BB we have comes from Tsai and Lee (2000, 2001) and from experience and notes members of this laboratory gathered over many years of growing and experimenting on this species. The information on BG is more widespread. Together with the same sources as for BB, we also collected information from Lee and Wu (1994) and many US and other web sites where apparently many universities, companies and organizations are involved in fighting this unwelcome but very sturdy species. Among these sites are the following:

- [creatures.ifas.ufl.edu/urban/roaches/german.htm](http://creatures.ifas.ufl.edu/urban/roaches/german.htm)
- [insects.tamu.edu/fieldguide/aimg25.html](http://insects.tamu.edu/fieldguide/aimg25.html)
- [www.pestworld.org/homeowners/spotlight/german_cockroach.asp](http://www.pestworld.org/homeowners/spotlight/german_cockroach.asp)
- [www.the-piedpiper.co.uk/th2b.htm](http://www.the-piedpiper.co.uk/th2b.htm)
- [www.west-ext.com/german_cockroach.html](http://www.west-ext.com/german_cockroach.html)
- [www.ento.psu.edu/extension/factsheets/german_cockroach.htm](http://www.ento.psu.edu/extension/factsheets/german_cockroach.htm)


Heterogeneity present in the available data (units, ranges, sampling effort, laboratory vs. natural populations) gave us no clear hint on which values to prefer. We took a range midpoint in some cases, what we considered the most precise value in others, based on long-term experience of two of us (HJL and HHW), and the mean in still other cases. We do not claim that our choice is the best possible one, and this is also one of the reasons we carried out the sensitivity and elasticity analysis of our model predictions with respect to all parameters considered. Obviously, the parameters to which model predictions are most sensitive require conducting further experiments so as to make their values as precise as possible.

### 2.5. Female mating rate

A submodel for the female mating rate, that is, a functional form for \( \Phi_n \), is the most delicate part of the current model. To get fertilized, a receptive female has to find a receptive male and then to mate with that male. Neither the daily encounter rate (i.e. probability of a receptive female to find at least one receptive male at a given day) nor the probability of a female to mate upon male encounter are quantities we have at disposal. What we actually do is to utilize the information on locomotion activity for estimating the former (below) and the data on mating probabilities (Table 1) as estimates of the latter.
Female mating rate is obviously a function of the number or density of receptive males $M_{a}$. Simple but rather general arguments led McCarthy (1997) and Philip (1957) to propose the following functional form:

$$\Phi_i = k_i (1 - \exp(-S_i M_{a})),$$

Table 2

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>German cockroach, <em>Blattella germanica</em></th>
<th>Double-striped cockroach, <em>Blattella bisignata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of nymphal stage</td>
<td>$1/r_N$</td>
<td>60 d, 1.5–4 months, 74–85 d, 6–31 weeks, 6 weeks–6 months</td>
<td>$43.7 \pm 0.4$ d (male), $44.8 \pm 0.6$ d (female)</td>
</tr>
<tr>
<td>Number of eggs per fertilized ootheca</td>
<td>$b$</td>
<td>30–40, 30–48, 18–50 (mean 32), 30.9 ± 1.8</td>
<td>$18.5 \pm 3.3$</td>
</tr>
<tr>
<td>Mortality rate of nymphs</td>
<td>$d_N$</td>
<td>0.005 d$^{-1}$</td>
<td>$0.005$</td>
</tr>
<tr>
<td>Fraction of nymphs surviving to the next time step</td>
<td>$s_N$</td>
<td>$\exp(-d_N) = 0.995$</td>
<td>Unknown (value equal to that of German cockroach chosen)</td>
</tr>
<tr>
<td>Time span between entering the adult stage and becoming sexually receptive (males)</td>
<td>$1/r_M$</td>
<td>3 d, 5 d</td>
<td>3 d, 4 d, 3 d</td>
</tr>
<tr>
<td>Life span of adult males</td>
<td>$1/d_M$</td>
<td>100–200 d (range 1–303 d), 3–7 months, 20–30 weeks, slightly less than 6.5 months</td>
<td>$105.2 \pm 2.2$ d</td>
</tr>
<tr>
<td>Fraction of adult males surviving to the next time step</td>
<td>$s_M$</td>
<td>$\exp(-d_M)$</td>
<td>$\exp(-d_M)$</td>
</tr>
<tr>
<td>Time span between entering the adult stage and becoming sexually receptive (females)</td>
<td>$1/r_F$</td>
<td>4–6 d, 3 d</td>
<td>4–6 d, 3 d, 4–7 d</td>
</tr>
<tr>
<td>Life span of adult females</td>
<td>$1/d_F$</td>
<td>100–200 d (range 1–303 d), 3–7 months, 20–30 weeks, 6.5 months</td>
<td>$180.8 \pm 14.1$ d (mated once), $162.1 \pm 3.5$ d (virgin)</td>
</tr>
<tr>
<td>Fraction of adult females surviving to the next time step</td>
<td>$s_F$</td>
<td>$\exp(-d_F)$</td>
<td>$\exp(-d_F)$</td>
</tr>
<tr>
<td>Length of pseudo-pregnancy (virgin females)</td>
<td>$1/r_{VP}$</td>
<td>First about 2 d, later average 12 d</td>
<td>12 d</td>
</tr>
<tr>
<td>Length of recovery after pseudo-pregnancy (virgin females)</td>
<td>$1/r_{VR}$</td>
<td>3 d, 5 d</td>
<td>4–5 d, 5–11 d, at least 5 d</td>
</tr>
<tr>
<td>Length of pregnancy (mated females)</td>
<td>$1/r_{MP}$</td>
<td>About 30 d, 14–35 d, $17 \pm 0.6$ d</td>
<td>17 d</td>
</tr>
<tr>
<td>Length of recovery after pregnancy (mated females)</td>
<td>$1/r_{MR}$</td>
<td>5 ± 0.6 d</td>
<td>About 5 d, 3–4 d</td>
</tr>
<tr>
<td>Length of mating window (that is, number of $F_{a}$ classes)</td>
<td>$r_{MR}$</td>
<td>3–4 d, 5 d</td>
<td>5 d, 6 d, 7 d, 8 d</td>
</tr>
<tr>
<td>Probability that a female that has just dropped a fertile ootheca still has enough sperm to enter new pregnancy period without need of re-mating</td>
<td>$p_S$</td>
<td>One mating suffices to provide sperm for (on average) $3.4 \pm 1.6$ oothecae</td>
<td>One mating suffices to provide sperm for (on average) $2.7 \pm 0.2$ oothecae</td>
</tr>
</tbody>
</table>

Some parameters were measured under dark–dark conditions, while some under light–dark ones. Sources: Lee and Wu (1994), Tsai and Lee (2000, 2001), various US and other web sites. See the main text for more on how specific model parameters were chosen for model simulations.
where $k_i$ is the probability of a receptive female to mate on the $i$th day of the female window provided it still needs mating, and $S_d$ is the effective area searched by the female per day. This expression preserves holds if males are randomly distributed with density $M_A$ and females search randomly until a male ‘falls’ within the female reception range in which case the female goes directly to the male. We can write

$$S_d = \int_{t_0}^{t_1} S(t) \, dt,$$

where $S(t)$ is the effective area searched within a small time interval $(t, t+dt)$.

As both sexes have to be simultaneously active to initiate copulation, we can write $S(t) = a(L_M(t) + L_F(t))$ in that case and $S(t) = 0$ when at least one of the sexes is not active. Here $L_M(t)$ and $L_F(t)$ quantify locomotion activity of males and females, respectively, scaled to the maximum of one-half (to have their sum scaled to the maximum of one). The ‘movement efficiency’ constant $a$ is introduced to account for this scaling. Also, it comprises other features affecting the female mating rate, such as degree of species gregariousness, individual perception range, movement rate, fraction of receptive males and females active at any time, etc. All these features are currently assumed time invariant, although the model is open to any change in this respect.

As the locomotion activity is a function of the circadian clock, it is here where the circadian clock enters the cockroach population model. For the phase-related scenarios, $S_d$ equals $a$ times the length of the overlap of the male and female types considered. For BG, $S_d = 12$ irrespectively of the scenario, as BG females are found active all of the day within their mating window. In contrast, for BB, $S_d = 12$ for the on-phase scenarios and $S_d = 2$ for the off-phase ones (we assume the off-phase overlap in their activity for 1 h so that there are 2 h of common activity each day. For our thought experiment on clock-related mutants, $S_d$ equals $a$ times the length of the active time period. For the arrhythmic BB genotype, $M_A$ was replaced by $M_A/2$, the effective receptive male population size, as each female on average perceives only half the male population at any moment of activity and her active time period comprise only half a day; this is in contrast to BG females which is found active all of the day within her mating window.

Unfortunately, we have no idea of the value or at least an order of magnitude of the positive constant $a$. Obviously, $a = 0$ means no reproduction and hence population extinction, while sufficiently large $a$ represents almost certain reproduction of any receptive female. For some fixed initial conditions on population size and composition we explore dependence of the cockroach population growth on $a$. Some of the results in this paper are based on the assumption that for a receptive female there is no problem to find at least one receptive male a given day, which formally corresponds to an infinite value of $a$ and hence $\Phi = k_i$—we emphasize that we use this assumption where appropriate.

### 2.6. Intraspecific competition

Populations are often limited in growth when at large numbers. Although the density-independent model version is sufficient to describe initial phases of invasion of an empty house, we also consider adding negative density dependence to the above population model, in order to prevent unchecked growth of cockroach populations and allow for modeling competition between the two cockroach species for a limiting resource (below). Among cockroaches, negative density dependence is likely to operate due to competition for food (Müller-Graf et al., 2001). As competition among nymphs and adults appears low relative to aggressive interactions on food sources between cockroaches within the same age class (Rivault and Cloarec, 1992), we do not consider the former in our model.

Any life history parameter can in principle be density-dependent, be it the number of eggs, rates of development, or survival. In line with Müller-Graf et al. (2001), we choose survival to be negatively density-dependent. This corresponds to replacing $s_N$ by $s_N(1-z_N N)$ and $s_M$ or $s_F$ by $s_M + F_M(s_N + s_M + s_F)$, for some positive constants $z_N$ and $z_A$. We assume $z_A = 10 z_N$, that is, competition between adults is ten times higher than that between (smaller) nymphs (Müller-Graf et al., 2001), and, to avoid negative survival probabilities, we use $z_N = 10^{-5}$. We use the same values of $z_A$ and $z_N$ for both cockroach species. This may seem strange since BB prefers a solitary way of life, but as we are interested in a potential of this species to establish in human households we expect to find at least loose aggregations of BB and thus competition for food in this habitat roughly comparable to BG. Last but not least, we are interested only in the relative ordering of the four phase-related scenarios with respect to dynamic properties of the population. Exploration of sensitivity of the cockroach population dynamics to the strength of interspecific competition is beyond the scope of this article as we think it should be coupled with parallel experiments aimed to estimate this strength.

### 2.7. Interspecific competition

BG is obviously one of the most spread household pests in the world, and is now virtually impossible to sustain outside human constructions. BB, on the other hand, is limited to Southeast Asia and mostly living in the open space. Since BB is able to establish in cockroach-free households, too, it is relevant to ask whether it is also able to invade domicile habitats occupied by BG, or, put the other way round, whether BB can resist likely invasions of BG. An extended version of the above-described model can address this question in a straightforward way (Appendix B). Apart from an indirect interaction mediated by consumption of limiting resources, populations of the two species that live together directly interact in the following way: BB females often mate with BG males,
2.8. Sensitivity, elasticity and perturbation experiments

For density-independent matrix models sensitivity is defined as the partial derivative of the population growth rate with respect to any matrix element (Caswell, 2001). If the matrix elements are composed of lower-level parameters, sensitivity of the population growth rate with respect to any such parameter \( p \) is defined as

\[
\frac{\partial \lambda}{\partial p} = \sum_{ij} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial p} 
\]

where the summation runs over all such elements \( a_{ij} \) of the interaction matrix \( A \) which are composed of the lower-level parameter \( p \). Elasticity is defined as the sensitivity divided by the ratio \( \lambda / p \). Hence, while sensitivity expresses the absolute change in the population growth rate as a result of an absolute change in a parameter value, elasticity works on relative changes. Elasticity “is frequently used instead of sensitivity since reproduction and growth transitions are measured at different scales” (Rogers-Bennett and Leaf, 2006) yet there is no real reason to prefer one over another (Caswell, 2001). Here we calculate both sensitivity and elasticity.

Models of the type analyzed here can also be used to assess population responses to larger perturbations, such as to various potential pest control strategies. We simulate the impacts on BG of two such strategies: (1) reduction of survival of cockroach nymphs, lowering their rate of development, and reduction of female fecundity, effects implied by an interaction of BG and its parasite Blatticola blattae (Oxyurida, Thelastomatoidea) (Müller-Graf et al., 2001), and (2) reduced longevity of adult males and females and female fecundity, an effect of various types and concentrations of chemicals (Abdelghafar and Appel, 1992; see also Section 4). We use natural populations of BG, i.e. 10 L \( \Delta \) 10 L \( \nabla \) data, to address all these issues.

3. Results

3.1. Single-species dynamics

3.1.1. Impacts of circadian clock

With density-independent transition matrix (i.e. no intraspecific competition and \( \Phi_i = k_i \)), the matrix model is linear and the population grows exponentially, approaching a constant population growth rate and a stable stage distribution. Table 3 summarizes how these two quantities differ for the four phase-related scenarios examined. The differences are indeed minor for any of the species. The stage structure of the populations soon stabilizes, with nymphs’ prevalence \( \sim 83\% \) for BG and \( \sim 71\% \) for BB. With negative density dependence, populations approach respective carrying capacities (Table 4).

<table>
<thead>
<tr>
<th>Scenario</th>
<th>( \lambda )</th>
<th>( N )</th>
<th>( M_n )</th>
<th>( M_a )</th>
<th>( F_n )</th>
<th>( F_a )</th>
<th>( F_m )</th>
<th>( F_v )</th>
<th>( F_{mr} )</th>
<th>( F_{vr} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blattella germanica</td>
<td>10 L ( \Delta ) 10 L ( \nabla )</td>
<td>1.0566</td>
<td>79.23</td>
<td>1.67</td>
<td>8.72</td>
<td>1.67</td>
<td>2.28</td>
<td>3.42</td>
<td>1.72</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>10 L ( \Delta ) 22 L ( \nabla )</td>
<td>1.0581</td>
<td>79.61</td>
<td>1.67</td>
<td>8.53</td>
<td>1.67</td>
<td>2.32</td>
<td>3.50</td>
<td>1.47</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>10 L ( \Delta ) 22 L ( \nabla )</td>
<td>1.0584</td>
<td>79.70</td>
<td>1.67</td>
<td>8.48</td>
<td>1.67</td>
<td>2.34</td>
<td>3.52</td>
<td>1.40</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>10 L ( \Delta ) 22 L ( \nabla )</td>
<td>1.0612</td>
<td>80.37</td>
<td>1.67</td>
<td>8.15</td>
<td>1.67</td>
<td>1.99</td>
<td>3.67</td>
<td>1.28</td>
<td>0.81</td>
</tr>
</tbody>
</table>

Also here, the differences between the four examined scenarios are marginal. The stage structure now stabilizes at nymphs’ prevalence \( \sim 83\% \) for BG and \( \sim 76\% \) for BB. There are only minor differences in the stable stage distributions between the density-independent model and the model with negative density dependence.

Obviously, small enough value of the scaling constant \( a \) will cause the population not to grow, whereas sufficiently large \( a \) means that females have no problem to locate receptive mates. Figs. 2A and B show how the carrying capacity of the cockroach populations changes with \( a \). Differences are marginal for BG, due to the masking effect of females. On the other hand, differences between on-phase and off-phase scenarios for BB are substantial, since in the off-phase scenarios receptive males and females are jointly prone to copulation only in a small period between the end of activity of one sex and the beginning of activity of the other (assumed 2 h a day in our model).
The female mating rate described by the exponential function gives rise to a demographic Allee effect (that is, decrease in individual fitness with declining population density). In particular, small enough populations can go extinct due to their internal demography—insufficient ability to find mates. The smaller is the initial population size the higher \( \alpha \) (searching efficiency) has to be for the population to overcome the deficiency of mates (Fig. 2C,D).

Regarding population dynamics of the circadian clock genotypes of BG, the longer the active phase of the day relative to the inactive one, the lower the scaling constant \( \alpha \) can be for the population not to go extinct (Fig. 3A) and the shorter time will be needed for the population to grow to large sizes (Fig. 3B). Results for the ‘normal’ and ‘arrhythmic’ genotypes coincide for BG, as females are active all of the day within the mating window and males of both genotypes are altogether active for 12 h. Whereas the same ranking of the ‘normal’, ‘long’ and ‘short’ genotypes holds also for BB, the ‘arrhythmic’ genotype is the least viable here, as female and male genotypes are assumed to be the same—the difference between ‘normal’ and ‘arrhythmic’ genotypes thus matters in this case (Fig. 3C,D).

### 3.1.2. Sensitivity, elasticity and perturbation experiments

For the BG model version with five \( F_a \) classes and density-independent transition matrix, sensitivity and elasticity of the asymptotic population growth rate \( \lambda \) to female mating rates \( \Phi_i = k_i \) and to other lower-level model parameters are summarized in Fig. 4A. This analysis suggests that the population growth rate is most sensitive to the length of the nymphal period \( r_N \), followed by the female survivorship \( s_F \), the length of pregnancy period \( r_{MP} \),
and the nymph survivorship $s_N$; it is not sensitive to male characteristics $s_M$ and $r_M$. Elasticity ranks the five most important parameters, from the highest to the lowest impact, as $s_F$, $s_N$, $b$, and $r_{MP}$ and $r_N$ having a comparable effect.

Fig. 4B indicates changes in the population growth rate of the density-independent model version as a result of changes in respective model parameters, calculated as $(\lambda - 1) \times 100\%$. The baseline growth rate is $\lambda = 1.0566$ ($= 5.66\%$) in this case. Percentage values next to bars indicate percentage decreases in the respective baseline parameters, with control 1 scenario affecting $s_N$, $r_N$, and $b$ and control 2 scenario affecting $s_M$, $s_F$, and $b$ (see Methods). The other scenarios represent population responses to changes of some model parameters to their lowest and highest values found in the literature (Table 2). Only 50% reductions corresponding to both control strategies bring the population growth rate below the self-replacing value $\lambda = 1$ ($= 0\%$); 50% decrease in nymph survival also significantly reduced $\lambda$, this time very slightly below 1. This indicates that the life history of BG is quite vital and only a control strategy that targets several most sensitive parameters simultaneously and significantly has a chance to be successful.

Sensitivity of the carrying capacity to the same stimuli in the model version with intraspecific competition demonstrates an analogous pattern: 50% reductions in both control strategies eliminate the population and 50% decrease in the nymph survival does almost the same job (Fig. 4C). Of some practical interest can also be that 10% reductions in both control strategies and in $r_N$ reduce the cockroach populations to about one fourth of its pre-control level.

### 3.2. Interspecific competition

Using model combined for both species allows us to examine how one of the species is able to invade the established population of the other (Fig. 5). While BG populations can invade established BB populations from any small population density, BB populations cannot do the reverse even if starting at their own carrying capacity. Fig. 5A shows that for communities initially composed of the same small number of BG and BB the former species soon brings the latter to extinction and itself stabilizes at a level where newly emerging nymphs exactly balance individuals that are dying. Fig. 5B shows what happens when BB first invades an empty human construction, and followed by BG. Even in this case, BB takes a lead and out-competes the BB population in a few years. Finally, BB cannot invade established BG populations even when starting from its carrying capacity in BG absence (Fig. 5C).
These results have been obtained given no advantage of gregariousness in BG and no hybridization of BB females with BG males. Incorporation of both these features further decreases already low competitive ability of BB with respect to BG (results not shown).

4. Discussion

In this article, we have developed a stage-structured model of cockroach population dynamics, parameterized it by available data on the German cockroach *Blattella germanica* (BG) and the double-striped cockroach *B. bisignata* (BB), and explored a potential of these species to establish from initially small populations. Population models play three essential roles in understanding and/or ‘manipulating’ nature. Firstly, they help us organize and synthesize knowledge on a species’ life cycle and its intra- and inter-specific processes, together with identification of directions in which available data are deficient and underlying processes poorly understood. Secondly, simulating such a life cycle over and over...
again, population models assist us not only in understanding current population characteristics, such as the population growth rate or juveniles-to-adults ratio, but also in projecting these characteristics farther into the future. Finally, models can assess potential impacts and efficiency of diverse control or conservation measures applied to regulate pest or reinforce endangered populations, respectively, including the effects interactions with other species might have for their dynamics. As a consequence, models can support our decision-making provided that biology of the involved species is sufficiently understood and the candidate models tested against carefully collected, adequate data.

4.1. Circadian clock and population dynamics

One of the questions posed in this article has been whether the circadian clock has a role in dynamics of BG and BB populations. We have examined how populations composed of (i) males and females adapted to different LD conditions and (ii) hypothesized circadian clock mutants performed in the long run. Regarding the former, our results show that, even if the adaptations would persist indefinitely, there is virtually no effect of them on BG dynamics (due to the masking effect of females; Lin and Lee, 1996, 1998) and that dynamics of BB are affected only in a narrow range of *searching efficiency* \(a\) where the on-phase populations survive but the off-phase ones do go extinct. In the Egyptian cotton leafworm *Spodoptera littoralis*, pairs mated significantly less often when either the male or female had been raised in an LD cycle with 10 h phase shift, suggesting that “the proposed circadian rhythm in mating activity is composed of rhythmic mating preference/ability in both sexes” (Silvegren et al., 2005). For the hypothesized circadian clock genotypes, we have shown that the shorter is the inactivity period relative to the activity one or the less arrhythmic is the population, the more viable the population is and the quicker it grows to large numbers. Whether and how these results can be utilized to fight the cockroach infestations remains to be determined.

Our results have to be considered cautiously, however, in part because the circadian clock has been considered to only affect the cockroach locomotion activity. There are likely to be other behavioral or ecological features that might be under its direct or indirect control, such as the daily course of individual mortality rate which could be especially the case of BB living in the open space and thus likely subject to strong predation in the daylight or activity hours.

4.2. Interspecific competition

The German cockroach is obviously one of the most spread household pests in the world, and it is now virtually impossible to sustain outside human constructions. The
double-striped cockroach, on the other hand, is limited to Southeast Asia and mostly living in the open space. Since BB is able to establish in cockroach-free households, too, it is relevant to ask whether it is able to invade domicile habitats occupied by BG, or, put the other way round, whether BB can resist likely invasions of BG. An extended version of the single-species population model (Appendix B) was used to address this question.

No matter what the initial pattern of BG and BB occupancy, BG is a stronger competitor that always drives BB to extinction. This is also true for the most optimistic BB life history, that is, no need to find males (i.e. group effects comparable to BG) and no hybridization with BG. Incorporation of these features only worsens the already weak competitive abilities of BB and increases the rate at which this species is outcompeted.

Experimental evidence, although short-term and carried out in a rather limited environment (2-l containers), appears to confirm this conclusion (Tsai and Lee, 2001). In that experiment, 10 adult pairs of each species were reared together in the same container for 3 months. In each replicate, BG had always taken a lead and drove BB to extinction. Observations of decreasing percentage of pregnant females in BB likely indicate a lack of successful reproduction (Tsai and Lee, 2001). It would be helpful to repeat these experiments in larger containers that would more closely resemble natural conditions of common household habitats, and see whether the inferiority of BB still holds and whether model predictions fit these observations not only qualitatively, but also quantitatively.

4.3. Pest control

Pest control has been an area of extensive research and a significant portion of it is theoretical. This is not that surprising as population models are ideal tools to a priori assess impacts and efficiency of diverse plausible control strategies. Indeed, there are at least two studies that went in this direction as regards control of German cockroach populations.

Müller-Graf et al. (2001) developed a model of an interaction between the German cockroach and its parasite Blatticola blattae (Oxyurida, Thelastomatoidea), so as to assess an impact the parasite might inflict on population growth and establishment density of German cockroaches. B. blattae reduces survival of cockroach larvae, slows down their development, and reduces female fecundity. The model consisted of four compartments: uninfected and infected larval hosts, and uninfected and infected adult hosts. In fact, this model is a highly simplified version of our continuous-time model (Appendix A) which does not discern between the sexes and aggregates all adult stages into one population class. Müller-Graf et al. (2001) reported that the parasite had inflicted a reduction of both juvenile and adult densities and that the overall population density in the presence of parasites had been depressed by about 11% compared to that in their absence. We have simulated impacts of effects analogous to those of B. blattae by applying a 10% and 50% reduction to the three affected parameters. Only the 50% reduction causes the cockroach population to go extinct.

Zeman (1993) studied an effect of juvenoids (chemical substances that mimic the insect juvenile hormone) that act in many ways on all cockroach stages, yet their key effect is sterilization during the last nymphal instar. Modeling accumulation and depletion of juvenoids in the insect’s body, nymphs that matured with a juvenoid concentration exceeding a critical level were considered sterile. In his discrete-time matrix model, Zeman distinguished the egg stage, six nymphal instars, and adults (with 1:1 sex ratio). Contrary to our model and the model by Müller-Graf et al. (2001), it was the net fertility rate of the population that was subject to negative density dependence. Zeman’s model is methodologically close to our discrete-time model, yet it focuses on modeling individual nymphal instars, whereas we focus on distinguishing various stages among cockroach adults. There was a temporal lag between the juvenoid application and its observable effect. In addition, there was no population reduction until an 80% sterility level was achieved. Based on these results, Zeman (1993) calculated that to eliminate the cockroach population the juvenoid bait density should be such that the probability of encountering it within 3 days exceeded 0.6.

Any control strategy affects the life history processes and parameters in a different way and a specific model adjustment is therefore required in each specific case. In German cockroaches, higher concentrations of monoterpenoids in the diet reduced development time of nymphs and applications of high doses of n-limonene and linalool to oothecae in gravid females significantly decreased the probability of young emerging from them (Karr and Coats, 1992). Similarly, Abdelghafar and Appel (1992) reported effects of various types and concentrations of insecticides on longevity of adult males and females and fecundity of female German cockroaches. Application of juvenile hormone analogs is also an essence of a control strategy of German cockroaches suggested by Schal et al. (1997). Juvenile hormone analogs cause abortion of fertile oothecae in gravid females and in turn induce feeding. Strategic placement of juvenile hormone analogs and insecticidal baits hence allows for an effective control of gravid females that normally feed little and are thus difficult to control. Simulating the impact of insecticides on longevity of adult males and females and female fecundity has again demonstrated that only a significant reduction of the corresponding parameters is needed to bring the BG population to extinction.

Exploration of the effects of variation in parameters that demonstrate the highest sensitivity or elasticity of the population growth rate indicates that only a simultaneous reduction in a number of ‘important’ parameters (e.g. survival and maturation rates of nymphs and adult female fecundity, as in the ‘control 1’ scenario) gives us a chance of achieving successful control.
4.4. Future avenues

The models we have used to address the questions posed in this article are analytical, be it the discrete-time matrix model analyzed in detail or the analogous continuous-time model (Appendix A) that leads to the same results (not shown), meaning that they do not fully capture individual variability within populations. On the other hand, individual-based models help quantify costs and benefits of individual behavioral strategies at a much finer scale. Also, time intervals within which animals belong to a population stage, which are exponentially distributed in analytical models, are under a direct modeler’s control in individual-based models. One of the future directions in modeling cockroach population dynamics could thus be to develop an appropriate individual-based model. This effort should, however, be preceded by an experiment in which population dynamics of both cockroach species are followed over a long enough time and compared to those generated by currently available models. Replicated trials in which sufficiently large containers with populations of one or both (competing) species would live and be counted at regular intervals, would best suit this purpose.

To explore impacts of the circadian clock on cockroach population dynamics in more detail, whether for the phase-related scenarios or circadian clock genotypes, the female mating rate \( \Phi \) should be estimated as a function of male and female synchronization and availability. Currently available knowledge of the locomotion activity as driven by the circadian clock could turn insufficient in this respect, as the locomotion activity (determining the encounter rate with other conspecifics) and the mating activity (determining the mating rate) may not coincide. The way these two can be determined simultaneously includes performing an experiment which explored behavior of males and females in mating arenas of different sizes. Also, the potential role of chemical communication in mate finding that itself may be (and often is) affected by the circadian clock are to be clarified. Therefore, we call for carrying out experiments that would help us verify (or not) the exponential form of the female mating rate adopted in this study and its estimate scaling constant \( a \). Finally, we have already mentioned a need for performing more competition experiments, to further verify predictions of our models. In any case, only carefully designed and data-based models of German cockroach population dynamics can be helpful in our quest to win the fight over this unwelcome but very sturdy species.

Acknowledgments

LB acknowledges funding by the Institute of Entomology of the Biology Centre ASCR (Z50070508).

Appendix A. Definition of a continuous-time cockroach population model

Multidimensional, continuous-time population models can generally be represented as
\[
\frac{dx}{dt} = Ax,
\]
where \( x \) is again the vector of state variables and \( A \) is the transition matrix (each matrix element has now the meaning of rate at which an individual ‘moves’ from one state to another, rather than transition probability which was the case in the discrete-time matrix model). Regarding BG and BB, \( x = (N, M_n, M_a, F_n, F_a, F_v, F_{mr}, F_{vr}) \) where \( F_v \) is further divided into five (BG) or eight (BB) classes. For BG, the transition matrix \( A \) has now the following form (the corresponding model for BB differs only by having eight \( F_v \) classes instead of five):

\[
\begin{vmatrix}
-d_N - r_N & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
-d_M - r_M & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
r_M & d_M & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
r_N/2 & 0 & 0 & -d_F - r_F & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & r_F & -(d_F + \phi_1 + 1) & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & -(d_F + \phi_F + 1) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & -(d_F + \phi_F + 1) & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -(d_F + \phi_F + 1) \\
\end{vmatrix}
\]

When negative density dependence in survival is considered, the nymph mortality rate \( d_N \) is to be replaced by \( d_M(1 + \alpha_N N) \) and analogously \( d_M \) or \( F \) by \( d_M(1 + \alpha_M (M_n + M_a + F_n + F_a + F_v + F_{mr} + F_{vr} + F_{mr} + F_{vr})) \). We used \( \alpha_N = 0.001 \) and \( \alpha_M = 0.01 \) for simulations of the continuous-time model (Müller-Graf et al., 2001).

Expression for the female mating rate becomes simpler for the continuous-time model,
\[
\Phi_i = k_i S(t) M_{si}(t)
\]
as we now count time in infinitesimal steps \( dt \). The \( k_i \) values are again approximated by those given in Table 1.
Appendix B. The two-species matrix model

In the two-species matrix model (and analogously in the two-species continuous-time model), two single-species models corresponding to BG and BB are put together and coupled in several ways. First and most importantly, both species compete for a limited amount of resources. This makes all survival parameters dependent on appropriate stage densities of both species. In particular, nymph survival becomes \( s_F(1-\alpha_i(N_{BG}+N_{BB})) \), where \( i = BG \) or \( BB \) specifies a particular species. Adult male and female survival is defined analogously, summing in the inner parentheses all of the life stages of both species excluding the nymphs.

Hybridization of BB females with BG males is modeled as follows. The terms \( s_F(1-\Phi_i) \) in the BB model now become \( s_F(1-\Phi_i-\Phi_{BG}) \) for a hybridization probability \( \Phi_{BG} \) and \( F_v^i \) classes \( i = 1-7 \). At the same time, zeros in the \( F_i \) line and \( F_a^1 \) to \( F_a^7 \) columns of the BB transition matrix become \( s_F \Phi_{BG} \) representing the fact that hybridized females are sterile and hence formally analogous to virgin pregnant females. All else remains unchanged (we only note that the original term \( s_F(1-\Phi_i) \) now becomes \( s_F(1-\Phi_i-\Phi_{BG})+s_F \Phi_{BG} = s_F(1-\Phi_i) \), so that it does not change either).

References