

## Optimal Reproduction Strategies in Two Species of Mound-Building Termites

David A. Cameron<sup>a</sup>, David J. Ivers<sup>a</sup>, Theodore A. Evans<sup>b</sup>,  
Mary R. Myerscough<sup>a,\*</sup>

<sup>a</sup>*School of Mathematics and Statistics, University of Sydney, Sydney, NSW 2006, Australia*

<sup>b</sup>*CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia*

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**Abstract** We formulate a mathematical model for food collection and production of workers and nymphs in 2 species of mound building termites. We maximise the number of nymphs (reproductives) produced by each colony over its lifetime with respect to the proportion of eggs that hatch as nymphs as opposed to workers. The results predict that food storage has a very important influence on the pattern of nymph and worker production. Food storage affects the part of the year that nymph production dominates, whether nymphs and workers are produced at the same time or not, and the existence of a final phase in the colony's life when a very large number of nymphs but no workers are produced.

**Keywords** Optimal control · Ordinary differential equations · Bang-bang control · Termites · Isoptera · *Coptotermes lacteus* · *Nasutitermes exitiosus*

### 1. Reproduction by mound-building termites

Termites (Isoptera) are ubiquitous throughout the tropical and temperate areas of the world. Termites are essentially social cockroaches that have evolved to feed on dead plant matter, especially cellulose. Primitively, termites eat wood and many species live in living or dead wood, or in cryptic underground nests. The most obvious and famous examples of termites live in mounds that are constructed by large colonies over a number of years.

In general, colonies are established by a reproductive pair, the founding king and queen. These reproductives produce all the brood in the colony, which are of three types called castes: workers, soldiers and nymphs. Workers build and maintain the nest and mound, forage for food, clean and care for the eggs, young, and the reproductives, and perform other tasks that are needed to keep the colony healthy (Grassé, 1986). Soldiers are derived developmentally from workers and are specialised for defence. Workers and

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\*Corresponding author.

E-mail address: M.Myerscough@maths.usyd.edu.au (Mary R. Myerscough).

soldiers are sterile in mound building termites although in other species they may develop into reproductives. Nymphs are the reproductive caste and perform little work. Instead, they channel energy into growth; nymphs are larger than workers and soldiers and develop wings and eyes. The final adult stage of the nymph is the imago or alate, which disperses from the natal colony to find a mate and establish a new colony.

It appears that all termite eggs have the potential to develop into any caste. Differentiation occurs at the second larval instar; that is, after the second moult. The colony appears to have an influence on differentiation, but it is not known how this influence operates (Watson and Sewell, 1981). The more alates the colony produces, the greater the reproductive fitness of the colony and its established reproductives. The number of alates that are produced will depend on the queen's laying capacity, the proportion of eggs that become nymphs and not other castes, and the proportion that survives to adulthood to become alates. Evolutionary theory suggests that termites evolve so that alate production is maximised.

Workers are essential to the growth of the colony and the development of healthy nymphs and alates. They provide the resources such as food and water, and construct and maintain the mound. In this study, we will focus on food as the limiting factor on nymph production. Under this assumption, the most critical role of the worker is as a collector and consumer of food.

Modelling has a useful role to play in prediction and in establishing hypotheses about termite behaviour. In general, termite behaviour is not well studied, especially life history and reproductive strategies. Field studies are expensive, particularly for insects with colonies comprised of millions of individuals and with foraging territories of over 10,000 square metres (Holdaway et al., 1935; Gay and Greaves, 1940; Ratcliffe and Greaves, 1940; Lee and Wood, 1971; Evans et al., 1998; Evans, 2002). Given that colonies may persist for 50 years (Ratcliffe et al., 1952) or even 100 years (Watson, 1972), lifetime reproductive success may not be measurable by any individual scientist. Laboratory experiments are also problematic. Large scale foraging and the total population of colonies must be restricted for termite colonies to be kept indoors and this will almost certainly alter reproductive behaviour. Termites are sensitive to their environment and difficult to observe even without disturbing their behaviour.

Because of the paucity of observational data, the models we present here are very simple and contain a number of assumptions that might be viewed as oversimplifications of what actually happens in a termite colony. It is of little value, however, to have an elaborate model when some parts of the model are purely speculative and numerical parameters may only be known to within an order of magnitude at best. For this reason, we have chosen to make the model as simple as possible while still incorporating essential behaviour, and to use a straightforward differential equation model rather than a more complicated approach such as individual-oriented simulation.

The philosophy of this model is to work with fundamental ecological processes—reproduction and food collection and consumption—to explore the effects of these processes over the lifetime of the colony.

The termites are an amazingly diverse order. Some species live in small colonies with multiple reproductives with populations in the tens or hundreds inside the wood that they feed on. Other species have only a single pair of reproductives in each colony, but millions of workers that cultivate fungus gardens inside massive mounds. Reproductive behaviour,

foraging behaviour, individual development and life cycles vary enormously across the order.

In this study, we formulate and use models specifically for two particular termite species. This ensures that there is no confusion about the type of behaviours that the models represent and that the modelling can produce testable predictions that may, in principle, be investigated in field studies.

The two species, *Coptotermes lacteus* (subfamily Rhinotermitidae) and *Nasutitermes exitiosus* (subfamily Termitidae), that we use as a focus for modelling are both native to broad areas of southern Australia, often found in the same habitats (Hill, 1942; Watson and Abbey, 1993) and both build mounds (Hill, 1942; Lee and Wood, 1971). They eat sound or partially decayed wood, which is foraged by obligately sterile workers who never become reproductives. Nests, built as mounds on the surface of the ground, have many functions including the maintenance of constant conditions conducive to termite growth and reproduction (Fyfe and Gay, 1938; Watson and Abbey, 1986).

The two species have differences also. *C. lacteus* workers do not digest their wooden food completely, but produce a nutrient rich material that encloses their nests (i.e., nursery chambers and royal cells) and forms the bulk of their mounds (Hill, 1942; Lee and Wood, 1971). This mound material represents stored food (Gay et al., 1955) and can be eaten. The *C. lacteus* mound is covered with a thick layer of mud (Hill, 1942), presumably to protect the contents, including the mound material. Interestingly, old mounds of this species appear hollow, with little mound material remaining. In contrast, *N. exitiosus* workers appear to digest the majority of the cellulose from their wooden food, so the mound material is of little nutritional value (around 5% cellulose: Cohen, 1933; Holdaway, 1933; Fyfe and Gay, 1938). Perhaps corresponding to this, *N. exitiosus* mounds have only a thin layer of mud (Hill, 1942). *N. exitiosus* mounds in which the colony of termites has died are very similar to those containing live termites; the major difference is the ambient temperature inside the mound (Watson and Abbey, 1986).

In the paper, we formulate a model for food collection and consumption, and for the population of nymphs and workers in a colony for each species. We use this model to find the optimal proportion of eggs that should develop into nymphs as a function of time. In each section of the paper, the model for *C. lacteus* is discussed first, followed by the model for *N. exitiosus*. This enables the models to be compared easily and keeps repetition to a minimum.

## 2. Formulating the models

### 2.1. *Coptotermes lacteus*

Let  $t$  be the age of the colony in years,  $n(t)$  the number of nymphs and  $w(t)$  the number of workers at time  $t$ . We model the nymphs and workers only, and assume that the numbers of soldiers are sufficiently small that the presence of soldiers has little direct influence on the population and food dynamics of the colony. Let  $f(t)$  be the amount of food stored in the mound at time  $t$ , in suitable units. We assume that each egg laid by the queen becomes either a worker or a nymph. Let  $p(t)$  be the proportion of eggs laid at time  $t$ , that will develop into nymphs. Then  $(1 - p(t))$  is the proportion of eggs laid at time  $t$ , that will develop into workers.

We assume that the lifetime of the colony is fixed at  $t_f$ , which we take to be 20 years when obtaining our results. Once a *Coptotermes lacteus* colony has become mature enough to produce alates, its average lifespan is roughly 20 to 30 years. A colony may suffer premature death or be disrupted in some other way after starting to produce alates before reaching this age, but we assume that such occurrences are sufficiently rare that they have had little impact on the evolution of the pattern of alate production.

It is not known what mechanism would enable a colony to sense its approaching end. A colony that is not invaded by predators will die when its reproductives die or cease to lay viable eggs. Few animals in their natural state die of old age, but is it possible that this is the case with termite reproductives. The mound defenses reduce the effect of predation and disease and because the colony relies on dead or living wood, food supply is usually very reliable. There may be hormonal changes in aging *C. lacteus* queens that are perceptible in the colony. It is also known (Roisin and Lenz, 1993) that following the death of the founding reproductives, *C. lacteus* colonies install one or more pairs of “home-grown” neotenic reproductives in the mound. The presence of secondary reproductives may signal that the colony is coming to an end of its life.

### 2.1.1. Egg laying

In this model, the queen lays eggs at a constant rate of  $r$  eggs per year. In reality, the egg laying rate is relatively constant for an established colony, but lower at the start of the colony’s life when the queen is involved in foraging and building as well as reproduction. As the colony grows and acquires a large number of workers, the queen’s fecundity increases as she develops highly enlarged ovaries and abdomen (physogastry). We chose to keep  $r$  constant here, however, to keep the model as simple as possible.

We assume that the effect of seasonal climate change is negligible, so that the egg laying rate does not change over the course of each year. This assumption is likely to be valid for tropical areas with more constant climate, such as temperature, but is less likely to be valid for temperate areas with fluctuating climate. Because both *C. lacteus* and *N. exitiosus* are wood feeders, they are likely to experience less seasonal disturbance than species which rely on more seasonally dependent food source such as grass or litter. Evans and Gleeson (2001) showed that the foraging worker populations are larger in summer compared with winter in both *C. lacteus* and *N. exitiosus*, which suggests that the queen’s egg laying rate will be affected. Nest temperature fluctuations observed in temperate areas are likely to slow the queen’s egg laying rate (Holdaway and Gay, 1948), but again, in the interests of keeping the model simple, we assume that  $r$  is constant.

### 2.1.2. Food collection and consumption

Food is gathered primarily by workers. We assume that only workers collect food, that there is always plenty of available food to collect, and that the rate of food collection per worker, denoted by  $q$ , is constant. Because both the species under consideration rely on large, immovable sources of forage (living and dead trees), this is a reasonable assumption.

Food consumption per individual is assumed to be at constant rates,  $c_w$  and  $c_n$  for the worker and nymph castes, respectively. Since nymphs grow to around three times the size of workers (Hill, 1942),  $c_n$  will most likely be larger than  $c_w$ . No quantitative experimental data exists for food consumption in either species of termite modelled in this study. We choose  $c_n/c_w$  to be 1.5, for the purpose of finding numerical solutions to

the models. Similarly, we choose  $q/c_n$  to be 1.5, since the workers collect more food than they can eat themselves. These values are arbitrary, but reasonable. Parameter searches (see Section 4.3) show that changes to the values of  $c_n/c_w$  and  $q/c_w$  do not change the qualitative nature of the solutions significantly, although they are quantitatively sensitive to changes in either.

### 2.1.3. Food stores

The colony populations of *C. lacteus* are eventually large (Gay and Greaves, 1940; Evans et al., 1998), but colony growth rates are poorly known, although some indication can be inferred from other species (e.g., Thorne et al., 1997; Fei and Henderson, 2003). We will assume that colony populations are sufficiently large that food storage and nymph and worker populations can be modelled as continuous variables using ordinary differential equations (ODEs). Changes in stored food are given by

$$\frac{df}{dt} = qw - c_w w - c_n n, \quad (1)$$

where  $f(t)$  is the food stored in the nest,  $w(t)$  is the number of workers in the nest,  $n(t)$  is the number of nymphs,  $c_w$  is the rate of food consumption per worker per year, and  $c_n$  is the rate of food consumption per nymph per year. Equation (1) is valid for  $t \in [0, t_f]$ , and depends on  $w(t)$  and  $n(t)$ .

Clearly  $f(0) = 0$ , because the colony starts without any stored food. Also, because food stores in the model cannot become negative,  $f(t)$  is subject to the constraint

$$f(t) \geq 0, \quad \forall t \in [0, t_f]. \quad (2)$$

Furthermore, it is reasonable to assume that the colony has no food left over at the end of its lifetime:

$$f(t_f) = 0. \quad (3)$$

This constraint is likely to be optimal since excess food could be used to produce more nymphs. It has also been observed that extinct *Coptotermes lacteus* mounds are rarely found with leftover food.

### 2.1.4. Worker population

The rate of change of the worker population is modelled by

$$\frac{dw}{dt} = r(1 - p(t)) - \beta(t)w. \quad (4)$$

The first term represents the birth rate of workers which is given by the egg laying rate  $r$  multiplied by the proportion of eggs that develop into workers. The second term represents the death rate of workers, where  $\beta(t)$  is the death rate per worker, i.e. the number of deaths per worker per unit time. If the age of workers is always uniformly distributed, and all workers live the same length of time  $\tau_w$ , then

$$\beta(t) \equiv \frac{1}{\tau_w}.$$

The age profile, however, is not constant throughout the life of the colony. The average age of the workers is younger at the start of the colony, because the colony begins with no workers and so the death rate is lower in the early years. As  $t$  gets larger, the age distribution becomes more uniform, and so  $\beta(t) \rightarrow 1/\tau_w$ , as  $t \rightarrow \infty$ . This suggests that a reasonable form for  $\beta(t)$  is

$$\beta(t) = a \left( 1 - \frac{1}{1 + bt} \right), \quad (5)$$

where  $a$  and  $b$  are positive constants with  $a = 1/\tau_w \approx \frac{1}{3}$ . This assumes that the average age of a *C. lacteus* worker at death is 3 years. This is a reasonable assumption for this species. Mark and recapture studies show that *C. lacteus* workers can live at least 16 months (Evans et al., 1998), and it is known that workers of other species may live for several years; for example, *Reticulitermes* workers can survive for up to 10 years (Lainé and Wright, 2003). The constant  $b$  controls the rate that  $\beta(t)$  approaches  $a$  and we choose  $b = 3$  as this allows  $\beta(t)$  to be within 10% of  $a$  after 3 years.

*C. lacteus* and *N. exitiosus* workers start to forage outside the nest from a few months of age, well before they reach their final instar. To model this explicitly would require the introduction of delays into the differential equations which introduces considerable mathematical complexity. Analysis of similar models (Evans et al., in preparation) suggest that including such delays has no significant effect on the qualitative outcomes on the model. Therefore, we will not include these delays here.

A suitable initial condition for  $w(t)$  is  $w(0) = 0$ . This assumes that the colony starts with zero workers.

### 2.1.5. Nymph population

Young nymphs do not appear to feed themselves, as they lack the necessary gut microflora and their mandibles have little or no wear (Watson and Abbey, 1977; Lee and Wood, 1971; Watson et al., 1978). Furthermore, few nymphs are found in foraging sites away from the mound (Evans et al., 1998), suggesting that nymphs rely on workers for all or part of their food. Consequently, nymph mortality is likely to be low. Hence, we model the change in nymph population with a *leaving rate* rather than a death rate:

$$\frac{dn}{dt} = rp(t) - \gamma(t)n, \quad (6)$$

where  $rp(t)$  is the egg laying rate multiplied by the proportion of eggs that develop into nymphs, and  $\gamma(t)$  is the leaving rate of nymphs. We ideally take

$$\gamma(t) = 10 \sum_{i=1}^{\lfloor t_f \rfloor} \delta(t - i), \quad (7)$$

where  $\lfloor t_f \rfloor = \max\{i \in \mathbb{Z} \mid i \leq t_f\}$  is the floor of  $t_f$ , that is, the greatest integer that is less than or equal to  $t_f$ , and  $\delta(t)$  is the Dirac delta function. This expression ensures that the nymphs leave annually when  $t$  is an integer. We use the factor of 10 in Eq. (7) to amplify the delta-functions, so that  $n(t)$  drops to nearly zero at the end of each year, modelling the mass departure of nearly all of the nymphs. In fact,  $n(i+) = e^{-10}n(i-)$ , i.e.  $n$  decreases by a factor  $e^{-10}$  at  $t = i$ .

The delay between the hatching of the alates and their release is not included in this model. Including such a delay merely moves the time of alate hatching back in time by an amount equivalent to the delay between hatching and emergence from the mound and produces no new insights. Therefore, we have chosen not to include it in this very simple model.

### 2.1.6. Total nymph output

The purpose of this model is to find a breeding strategy, which maximises the total nymph output of a colony over its lifetime. This is given by the integral of the birth rate of nymphs over  $[0, t_f]$ . Let the total number of nymphs be denoted by  $I$ , where

$$I = \int_0^{t_f} rp(t) dt = r \int_0^{t_f} p(t) dt. \quad (8)$$

The function  $p(t)$  must lie between 0 and 1, as it is a proportion:

$$0 \leq p(t) \leq 1, \quad \forall t \in [0, t_f]. \quad (9)$$

Therefore, the optimisation problem is to determine the optimal functions  $f^*$ ,  $w^*$ ,  $n^*$  and  $p^*$ , which satisfy the ODE's (1), (4) and (6) subject to the constraints (2), (3) and (9), and which maximise the integral (8).

If  $\beta(t)$  is given by (5),  $f(t)$  is always positive, so the constraint (2) is non-active and can be ignored. This makes the problem much easier to solve. If  $\beta$  is a constant, then  $f(t)$  is negative for small  $t$ , and so in this case, the constraint (2) is active and must be retained.

### 2.1.7. Non-dimensionalisation

We partially non-dimensionalise the equations in the model to remove the constant  $c_w$ . We denote old variables with a bar and let the new variables be barless.

$$f = \frac{\bar{f}}{c_w}, \quad (10)$$

$$q = \frac{\bar{q}}{c_w}, \quad (11)$$

$$c_n = \frac{\bar{c}_n}{c_w}. \quad (12)$$

It is also possible to non-dimensionalise the time but we prefer the timescale to be in years so that  $\gamma(t)$  has a spike at every integer, and so that important qualitative information contained in the optimal solution is not obscured.

## 2.2. *Nasutitermes exitiosus*

*Nasutitermes exitiosus*, unlike *Coptotermes lacteus* do not store food in their mound. This difference requires a modification to the model and to the optimisation problem. It is interesting to see how this modification affects the nature of the solutions.

Because no food is stored in the mound, it is unnecessary to include a differential equation for  $f(t)$ . It is necessary, however, to ensure that the amount of food collected is always greater than or equal to the amount of food consumed. This leads to the constraint

$$qw \geq c_w w + c_n n, \quad (13)$$

or, in non-dimensional form,

$$(q - 1)w \geq c_n n, \quad (14)$$

where the new variables are given by Eqs. (10)–(12).

Removing food storage from the colony does not change the differential equations for worker population or nymph population, since  $f(t)$  is not present in either of these equations.

Therefore, the *N. exitiosus* problem is to maximise (8) subject to the constraints (9) and (14) where the dynamics are given by (4) and (6).

Differences between the constraints in the *C. lacteus* problem and on the *N. exitiosus* problem necessitate quite different approaches to the optimisation and are reflected in the nature of the solutions.

### 3. Solving the optimisation problems

#### 3.1. *Coptotermes lacteus*

We use the Pontryagin Maximum Principle (PMP) (see, for example, Seierstad and Sydsaeter, 1987) to solve the optimisation problem described in Section 2.1. We use the PMP to obtain a feasible solution, which we argue satisfies the necessary conditions for optimality. We then show that the solution also satisfies sufficient conditions for the PMP (see, for example, Seierstad and Sydsaeter, 1987) and hence, maximises the total nymph output  $I$ .

Let

$$\mathbf{x}(t) = \begin{bmatrix} f(t) \\ w(t) \\ n(t) \end{bmatrix}$$

and define  $\mathbf{f} : \mathbb{R}^3 \times [0, 1] \times \mathbb{R} \rightarrow \mathbb{R}^3$  to be the function

$$\mathbf{f}(\mathbf{x}, p, t) := \dot{\mathbf{x}} = \begin{bmatrix} (q - 1)w - c_n n \\ r(1 - p(t)) - \beta(t)w \\ rp(t) - \gamma(t)n \end{bmatrix}.$$

Care must be taken not to confuse  $\mathbf{f}(\mathbf{x}, p, t)$  with the food variable  $f(t)$ .

For the PMP to be valid, we need to check the continuity conditions that  $f_i, \partial f_i / \partial x_j \in C^0, \forall i, j \in \{1, 2, 3\}$  with respect to  $\mathbf{x}, p$  and  $t$ . These conditions are clearly satisfied if  $\gamma(t) \in C^0$ , but we defined  $\gamma(t)$  in Eq. (7) as a sum of Dirac delta functions, so it cannot



be  $C^0$ . We can, however, approximate each Dirac delta function with a very tall  $C^\infty$  spike, that has unit area. This approximation is consistent with the biological modelling because it still reduces the nymph population to almost zero at the end of every year. Moreover, we expect the approximation to be mathematically valid, because we can take the widths of the spikes to be arbitrarily small, such that they simulate Dirac delta functions arbitrarily closely.

For now, we ignore the constraint (2), that the food stores cannot be negative, on the assumption that (2) is not active. If, however, the final solution violates this assumption, we would need to solve the problem with (2), which would require more complicated techniques. We verify that the constraint is not active by observing the value of  $f(t)$  in the results. The inactivity of this constraint is necessary for us to obtain an analytic solution.

We find the Hamiltonian of the dynamical system, in a suitable form for the application of the PMP:

$$H = g + \lambda \cdot f, \tag{15}$$

where  $g = rp(t)$  is the function whose integral is to be maximised,  $f$  has already been defined and  $\lambda$  is found from the relation

$$\dot{\lambda}_i = -\frac{\partial H}{\partial x_i}, \quad \text{for } i = 1, 2, 3. \tag{16}$$

So the Hamiltonian is

$$H = r[1 - \lambda_2(t) + \lambda_3(t)]p(t) + r\lambda_2(t) + w[\lambda_1(t)(q - 1) - \lambda_2(t)\beta(t)] + n[-\lambda_1(t)c_n - \lambda_3(t)\gamma(t)]. \tag{17}$$

Given  $H$ , we find the equations for  $\lambda_1(t)$ ,  $\lambda_2(t)$ , and  $\lambda_3(t)$  using Eq. (16).

$$\dot{\lambda}_1 = -\frac{\partial H}{\partial f} = 0, \tag{18}$$

$$\dot{\lambda}_2 = -\frac{\partial H}{\partial w} = -\lambda_1(q - 1) + \lambda_2\beta(t), \tag{19}$$

$$\dot{\lambda}_3 = -\frac{\partial H}{\partial n} = \lambda_1c_n + \lambda_3\gamma(t). \tag{20}$$

Equation (18) gives  $\lambda_1(t) \equiv \lambda_0$ , a constant. However, we cannot immediately solve for  $\lambda_0$  because  $f(t_f)$  is fixed at 0, implying  $\lambda_1$  has no transversality condition. Finding  $\lambda_0$  accurately turns out to be the crux of the problem.

Solving Eq. (19), using the transversality condition  $\lambda_2(t_f) = 0$ , gives

$$\lambda_2(t) = \lambda_0(q - 1) \int_t^{t_f} e^{B(t)-B(s)} ds, \tag{21}$$

where we have defined

$$B(t) := \int_0^t \beta(\tau) d\tau = at - (a/b) \ln(1 + bt).$$

We can solve Eq. (21) analytically, in terms of the upper incomplete Gamma function to give

$$\lambda_2(t) = \lambda_0(q - 1)e^{B(t)} \left[ -\frac{1}{a} \left( \frac{eb}{a} \right)^{a/b} \Gamma \left( \frac{a+b}{b}, \frac{a}{b} (1+bs) \right) \right]_t^{t_f}.$$

However, this form of the solution is not useful for computation in `Matlab`.

Solving Eq. (20), using the transversality condition  $\lambda_3(t_f) = 0$ , gives

$$\lambda_3(t) = -\lambda_0 c_n e^{\int_0^t \gamma(\tau) d\tau} \int_t^{t_f} e^{-\int_0^s \gamma(\tau) d\tau} ds.$$

If we use the assumption that  $\gamma(t)$  is a  $C^\infty$  function, which closely approximates  $10 \sum_{i=1}^{t_f} \delta(t - i)$ , then we can simplify the expression for  $\lambda_3$  to

$$\lambda_3(t) \approx \lambda_0 c_n \left( t - [t] - \sum_{i=[t]}^{t_f-1} e^{10([t]-i)} \right), \tag{22}$$

where for all intents and purposes, we may assume equality.

Hence, if  $\lambda_0$  is known, both  $\lambda_2$  and  $\lambda_3$  can be found explicitly.

By the PMP, any control that optimises the problem, must also maximise the Hamiltonian at  $\mathbf{x}^*$ , where  $\mathbf{x}^*$  is the state variable that corresponds to the optimal control  $p^*$ . That is,

$$H(\mathbf{x}^*, p^*, \lambda, t) \geq H(\mathbf{x}^*, p, \lambda, t), \quad \forall p(t) \in [0, 1].$$

From (17),  $H$  is maximised at a fixed  $\mathbf{x}$  with respect to  $p$  by a bang-bang solution with  $p = 1$  or  $p = 0$  (that is, where either all nymphs are produced or all workers), since  $H$  is linear in  $p$ . As the coefficient of  $p$  in  $H$  is  $r[1 - \lambda_2(t) + \lambda_3(t)]$ ,  $p$  must be maximal when  $1 - \lambda_2(t) + \lambda_3(t) > 0$ , and minimal when  $1 - \lambda_2(t) + \lambda_3(t) < 0$ . Since  $p$  is constrained to the closed set  $[0, 1]$ , we get

$$p^*(t) = \begin{cases} 1, & \text{when } 1 - \lambda_2(t) + \lambda_3(t) > 0; \\ 0, & \text{when } 1 - \lambda_2(t) + \lambda_3(t) < 0. \end{cases} \tag{23}$$

Notice that Eqs. (21), (22) and (23) determine the functions  $\lambda_2$  and  $\lambda_3$ , and hence the function  $p^*$ , in terms of the unknown constant  $\lambda_0$ . To find  $\lambda_0$ , we use the constraint condition  $f^*(t_f) = 0$ . We regard  $f^*(t_f)$  as a function of  $\lambda_0$ , and use a numerical root finding routine to find the value of  $\lambda_0$ , for which the constraint condition is satisfied.

To determine the optimal function  $f^*(t)$  we must first find  $w^*(t)$  and  $n^*(t)$  in terms of  $\lambda_0$ . Using the expression for  $p^*(t)$  given in (23), we can solve (4) for  $w^*(t)$ :

$$w^*(t) = \int_0^t r(1 - p^*(s))e^{B(s)-B(t)} ds. \tag{24}$$

The integral depends on  $\lambda_0$  through  $p^*(t)$ , which ultimately depends on the unknown  $\lambda_0$  through  $\lambda_2(t)$  and  $\lambda_3(t)$ . The nymph population  $n(t)$  is reset to almost zero at the end of each year, when  $t$  is an integer. Therefore, we can approximate  $n^*(t)$  as

$$n^*(t) \approx \int_{\lfloor t \rfloor}^t r p^*(s) ds. \tag{25}$$

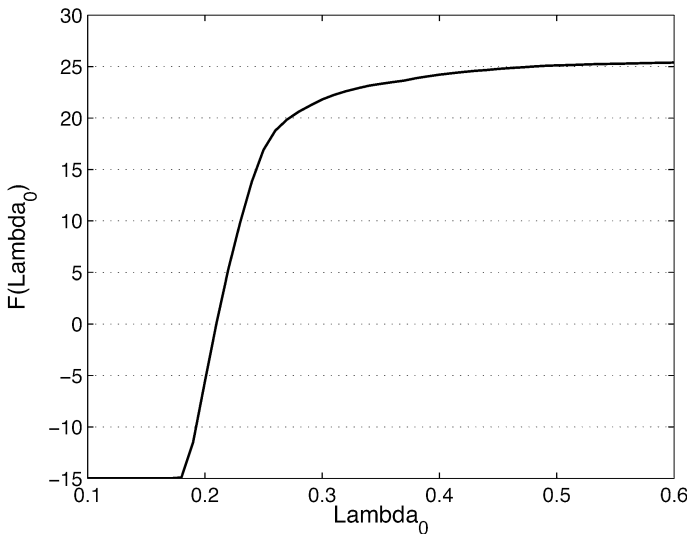
Since  $w^*(t)$  and  $n^*(t)$  are now known we can write

$$f^*(t_f) = \int_0^{t_f} [(q - 1)w^*(t) - c_n n^*(t)] dt = 0. \tag{26}$$

The integral depends on the remaining unknown  $\lambda_0$  through  $w^*(t)$  and  $n^*(t)$ .

We define the function  $F(\lambda_0) = f^*(t_f)$  and use standard numerical root-finding procedures to find where  $F(\lambda_0) = 0$ . The evaluation of  $F(\lambda_0)$  requires  $p^*(t)$  to be found for the given input  $\lambda_0$ , which in turn depends on finding where  $1 - \lambda_2(t) + \lambda_3(t) = 0$ , and using this to evaluate  $w^*(t)$  and  $n^*(t)$ . To do this, the time domain is discretised with a variable mesh which is finest close to where  $t$  is an integer, as this is most likely to be where  $p(t)$  switches from 0 to 1. The trapezoidal rule was used to calculate integrals over the time domain. We found that higher level integration techniques were not well suited to the bang-bang variable  $p^*$ . Analytic solutions for  $w$  and  $n$  were found for fixed values of  $p$ , but these solutions did not significantly aid the computation of results.

The function  $F(\lambda_0)$  is illustrated in Fig. 1. For the given parameters, it has one root near 0.225.



**Fig. 1** The function  $F(\lambda_0)/r$  is plotted over the domain  $[0, 1]$ . The values of the parameters in this case are:  $q = 1.5$ ,  $c_n = 1.5$ ,  $t_f = 20$ ,  $a = 1/3$  and  $b = 3$ . As  $\lambda_0 \rightarrow -\infty$ , the graph tends to a horizontal asymptote, since the function  $\text{sgn}(1 - \lambda_2 + \lambda_3)$  is little changed and hence there is little change to  $p^*$ . For the same reason, the graph will tend toward a horizontal asymptote as  $\lambda_0 \rightarrow \infty$ . The graph suggests that  $F(\lambda_0)$  is a monotonic function and has only one root, which is near 0.225.

We have used the PMP to show that this solution satisfies the necessary conditions for optimality. But in order to satisfy sufficient conditions for optimality, we also need to show that the maximum of the Hamiltonian with respect to  $p$ , which is given by the bang-bang solution calculated above, is concave in  $\mathbf{x}$  for all  $t \in [0, t_f]$  (see, for example, Seierstad and Sydsaeter, 1987).

Let

$$\hat{H}(\mathbf{x}, \boldsymbol{\lambda}, t) := \max_{p \in [0,1]} H(\mathbf{x}, \boldsymbol{\lambda}, p, t). \quad (27)$$

We show that  $\hat{H}$  is concave in  $\mathbf{x}$  by showing that  $-\hat{H}$  is convex in  $\mathbf{x}$ . Both  $\hat{H}$  and  $-\hat{H}$  are  $C^1$ . Let  $\mathbf{x}, \mathbf{y} \in [0, \infty)^3$ . By inspection, we can see that

$$-\nabla \hat{H}(\mathbf{x}) \cdot (\mathbf{x} - \mathbf{y}) = -\hat{H}(\mathbf{x}) + \hat{H}(\mathbf{y}),$$

so clearly,

$$(-\hat{H})(\mathbf{x}) - (-\hat{H})(\mathbf{y}) \leq \nabla(-\hat{H})(\mathbf{x}) \cdot (\mathbf{x} - \mathbf{y}), \quad \forall \mathbf{x}, \mathbf{y} \in [0, \infty)^3.$$

Hence,  $-\hat{H}$  is convex, i.e.  $\hat{H}$  is concave, and the bang-bang solution with appropriate choice of  $\lambda_0$  is indeed optimal.

### 3.2. *Nasutitermes exitiosus*

Although the equations for the *Nasutitermes exitiosus* model are not very different from those of the *C. lacteus* model, the active constraint (14) precludes an analytic solution similar to that of the *C. lacteus* case. We chose instead to discretise the system and use linear programming. The advantage of this approach is that it is easy to implement but the discretisation, and hence, the accuracy is limited by the size of the LP problems which can be solved.

We discretise the interval  $[0, t_f]$  into  $N$  subintervals of width  $h = t_f/N$  by setting

$$\mathbf{t} = \left( \frac{h}{2}, \frac{3h}{2}, \dots, t_f - \frac{h}{2} \right) = (t_1, \dots, t_N)$$

and assign values  $w_i, n_i$  and  $p_i$  to  $w(t), n(t)$  and  $p(t)$ , respectively, at integer values of  $h$ . That is, values of  $w_i, n_i$  and  $p_i$  are defined midway between the points  $t_i$  and at  $t = 0$  and  $t = t_f$ . Using the integral expressions (24) and (25) for  $w(t)$  and  $n(t)$ , we write  $w_i$  and  $n_i$  in terms of  $p_i$ . So

$$w_i = rh \left[ \sum_{k=1}^i e^{B(t_k) - B(t_i + \frac{h}{2})} (1 - p(t_k)) \right],$$

for  $i \in \{1, \dots, N\}$  or in matrix form

$$\mathbf{w} = \mathbf{c} - \mathbf{A}\mathbf{p},$$

where

$$c_i = rh \sum_{k=1}^i e^{B(t_k) - B(t_i + \frac{h}{2})},$$

and the matrix  $A$  is defined by

$$A_{i,k} = rh \begin{cases} e^{B(t_k) - B(t_i + \frac{h}{2})}, & \text{for } 1 \leq k \leq i; \\ 0, & \text{for } k > i. \end{cases}$$

Similarly, we can find an approximation to  $n_i = n(t_i + h/2)$  in terms of  $\mathbf{p}$ , by applying the same discretisation to Eq. (25). An important difference is that when  $t = \lfloor t \rfloor$ ,  $n(t) = 0$ . So using the composite midpoint quadrature rule,

$$n_i = \begin{cases} 0, & \text{for } t_i \in \mathbb{N}; \\ rh \sum_{k=m_i}^i p(t_k), & \text{for } t_i \notin \mathbb{N}, \end{cases}$$

where  $m_i := \lfloor t_i \rfloor / h + 1$ , and we choose  $h$  such that this  $m_i$  is an integer. In matrix form,

$$\mathbf{n} = D\mathbf{p},$$

where, for  $t_i \in \mathbb{N}$ ,  $D_{i,k} = 0$ , and for  $t_i \notin \mathbb{N}$ , the matrix  $D$  is defined by

$$D_{i,k} = rh \begin{cases} 1, & m_i \leq k \leq i; \\ 0, & k > i \text{ or } k < m_i. \end{cases}$$

We note that both  $A$  and  $D$  are lower triangular matrices. In this discretisation, we use Riemann sum approximations rather than the midpoint, trapezoidal or other more sophisticated integration methods. The more sophisticated methods appear to introduce instabilities into the linear programming routine in `Matlab`, which we used.

In the discretised problem, the constraints (14) and (9) become

$$(\mathbf{c} - A\mathbf{p})(q - 1) \geq c_n D\mathbf{p}, \tag{28}$$

$$0 \leq \mathbf{p} \leq 1. \tag{29}$$

The first inequality can be rewritten as

$$E\mathbf{p} \leq \mathbf{c}, \quad \text{where } E = \frac{c_n}{q - 1} D + A. \tag{30}$$

Therefore, the problem reduces to finding the  $\mathbf{p}$  that maximises

$$I = rh \sum_{j=1}^N p(t_j),$$

with respect to the constraints (29) and (30).

This problem can be directly solved in `Matlab` without further analytical manipulation, using the command `linprog`. We found that we could not take our step size  $h$  to

be arbitrarily small, because `Matlab` cannot handle linear programming problems with vectors longer than a particular length. Tests with smaller and larger step sizes for various values of  $t_f$ , indicated that the results were not too sensitive to step size changes, around the value that was used ( $h = 0.05$ ).

## 4. Results

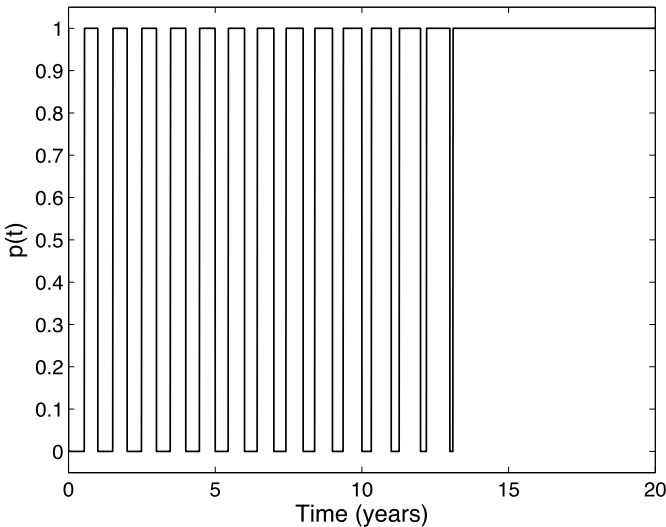
Figures 2–6 show the optimised variables  $p^*(t)$ ,  $w^*(t)$ ,  $n^*(t)$  and  $f^*(t)$  for *Coptotermes lacteus* and *Nasutitermes exitiosus*. These figures were obtained with the specific parameter values:  $t_f = 20$ ,  $q = 1.5$ ,  $c_n = 1.5$ ,  $a = 1/3$ ,  $b = 3$ . The function  $p^*$  is independent of  $r$ , and the equations for  $w^*$ ,  $n^*$  and  $f^*$  contain  $r$  only as a constant multiple. Calculating  $w^*/r$ ,  $n^*/r$  and  $f^*/r$  avoids the need to estimate  $r$  and gives a useful measure of nymph production relative to the queen's egg laying rate.

### 4.1. *Coptotermes lacteus*

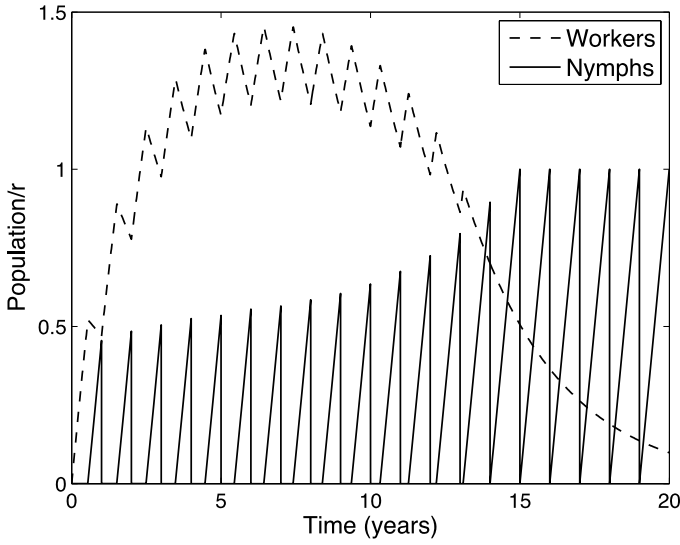
Figure 2 clearly displays the bang-bang nature of  $p^*(t)$  for *C. lacteus*. Workers are always produced at the start of each year (corresponding to  $p = 0$ ), and nymphs at the end (corresponding to  $p = 1$ ). This is optimal as the colony uses less food per nymph, because the nymphs are in the nest for the shortest possible time.

Looking at the widths of the  $p = 1$  segments of  $p^*$  in Fig. 2, we see that the number of nymphs produced each year increases with time. The model predicts that only nymphs will be produced in the final years of the colony's life.

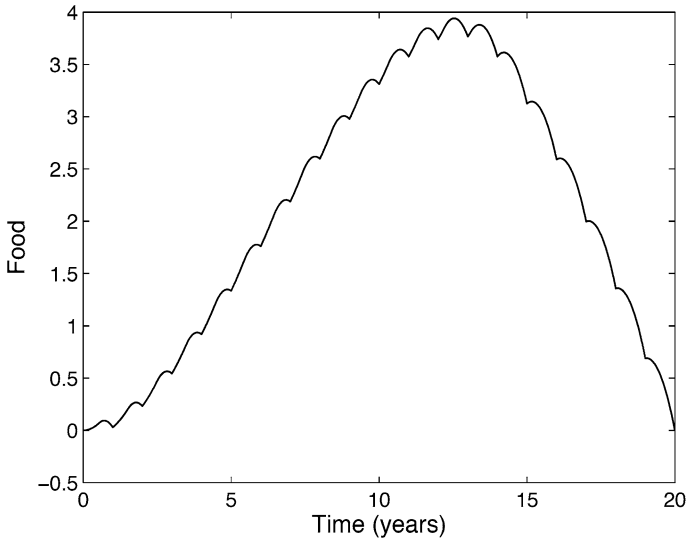
Figure 3 shows the optimal worker and nymph populations. As expected, the worker population climbs rapidly when the colony is very young. It remains steady, apart from



**Fig. 2** Optimised  $p^*(t)$  (the ratio of eggs laid that will become nymphs) in the *C. lacteus* model.

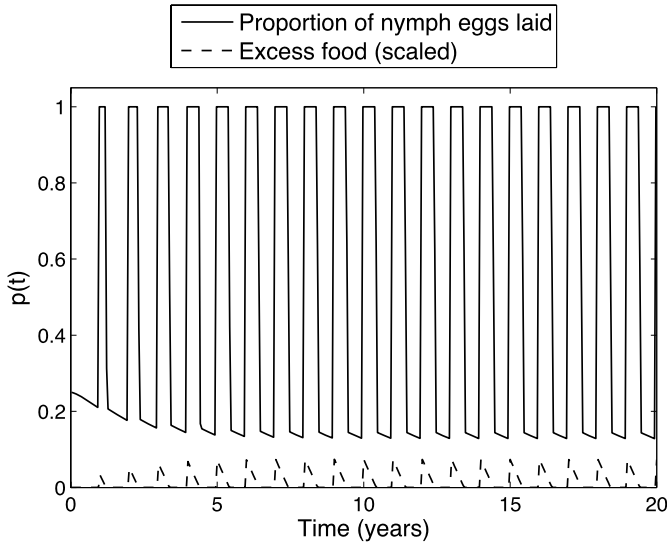


**Fig. 3** Optimised  $w^*$  (worker population) and  $n^*$  (nymph population) in the *C. lacteus* model.

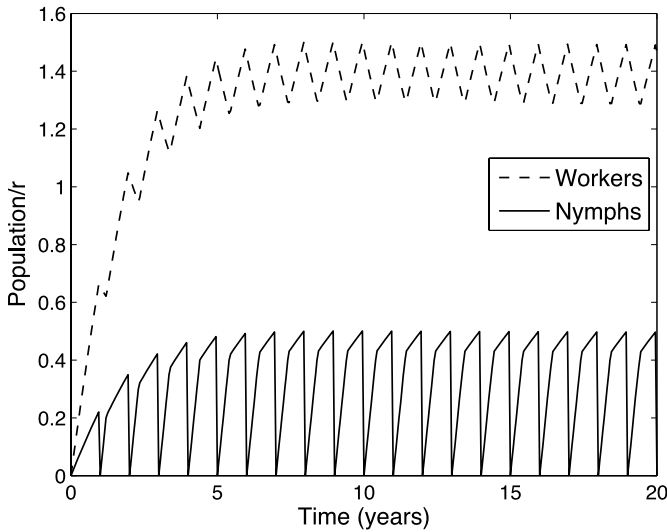


**Fig. 4** Optimised  $f^*(t)$  in the *C. lacteus* model. The characterising constraint on the solution was that  $f(t_f) = 0$ . Notice also that  $f(t) \geq 0$  is always satisfied.

annual fluctuations, through the middle part of the colony’s life and declines significantly toward  $t_f$  once no further workers are produced. The nymph population fluctuates seasonally. The peak each season gives the total number of nymphs produced in that year.



**Fig. 5** Optimised  $p^*$  (proportion of eggs laid that become nymphs) for the *N. exitiosus* problem is shown as a solid line. The optimal excess food  $g^*(t)$  (multiplied by the constant  $\frac{1}{10r}$ , so that is easy to compare with  $p^*(t)$ ) is shown as a dashed line.



**Fig. 6** Optimised  $w^*$  (worker population) and  $n^*$  (nymph population), for the *N. exitiosus* problem.

This is more or less constant through the middle of the colony's life, but increases rapidly in the last few years before the colony dies.



Colony food stores are shown in Fig. 4. The total stored food increases (aside from seasonal variations) until the last phase of the colony's life when the food stores are rapidly consumed by the large number of nymphs that the colony produces. In the seasonal cycle, food stores are always lowest just after the nymphs leave the nest. In the first part of the year, when there are no nymphs in the nest, workers collect more than they consume. Once nymph production starts, as the number of nymphs increase, food levels start to decline until the next group of nymphs leave.

#### 4.2. *Nasutitermes exitiosus*

Figure 5 shows the optimal  $p(t)$  for *N. exitiosus* (upper line) and the amount of excess food collected as a function of time (lower line). For this model,  $p(t)$  is never zero; there are always some nymphs being produced. In contrast to *C. lacteus*, the main season of nymph production, when  $p(t) = 1$ , takes place immediately after the mature nymphs have left the nest. This effectively minimises the amount of food that goes to waste, or, alternatively, makes best use of the nest's food collection capacity. After an initial period of higher worker production as the nest becomes established, the annual pattern of nymph and worker production settles to a repeating stable cycle that is not disrupted by the impending end of the nest at  $t_f$ . The populations of workers and nymphs in Fig. 6 show similar behaviour.

#### 4.3. Parameter searches

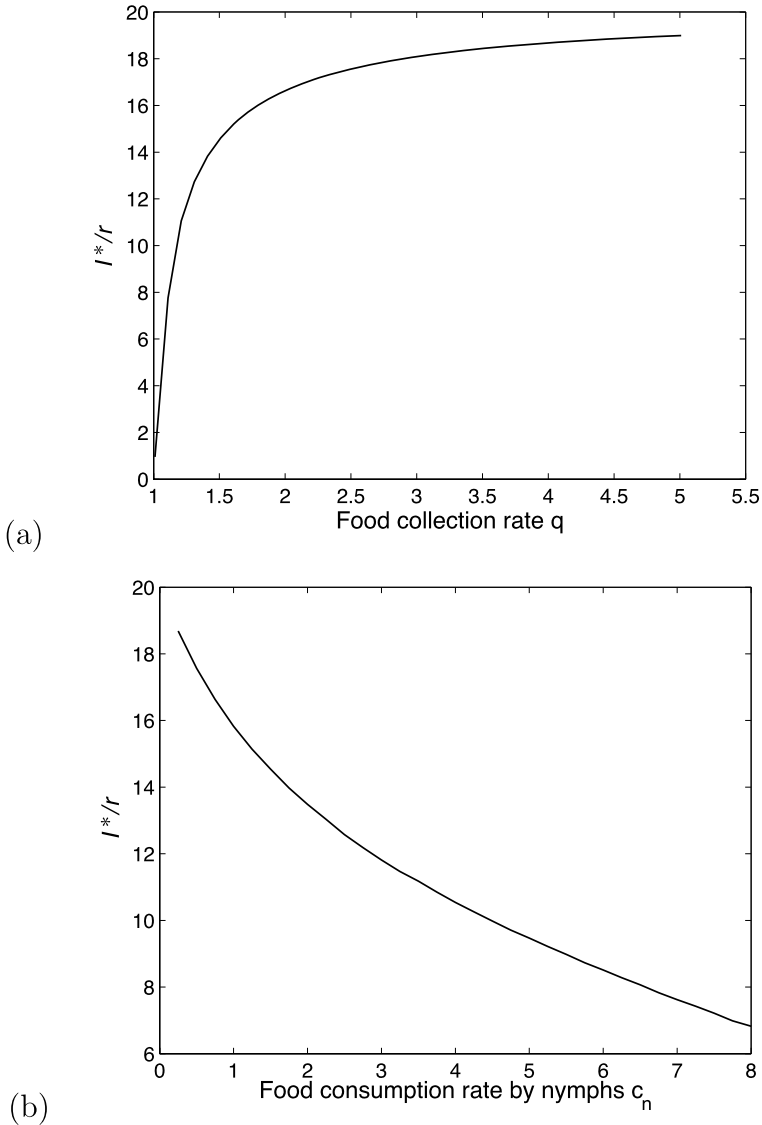
As there is very little firm observational data on the values of parameters in the models, we investigated whether these results were robust to parameter changes. We changed  $q$ ,  $c_n$  and  $t_f$  for each species in turn, and found the value for  $I^*/r$  where  $I^*$  is the optimal number of nymphs produced over the colony's lifetime. Figure 7 shows the results for varying  $q$ ,  $c_n$ , and  $t_f$  for *C. lacteus*. The results for *N. exitiosus* were similar.

In Fig. 7(a), the independent variable,  $q$ , is the rate of food collection per worker, scaled by the rate of food consumption per worker. As  $q$  increases, the nymph output rises rapidly at low  $q$  and more slowly as  $q$  gets larger. The value of  $q$  used in the model is 1.5 and is on a part of the curve where the total number of nymphs increases rapidly. Hence, we expect the model to be somewhat sensitive to changes in  $q$ . In Fig. 7(b), the total number of nymphs produced by a colony falls as  $c_n$  (the ratio of the rate of food consumption by nymphs to food consumption by workers) decreases. At  $c_n = 8$  the curve appears to be levelling out. In our model, we used  $c_n = 1.5$ , and so we might expect some sensitivity of our results to changes in  $c_n$ .

In Fig. 7(c), the dependent variable is the average scaled number of nymphs produced per year  $I^*/rt_f$ , rather than  $I^*/r$ , which was graphed in (a) and (b). The trend indicates that the longer a colony lives, the more nymphs it can produce per year, tending toward a horizontal asymptote at around  $t_f = 10$ . The calculations in this study take  $t_f = 20$ . This value lies in an area of the graph that is not changing rapidly for either species of termite, and hence, the solution is not sensitive to changes in  $t_f$ .

## 5. Discussion

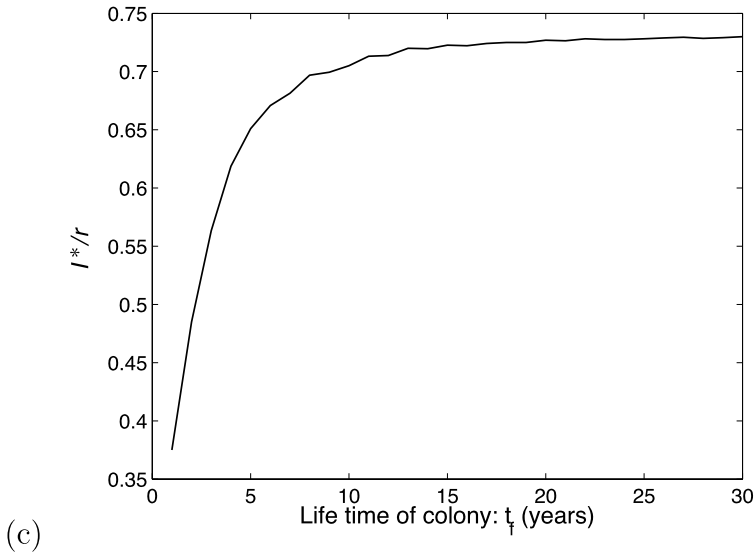
This study is the first to use a mathematical model to investigate reproductive patterns in termites. There are few observational studies in this area and most of the information



**Fig. 7** Parameter sensitivity in the *C. lacteus* model. Each plot shows the effect on nymph output  $I^*/r$  of varying a particular parameter. When parameters are fixed, their values are,  $q = 1.5$ ,  $c_n = 1.5$ ,  $a = \frac{1}{3}$ ,  $b = 3$ ,  $t_f = 20$  (a) varying the food collection rate  $q$ ; (b) varying the nymph food consumption rate  $c_n$ ; (c) varying the colony lifespan  $t_f$ .

available is anecdotal rather than systematically obtained. Therefore, the predictions of the model and the questions that it raises are significant and useful.

The most important outcome of the model is to predict that whether or not a mound-building termite stores food will determine both its seasonal pattern of nymph and alate



**Fig. 7** (Continued.)

production, and the overall pattern of worker and nymph production over the life of the colony. At one level, this is surprising: *C. lacteus* and *N. exitiosus* live in similar environments and have similar behaviours (Hill, 1942; Evans and Gleeson, 2001). The similarities of the models reflect this. Once the mathematical theory for solving the optimisation problem is invoked, however, it becomes clear that the difference in food storage leads to structurally different mathematical optimisation problems and, not surprisingly, qualitatively different results.

Food storage by *Coptotermes lacteus* has a number of consequences. First, nymph production occurs as close as possible to the time when they will leave the nest. In the model, we have not introduced a delay between hatching and leaving, but it is unlikely that such a delay will significantly change the prediction that *C. lacteus* nymphs spend as little time in the nest as possible. Further, the bang-bang solution to the optimisation problem predicts that at any given time, all the new offspring produced in a *C. lacteus* mound will either be workers or be all nymphs. Secondly, the model predicts that *C. lacteus* mounds will have a distinct phase at the end of their natural life where almost all new offspring are nymphs, worker production is minimal, and stored food is rapidly consumed.

In contrast, the model predicts that once a *N. exitiosus* mound is well established, it will settle down into what is essentially a steady state with a recurrent annual cycle, that is not affected by the impending extinction of the mound. Nymphs are produced throughout the year, but mainly immediately after the previous year's nymphs have left the mound, so that the colony's food collection capacity can be used to the best advantage. This suggests that there should always be nymphs of every stage of growth in a *N. exitiosus* mound, unlike a *C. lacteus* mound where the model predicts that for some of the year, immediately after the alates leave, there will be no nymphs.

In this study we set out to maximise the number of nymphs that a colony could produce with a fixed egg-laying rate. For *N. exitiosus*, exactly the same results can be obtained by

minimising the amount of food wasted, that is, minimising  $(1 - q)f(t) - c_n n(t)$  under the constraint that it must always be non-negative. This can also be interpreted as minimising the amount of unused foraging capacity.

The models in this study are very simple and clearly could be made more realistic. Changes that could be made include introducing a delay in the equation for nymph populations so that nymphs do not leave the nest until they are mature, introducing explicit age structure into the worker population so that the age-dependent death rates at the start and end of the colony's life can be more accurately modelled, introducing a time dependent egg-laying rate to reflect the queen's development early in the colony's life, including seasonal cycles in temperature and food consumption and availability, and introducing a soldier caste. Workers develop into soldiers, but can do so from mid to late instars, (that is, as they approach maturity) which would be a loss to the worker population. Soldiers are unable to feed themselves and must be fed by workers, which is another constraint on the food available for nymph development. We have chosen, however, to keep the model uncomplicated so as not to obscure the main results and to permit some measure of analysis.

This study predicts observable differences in nymph and alate production between two species of Australian termites that relate to their foraging strategies. We hope that it will provide a focus for experimental research in the area of termite reproductive strategies not only for the species investigated here, but also for other types of termite in other ecologies and in other parts of the world.

## Acknowledgements

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