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Dynamics of colony development in *Polistes dominulus*: a modeling approach

Abstract A simple model based on feedback mechanisms is developed to describe the dynamics of brood production and colony development of primitively eusocial paper wasps. The presence of pupae and empty cells stimulate egg laying, which varies between a basic rate and a physiological maximum. Newly hatched larvae are fed eggs, causing fluctuations in brood demography and forming cohorts of offspring. The basic feedback mechanisms produce emergent colony-level properties such as synchronized development of the brood and mature nest size. Results suggest that it is incorrect to imply colony decline from lack of nest growth, and that production of waves of offspring can be interpreted as the inevitable result of these simple feedback mechanisms rather than the solution to ultimate optimality criteria. Simulations using the parameters estimated in *Polistes dominulus* Christ are compared to studies of live wasps to test the validity of the model. Comparing simulated results with a perturbation experiment in nature suggests that feedback relationships establish a system that is robust and resilient against severe disturbance.

Key words Paper wasps · Colony development · Model · Feedback · Dynamics

Introduction

The rate and pattern of productivity are often at the heart of studies of sociality (Wilson 1971). Ultimate, adaptive causality is often invoked to explain details of reproductive biology. For example, Oster and Wilson (1978) found advantages to producing either of the complementary patterns of continuous growth or periodic cohorts of offspring, but the mechanisms by which such patterns evolve were generally left as speculation or avenues for future research.

Early models of colony dynamics of social insects focused mainly on the larva/worker ratio as the main factor governing colony development (Richards and Richards 1951; Lövgren 1958). In a more general model (Brian 1965) the rate and timing of the emergence of reproductives were taken as the principal population-limiting factor. Brian's model, depending on the coefficient of queen production, was able to simulate the main type of natural dynamics of social insects. The presumed regulatory role of the workers linked with the "ultimate goal" of the queen led to the so called bang-bang theory of colony growth (Oster and Wilson 1978). Several more recent models (e.g., Archer 1981; Martin 1991) are based on similar assumptions, but although the elementary functions of these models are simple, the great number of variables and complex relations make the models quite complicated.

All the models outlined above simulated the colony dynamics of highly eusocial insects, where the workers certainly play an important role in the productivity of the colony (Spradbery 1965; Oster and Wilson 1978). Primitively social wasps, the subject of this study, build small colonies with a small number of workers under the physical control of the queen. Patterns of brood production in these colonies generally suggest an initial production of a small number of workers followed by a hiatus and eventually a second phase of increased production. In this second phase both workers and reproductives are commonly produced together in waves. This temporal pattern in colony growth is commonly reported as a temporary drop in egg production or a short plateau in a plot of nest size against date (Morimoto 1954a, b, c; Deleurance 1957; Jeanne 1972; Kojima 1989). Once production is resumed, it may

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proceed more or less smoothly until the colony begins to "decline", when construction and brood production cease. This final nest size may be a life history trait in itself, thus nest growth patterns may be adequate to characterize species (Karsai and Pénzes 1996).

Empirical and theoretical evidence indicates several mechanisms and parameters that influence brood demography in paper wasps. One of the first observed was oophagy (Heldmann 1936; Pardi 1942; Deleurance 1956; Gervet 1964b, 1956; Miyano 1980). Much of the thinking about the causes and results of oophagy has been dominated by concerns about the differential reproductivity of multiple females on the same nest (Pardi 1942; West Eberhard 1969), and demographic concerns have been somewhat eclipsed.

Another main parameter that influences the brood demography is the egg-laying rate of the queen. Although numerous authors count the daily egg number in the nests (e.g., Strassmann 1981; Kojima 1989; Karsai 1996), few studies record the actual number of eggs laid per day. Physiological constraints fix the upper limit of the egg-laying rate (Gervet 1964a) but within the given range, its actual value varies, depending on the social milieu (number of empty cells, pupae and nestmates) of the colony (Deleurance 1950; Gervet 1965; Mead et al. 1994; Karsai 1996).

The rich literature on *Polistes* and related genera offers empirical derivation of life history parameters appropriate for building models of colony growth. The aim of this paper is to develop a discrete deterministic model based on simple feedback mechanisms to describe the dynamics of brood production and colony development of primitively eusocial paper wasps. Simulations using the parameters estimated in *Polistes dominulus* are compared to studies of live wasps to test the validity of the model. Such models may also allow qualitative evaluation of the relative importance of given parameters for producing well-known colony-level phenomena. In this paper we draw attention to forgotten patterns in reproductivity of primitively social wasps and use a simple model to explain how the cadence of reproductivity is produced. Ultimate, adaptationist reasoning or traditional views of causality are omitted so that the study may offer an appraisal of the minimum assumptions necessary to generate natural patterns.

Methods

Assumptions of the model

The models intend to describe the dynamics of the growth period of a determinate nesting cycle, where one individual develops in one cell which is then reused for brood rearing (Fig. 1). In the presence of enough empty cells (F), no initiation of new cells takes place. Eggs are laid into empty cells, which are built by the queen or appear due to the emergence of a new adult (W). It is assumed that as many cells are initiated as will be filled with eggs on the same
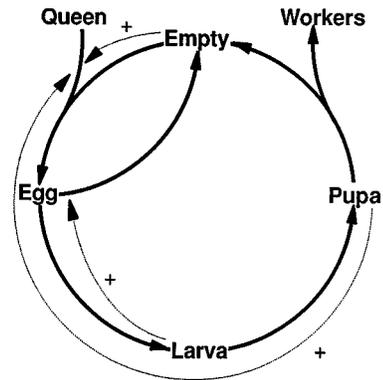

Fig. 1 Cell cycle, larval development and positive feedback in *Polistes* wasps. Pupae and empty cells stimulate queen egg-laying (+), larvae eat eggs (+) resulting in empty cells

day. It is supposed that only the queen lays eggs and her egg laying rate (R) is constant (model I) or a function of the number of pupae and empty cells (model II). The development time of every individual is constant, encompassing the days spent as an egg (T_E), a larva (T_L), and a pupa (T_P). Each larva consumes a given quantity of eggs (OO) early in its life (model III).

The simulations are based on a daily timescale as are most studies of live wasps, from nest initiation to the end of 4 months ($T = 120$ days). The daily schedule of the colony is fixed, the different behaviors are separated and set in the following sequence:

1. Development (brood becomes 1 day older) and eclosion of adults (providing empty cells)
2. Egg laying, which is affected by recent stimuli (e.g., empty cells from behaviour 1 stimulate the egg-laying in current day)
3. Cell construction, if the queen is able to lay more eggs than the number of available empty cells
4. Feeding larvae or oophagy (eggs that have been laid on current day at behaviour 2 may also be used to feed larvae)
5. Recording data (census of brood stages, numbers of wasps, empty and total cells).

The numbers of eggs laid and consumed are rounded to integers to provide discrete values for comparisons with natural data.

Estimation of parameters for *Polistes dominulus*

Egg laying rate, oophagy, and the time spent in different stages in this species have been estimated by several authors (Table 1) Results suggest that the pupae and empty cells independently affect egg laying rate through logistic stimulus-response curves. The parameters of the function relating number of pupae to egg laying rate are based on the experimental study of Mead et al. (1994). Parameters for the stimulus effect of empty cells on egg laying rate are based on an experiment where half of the brood was removed from medium sized nests (50–70 cells), providing 25–35 empty cells (see detailed description of the experiment in Karsai 1996). The number of empty cells and eggs laid on the same day are plotted in Fig. 2 (pooled data of ten experiments).

Results

The models describe the dynamics of the growth period of a determinate nesting cycle. After demonstrating the basic constitution of the system (model I) the effects

Table 1 Life-history parameters of *Polistes dominulus*. Effect of empty cells and pupa on egg laying are described by sigmoid stimulus reaction curves where *C:* basic egg laying rate; C_F and C_P: maximal egg laying rate due to the effect of empty cell and pupa; *F* and *P*: number of empty cells and pupa; B_F, A_F and B_P, A_P are the parameters of sigmoid function in case of empty cell and pupa, respectively

Parameters	Estimated value	Source
Expansive period of a colony (days) (*T*)	120	Turillazzi 1980
Development time of egg (days) (T_E)	10	Pardi 1951
Development time of larva (days) (T_L)	16	Pardi 1951
Development time of pupa (days) (T_P)	13	Pardi 1951
Basic egg laying rate (*C*)	2.5	Mead et al. 1994
Effect of pupae on egg laying:		
$(C_P–C)/(1+\exp(−B_P×(P–A_P)))$	$A_P = 10$ $B_P = 0.4$ $C_P = 5$	based on Mead et al. 1994
Effect of empty cells on egg laying:		
$(C_F–C)/(1+\exp(−B_F×(F–A_F)))$	$A_F = 15$ $B_F = 0.8$ $C_F = 6$	This study (Fig. 2)
Oophagy (egg/larva) (*OO*)	1.3	Mead et al. 1994

of the feedbacks (see Fig. 1) are studied separately (models II and III). Finally all processes studied in these models are built into a complete model and its predictions are compared with natural data.

Model I

The dynamics of the different brood stages are simple. With constant egg laying, the numbers of each brood stage (egg, larva and pupa) increase only until the oldest individuals graduate to the next stage, when recruitment to the cohort (e.g., eggs hatching to larvae) is exactly balanced by graduation from the cohort (larvae pupating) (Fig. 3). After the growth period, the proportion of the different brood in the comb is determined by the ratio of development times of the different stages. The nest size [measured as cell number (*N*)] does not increase after the first adults emerge because the vacated cells provide enough places for new eggs (*F* = *C* = 2). The final size of the nest can be calculated by multiplying egg-laying rate by total development time ($N = C × (T_E + T_L + T_P) = 78$ cells).
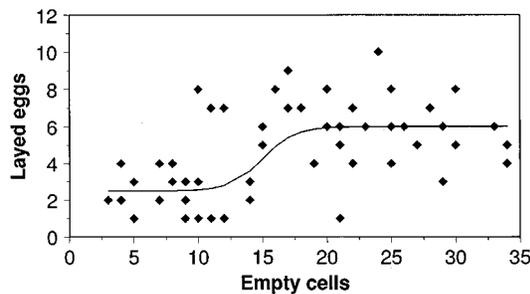
Fig. 2 Stimulation of egg-laying by empty cells in *P. dominulus*. Half of the brood from combs consisting of 50–70 cells was removed to liberate cells. Eggs laid per day are plotted as a function of the number of empty cells on the nests on the day in question. Fitted curve $R(t) = C+[(C_F−C)]/\{1+\exp[−B_F×(F–A_F)]\}$, where *C* is the basic egg laying rate (= 2.5), C_F is the maximal egg laying rate due to the effect of empty cell, *F* is the number of empty cells, B_F and A_F are parameters of the sigmoid function (see also Table 1)

Model II

This model differs from Model I only in allowing a variable egg-laying rate. Pupae and empty cells provide positive feedback to stimulate egg laying (Fig. 1). It is assumed that without any time-lag, only recent stimuli (the numbers of pupae and empty cells after the eclosion of adults) influence the egg-laying of the queen. These two colony components affect the rate independently, assuming logistic stimulus response curves (see also Table 1, Fig. 2):

$$R(t) = C + \frac{(C_P−C)}{1+\exp(−B_P \cdot (P−A_P))}$$
$$+ \frac{(C_F−C)}{1+\exp(−B_F \cdot (F−A_F))}$$

The egg-laying rate, depending on the parameters of the stimulus functions, may vary between *C* and
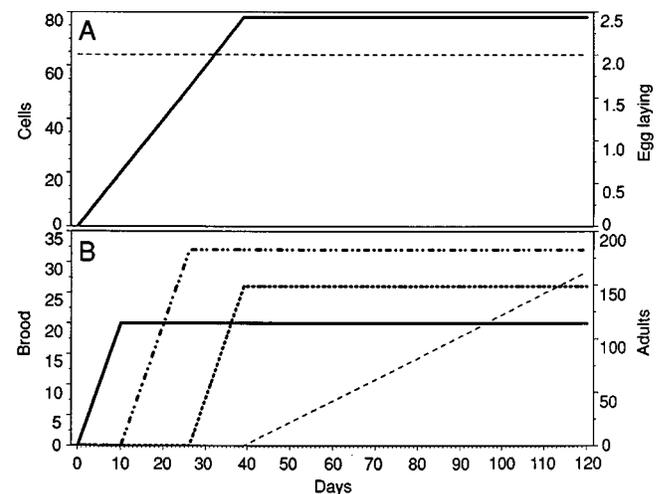
Fig. 3A, B Simulation of colony development of *P. dominulus*, model I. All broods reach their maximum when recruitment into a given stage is balanced by graduation to next stage. Parameters as in Table 1, except $C_P = C_F = C = 2$ and $OO = 0$. **A** nest size, *solid line*, number of eggs laid *dashed line*. **B** Egg *solid line*, larva *dot-dash* line, pupa *dotted* line, adults *dashed* line. Nest size and adult number are cumulative, other values are instantaneous
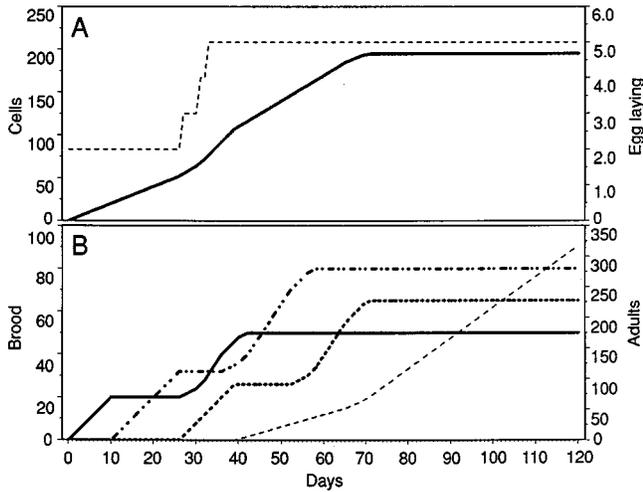
Fig. 4A, B Simulation of colony development of *P. dominulus*, model II. Positive feedback increases nest size and the number of brood. Parameters as in Table 1, except *OO* = 0. **A** Nest size *solid line*, number of eggs laid *dashed line*. **B** Egg *solid line*, larva *dot-dash line*, pupa *dotted line*, adults *dashed line*. Nest size and adult number are cumulative, other values are instantaneous

Fig. 5A, B Simulation of colony development of *P. dominulus*, model III. Oophagy results in empty cells and fluctuation of brood demography. Parameters as in Table 1, except $C_P = C_F = C = 2$. **A** Nest size *solid line*, number of eggs laid *dashed line*, empty cell *dotted line*. **B** Egg *solid line*, larva *dot-dash line*, pupa *dotted line*, adults *dashed line*. Nest size and adult number are cumulative, other values are instantaneous
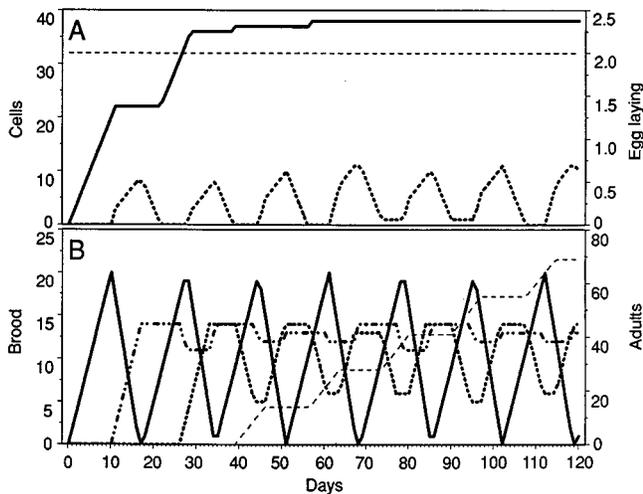
the theoretical maximum $[C_{max} = (C_P+C_F- C) = 8]$. The dynamics of colony development are the same as in model I before the first pupae emerge (Fig. 4). As pupae (and later empty cells) increase, egg-laying rate increases. When pupae and empty cells remain constant, egg laying remains constant resulting in plateaus in the brood dynamics and nest size. After egg-laying rate reaches a maximum, the brood reaches equilib-

rium and the nest its final size. At equilibrium, the number of the different brood stages are proportional to their development time and can be calculated (as in model I) by multiplying the theoretical maximal egg laying rate and the development time of the given stage. The theoretical maximal nest consists of 312 cells $(N_{max} = C_{max} \times (T_E+T_L+T_P))$, but due to the small number of empty cells in this model, the actual egg laying rate is not affected significantly by empty cells (Fig. 2), therefore the rate stabilizes at the limit determined by pupae $(C_P = 5)$ resulting in a smaller nest $(N = 195)$.

Model III

This model differs from model I only in that the larvae are fed a given quantity of eggs (*OO*). Adults fulfil the larval demands as soon as possible, removing as many eggs from cells as are required for oophagy. Based on experiments of Mead et al. (1994), it is assumed that adults prefer to feed the larvae with the younger eggs. Oophagy decreases the number of eggs and henceforward every brood stage leading to fluctuations in brood dynamics (Fig. 5). If more eggs are eaten than laid on the same day, there are gaps T_E days later in hatching, and henceforward later in adult emergence. The emptied cells cause the nest to cease growth because these cells are available for oviposition. The first plateau in cell number may occur when the first larvae hatch ($t = T_E+1$) if they eat more eggs than are laid per day. Due to oophagy the final nest size is small $(N = 38)$.

Modeling colony development of *Polistes dominulus*

The processes studied above were built into a complete model that resulted in complex colony dynamics (Fig. 6). Due to oophagy, there are gaps between the periods of hatching leading to formation of brood cohorts and fluctuating demography. Positive feedback mechanisms enhance these fluctuations, because they increase egg-laying rate (model III). Contrary to model II (due to oophagy), here empty cells become numerous periodically making it possible to reach the maximal egg laying rate $(C_{max} = 8)$.

The size of the nest increases gradually. Oophagy following the first hatch stops nest growth during the following 9 days as first cohort of brood are fed eggs. After the oophagic period the queen fills empty cells with new eggs and after this cell construction is resumed. Later, depending on the timing of oophagic periods and egg laying stimulation, the nest growth consists of increasing and constant periods. After 90 days, the nest does not increase further $(N = 102)$ because emerging adults and oophagy liberate enough empty cells for oviposition.

 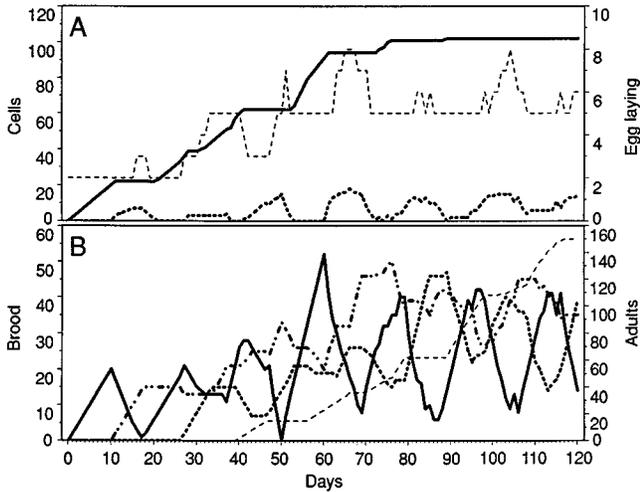
A
120
100
80
60
40
20
0
Cells
10
8
6
4
2
0
Egg laying
B
60
50
40
30
20
10
0
Brood
160
140
120
100
80
60
40
20
0
Adults
0 10 20 30 40 50 60 70 80 90 100 110 120
Days

Fig. 6A, B Simulation of colony development of *P. dominulus*, complete model. Increasing tendency with fluctuation (see text). Parameters as in Table 1. **A** Nest size *solid line*, number of eggs laid *dashed line*, empty cells *dotted line*. **B** Egg *solid line*, larva *dot-dash line*, pupa *dotted line*, adults *dashed line*. Nest size and adult number are cumulative, other values are instantaneous

Model performance in predicting natural data

For all comparisons, the complete model is used with the parameters presented in Table 1, including positive feedback and oophagy. Parameters are only changed in the cases where authors explicitly presented different ones from Table 1 [e.g., development time of brood in Röseler and Röseler (1989) was longer, but in Mead et al. (1994) shorter than in Pardi (1951)].

The model predicted well the timing of minimum and maximum hatching, and appearance of cohorts (Fig. 7) (cf. Mead et al., (1994)). Despite considerable differences in development period, the number of pupae and emerged adults were also predicted well by the models; their values were within the range that authors had recorded in the natural nests (Fig. 8). The size of the simulated nest increases in the same way as in the nests of Röseler and Röseler (1989) and Mead et al. (1994). The field nests of Turilazzi (1980) were smaller than the model predicted only in the middle part of the colony development when the number of pupae also dropped.

Perturbation of the colony growth

Wenzel (1989, 1996) presented an experiment where the perimeter of nests of *Polistes annularis* was excised and nest regeneration was followed. We simulated this experiment using the general model (with parameters from Table 1), because the life and cell cycle of this species are similar to those of *P. dominulus* (Fig. 1):

1. Nest was allowed to grow until the first pupae emerge.

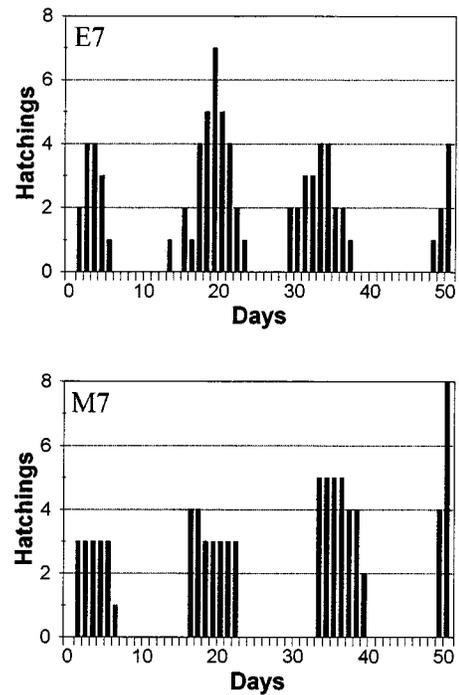
E7
Hatchings
0
2
4
6
8
0 10 20 30 40 50
Days
M7
Hatchings
0
2
4
6
8
0 10 20 30 40 50
Days

Fig. 7 Number hatching per day from the first hatching (*E7* empirical data of Mead et al. (1994), where the number denotes their colony codes, *M7* simulated model based on the parameters of Table 1 and data were given by Mead et al. 1994: $T_L = 12$; $C = 3.3$, $OO = 2.1$). Comparison shows that the model predicts the minimum and maximum values in demography

2. Fifty percent of the cells were removed from the periphery of the comb, keeping the shape of the nest constant as far as possible.
3. Nest was allowed to grow until the end of the season ($T = 120$ days).

The simulated experimental nest increased rapidly in size and reached the cell number of the control simulation before the first workers emerged (within 13 days) as in natural nests of Wenzel (1989, 1996) (Fig. 9). Excising the cells in the early pupa stage [27–33 days, before the number of pupae is constant (Fig. 6)] allows quick regeneration to natural size. If cells are excised after the number of pupae stabilizes (36 days) or after the emergence of workers (50 days), the nest reaches the size of control nests much later (after 90 days).

Although the simulated experimental (excised) nest did not increase as rapidly as the control nest (simulated nests without excising) in the middle of the colony cycle, the final nest size and the dynamics of brood in the last third of colony life were very similar in all kind of nests (Fig. 9). Destruction of brood results in a short-term disturbance in brood demography, but all the simulated experimental nests achieved synchronized fluctuation of brood after approximately 90 days. These cycles closely approximate the unmanipulated nests of the model (Fig. 9),
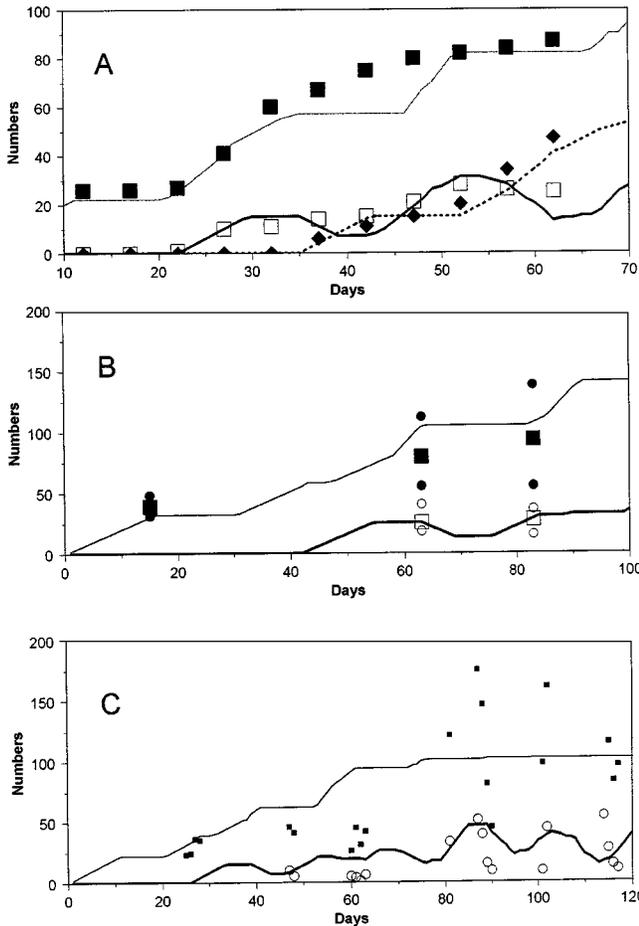
Fig. 8A–C Comparison of natural data (*symbols*) with the predictions of the models (*lines*). Parameters for models as in Table 1 with the indicated exceptions that are based on the given study. Nest size and adult number are cumulative (*thin and broken lines* or *filled symbols*), number of pupae is instantaneous (*thick lines* and *empty symbols*). **A** Model parameter and data are based on the average values of five colonies of Mead et al. (1994): $T_L = 12$; adults *broken line* and *diamond*, nest size *thin line* and *black square*, pupa *thick line* and *empty square*. **B** Model parameter and data are based on the average (*large symbols*) and range (*small circles*) of six colonies of Röseler and Röseler (1989): $T_E = 15$; $T_L = 27$; $T_P = 21$; nest size: *solid line* and *black square*, pupa *thick line* and *empty square*. **C** Individual data are based on the 21 field nest of Turillazzi (1980) collected between 2 May and 1 August

demonstrating regeneration of brood dynamics after early pertubation.

Discussion

Recent advances in modeling social insect biology (Franks et al. 1990; Camazine 1991; Theraulaz and Bonabeau 1995) and the application of principles of self-organization (Deneubourg and Goss 1989; Camazine et al. 1990; Karsai and Pénzes 1993) have stimulated interest in how far simple mechanisms may go toward producing complex phenomena. Jeanne
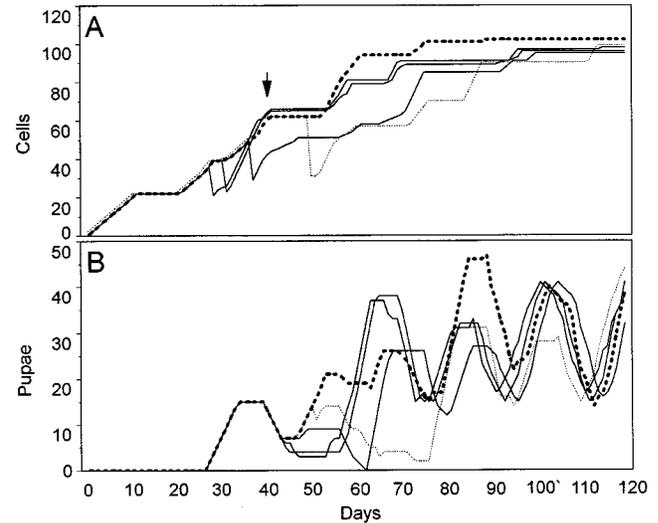

Fig. 9A, B Simulation of the perturbation experiment of Wenzel (1989, 1996) using parameters of Table 1 (undisturbed nest *thick dotted line*). Perturbation: half of the cells were removed from the periphery of the nests on the 27th, 30th, and 36th days (*solid lines*) and 50th day (*dotted line*), respectively. *Arrow* shows stage of comparison equivalent to that of Wenzel (1996) corresponding to first worker emergence. **A** Cell number, **B** Pupa number

(1972) doubted that extrinsic factors are able to govern the regular and delimited life cycles of wasps, suggesting that intrinsic factors are involved. We demonstrate here that colony-level properties can be deduced from the regulatory effect of simple feedback mechanisms. We show how these mechanisms are able to produce the main trends of colony growth of primitively eusocial paper wasps.

Elementary feedbacks

Oophagy transforms continous egg-laying into brood waves. It has a dramatic effect in colonies where the egg laying rate is low or the oophagy is intense. Oophagy represents not only simple destruction of eggs, but, through the stimulating effect of empty cells that result from egg removal, it increases the egg laying rate as well. Mead et al. (1994), experimenting on *P. dominulus*, argued that waves of hatching are dependent on available food and the rate of oophagy. Using the parameters of Mead et al. (1994) our model was able to generate hatching profiles similar to those measured in their laboratory colonies. The model predicted well the timing of minimum and maximum hatching, but sometimes predicted more or less larvae in a given period. This difference stems from simplifications and the deterministic property of the model. For example, in nature the development time of individuals may vary (Mead et al. 1994) resulting in smaller gaps between cohorts and more smooth transitions in natural colonies.

Analyzing the effect of the simple feedback mechanisms separately revealed that the stimulating effect of the pupae is very important in the intensive growth of the late pre-emergence and early post-emergence phase. The rate of oviposition rose gradually in the presence of pupae not only in the case of several wasp species (Jeanne 1972; Gervet 1964b; Morimoto 1954b), but also in some bees (*Bombus*) and several ant species (*Myrmica*) (Brian and Brian 1948). In case of wasp colonies the period when first pupae emerge commonly includes the emergence of first male eggs (Jeanne 1972; Deleurance 1948; West Eberhard 1969) or a signal to begin new comb in species that use several independent combs simultaneously (e.g., *P. canadensis*, Jeanne 1979). Qualitative and quantitative changes in primitively social wasps colonies may be regulated by stimuli coming from pupae rather than by workers.

The rate of colony growth in highly eusocial wasps is linked primarily to the workforce (Spradbery 1965), resulting in an exponential increase of colony size with worker number (Oster and Wilson 1978). In the case of *Polistes*, colony dynamics do not fit an exponential increase, which is why an unspecified logistic density-dependent term was included in the model of Oster and Wilson. Assuming the existence of similar elementary feedback mechanisms in both groups, the basic difference between these two growth functions may be in the egg-laying capacity of the two groups. While both types of queen lay 1 or 2 eggs per day initially, the vespine wasps may increase to over 100 per day (Martin 1991), whereas *Polistes* are rarely able to lay more than 10 eggs (Karsai 1996).

The approach of the present model does not deny that the work force may play a role in case of the primitively eusocial wasps as well (the queen may remain on the nest, can invest more energy in eggs, and oophagy decreases due to more foragers), but to invoke this parameter to obtain the main trends of natural patterns proves to be unnecessary. *Polistes dominulus* builds small societies where later workers (beyond six) have few contacts with higher-ranked individuals and the brood; they are the reserve workforce of the colony (Theraulaz et al. 1992). The dynamics would not change significantly if, due to this moderate worker effect, the maximum or actual number of eggs laid was somewhat higher. The current modeling framework, with different kinds of feedback mechanisms and appropriate life history parameters, may be used to describe the colony dynamics of other social insects too.

Global performance

Examining many species Richards and Richards (1951) commonly found 19–40% of the cells empty. They discussed the significance of this phenomenon, suggesting that cell construction is dependent on the egg-laying rate. Deleurance (1957) showed that in *P. dominulus* initiation of new cells is suspended or rare in the presence of empty cells and egg-laying is stimulated. The present study demonstrates that egg-laying rate may increase by 2–3 times due purely to the increased number of empty cells. This phenomenon increases the homogeneity of the brood (see below) and by keeping all cells filled with her own eggs the queen also prevents subordinates from ovipositing (Brian 1958).

In the pre-emergence stage vacated cells appear where eggs are removed for oophagy, causing a plateau in nest growth. The youngest eggs are removed preferentially (Mead et al. 1994) resulting in discontinuity in brood and empty cells for egg laying. Empty cells and small larvae do not stimulate cell initiation (Deleurance 1957; Yamane 1971; Karsai 1996; but see Yamane 1969, 1971), so this plateau may exist until empty cells are refilled after the enhanced oophagy period. Jeanne (1972) observed that this plateau was more distinct for single-foundress nests than for multiple-foundress nests in *Mischocyttarus drewseni*. The higher egglaying rate and greater number of foragers may decrease the effect of oophagy on colony development in multi-foundresses colonies, but the rate of nest growth nevertheless shows a significant decrease after the first eggs progress to larvae (Kojima 1989).

The modeled nests increased gradually approaching a "final mature value". Due to the oophagy, the nest size remained below the maximum value predicted by model II, although in the complete model egg-laying rate was occasionally strongly stimulated by the great number of empty cells. The smaller nest size can be ascribed to the fact that increased egg-laying is not able to counterbalance the considerable oophagy within the studied parameters.

The dynamics of modeled nests exhibited good agreement with the growth of natural nests with noteworthy exception of field data of Turillazzi (1980). Field nests tend to be smaller than modelled nests between 40 and 80 days, and larger at senescence. Ecological factors [e.g., changes in temperature and availability of prey (Mead et al. 1994)] may explain these differences. None of the studies made in controlled laboratory circumstances (Mead et al. 1994; Röseler and Röseler 1989) showed similar divergence.

Cessation of construction is generally recognized as the onset of final senescence, and is typically ascribed to several factors including decreasing fecundity of the ageing egglayer, the decreasing worker/brood ratio, or the emergence of future reproductives who do not work on their natal nest (Deleurance 1948; Reeve 1991; M.G. Keeping, unpublished work). These causal relations are logical and certainly play some role, but the degree to which they are responsible for the fundamental "collapse" of the colony is usually left to speculation or detailed on a case-study basis. The present model proposes that final nest size is an emergent property of the system determined by few simple feedback

mechanisms. In species that reuse cells, depending on the values of life-history parameters, an equilibrium occurs where the number of eggs laid needs no more cells than are provided by oophagy and eclosion of adults. This equlibrium may occur before and independently from ecological and other factors mentioned above, resulting in a static nest size of a flourishing colony.

Mapping the nest of *P. dominulus* regularly reveals large variance in nest size and demography of different stages (Turillazzi 1980; Röseler and Röseler 1989). This variance may stem from ecological factors and the egg laying capacity of the queen (Mead et al. 1994). However, the present model suggests that considerable fluctuations are an innate property of the system in that homogenous brood patches emerge with more or less synchronized development. The nutritional oophagy produces a developmental gap in the brood. In the periods when small larvae are widespread in the comb, empty cells emerge purely as a result of oophagy. Small larvae do not stimulate cell initiation (Karsai 1996), but the emptied cells (stimulating egg laying) are filled with eggs quickly. Eggs laid after the peak of small larvae (and oophagy) have a good chance of developing further forming a cohort of the brood. When this cohort reaches the pupa stage, the large number of pupae stimulate cell initiation and egg laying (Mead et al. 1994; Karsai 1996) forming another peak of egg-laying. Across many colonies small differences in development time and oophagy accumulate and are enchanced by positive feedback causing similar dynamics but with shorter and longer periods. Instantaneous and rare (e.g., weekly) census of many nests would show apparent variance in brood constitution where the fundamentally similar dynamic property of colony development is neglected.

Perturbation of colony growth

A strong test of any model is to disturb the simulated system and examine its performance relative to natural data that were not used to build the model. Wenzel reduced the size of natural nests of *Polistes annularis* to roughly one half by excising the marginal cells (generally containing eggs and small larvae) shortly after the appearance of the first pupa (Wenzel 1989). Regression analysis demonstrated that foundress groups ranging from two to eight females roughly doubled their construction rate, compensated for the loss by the time the first worker emerged such that the experimental nests were then about the same size as natural nests that had never been reduced (Wenzel 1994, 1996). These results were interpreted to represent a form of homeostasis more complex than a simple stepwise construction procedure. Wenzel discussed demographic distortions only far enough to reject the idea that the increase in construction rate was due to relaxation of demands of the brood upon foragers, but he did not consider the effect of eliminating eggs that were about to hatch.

The present model suggest that Wenzel's results are the consequence of the elementary feedback mechanisms of colony development. The experimental elimination of eggs with the peripheral cells must eventually translate into a temporary reduction in hatching rates in the following days. Reduced oophagy results in fewer emptied cells. New cells must be built to provide space for the eggs the queen will lay, and thus the construction rate must increase above that of a colony containing oophagic larvae. The stimulating effect of the increasing number of pupae (they are developing in the core of the comb in the preemergence stage) intensifies the egg laying rate resulting in enhanced building rate if empty cells are not present. Simulations reveal that perturbation in preemergence stage after the pupae reached their peak allows only delayed nest size regeneration.

Severe distortion of brood ratios and development patterns due to the experimental destruction of younger brood do not last throughout the colony's life. After about 90 days, the fluctuations in the number of pupae begin closely to approximate the dynamics of the unmanipulated model: all simulations fluctuate in a synchronized manner. Thus, although productivity may occur in waves, the subtle feedback loops used in this model are enough to produce waves that recover from severe perturbation.

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