Bulletin of Mathematical Biology (1998) **60**, 307–327

Distinguishing the Effects of Dilution and Restricted Movement on the Intra-nest Transmission of Honey-Bee Queen Pheromones

JAMES WATMOUGH*
Department of Biology,
Viginia Polytechnic Institute and State University,
Blackburg, Virginia 24061, U.S.A.
E-mail: `watmough@vt.edu`

MARK WINSTON
Department of Biology,
Simon Fraser University, Burnaby, B.C., V5A 1S6, U.S.A.

KEITH SLESSOR
Department of Chemistry,
Simon Fraser University, Burnaby, B.C., V5A 1S6, U.S.A.

This paper develops a simple model for the movement of a non-volatile pheromone through a honey-bee hive. The model is specifically developed for a pheromone produced by the queen which is thought to regulate colony swarming. Although the model begins as a system of partial integro-differential equations, it is in the end reduced to a system of linear, first-order partial differential equations for the average pheromone level per worker, the pheromone level of the hive substrate, and the pheromone level of the queen. Analysis of this system shows that both colony size and hive area have independent effects on the average pheromone levels of the workers, but that worker congestion can have an even stronger effect on the pheromone distribution. These results establish a relationship between colony size, hive area, worker crowding, and queen-pheromone transmission.

1. INTRODUCTION

Honey-bee queens produce a pheromone which suppresses queen rearing and can delay swarming (Winston *et al.*, 1991). It is also known that colony crowding leads to swarming, and that the addition of extra space to a hive can delay swarming, allowing for larger colonies and greater honey production. One hypothesis linking colony size, queen-pheromone production, and hive space is that colony congestion hinders the transmission of the pheromone and decreases the amount of pheromone received by each bee, and that this decreased pheromone level is

---

*To whom reprint requests should be addressed.

0092-8240/98/020307 + 21 $25.00/0 bu970006

one of the triggers for swarming (Winston and Taylor, 1980; Winston, 1987). Thus, increasing the number of workers in a colony leads to a *dilution* of pheromone (i.e. less pheromone per bee). In addition, increased colony size may restrict movement and lead to a poor distribution of pheromone. Increasing hive space relieves *congestion* and results in a more even distribution of pheromone. The purpose of this paper is to develop a model of pheromone transmission that can be used to examine this hypothesis.

Since the pheromone is non-volatile and is transmitted by contacts between workers, rather than by diffusion through the air, the following questions are of interest:

(1) How does worker congestion affect the transmission of the pheromone and how can the effects of congestion and dilution be compared?
(2) Is the indirect transmission through the wax more, or less important than direct transmission by contacts between workers?
(3) How long does the pheromone remain in the system after the queen is removed?

Answering the first question is the main purpose of this paper. The pheromone transmission hypothesis cannot be evaluated without some means of quantifying congestion and dilution. The second question concerns the possibility that the wax is a potential transfer mechanism, especially since the queen may leave large deposits of pheromone (footprints) on the wax. In addition, if the wax is a pheromone sink, then increasing hive space should increase the dilution effect. Thus, there must be a balance between dilution and congestion. The final question concerns the time constants of the system. It is known that the queen's pheromone signal must not persist if the queen is injured or killed. In such an event, the colony must proceed to rear a new queen. In experiments, the visible effects of removing the queen, such as worker agitation, occur approximately 30 min after the event (Winston *et al.*, 1991).

The model consists of a system of partial integro-differential equations (PIDEs) governing the density of pheromone on the wax and the density of workers as a function of pheromone level and position in the hive. The model is studied by taking moments of the worker density with respect to pheromone levels. Due to the nature of the exchange of pheromone between individuals, the equations for the evolution of the first two moments form a closed system of linear partial differential equations (PDEs). Thus, I determine the average pheromone level of the workers as a function of position and estimate the deviations from this average level. In a related paper, I developed a general model for pheromone transmission and studied it using numerical simulations (Watmough, 1997). Although the current model is based on my previous model, it is simplified enough to allow some analysis.

Using the model, I predict that a reduced motility of the bees will lead to a spatially uneven distribution of the pheromone. It is therefore plausible that colony congestion constricts worker movements and thus hinders the transmission

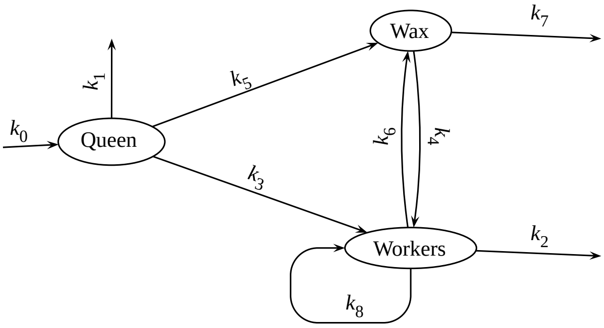

Figure 1. The pathways for the pheromone transmission were determined by Naumann *et al.* (1991)in a series of experiments. The pheromone is produced by the queen and transmitted to the workers and the wax. Pheromone is also exchanged between workers and between the workers and the wax. Pheromone is removed from the system by absorption through the bees' cuticle and by absorption into the wax.

of the queen pheromone. The analysis also reveals that the wax does not play a significant role in the pheromone transmission. Although large amounts of pheromone can be found on the wax, only a small fraction is picked up by the workers. Finally, the decay rate of the pheromone in the entire system is consistent with the time lag seen between the removal of the queen and the onset of worker agitation.

2. THE GENERAL MODEL

The general model upon which the present model is based consists of a system of $(N+1)$ pairs of equations for the evolution of the pheromone level and position of N individual bees and a single queen coupled with a single differential equation for the evolution of the pheromone level in the wax as a function of time and position. This model is discussed in detail by Watmough (1997). In this section I briefly summarize the model and explain the key features.

The flow of the pheromone though a honey-bee colony is summarized in Fig. 1. The parameters $k_0 \dots k_8$ are first-order rate constants for the transmission along each branch. Pheromone is produced by the queen (k_0) and transmitted, by contact, to the workers (k_3) and the wax (k_5). Pheromone is also transmitted between the workers and the wax (k_4, k_6) and exchanged between workers (k_8). Finally, pheromone is absorbed into the wax (k_7) and through the cuticle of the queen (k_1) and workers (k_2).

The equations derived by Watmough (1997) for the pheromone level of the bees and the wax are

$$\frac{dp}{dt} = -(k_2 + k_6)p + k_4 A_b w(x_i, t) + \sum_{j=1}^{N} \kappa(p_i, p_j)\delta_e(x_i - x_j)$$
$$+\kappa(p_i, Q)\delta_e(x_i - x_j), \qquad (1)$$

$$\frac{\partial w}{\partial t} = -k_7 w \sum_{i=1}^{N} \left(k_6 \frac{p_i}{A_b} - k_4 w \right) \delta_b(x - x_i) + k_5 \frac{Q}{A_q} \delta_q(x - x_q), \tag{2}$$

$$\frac{dQ}{dt} = k_0 - (k_1 + k_5)Q + \sum_{i=1}^{N} \kappa(Q, p_i)\delta_e(x_i - x_q), \tag{3}$$

where $w(x, t)$ is the level of pheromone per unit area on the wax substrate at (x, t), $x_q(t)$ is the position of the queen at time t, $Q(t)$ is the pheromone level of the queen at time t, $x_i(t)$ is the position of bee i at time t, and $p_i(t)$ pheromone level of bee i at time t.

The hive is represented as a square with sides of length R and is designated by $\Omega = (0, R) \times (0, R)$. Typical hives are composed of several parallel frames and have total areas (R^2) in the range of 8000–32 000 cm^2. The positions x, x_i, and x_q are vectors in Ω and the pheromone levels p_i, Q, and w are non-negative real numbers. (The index i runs from 1 to N.) Movement is modelled by a simple random walk with zero mean and a variance of σ^2. This variance results from steps of roughly 6 cm each minute and is estimated to be 0.6 cm^2 s^{-1} within one order of magnitude (Watmough, 1996, 1997). The lengths b, q, and e are the sizes of workers, queen, and the distance over which bees will interact, respectively. The corresponding areas A_b, A_q, and A_e are simply circles of the appropriate radius. The areas of interaction are determined by the neighborhood function

$$\delta_r(x - y) = \begin{cases} 1 & \text{if } |x - y| < r, \\ 0 & \text{otherwise.} \end{cases} \tag{4}$$

The function $\kappa(p_i, p_j)$ is the net rate of pheromone transferred between worker i and worker j. This function depends not only on the pheromone levels of the two workers, but also on their current behaviour. In the study of the general model Watmough (1997) simulated this function using a random-number generator to model the switching between activities.

3. THE DENSITY MODEL

The goal of this research is to develop a simple model for pheromone transmission which, unlike the general model outlined in the previous section, can be studied analytically. The density model shifts the focus from tracking the position and pheromone level of each bee to tracking the number of bees at each position and pheromone level. Let $u(x, p, t)$ be the probability density of workers as a function of pheromone level p and position x at time t. Note that, since $u(x, p, t)$ is a density,

$$\int_0^\infty \int_\Omega u(x, p, t)\, dx\, dp = 1. \tag{5}$$

Thus, integrating $Nu(x, p, t)$ over all pheromone levels yields the number of workers per unit area of the hive at position x, and integrating $Npu(x, p, t)$ over all pheromone levels yields the total amount of pheromone per unit area of the hive on all workers at position x.

The equations for the evolution of the pheromone levels and positions of the workers can be approximated by a single partial integro-differential for the evolution of the density $u(x, p, t)$. Similarly, the summations appearing in the remaining two equations can be approximated by integrals as described in the previous paragraph. The equations contain a non-linear integral term that makes analysis difficult. As a simplification the moments of the density $u(x, p, t)$ with respect to the pheromone level of the workers are examined. The equations for these moments can be reduced to a pair of linear ordinary differential equations for the evolution of the expected pheromone levels of the wax and the workers as a function of the position. The solutions of these equations clarify the effect of congestion on the transmission of the pheromone.

3.1. ***Development of the density model.*** The worker–worker interactions can be greatly simplified by the assumptions that pheromone is conserved during the interactions, and that the exchange proceeds at the same rate for all encounters. Thus, the amount of pheromone transferred will depend only on the pheromone levels of the bees and the duration of the encounter. For the case of the queen mandibular-gland pheromone, which is the motivation for this model, the transmission between bees is known to proceed at two different rates. The bees either remove pheromone using only their antenna (antennating), or using their mouthparts (licking). The latter method transmits the pheromone at a far greater rate, but pheromone is known to be ingested during the exchange (Naumann *et al.*, 1991). Hence, both of these assumptions are invalidated. However, since licking behaviour has only been observed during queen–worker encounters, and not during worker–worker encounters (Seeley, 1979), it will be assumed that all exchanges between workers are antennations.

Under this assumption, the transmission rates $\kappa(p_i, p_j)$ can be set to $k_8 p_j$ or $-k_8 p_i$ if the bees are in contact, and zero otherwise. By defining $P_a(p, q)$ to be the probability that a bee of pheromone level q is antennating a bee of pheromone level p, the (deterministic) function can be introduced

$$K(p, q) = -pP_a(p, q) + qP_a(q, p), \tag{6}$$

such that $\kappa(p_i, p_j) = k_8 K(p_i, p_j)$. That is, $k_8 K(p, q)$ is the expected rate of pheromone transfer (units of pheromone per unit time) between bees of pheromone level p and q.

The workers interacting with the queen are both lickers and antennators. The ratio of lickers to antennators in the queen's retinue depends on the activity of the queen, but is usually near 1:9 (Seeley, 1979). If we assume this ratio to be constant, then the two rates for licking and antennating can be combined into a single-rate constant representing the rate of pheromone removal from the queen per worker in her retinue, k_3. This constant has been determined experimentally (Naumann *et al.*, 1991).

The rate of pheromone removal from the queen by the workers can now be approximated as follows:

$$\sum_{i=1}^{N} \kappa(Q, p_i)\delta_e(x_i - x_q) = -(k_3 Q) \times \begin{pmatrix} \text{number of bees in the} \\ \text{neighborhood of the queen,} \end{pmatrix} \tag{7}$$

$$= -(k_3 Q) \times \begin{pmatrix} \text{area of} \\ \text{neighborhood} \end{pmatrix} \times \begin{pmatrix} \text{bees per} \\ \text{unit area} \\ \text{near the queen,} \end{pmatrix} \tag{8}$$

$$\approx -k_3 Q A_e N \int_0^\infty u(x_i, p, t)\, dp. \tag{9}$$

Using this approximation, the level of pheromone on the queen evolves as follows:

$$\frac{d}{dt}Q(t) = k_0 - \left(k_1 + k_5 + N k_3 A_q \int_0^\infty u(x_q, p, t)\, dp\right) Q(t). \tag{10}$$

To develop an evolution equation for the density function $u(x, p, t)$ we use the above assumptions to approximate the 'flux' of the workers through pheromone levels [equation (1)] given a pheromone level p and a position x.

$$\frac{\partial}{\partial t}u(x, p, t) = \frac{\sigma^2}{2}\Delta u(x, p, t) - \frac{\partial}{\partial p}(J_p u(x, p, t)), \tag{11}$$

where

$$J_p = -(k_2 + k_6)p + k_4 A_b w(x, t) + N A_e k_8 \boldsymbol{K} u + k_3(1 - I) A_q Q(t)\delta(x - x_q), \tag{12}$$

and Δ is the Laplacian in two spatial dimensions (i.e. the domain Ω). A fraction I of the pheromone is ingested during transmission from the queen. Note that the following shorthand notation for the integral operator has been used:

$$\boldsymbol{K}u = \int_0^\infty K(p, q) u(x, q, t)\, dq. \tag{13}$$

This equation can also be derived from a Boltzman-like formulation. For example, Jäger and Segel (1992) obtain a similar equation in their model of dominance in bumble bees. This similarity is not surprising since dominance can conceivably be linked to pheromone transmission.

To compute the rate of change of the pheromone level of the wax use equation (2), replacing the summations by integrations over pheromone levels, to determine the total number of bees and the total amount of pheromone on the bees as a function of position. Thus,

$$\frac{\partial}{\partial t} w(x,t) = -k_7 w + N \int_0^\infty (k_6 p - k_4 A_b w(x,t)) u(x,p,t)\, dp + k_5 Q(t) \delta(x - x_q). \tag{14}$$

In summary, equations (10), (11) and (14) represent the evolution of the expected pheromone levels of the queen, the workers and the wax respectively. I have approximated the rate of pheromone exchange between workers based on the distribution of worker pheromone levels at each point. This simplification results in a continuous pheromone transfer between workers and does not properly represent the fact that the workers move a finite distance between contacts. Yet, the results of the analysis are supported in part by the simulations of the general model, so this simplification does not appear to detract significantly from the usefulness of the model.

3.2. *Non-dimensionalization of the system.* Equations (10), (11), and (14) can be non-dimensionalized using the following rescalings:

independent variables	dependent variables
$\bar{x} = R$	$\bar{u} = \frac{(k_1+k_5)(k_2+k_6)}{k_3(1-I)k_0 A_q}$
$\bar{t} = \frac{1}{k_2+k_6}$	$\bar{Q} = \frac{k_0}{k_1+k_5}$
$\bar{p} = \frac{k_3(1-I)k_0 A_q}{(k_1+k_5)(k_2+k_6)R^2}$	$\bar{w} = \frac{k_6 N k_3(1-I)k_0 A_q}{k_7(k_1+k_5)(k_2+k_6)R^4}$

For example, $t^* = t/\bar{t}$ is the time in dimensionless units. For convenience and readability new notation is not introduced for the dimensionless variables. The reader may assume that all variables and functions are dimensionless from this point forward, unless clearly noted otherwise.

The spatial scale $\bar{x}$ simply reflects the size of the domain. Recall that x is a position in two dimensions, and therefore has two components. Both components are scaled by $\bar{x}$. The temporal scale is related to the rate of decay of pheromone on the workers. Recall that k_2 is the rate of pheromone absorption into the workers' cuticle, and that k_6 is the rate of pheromone transmission from the workers to the wax. Hence, $\bar{t} \ln 2 \approx 14$ min is the half-life of the pheromone on an isolated worker. The pheromone level of the queen is rescaled by the ratio of the production rate k_0 to the rate of pheromone removal from the queen by absorption and transmission to the wax $(k_1 + k_5)$. Therefore, $\bar{Q}$ is the steady-state pheromone level of a solitary queen isolated on a section of wax. The rescaling of the pheromone level of the workers is the product of $\bar{Q}$, the rate of pheromone removal from the queen to the workers (k_3), and the rate of removal of pheromone from the workers $(k_2 + k_6)$. Thus $\bar{p}$ is the expected steady-state pheromone level of an isolated worker in contact with a pheromone source of pheromone level $\bar{Q}$. This is an estimate of the pheromone level of a single worker. Finally, the rescaling of the pheromone level of the wax is the product of $\bar{p}$ and the ratio of k_6 (the rate of transmission of pheromone from worker to wax) to k_7 (the rate of absorption of pheromone into the wax). Therefore, $\bar{w}$ is the steady-state pheromone level of the wax in a colony whose workers all have a pheromone level of $\bar{p}$. These rescalings reflect the transmission of pheromone from the queen to the workers and finally to the wax. The scaling of the density $\bar{u}$ preserves the value of the integral of equation (5).

These rescalings lead to the following dimensionless system of PIDEs:

$$\frac{\partial u}{\partial t} = \mu \Delta u - \frac{\partial}{\partial p}\left(-pu + \eta w u + \epsilon u \boldsymbol{K} u + Q\delta(x - x_q)u\right), \tag{15}$$

$$\tau_w \frac{\partial w}{\partial t} = -w - \beta w \int_0^\infty u\, dp + \int_0^\infty pu\, dp + \gamma Q \delta(x - x_q), \tag{16}$$

$$\tau_q \frac{dQ}{dt} = 1 - Q - \alpha Q \int_0^\infty u(x_q, p, t)\, dp. \tag{17}$$

The dimensionless parameters are

$$\begin{aligned} \mu &= \frac{\sigma^2}{2R^2(k_2+k_6)}, & \eta &= \frac{k_6}{k_2+k_6}\beta, & \epsilon &= \frac{k_8 A_e N}{R^2(k_2+k_6)}, \\ \tau_w &= \frac{k_2+k_6}{k_7}, & \beta &= \frac{k_4 N A_b}{k_7 R^2}, & \gamma &= \frac{k_5 R^2 (k_2+k_6)}{k_3(1-I)k_6 N A_q}, \\ \tau_q &= \frac{k_2+k_6}{k_1+k_5}, & \alpha &= \frac{k_3 A_q N}{R^2(k_1+k_5)}. \end{aligned} \tag{18}$$

Using the values for the dimensioned parameters computed for the general model (Watmough, 1997) gives the following values for the dimensionless parameters:

$$\begin{aligned} \mu &= 0.02, & \eta &= 0.3, & \epsilon &= 0.2, \\ \tau_w &= 0.8, & \beta &= 2, & \gamma &= 0.8, \\ \tau_q &= 0.9, & \alpha &= 0.8. \end{aligned} \tag{19}$$

Note that the experimental error in these values is of the same order as the values themselves. Hence, they are order of magnitude estimates only, and have been rounded to the most significant digit.

The motility, μ, is a measure of the scale of worker movements relative to the dimensions of the hive and the decay rate of the pheromone on the workers. The half-lives of the pheromone on the wax and the queen in relation to $\bar{t}$ are given by τ_w and τ_q respectively. The transmission of pheromone from the wax to the workers is represented by the two parameters η and β, which measure the transmission rates from wax to workers relative to the scalings of the workers and the wax respectively. The fact that η is small suggests that the pheromone transmission from the wax to the workers has little impact on the pheromone level of each worker. The rate of increase of the level of pheromone on the wax due to deposition by the queen is given by γ. The final two parameters, ϵ and α, represent the rate of pheromone transmission between workers and from the queen to the workers respectively. The parameters measure the transmission rates per worker (k_3 and k_8) relative to the rates of absorption and deposition ($k_1 + k_5$ and $k_2 + k_6$) and to the number of workers per unit area. Therefore, these parameters increase as colony congestion increases.

3.3. *Analysis.*

3.3.1. *The moment equations.* The fact that the integral term in the system is quadratic in u makes analysis difficult. However, many properties of the system can be obtained from a study of the moments of the density $u(x, p, t)$ over p. These moments are defined as

$$n(x,t) = \int_0^\infty u(p,x,t)\,dp, \tag{20}$$

$$m(x,t) = \int_0^\infty pu(p,x,t)\,dp, \tag{21}$$

Evolution equations for these moments are derived by integrating equation (15) over all pheromone levels. This requires several integrations by parts, which are simplified by the following two assumptions:

Assumption A1. $\lim_{p\to 0} u(x,p,t) = 0,$

Assumption A2. $\lim_{p\to\infty} p^k u(x,p,t) = 0, \qquad k = 0, 1, 2.$

These assumptions ensure that the boundary terms arising from integration by parts vanish. Since there should be no bees with pheromone levels larger than that of the queen, Assumption A2 is reasonable. The reasoning behind Assumption A1 is that, although the pheromone levels of the workers may be arbitrarily small, there should be no workers with zero pheromone levels. This will be violated if some workers initially have pheromone levels of zero.

Evolution equations for the moments are obtained by multiplying equation (15) through by p^k ($k \in \{0, 1, 2\}$) and integrating once. This leads to the following system of evolution equations for the mean worker pheromone level, the wax pheromone level, and the queen pheromone level:

$$n_t = \mu\Delta n, \tag{22}$$

$$m_t = \mu\Delta m - m + \eta w n + Qn\delta(x - x_q), \tag{23}$$

$$\tau_w w_t = -w - \beta w n + m + \gamma Q\delta(x - x_q), \tag{24}$$

$$\tau_q \frac{dQ}{dt} = 1 - (1+\alpha)Qn(x_q, t). \tag{25}$$

Zero-flux boundary conditions are assumed for $n(x, t)$, $m(x, t)$, and $v(x, t)$ at the edge of the domain.

The analysis of these equations proceeds as follows. First, equations (22) and (25) do not involve m, or w and can be solved separately. Secondly, Equations (23) and (24) do not depend on higher moments of the density. These higher moments would arise through the integral of $\boldsymbol{K}u$ that would appear in equation (23). However, this integral equates to zero under the assumption that there is no ingestion during pheromone exchange between workers. Third, I present a more realistic scaling of w is presented such that equation (23) can be completely decoupled from Equation (24) by neglecting terms of order $\eta/(1+\beta)$, which is a small parameter grouping. This leaves equation (23) as a linear diffusion equation with a randomly moving source. The speed of the source is compared with the motility of the bees to determine the effect of reducing bee motility on the distribution of the pheromone.

3.3.2. *The linear system.* Equation (22) implies that the worker density evolves towards the globally stable steady state solution $n(x, t) = 1$. (Recall that n must satisfy the condition

$$\int_{\Omega} n(x, t)\, dx = 1$$

where Ω is the non-dimensional hive area, which is the unit square.)

Since $n(x, t)$ is a constant, equation (25) is decoupled from the rest of the system. This implies that the pheromone level of the queen also approaches a steady state of

$$Q_s = \frac{1}{1+\alpha}. \tag{26}$$

The above observations imply that, after a time, the spatial distribution of workers becomes homogeneous and the pheromone level of the queen approaches Q_s. With these simplifications, equations (23) and (24) become

$$m_t = \mu \Delta m - m + \eta w + Q_s \delta(x - x_q), \tag{27}$$

$$\tau_w w_t = -w - \beta w + m + \gamma Q_s \delta(x - x_q). \tag{28}$$

Since equations (27) and (28) are linear, their solutions can be written as a series in the eigenfunctions of the Laplacian with zero-flux boundary conditions. Thus,

$$\begin{pmatrix} m(x, t) \\ w(x, t) \end{pmatrix} = \sum_{j,k=0}^{\infty} \begin{pmatrix} a_{jk}(t) \\ b_{jk}(t) \end{pmatrix} \phi_{jk}(x), \tag{29}$$

where the normalized eigenfunctions for the Laplacian on the unit square with zero-flux boundary conditions are

$$\phi_{00} = 1, \qquad \phi_{jk}(x) = 4\cos(j\pi \mathrm{x})\cos(k\pi \mathrm{y}), \qquad j, k = 1, 2, 3, \ldots$$

and $x = (\mathrm{x,y})$.

Substituting this expansion into equation (27) and equation (28), the coefficients of the series satisfy the relations

$$\begin{pmatrix} a'_{jk} \\ b'_{jk} \end{pmatrix} = \begin{pmatrix} -1 - L_{jk} & \eta \\ 1/\tau_w & -(1+\beta)/\tau_w \end{pmatrix} \begin{pmatrix} a_{jk} \\ b_{jk} \end{pmatrix} + \begin{pmatrix} 1 \\ \gamma/\tau_w \end{pmatrix} Q_s \phi_{jk}(x_q), \quad (30)$$

where

$$L_{jk} = (j^2 + k^2)\pi^2 \mu.$$

The eigenvalues of this system are

$$\lambda^{\pm}_{jk} = -\frac{1}{2}\left(1 + L_{jk} + \frac{1+\beta}{\tau_w}\right) \pm \frac{1}{2}\sqrt{\left(1 + L_{jk} - \frac{1+\beta}{\tau_w}\right)^2 + 4\frac{\eta}{\tau_w}}, \quad (31)$$

and the eigenvectors are

$$\xi^{\pm}_{jk} = \begin{pmatrix} \tau_w \lambda^{\pm}_{jk} + 1 + \beta \\ 1 \end{pmatrix}. \quad (32)$$

Note that this yields a pair of eigenvalues for each eigenfunction ϕ_{jk}. Further, these eigenvalues are all negative, real numbers, since, by definition, $\eta < \beta$.

The eigenvalues are shown in Fig. 2 as functions of the mode L_{jk} for $\tau_w = 0.8$, $\eta = 0.25$, and $\beta = 2.6$. For all parameter values the two curves asymptote to the lines $\lambda = -(1+\beta)/\tau_w$ and $\lambda = -(1 + L_{jk})$. For eigenvalues near the horizontal asymptote, the corresponding eigenvector approaches

$$\xi_{\mathrm{w}} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad (33)$$

which corresponds to the pheromone level of the wax, w. In contrast, as the lower eigenvalue approaches the oblique asymptote, such that

$$\lim_{L_{ij} \to \infty} \xi^{-}_{ij} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}. \quad (34)$$

This vector corresponds to the mean worker pheromone level, m. Together, these limits state that the higher modes of the pattern die out quicker in the worker pheromone distribution than in the wax pheromone distribution. Thus, upon removal of the queen from the system, any pattern to the pheromone distribution of the workers will quickly disappear, leaving all workers with equal pheromone levels. In contrast, a pattern in the wax pheromone distribution will remain longer, as all modes of the pattern decay at nearly the same rate.

The overall time scale for pheromone decay from the system is given by the largest eigenvalue which is $\lambda^{+}_{00} \lessapprox -1$ (the intercept of the top curve in Fig. 2 with the vertical axis). This implies that upon removal of the queen, the slowest mode to decay is ϕ_{00}. Note that the time scaling is $\bar{t} = 1/(k_2 + k_6)$. Hence, λ^{+}_{00} corresponds to pheromone absorption into the worker cuticle.

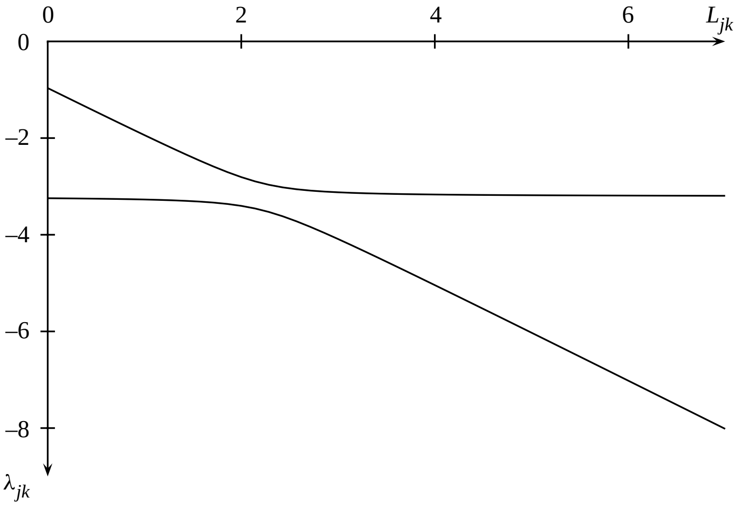

Figure 2. The above two curves show the eigenvalues λ^{+}_{jk} and λ^{-}_{jk} as functions of L_{jk}. Both curves have a horizontal asymptote $\lambda = -(1+\beta)/\tau_w$ and an oblique of $\lambda^{-} = -(1+L_{jk})$. The parameter values used to produced the figures were $\tau_w = 0.8$, $\eta = 0.25$, and $\beta = 2.6$.

3.3.3. *Further simplifications* I now examine three cases. First, it is shown that, as a first approximation, equation (27) can be decoupled from Equation (28). The resulting equation is examined, with a moving queen, using numerical simulations. Secondly, to isolate the effect of worker movements from the effect of queen movements, the steady-state solutions are examined for the case where the queen's position is fixed at the centre of the hive. Finally, in order to estimate the average pheromone level per worker over the entire colony, a case is studied in which both the queen and the workers have unrestricted longer-range movements. This assumes that the bees move from one region of the hive to another on a faster timescale than the pheromone decay. Although the bees and the queen do not move this fast under natural colony conditions, it is physically possible.

CASE I: MOVING QUEEN. Substituting

$$\tilde{w} = \frac{1+\beta}{1+\alpha} w \tag{35}$$

$$\tilde{m} = \frac{1}{1+\alpha} m \tag{36}$$

in equation (27) yields

$$\tilde{m}_t = \mu \Delta \tilde{m} - \tilde{m} + \frac{\eta}{1+\beta} \tilde{w} + \delta(x - x_q). \tag{37}$$

Since $\eta << 1 + \beta$, we can approximate this equality by

$$\tilde{m}_t = \mu \Delta \tilde{m} - \tilde{m} + \delta(x - x_q). \tag{38}$$

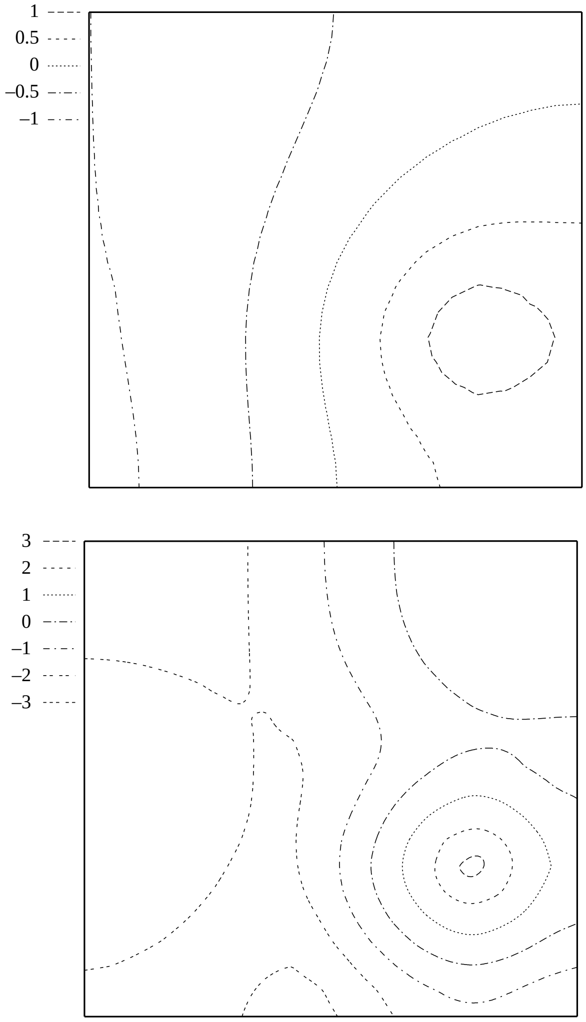

Figure 3. The two plots show solutions to equation (38) for $\mu = 0.1$ (top) and $\mu = 0.01$ (bottom). The domain is the unit square. The contours show the mean worker-pheromone level using a logarithmic scale. Thus, the zero contour represents workers with pheromone levels equal to the colony average, and the next contour higher represents workers with pheromone levels a factor of 10 above the colony average. With the lower motility ($\mu = 0.01$), the previous positions of the queen can be seen in the contours, and the pheromone levels vary by six orders of magnitude over the hive. In contrast, the higher motility leads to a more uniform distribution of the pheromone. The movements of the queen are identical in the two cases.

Figure 3 shows the results of numerical simulations of equation (38) for two values of μ. Recall that, in the dimensionless coordinates, the domain is a unit square, with zero-flux boundary conditions. The position of the queen (x_q) is a random variable whose values are uniformly distributed over the unit square and change at 10 min intervals. This reproduces the general features of the queen's movement. Both simulations use the same sequence for x_q. The graph uses a logarithmic scale for the pheromone level; thus, a value of zero indicates a pheromone level of $m = 1/(1+\alpha)$. For smaller values of μ, the pheromone level decays by several orders of magnitude as we move away from the queen. Workers in the queen's retinue have pheromone levels of several hundred picograms, while those far away from regions where the queen has recently visited have pheromone levels well below one picogram.

CASE II: FIXED QUEEN. As a further restriction, I assume that the queen is situated in the center of the hive. This situation can be tested experimentally by placing the queen in a wire cage, thus fixing her position, but allowing the workers to contact her. Workers from various positions within the hive can then be removed and their pheromone levels analysed. These pheromone levels can be compared with the solution described below as a test of the model. Unfortunately, the amount of pheromone typically found on the workers is below the minimum level detectable using current techniques. Once these techniques are refined, the model can be rigorously tested.

Since, the spatial scale of equation (38) is of the order $\sqrt{\mu}$, and μ is thought to be small, the boundaries of the hive are effectively far from the queen, and the general characteristic of the solution can be found by examining the solution on an infinite domain. This solution is

$$\tilde{m}(x,t) = \int_0^t \frac{e^{-\xi - |x-x_q|^2/(4\mu\xi)}}{2\pi\mu\xi}\, d\xi. \tag{39}$$

Thus, the steady-state solution to equation (27) can be approximated by

$$\lim_{t\to\infty} \tilde{m}(x,t) = \int_0^\infty \frac{e^{-\xi - |x-x_q|^2/(4\mu\xi)}}{2\pi\mu\xi}\, d\xi + \mathcal{O}(\eta/\beta), \tag{40}$$

which is the modified Bessel function $K_o(x/\sqrt{\mu})/\pi\mu$ (Gradshtyen and Ryzhik, 1980). This solution is shown by the graph in Fig. 4 for $\mu = 0.1$ and $\mu = 0.01$. As shown in Case III the scaling of $\tilde{m}$ is such that a value of unity corresponds to the colony average pheromone level.

If the position of the queen, x_q, is constant, then the steady-state solutions of equation (28) is

$$w_s = \lim_{t\to\infty} w(x,t) = \frac{m_s + \gamma Q_s \delta(x - x_q)}{1+\beta}. \tag{41}$$

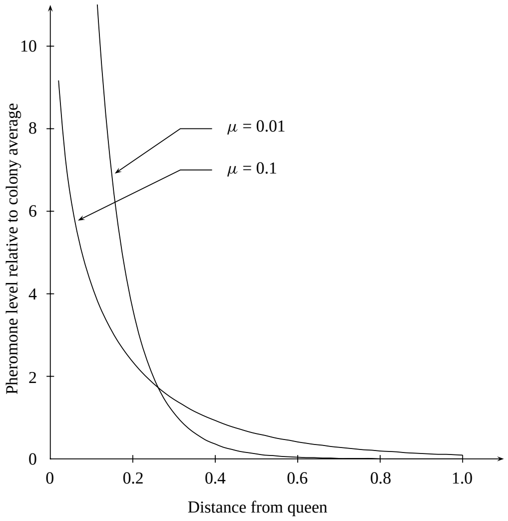

Figure 4. These two plots show equation (39) for $\mu = 0.1$ and $\mu = 0.01$. At lower values of the motility, μ, worker pheromone levels drop more rapidly with distance from the queen.

Note that the pheromone distributions of the wax and the workers are identical save for a factor of $1+\beta$, indicating that the pheromone level in the wax is about 20% of that of the workers, and the large amount of pheromone directly under the queen.

CASE III: AVERAGE PEROMONE LEVELS. The queen's movement consists of periods of roughly stationary behaviour while laying eggs and grooming, punctuated by long-range movements (Seeley, 1979). Under the simplifying assumption that this movement makes the queen equally accessible to all bees, regardless of position, we can integrate equation (40) [and equation (41)] over space and compute the steady-state average pheromone levels. These are

$$Q_s = \frac{1}{1+\alpha},$$
$$m_s = Q_s + \mathcal{O}(\eta/\beta),$$
$$w_s = \frac{Q_s(1+\gamma)}{1+\beta}.$$

The dimensional values are

$$\begin{aligned} Q_s &= \frac{\bar{Q}}{1+\alpha} \approx 560 \text{ ng}, \\ m_s &\approx \frac{\bar{p}}{1+\alpha} \approx 26 \text{ pg}, \end{aligned} \tag{42}$$

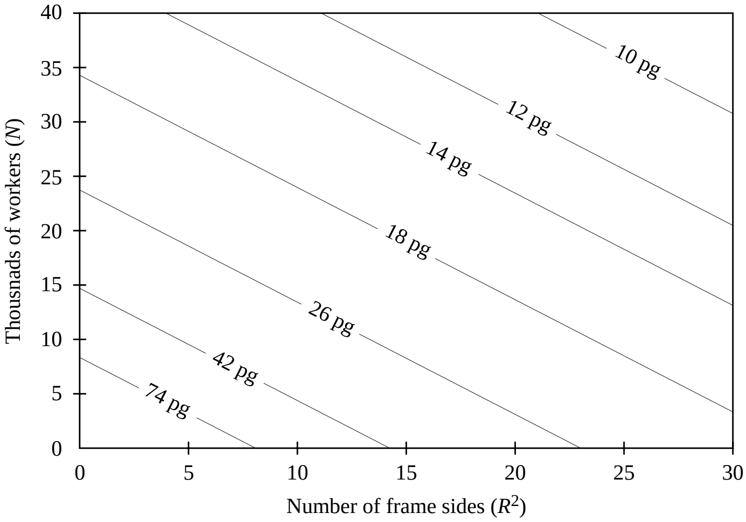

Figure 5. This contour plot of equation (44) shows the average amount of pheromone on a worker as a function of total hive area and number of workers. The hive area is shown as the number of 34 cm × 20 cm frame sides.

$$w_s \approx \frac{\bar{w}(1+\gamma)}{(1+\beta)(1+\alpha)} \approx 2.5 \text{ pg cm}^{-2}.$$

It is worthwhile to note that Q_s and m_s can be expressed as

$$Q_s = \frac{k_0}{k_1 + k_5 + k_3 A_q N/R^2}, \tag{43}$$

$$m_s = \frac{k_0(1-I)/(k_2+k_6)}{R^2(k_1+k_5)/(k_3 A_q) + N}. \tag{44}$$

Thus, Q_s depends on the density of workers, whereas m_s depends on the absolute colony size. The size of the colony is the sum of the number of workers and the dimensionless hive area. A contour plot of m_s versus the area of the hive (measured as the number of frame sides) and the number of workers is shown in Fig. 5.

4. SUMMARY OF PREDICTIONS

PREDICTION P1. *The level of pheromone on the queen is a decreasing function of colony congestion [N/R^2, equation (43)].*

The steady-state value of the level of pheromone on the queen, Q_s, is inversely proportional to the parameter α, and therefore decreases with increased colony congestion. Recall that α is proportional to the average worker density in the colony [see equation (18)]. Thus, the level of pheromone on the queen does not depend on the number of bees, but rather on the number of bees per unit area. Note that this dependence is of the form $1/(1+\alpha)$ [see equation (26)], and that for the 'typical' colony preparing to swarm, $\alpha = 0.8$ [see equation (19)]. Thus, as the number of workers doubles, raising α from 0.4 to 0.8 for example, there is only a 20% decrease in Q_s [see equation (26)]. The importance of this dependence is further decreased by the observation that the retinue response leads to crowding near the queen regardless of the average density of the colony. Hence, the average density of workers as seen by the queen is in all likelihood independent of the average density of the colony.

PREDICTION P2. *The mean pheromone level on the workers is a decreasing function of the number of bees [N, equation (44)].*

In contrast to the level of pheromone on the queen, the average level of pheromone on a worker, m_s, is not proportional to colony congestion, but rather inversely proportional to the *sum* of the area of the hive and the total number of workers. This result is not surprising since pheromone produced by the queen is divided between the wax comb and the workers. Hence, the amount on any given worker decreases with either an increased number of workers or an increased area of comb. The analysis leading to equation (44) shows how the pheromone is divided up between the *area* of wax and the *number* of workers. This effect is referred to as the dilution effect (Naumann *et al*., 1993). Note that the scale factor for the pheromone level, $\bar{p}$, does not depend on N. Hence, the dependence of the average worker pheromone level on changing colony size, N, will, again, be due to changes in the quantity $1/(1+\alpha)$. Thus, using the same calculations as in the previous paragraph, the doubling of workers in a 'typical' hive will result in a decrease in the mean worker pheromone level by 20%.

PREDICTION P3. *The worker pheromone levels also decrease with distance from the queen. This decrease is amplified by a reduced motility of the workers.*

The motility of the workers is significant in determining the distribution of pheromone through the colony, even if the movement of the queen is not hindered. Decreasing the motility increases the variation in worker pheromone levels with distance from the queen. This is consistent with the hypothesis that increased congestion of the colony restricts the movement of the workers and leads to an imbalance in the distribution of pheromone. Restricted movement is represented in the model by a smaller value for the motility μ. Decreasing μ yields a slower decay for the higher spatial modes (smaller magnitude of the eigenvalues), which results in a persistent spatial pattern to the pheromone distribution. The converse argument states that increasing the motility causes a faster decay of the higher spatial modes, which implies a faster spread of pheromone through the system and a more uniform distribution. In contrast to the 20% changes in worker pheromone levels that arise from the dilution effect discussed in the previous two paragraphs, changes in worker motility can lead to order of magnitude changes in pheromone levels (see Fig. 3).

PREDICTION P4. *Upon removal of the queen, the disappearance of pheromone from the workers is predominantly due to absorption through the cuticle.*

The largest eigenvalue of the system has a (dimensional) value slightly less than $-(k_2 + k_6)$ (the sum of absorption through the cuticle and transfer to the wax), which corresponds to a half-life of approximately 14 min. Thus, upon removal of the queen, the pheromone signal in the colony will decay at this rate, which is consistent with experiments.

PREDICTION P5. *The level of pheromone per square centimetre of the wax comb is comparable with the level of pheromone on the workers [equation (42)]. However, the rate of pheromone retrieval from the wax by the workers is much slower than the rate of pheromone removal from the workers.*

Although the pheromone is divided in nearly equal proportions between the workers and the wax, the results indicate that the rate at which pheromone is removed from the wax by the workers is much smaller than the rate at which pheromone is absorbed into the worker cuticle. This is indicated in the model by relation $\eta \ll 1 + \beta$, which implies that the rate of transfer of pheromone from the wax to the workers is very slow relative to the rate of pheromone removal from the workers. This suggests that normal pheromone levels in the wax will not present a significant signal to the workers. However, the pheromone level on tracks laid by the queen are significantly higher than the average, and the amount of pheromone acquired by workers moving over these queen tracks is similar to the amount removed from workers.

5. DISCUSSION

In this paper a model for the transmission of non-volatile pheromones through a honey-bee hive has been developed and analyzed. The model is based on a more detailed model and simulation, which were in turn based on the experiments of Naumann *et al.* (1991). We have used the model to examine the hypothesis that colony congestion can produce a significant reduction in the amount of queen pheromone detected by worker bees. This pheromone is known to suppress queen rearing and swarming behaviour. Hence, the results presented in this paper quantify the link between queen pheromone production, colony congestion, hive area and swarming.

The results of the model answer the three questions posed in the introduction. First, there is a definite distinction between the effects of colony size and colony crowding. Experimental evidence for this was obtained by Seeley and Fell (1981), who speculated that colony size was not significant in suppressing queen rearing. Their speculation is based on earlier results that congested, unpopulous colonies are likely to rear queens, yet populous, uncongested colonies are not (Seeley, 1979). This is consistent with the our model under the assumption that congestion restricts worker movements. As outlined in Prediction P2, increasing colony size does not dramatically decrease the mean pheromone levels of the workers. However, restricting worker movement by increasing colony crowding can lead to a dramatic imbalance in the distribution of pheromone among the workers.

The answer to the second question is that the pheromone in the wax of the hive frames does not play a significant role in the distribution of pheromone. As outlined in Prediction P5, the rate of removal of pheromone from the wax is quite slow. However, the wax does have a passive role in minimizing the effect of colony size on the pheromone distribution, since increasing the area of the wax will decrease α (see Prediction P2).

The answer to the final question is outlined in Prediction P4. In short, the time scale of pheromone removal from the colony is consistent with experimental observation of the time between queen removal from a colony and the onset of visible effects in worker behaviour. This time scale is determined from the rate of absorption of pheromone through the worker cuticle.

Experiments performed by Naumann *et al*. (1993) to determine the effect of colony congestion on pheromone transmission showed that the average pheromone levels on workers with detectable amounts of pheromone did not depend on colony size, but that the percentage of bees with detectable amounts of pheromone was lower in more populous colonies. They also noted that no spatial pattern to the worker pheromone distribution was observed (i.e. a spatially homogeneous distribution was observed) and concluded that worker motility was not important. Unfortunately, their experiments did not have a continuous source of pheromone (i.e. $k_0 = 0$), but rather a lure was coated with pheromone and placed in the hive. In this case, my model predicts that the bulk of the pheromone was removed from the lure during the first hour of the experiment. During this time, only one sample was taken. In order to see the spatial effects caused by congestion samples would have to be taken over a 15–30 min time frame rather than a 24 hr time frame. One interesting result of their experiments was that the pheromone was removed from the lure at a much slower rate than that determined from the earlier experiments of Naumann *et al.* (1991). In fact, the value suggested for k_3 was a full order of magnitude lower in the colony congestion experiments of Naumann *et al*. (1993) than in the laboratory experiments of Naumann *et al.* (1991). This would reduce the magnitude of α and hence further reduce the effect of colony size on the average pheromone level per worker.

In order to test the model properly, the experiments of Naumann *et al*. (1993) should be repeated with either more frequent sampling, or with a continuous pheromone source. Further, these experiments should be done in a simplified geometry where there is only a single frame. If these experiments verify the model, then it would be worth extending the model to more complicated geometries, specifically, hives composed of several square layers connected at the edges.

The analysis of the model performed in this paper did not determine the distribution of pheromone among the workers, but only determined the spatial distribution of the average worker pheromone level. A simulation of a more detailed version of this model has validated to some extent the implicit assumption that the worker pheromone levels are peaked around this average value. The development and results of this simulation are reported in a separate paper (Watmough, 1997).

ACKNOWLEDGEMENTS

JW would like to thank Leah Edelstein-Keshet for her advice and continuous support. The research reported in this paper was carried out as part of JW's PhD studies under the supervision of LEK at the Department of Mathematics and at the Institute of Applied Mathematics of the University of British Columbia. The research was made possible by a grant from the National Science and Engineering Research Council of Canada to LEK (grant number OGPIN 021).

REFERENCES

Gradshtyen, I. S. and I. M. Ryzhik (1980). *Table of Integrals, Series, and Products*, Academic Press, New York.

Jäger, E. and L. A. Segel (1992). On the ditribution of dominance in populations of social organisms. *SIAM J. Appl. Math.* **52**, 1442–1468.

Naumann, K., M. L. Winston, K. N. Slessor, G. D. Prestwich and F. X. Webster (1991). Production and transmission of honey bee queen (*Apis mellifera L*) mandibular gland pheromone. *Behav. Ecol. Sociobio.* **29**, 321.

Naumann, K., M. L. Winston, and K. N. Slessor (1993). Movement of honey bee (*Apis mellifera L*) queen mandibular gland pheromone in populous and unpopulous colonies. *J. Insect Behav.* **6**, 211.

Seeley, T. D. (1979). Queen substance dispersal by messenger workers in honeybee colonies. *Behav. Ecol. Sociobio.* **5**, 391.

Seeley, T. D. and R. D. Fell (1981). Queen substance production in the honeybee (*Apis mellifera*). *J. Kansas Entomol. Soc.* **54**, 192.

Watmough, J. (1996). PhD thesis, University of British Columbia, Canada.

Watmough, J. (1997). A general model of pheromone transmission within honey bee hives. *J. Theor. Bio.* **189**, 159–170.

Winston, M. L. (1987). *The Biology of the Honeybee*, Cambridge: Harvard University Press.

Winston, M. L. and O. R. Taylor (1980). Factors preceeding queen rearing in the Africanized honeybee (*Apis mellifera*). *Insectes Sociaux* **27**, 289.

Winston, M. L., H. A. Higo, S. J. Colley, T. Pankiw, and K. N. Slessor (1991). The role of queen mandibular pheromone and colony congestion in honey bee (*Apis mellifera L.*) reproductive swarming (Hymenoptera: Apidae). *J. Insect Behav.* **4**, 649.

Received 2 February 1997 and accepted 24 September 1997