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# The impact of clonal mixing on the evolution of social behaviour in aphids

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Reports of substantial clonal mixing measured in social aphid colonies seem, on the face of it, to rule out population structure as an explanation of this enigmatic insect's social behaviour. To clarify how selection operates in aphids, and to disentangle direct and indirect fitness components, we present a model of the life cycle of a typical colony-dwelling aphid. The model incorporates ecological factors and includes a trade-off between investing in social behaviour and investing in reproduction. Our focus on inclusive fitness contrasts with previous approaches that optimize colony output. Through deriving a variant of Hamilton's rule, we show that a simple relationship can be established between the patch-carrying capacity and immigration rates into patches. Our results indicate that the levels of clonal mixing reported are not inconsistent with social behaviour. We discuss our model in terms of the evolutionary origins of social behaviour in aphids.

**Keywords:** Hamilton's rule; kin structure; relatedness; adaptive dynamics; social insects

## 1. INTRODUCTION

The majority of aphids show little or no social behaviour. This is surprising given that they generally reproduce asexually and form colonies of closely related individuals (Hamilton 1987). Social behaviour is commonly found in the 10 per cent of aphid species that form communal nests in galls or hollow spaces (Blackman & Eastop 1994). These nests result from a collective effort by the colony that includes colony defence (Aoki 1977), house-keeping (Benton & Foster 1992) and gall repair (Aoki & Kurosu 1991). Such nesting behaviour may be beneficial to the colony, but it will decrease the reproductive potential of the individual. At the extreme, some species have effectively sterile soldier castes that have so far been identified in the Hormaphidinae and Pemphiginae subfamilies (Pike & Foster 2008).

Also surprising are the high levels of *clonal mixing* (mixing between parthenogenetically reproducing organisms) that have been observed between some social aphid colonies—both at the foundation stage (Akimoto 1981; Miller 1998) and during growth (Abbot *et al.* 2001; Abbot & Chhatre 2007; Abbot 2009). No mechanism for kin recognition has been observed in aphids (Wool 2004), so it seems likely that free-riders could enter colonies and disrupt social behaviour. On the face of it, given the high levels of mixing reported, it seems puzzling that social behaviour can persist.

A key component in the evolution of social traits is assortment (Grafen 1985; Queller & Goodnight 1989). Assortment arises in structured populations and means that individuals interact with genetically similar individuals at a higher than average probability—promoting the evolution of social traits. This notion is classically captured in inclusive fitness theory where assortment is

expressed through relatedness: which measures the probability, relative to the population average, that two interacting individuals will carry the same neutral gene (Queller & Goodnight 1989). Much of inclusive fitness theory is based on modelling efforts where fitness costs and benefits are taken to be given. This disconnects the evolutionary models from the ecological embedding. Here, we consider a typical aphid life cycle to derive the costs and benefits of social behaviour.

There are a broad range of life cycles across the different aphid species, but most aphids have a life cycle characterized by the diagram shown in figure 1 (Dixon 1998). A key feature of this life cycle is the habitation of aphids in colonies (a *colony* is a group of aphids that share and freely mix within the same living space). Colonies are founded by a small number of aphids. In many gall-dwelling aphid species, colonies are generally founded by a single fundatrix (Wool 2004). However, conspecific fundatrix mixing has been observed in the gall-dwelling *Tamalia* (Miller 1998) and *Eriosoma* (Akimoto 1981) aphids. After starting the colony, aphids reproduce parthenogenetically and are relatively isolated for the first few generations. As colonies age, the proportion of alatae tends to increase, and an increasing number of aphids start to emigrate (Karley *et al.* 2004; Mashanova *et al.* 2007). The final destination for alatae and their offspring is an over-wintering site, but before this happens, some will join other colonies or search for secondary hosts to continue growth for several more generations.

Social aphids form galls during colony growth. After gall formation, migration is frequently observed, although migrating aphids only rarely form new galls (Wool 2004). Samples of *Pemphigus* galls (Abbot 2009) demonstrate that many social species have a large proportion of immigrants (around 25%). If these immigrants are free-riders (i.e. they invest less in defending and maintaining nests and invest more in their own offspring), this raises the question as to what impact such free-riding may have on social behaviour in the colonies.

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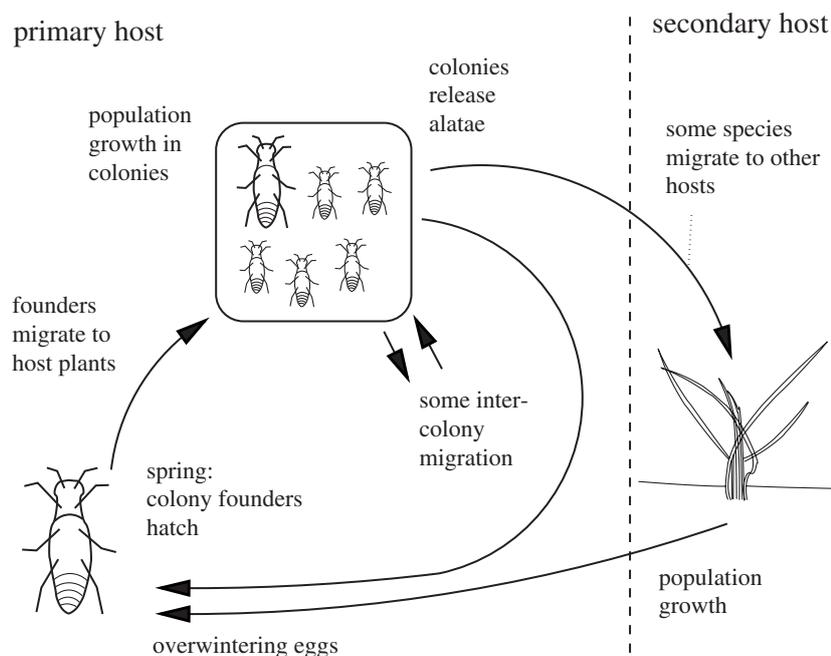


Figure 1. The typical aphid life cycle showing the movement of aphids between different habitats. Fundatrices hatch and find patches to start colonies where they reproduce parthenogenetically for several generations. After a period of several weeks, the colonies open and alatae are released. In most species, these move to a second host where they grow for further generations. Eventually aphids return to the overwintering site where eggs are laid, which hatch at the beginning of the next cycle.

Previous models of aphid social behaviour have focused on optimizing growth—with asocial aphids having inferior growth. This is done by maximizing either the colony growth rate (Stern & Foster 1996) or the alate output of the colonies (Aoki & Kurosu 2003, 2004; Pike & Manica 2006). However, analysis of sycamore aphids indicates that availability of space on trees can regulate overall population size (Dixon 2005). When the availability of patches is limited, increased competition for patches will reduce the pay-off from increasing output and thus increase the pay-off from free-riding (free-riders invest in individual growth rather than colony output). We thus model a trade-off between fast growth (free-riding) and increased output (nest investment).

To investigate the effects of free-riding aphids, it is important to understand the population structure: i.e. the way aphids mix with one another during the life cycle. Much inclusive fitness theory (Frank 1998) assumes that the relationship between the population structure, and the costs and benefits of a particular trait, is relatively constant. Such models cannot easily be applied to mixed aphid populations as both the population structure and the growth rate can change at many times during the life cycle. The population structure depends on the initial make-up of aphids at the start of growth, the amount of migration between colonies and the population mixing that can occur on second hosts and the overwintering site. The growth rate is probably density dependent within colonies. The presence of such significant environmental factors means it is not obvious how the elements of aphid life history translate into fitness components, how fitness costs and benefits can be calculated from their ecological determinants and how the population structure changes throughout the life cycle.

In this paper, we investigate the impact of clonal mixing in aphids by formulating and analysing a model of a typical, but caricatural, aphid life cycle. Aphids are randomly dispersed on patches (one patch contains one colony) at the start of each season. Mixing of aphids may happen at this stage, or during growth in colonies. To model free-riders, we model a trade-off between investment into growth within colonies and investment into production from the colony as a whole. We are thus able to determine the fitness components and analyse the model in terms of relatedness between individuals in the population.

## 2. MODELLING

Our model describes both social and non-social aphids. It considers an infinite number of colonies that are founded on identical patches at the beginning of each season. After these colonies mature, they will produce migrating individuals that will eventually give rise to females that produce the fundatrices of the new colonies of the next season. We will describe the biology using a variant of a seasonal patch model (Cohen & Eshel 1976; Jansen & Mulder 1999).

We begin by denoting the number of reproductive aphids in a colony by  $a$  and the intrinsic growth rate by  $r$ . We assume that the rate of increase of  $a$  is proportional to  $a$  and  $r$ , and also a regulating function  $u(r, a)$ . The rate of change of the number of reproductive aphids within a colony is thus given by

$$\frac{da}{dt} = aru(r, a). \quad (2.1)$$

The point where the population level is stationary is the carrying capacity  $K$  (defined as  $u(r, K) = 0$ ), which is a generally decreasing function of the growth rate  $r$ . Further

details of the regulating function  $u$  are left intentionally vague. We assume that it models both the effects of the nest (protection, food and density dependence) and social behaviour. The increased patch capacity owing to social behaviour—colony defence, housekeeping and nest repair—is modelled through the relationship of the function  $u$  with the function  $K$ . We thus model a trade-off between investment into growth (increasing  $r$ ) and investment into the good of the colony (increasing  $K$ ).

The output of the patch, in terms of fundatrices at the beginning of the next season, depends on overwinter survival. We define  $\eta$  as the frequency of surviving fundatrices per patch-dwelling reproductive aphid. This parameter will largely be dependent on environmental factors such as weather, predation levels, etc. It may also be modified by a further episode of reproduction on a secondary host. If we assume that all patches have reached carrying capacity by the end of growth, all patches must produce at least one fundatrix ( $\eta K > 1$ ) to sustain a population. This defines a lower limit for  $K$ , dubbed  $K_{\min}$ , and a corresponding (given  $K$  is a decreasing function of  $r$ ) upper limit for  $r$ , dubbed  $r_{\max}$ . The overwinter mortality  $\eta$  is thus a non-density-dependent process that is a key determinant of the density of colonies on trees.

At the beginning of the season, fundatrices are randomly distributed over the patches. When fundatrices start on the same patch, two or more will either grow together on the patch or a competition will result with a single winning fundatrix growing on the patch. When there is a single fundatrix, and no migration between patches during growth, all patches will have unmixed clones. The dominant strategy will be the one with the largest value of  $K(r)$ , and the corresponding lowest value of  $r$ . This can be limited by the time available for growth on patches (Pike *et al.* 2007), or the maximum size of a colony the plant may support. In many cases, however, there is mixing of fundatrices in the patches and/or migration between patches. Aphids with higher growth rates may invade patches and increase their frequency in the population at large. If this growth rate becomes too high ( $r > r_{\max}$ ), no aphid population will survive.

### (a) *The impact of clonal mixing*

We consider the impact of two different forms of clonal mixing: mixing of fundatrices and inter-colony migration. Mixing of fundatrices will have an impact because aphids using different strategies will grow at different rates and will also affect the carrying capacity of the colony. To study the effect of migration, we focus on the impact of mixing owing to immigrants (with different growth rates) entering colonies at early stages of growth.

We present an invasion analysis, looking at the growth rate of a small number of alien<sup>1</sup> invaders in a resident population at equilibrium. When there is competition between fundatrices, we assume only one survives (Whitham 1979). If the mean number of fundatrices is  $N$ , the proportion of patches with at least one fundatrix is  $1 - e^{-N}$ , and these patches, on average, give rise to  $\eta K$  new fundatrices in the next season (assuming all patches have reached carrying capacity). The mean number of fundatrices per patch will therefore approach

an equilibrium value  $\tilde{N} = \eta K(1 - e^{-\tilde{N}})$ . Although the equilibrium cannot be found in a closed form, it is easily calculated numerically.

We consider the impact of immigrants that grow at a faster rate than the native population by focusing on migrants of frequency  $m$  that enter colonies at an early stage (during colony growth to carrying capacity). To make analysis simple, we assume that all immigrants will have the maximum impact and are thus placed in their destination colonies at the start of growth. The variable  $m$  can be scaled accordingly to take account of the extra impact of this early growth. We assume that migrants are randomly spread over occupied patches, so that they are Poisson distributed.

We can now put together a picture of the dynamics of a rare alien strain invading a population of residents over a complete cycle. There are two variants of our model depending on whether there is a single fundatrix (denoted by the 's' subscript) or mixed fundatrices ('m' subscript) on the colonized patches. Considering the first variant, fundatrices are first randomly spread over the patches and a competition occurs between fundatrices resulting in a single winning fundatrix. Following this, but before growth starts, immigrants are added to those patches that are already occupied. Given a small frequency  $N^* \ll \tilde{N}$  of invading alien fundatrices per patch, a linear approximation can be made of the seasonal change in the frequency of aliens. For the variant where there is a single fundatrix on the patch after competition, this is given by  $N_s^{*'} = N_s^* W_s$ , where  $N_s^*$  and  $N_s^{*'}$  are the numbers of alien fundatrices before and after a single cycle, and the fitness of the alien strategy is  $W_s = (\eta/\tilde{N}) \sum_i P(i, m)[f(i, 1) + mf(i + 1, 1)]$ —see electronic supplementary material 1—where  $f(x, y)$  is the alien output of a patch starting growth with  $x$  residents and  $y$  aliens and  $i$  is the number of resident immigrants at the start of growth on each patch.

For the second variant, where there are mixed fundatrices, we simply randomly distribute both fundatrices and migrants across all the patches. Again, we have  $N_m^{*'} = N_m^* W_m$ , where  $W_m = (1 + m/\tilde{N}) \eta \sum_{a_0} P(a_0, \tilde{N} + m)f(a_0, 1)$ —see electronic supplementary material 1. Here  $a_0$  represents the number of residents at the start of growth on each patch.

To derive an expression for  $f(x, y)$ , we model growth within the colonies. We consider two different strains of aphids, the numbers of which are denoted  $a$  and  $a^*$ , and which have different intrinsic growth rates,  $r$  and  $r^*$ . Otherwise, these aphid strains are identical and, as they live in the same colony, their growth (see equation (2.1)) is regulated by the same function  $u(r, r^*, a, a^*)$ . The level of the mixed carrying capacity is given by averaging the carrying capacities of the aphids on the patch. In electronic supplementary material 2, we derive an expression for the alien output of a patch  $f(x, y)$ .

Given we know the fitness ( $W_s$  or  $W_m$ ) of invaders (strategy  $r^*$ ) into a resident population with strategy  $r$ , we can predict whether  $r$  is expected to evolve in a positive or negative direction by deriving the fitness gradient (see electronic supplementary material 3). A negative gradient indicates increasing social behaviour and is a variant of Hamilton's rule. Approximating that all patches start with one aphid and grow to carrying capacity  $K$ , we show how the rule is the same for both variants of our

model in electronic supplementary material 3. It is given by

$$-R \frac{d \ln K}{dr} > (1 - R) \frac{\ln K}{r}, \quad (2.2)$$

where  $R$  is the relatedness.<sup>2</sup> This shows how the benefits of larger colony output ( $d \ln K/dr$ ) are weighted by the relatedness  $R$  (note that  $K$  is generally a decreasing function of  $r$ , so the LHS will generally be positive). Similarly, the costs owing to reduced competitive ability caused by slower growth on the leaves ( $\ln K/r$ ) are weighted by  $1 - R$ . Such a cost will only be incurred in competition with non-kin (Jansen & Vitalis 2007).

We calculated the relatedness for the two cases. For the case with a single fundatrix, it is given by

$$R_s = \frac{1 - e^{-m}}{m}, \quad (2.3)$$

which is the frequency of patches immigrated to per immigrant. For the case with mixed fundatrices, the relatedness is,

$$R_m = \frac{\tilde{N} + m}{1 - e^{-\tilde{N}-m}} \sum_{a_0}^{\infty} \frac{P(a_0, \tilde{N} + m)}{(1 + a_0)^2}, \quad (2.4)$$

the normalized probability of sampling the same founder or migrant twice from a patch.

We predict a small correction to our variant of Hamilton's rule owing to the fact that, in the mixed-fundatrix case, many patches start growth with more than one fundatrix. Considering no migration, the RHS of equation (2.2) must be corrected (see electronic supplementary material 3) by

$$-\frac{cK}{r} \sum_{a_0}^{\infty} P(a_0, \tilde{N}) \frac{a_0 \ln(a_0 + 1)}{(1 + a_0)^2}. \quad (2.5)$$

This shows a further effect of population structure (assortment) outside that quantified by the relatedness. Comparison of the two forms of the equation indicates that the correction would not be significant when compared with empirical results (data not shown).

There is an evolutionarily stable strategy (ESS) when the local fitness gradient is equal to zero—i.e. when the LHS of equation (2.2) is equal to the RHS. This demonstrates how the relatedness modulates the costs and benefits to determine the level of the ESS; see electronic supplementary material 3 for stability analysis.

Considering the case where there is a single fundatrix, we may derive a simple relationship between the ESS carrying capacity  $\tilde{K}$  (which has a corresponding ESS growth rate  $\tilde{r}$ ) and the migration level. We assume that  $K$  has a linear approximation and may be rewritten in the form  $K = K_0 - r dK/dr$  (with constant  $K_0$ , the theoretical optimum carrying capacity when  $r \rightarrow 0$  and given unlimited time for growth). This allows us to generate a simple relationship between the ESS and the proportion of immigrants per patch ( $m/(1+m)$ )—plotted in figure 2 for the single-fundatrix variant. Considering samples from social aphid galls where immigrants are found at a mean proportion of around 0.25 per patch (Abbot 2009), the figure shows that we should expect a carrying capacity at 60 per cent of  $K_0$ .

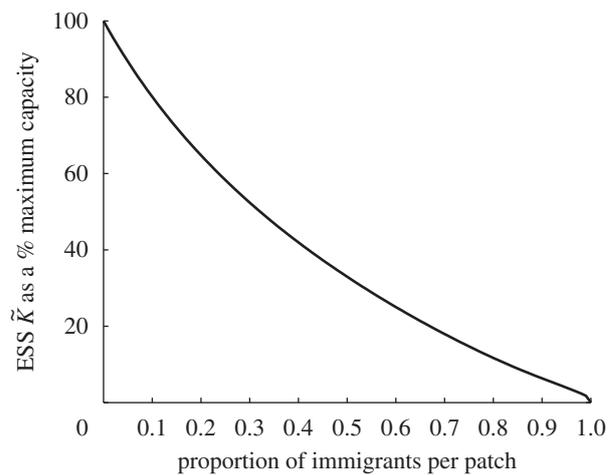


Figure 2. The ESS carrying capacity  $\tilde{K}$ , for the single-fundatrix case, as a function of the proportion of immigrants per patch. We plot  $\tilde{K}$ ,  $m$ , where  $(K_0 - \tilde{K})/(\tilde{K} \ln \tilde{K}) = (1 - R_s)/R_s$ . Here we have plotted  $\tilde{K}$  as a percentage of the value when patches are at optimum carrying capacity  $K_0$ .

### (b) Evolutionary history

Phylogenetic analysis of social aphids suggests that there have been several origins and losses of the sterile caste (Pike & Foster 2008). Given that there is also a continuum across the social spectrum in the present day, this demonstrates that the 'eusocial' behaviour of aphids is an adaptation to the environment. Evidence is accumulating which shows that environmental factors which may influence sociality are predation intensity (Stern & Foster 1996; Aoki & Kurosu 2003, 2004; Pike & Manica 2006; Pike *et al.* 2007) and the length of the time available for growth within colonies (Pike *et al.* 2007). Our model demonstrates that overwinter survival is also an important factor.

With both variants of the model, decreasing overwinter survival ( $\eta$ ) will shrink the range of possible values of  $\tilde{K}$ . This demonstrates the role of relatedness (and thus indirect fitness) in keeping the carrying capacity above  $K_{\min}$ , that required for overwinter survival.

The level of the relatedness for the single-fundatrix case depends on the number of immigrants per patch  $m$ . In the mixed-fundatrix case, the proportion of patches colonized (given by  $1 - e^{-N-m}$ ) is important. In this case, the proportion of immigrants is given by  $m/(N + m)$ . We calculated the values of  $m$  and  $N$  for the complete ranges of the proportion of colonized patches and the proportion of immigrants per patch. The relatedness for both the single- and mixed-fundatrix variants is plotted over the relevant values in figure 3.

When considering the evolutionary origins of aphid social behaviour, we look to areas of high relatedness in figure 3 to see how pre-social aphids may evolve social behaviour. Two paths to sociality stand out. First, when fundatrix competition does occur, we predict that lower levels of migration are needed (figure 3a). Since pre-social aphids will probably have a low carrying capacity on a host, perhaps a period of lower winter mortality is required while social behaviour is established. Second, when there is no competition for patches (perhaps more likely because patches are of lower value), it seems likely

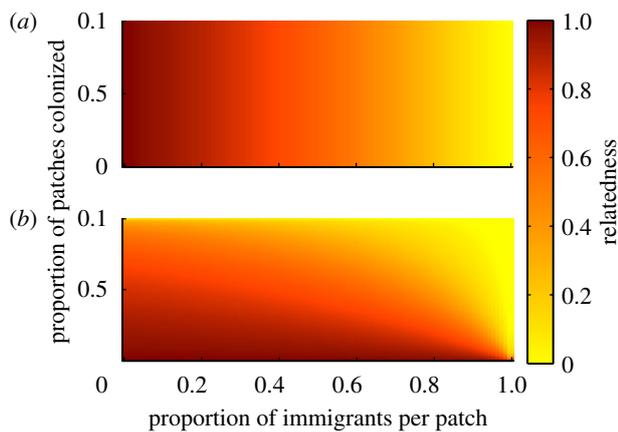


Figure 3. The relatedness for different levels of fundatrices and immigrants shows how immigration decreases the relatedness in both cases. (a) When there is a single fundatrix, the proportion of patches with fundatrices has no impact. (b) The impact of low- to mid-levels of immigration is not that significant compared with the level of patch colonization.

that the proportion of patches colonized will be influenced by the level of mortality overwinter. While increased mortality may shrink the range of possible values of  $\bar{K}$ , this effect can be balanced as relatedness will increase with overwinter mortality (see equation (2.4)). Contrasting with the first case, we thus predict that, when fundatrices mix with one another, social behaviour could originate through small increases in winter mortality (moving downward in figure 3b) perhaps over time, space or different host species.

### 3. SIMULATIONS

The simulations address our assumption that the effect of migration can be approximated by placing immigrants on patches at the start of growth. We have identified five factors for the effect of migration on social behaviour not covered by this approximation: (i) faster growing, less social colonies will generate emigrants earlier than slower growing colonies; (ii) emigration at carrying capacity will create space into which free-riders may grow; (iii) larger colonies will produce more emigrants; (iv) migration may decrease (through the death of migrants) colony output; and (v) migration will lower the growth rate of all strains. Intuitively, factors (i) and (ii) should increase, and factors (iii)–(v) should decrease, the ESS value of  $r$ .

To assess the significance of these factors, we have done computer simulations of the life cycle of the aphids shown in figure 1. The simulations, outlined in electronic supplementary material 4, model a set of patches with populations of individuals with varying growth rates ( $r$ ) and corresponding carrying capacities (a simple linear equation is used:  $K = K_0 - K_r r$ , with  $K_r$  constant). The carrying capacity of each patch is calculated by taking the mean of the carrying capacities on the patch. Based on logistic growth models used in Aoki & Kurosu (2003, 2004) and Pike & Manica (2006), growth on the patches is regulated by the local population density.

The ESS value  $\bar{r}$  was generated by simulations on both variants of the model. For the variant where fundatrices

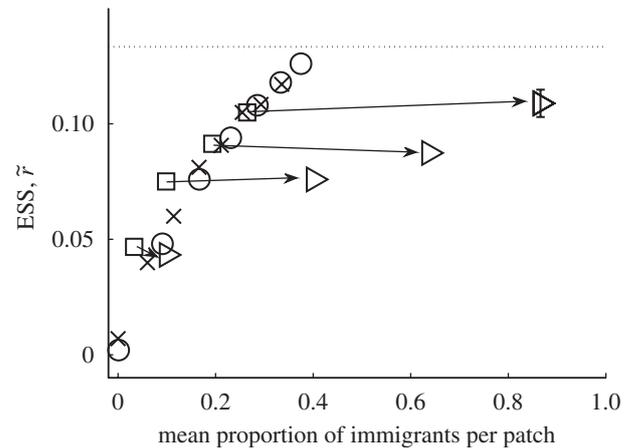


Figure 4. The mathematical treatment is largely similar to the simulation results. Comparing data points that have the same intrinsic migration level  $\gamma$  (linked with arrows), we see there is negligible impact to the ESS growth rate ( $\bar{r}$ ) from spending extra time on the patches. The error bar is shown for standard error greater than 0.005. The dotted line shows the value of  $r_{\max}$  for this parameter set:  $K_0 = 1000$ ,  $K_r = 5000$  and  $\eta = 0.003$ . Open circles, mathematical prediction; crosses, immigrants placed at start; open squares, growth stops at carrying capacity; triangles, growth over fixed period.

may mix at the start of growth, but ignoring migrants, we found very similar results to the mathematical prediction (data not shown). Migration was introduced with the single-fundatrix variant, with four different scenarios considered. First, in harmony with the mathematical treatment, a migrant population is produced and distributed before growth was initiated. Second, to consider the effect of factor (i), a group of randomly selected migrants (proportion  $\gamma$ ) are distributed at each time step—faster growing populations will thus produce more aphids more quickly. In this case, all migrants find populated patches and growth is stopped on patches once they have reached carrying capacity. The third scenario, considering factors (ii) and (iii), is the same as the second except that growth will continue for a fixed period—long after carrying capacity is reached. Finally, to test factors (iv) and (v), the fourth scenario is the same as the second, but migrants that reach empty patches die. Several simulations were run for each parameter set (chosen so that approximately half the patches are covered), and the mean value of  $\bar{r}$  for the first three scenarios is plotted against the mean proportion of immigrants per patch in figure 4.

In the main, the first three scenarios shown yield similar results to the mathematical treatment. The fourth scenario was also similar, though the intrinsic level of migration did need to be approximately doubled to make up for the migrants that find empty patches (data not shown). These results indicate that the main impact of migration on the ESS growth rate is due to early migration—i.e. migration while the population is still growing. Increasing the time spent growing and migrating on the patches did not significantly affect the relationship between the intrinsic migration level ( $\gamma$ ) and the ESS growth rate ( $\bar{r}$ ). However, the mean proportion of immigrants within patches did increase significantly. This demonstrates how, when estimating the relatedness of a

population, the point during growth when samples are taken can be acutely significant.

#### 4. DISCUSSION

The model and results presented here demonstrate how asexual organisms that reproduce parthenogenetically and grow within somewhat isolated colonies can evolve to social organisms that invest in the common good. The effect of clonal mixing on the level of sociality can be quantified with a relatedness measure. This demonstrates how social behaviour is not precluded by clonal mixing and may evolve without the need for some form of kin recognition.

The relatedness measure we have used quantifies assortment in the population. Our derivation of this measure and the costs and benefits came from a detailed ecological model. By demonstrating how inclusive fitness arguments follow from the ecology, without the need to invoke other mechanisms such as group selection, our work contributes to a growing body of literature that highlights the usefulness of inclusive fitness in complex ecological scenarios (e.g. Lehmann *et al.* 2007; Taylor *et al.* 2007).

Interestingly, as shown by equation (2.2), both variants of the relatedness measure apply to the same costs and benefits: the faster growth of less social strains and the extra colony output from more highly related colonies (owing to avoiding predation, better living conditions, etc.), respectively. The measure for the single-fundatrix variant  $R_s$  depends solely on the frequency of immigrants per patch. For mixed fundatrices, the second measure  $R_m$  depends largely on the frequency of fundatrices per patch when immigration is not at high levels (figure 3). It is rare to find social aphids with more than one fundatrix per patch—though whether this is due to competition between fundatrices or high levels of winter mortality has not been determined in many species.

It may be possible to test our model's predictions by taking measurements in the field. Our model demonstrates a simple relationship between the ESS carrying capacity of the patches, the maximum carrying capacity of the patches and proportion of immigrants in patches (figure 2). Estimates based on data for social *Pemphigus* aphids (Abbot 2009) indicate that even the more mixed populations (of mean 25% immigrants per patch) could have a carrying capacity at around 60 per cent of the maximum (where there is optimal investment). This means that, despite the observed high levels, our model predicts that social behaviour in aphids is not precluded by such clonal mixing.

The model demonstrates how population structure affects social behaviour through the relatedness measure in a variant of Hamilton's rule. In the main, the costs and benefits are due to environmental and phenotypic factors. However, population structure can have a small additional influence on the local fitness gradient. When there are a greater number of fundatrices, there will be less growth on the patches, reducing the competitive advantage of individuals that grow more quickly. While this will adjust the ESS, see equation (2.5), it is not likely to have a significant impact when measurement error is taken into consideration.

The levels of immigration shown in our results are compatible with those observed in data of social aphids (Abbot 2009). Our results also indicate that the timing of the migration is important. Interestingly in *Pemphigus obesinymphae*, migration is delayed until after the majority of nest investment has taken place (Abbot *et al.* 2001), after which it seems reproduction then becomes the priority. We find that migration that occurs after the population growth phase is largely inconsequential on the level of social behaviour. This highlights the importance of the timing of samples taken from the population. It also draws attention to an interesting behaviour observed in *Ceratoglyphina bambusae*, where soldiers will attack conspecific reproductives outside the gall (Aoki *et al.* 1991)—such behaviour can limit the level of free-riders intruding at early stages.

There is a growing body of literature that studies the evolution of sociality in aphids (Stern & Foster 1996; Pike *et al.* 2007). In this paper, we find that inclusive fitness (with relatedness depending on population structure at colony initiation) can explain social aphid evolution. An essential part of the model is the quantification of the costs and benefits of social behaviour within an ecological context. This approach may be usefully applied to studying the impact of environmental factors on the evolution of sociality in other model organisms such as slime mould (Bryden 2005, 2007).

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#### ENDNOTES

<sup>1</sup>In the adaptive dynamics literature, the term *alien* is normally referred to as *mutant* (Metz *et al.* 1992).

<sup>2</sup>We take relatedness as the normalized difference between the probability that two individuals (sampled with replacement) from the same patch carry the same neutral gene and the probability that two random individuals (again sampled with replacement) from the population carry the same neutral gene (Queller & Goodnight 1989).

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