Research article

Dominance hierarchies reduce the number of hopeful reproductives in polygynous queenless ants

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Summary. In many animal societies aggressive interactions regulate essential features such as feeding order and reproductive rights. Because aggressive interactions are costly the number of individuals competing for direct reproduction (hopeful reproductives) affects colony productivity. Using mathematical models, based on the costs/benefits trade-off for a worker to attempt to become a reproductive, we determine the number of hopeful reproductives expected to occur in insect societies with totipotent workers and several reproductives. The model is based on the biology of the polygynous queenless ant *Rhytidoponera confusa* (Formicidae: Ectatomminae), where every worker can potentially reproduce but only a few actually do, but is valid for all societies with totipotent individuals. We compare the number of hopeful reproductives predicted in the absence of a dominance hierarchy and with a linear dominance hierarchy, and we investigate the effects of colony size, relatedness, and mortality. The models show that a linear dominance hierarchy reduces the number of hopeful reproductives, and additional unpublished models show that this reduction is lower in non-linear hierarchies. Dominance hierarchies are thus favoured by natural selection. Larger colony size and higher mortalities result in longer hierarchy, whereas higher relatedness shortens hierarchy length. These predictions were successfully tested with eight colonies of *R. confusa*.

Key words: Regulation of reproduction, hopeful reproductive, hierarchy length, division of labour, probabilistic model.

Introduction

Dominance hierarchies are common in animal societies. They usually stem from competition for food, territory or reproduction. For example, in the chicken *Gallus gallus* the hierarchy determines feeding order (Schjelderup-Ebbe, 1935) and in the brown hyena *Hyaena brunnea* it regulates access to food and reproduction both among females and among males (Owens and Owens, 1996). Dominance hierarchies also regulate reproduction in some wasps, bees and ants (e.g. Premnath et al., 1996; Van Doorn and Heringa, 1986; Heinze et al., 1994). In ants, hierarchies among workers regulate male production by workers either in orphaned colonies only (e.g. *Pachycondyla* cf. *inversa*, Heinze et al., 2002) or in presence of the fertile queen (e.g. *Harpagoxenus sublaevis*, Bourke, 1988). Furthermore, hierarchies among queens result in one or a few queens monopolising reproduction in some multiple-queens (polygynous) ants (e.g. Heinze and Smith, 1990; Medeiros et al., 1992).

Queenless ants have secondarily lost the queen caste. Unlike in other ants, queenless ant workers have retained the ability to mate and reproduce sexually (Peeters, 1991). Mated egg-laying workers are called gamergates to differentiate them from queens of queenright species, but gamergates and workers are morphologically identical and the difference is strictly functional. Any worker can potentially become a gamergate, but not all workers actually do. An excess of gamergates would lower relatedness, thereby decreasing the benefits of altruism, and it would decrease colony productivity because reproductives typically work less than workers (e.g. Liebig et al., 1999; Gobin et al., 1999; Monnin and Peeters, 1999; Monnin and Ratnieks, 2001; Hartmann et al., 2003). Natural selection is thus expected to favour means to regulate gamergate number.

In most species gamergate number is socially determined through physical aggressions and/or chemical signals. For instance, only the top-ranking worker in a near-linear dominance hierarchy mates in *Pachycondyla sublaevis* and *Dinoponera quadriceps* (Ito and Higashi, 1991; Monnin and Peeters, 1998). Workers entering the dominance hierarchy aggressively compete to become gamergates, that is they are hopeful reproductives. Because they invest time and energy in aggressive interactions they work less than workers. Con-
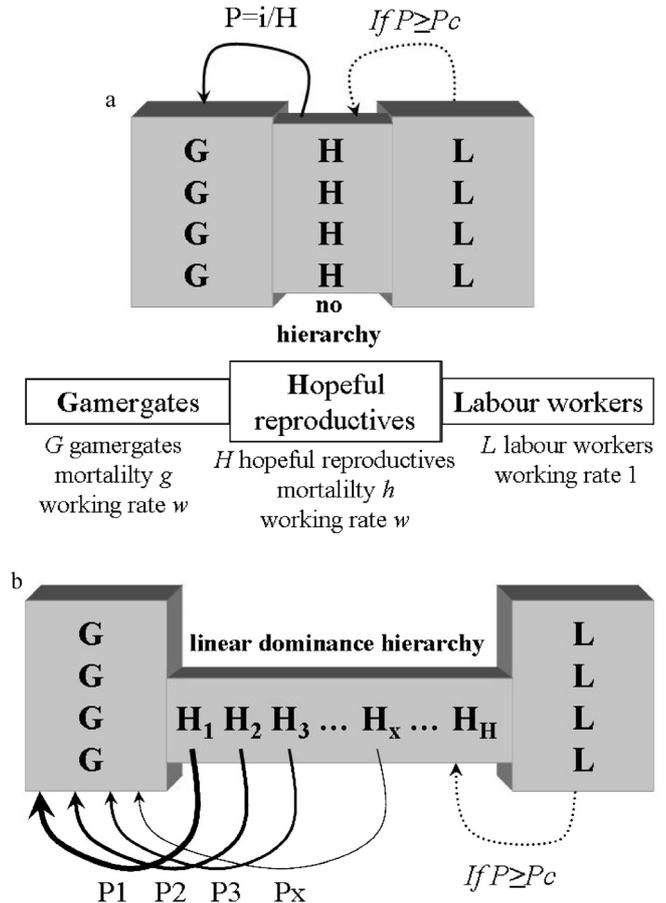
sequently, colony productivity decreases when the number of hopeful reproductives increases. Monnin and Ratnieks (1999) proposed a model based on the costs-benefits trade-off of being a hopeful reproductive that determines how many individuals should join the dominance hierarchy in queenless monogynous species. This model predicts that low relatedness and large colony size result in longer hierarchies, and this last prediction is supported by empirical data (Monnin et al., 2003). Here we generalise the model to polygynous species, and compare the number of hopeful reproductives expected in the absence of a dominance hierarchy with that expected in a linear dominance hierarchy. We also study how relatedness, colony size and mortality influence the number of hopeful reproductives, and we test numerical predictions of the models with eight colonies of the queenless polygynous ant *Rhytidoponera confusa*. The models show that the dominance hierarchy reduces the number of hopeful reproductives.

Methods

In our model we consider a colony consisting of three different classes of individuals: gamergates breed, hopeful reproductives aggressively compete with one another to become gamergates, and "labour workers" are not involved in aggressions (Fig. 1). Using such discrete classes of individuals is a useful simplification. In nature there is a continuum from hopeful reproductives to labour workers (e.g. Monnin and Peeters, 1999) but it is often impossible to precisely tell at which point hopeful reproductives give up the fight to become gamergates and become labour workers instead (e.g. Monnin and Ratnieks, 2001; Monnin et al., 2003). A hopeful reproductive can become a gamergate only if a breeding position becomes vacant following the death of a gamergate, but any labour worker can become a hopeful reproductive (i.e. join the competition for direct reproduction) if she decides to do so. We assume that all males are produced by gamergates. The number of gamergates, hopeful reproductives and labour workers is G, H and L, respectively (Table 1),

Figure 1. Sketch of the models without hierarchy (a) and with a linear dominance hierarchy (b). Workers form three groups: gamergates breed, hopeful reproductives aggressively compete with one another to become gamergates, and labour workers do not compete and work at maximum rate ($w = 1$). Hopeful reproductives can become gamergate only if a breeding position becomes vacant following the death of a gamergate. A labour worker becomes a hopeful reproductives (i.e. joins the hierarchy) if the probability P that she will become a gamergate is greater than the critical probability Pc

Table 1. Variables of the model

Variable	Significance
Px	Probability that the hopeful reproductive x becomes gamergate.
Pc	Critical probability of becoming gamergate above which the benefits of becoming a hopeful reproductive exceed the benefits of not joining.
G	Number of gamergates
H	Number of hopeful reproductives
L	Number of labour workers
N	Colony size ($N = G + H + L$)
g	Mortality of gamergates
h	Mortality of hopeful reproductives (includes the probability that they survive but give up the fight for direct reproduction and become labour workers)
r	Mean relatedness between workers and gamergates
w	Work rate of gamergates and hopeful reproductives ($0 \leq w \leq 1$)

and colony size is $N = G + H + L$. For simplification we assume that colony size is constant, that is emerging workers replace dying workers. In the model where hopeful reproductives are ranked in a linear hierarchy H is also the hierarchy length.

Hopeful reproductives and gamergates work at rate w, with $0 \leq w \leq 1$, whereas labour workers work at rate 1. This accounts for the fact that hopeful reproductives and gamergates usually work less than labour workers (Ito and Higashi, 1991; Monnin and Peeters, 1999). The probability that a gamergate dies is g, and the probability that a hopeful reproductive dies or gives up the fight for direct reproduction and becomes a labour worker is h. For simplicity we call g and h mortalities.

The mean relatedness between a focal gamergate and a worker, r, depends on the number of gamergates G. We assume that gamergates are equally fertile so that the focal gamergate mothers a fraction $1/G$ of the workers, with a mother-to-daughter relatedness $r = 0.5$. We further assume that gamergates are full-sisters, so that the fraction $(G - 1)/G$ of workers produced by the other gamergates are nieces to the focal gamergate, with relatedness $r = 0.375$. Therefore, the mean relatedness between the focal gamergate and workers is $r = \frac{1}{G} 0.5 + \frac{G-1}{G} 0.375$, so that $0.375 < r \leq 0.5$. These assumptions will be discussed later.

Critical probability of becoming gamergate, Pc

We define the payoff obtained by a worker as the product of the colony work force times the relatedness between the worker and the gamergates. For simplicity, we ignore any dynamical aspect and we treat the problem as a single, instantaneous costs/benefits analysis. Our model can thus be seen as an equilibrium analysis where we determine the number of hopeful reproductives in a stable colony. A worker should become a hopeful reproductive when the expected benefits (becoming gamergate and increasing the relatedness to the brood) exceed the costs (working less and thus decreasing colony productivity and producing less brood).

The benefit of remaining a labour worker is to increase colony productivity since labour workers work more than hopeful reproductives and gamergates. If the focal worker remains a labour worker the colony work force is $L + Hw + Gw$, that is L labour workers working at rate 1, and H hopeful reproductives and G gamergates working at rate w. The relatedness of the worker to the gamergates is r, so that her payoff is $(L + Hw + Gw)\, r$.

The benefit of being a hopeful reproductive is to become a gamergate oneself and reproduce, that is to increase one's relatedness to the brood reared by the colony. If the focal labour worker becomes a hopeful reproductive the number of labour workers decreases to $L - 1$ and the number of hopeful reproductives increases to $H + 1$. The colony work force becomes $(L - 1) + (H + 1)w + Gw$. This worker has a probability P of becoming gamergate, in which case she lays a fraction $1/G$ of the eggs and the other gamergates lay a fraction $(G - 1)/G$. The relatedness between the worker and the other gamergates remains r, and relatedness to self is 1. The worker also has a probability $1 - P$ of failing to become gamergate, in which case all the eggs are produced by the other gamergates. Therefore, the payoff for a hopeful reproductive is

$$((L - 1) + (H + 1)w + Gw)\left[P\left(\frac{1}{G} + \frac{G-1}{G}\, r \right) + (1 - P)r \right].$$

The critical probability of becoming gamergate, Pc, is the probability for which being a hopeful reproductive and being a labour worker yields the same payoff. Therefore, when $P = Pc$ then $(L + Hw + Gw)r$

$$= ((L - 1) + (H + 1)w + Gw)\left[Pc\left(\frac{1}{G} + \frac{G-1}{G}\, r \right) + (1 - Pc)r \right].$$ Since $L =$

$N - G - H$ this gives $Pc = \dfrac{r(1 - w)G}{(1 - r)[N - (1 - w)(G + H + 1)]}$.

The critical probability, Pc, decreases as colony size increases (Fig. 2a, dashed line). Thus being a hopeful reproductive is more rewarded in larger than in smaller colonies. This is because in larger colonies each hopeful reproductive working at a decreased rate w represents a smaller proportion of the total work force. Pc increases when r increases independently of other parameters (Fig. 3a left, dashed line). That is, workers are less likely to become hopeful reproductives. This is because workers have little to gain by competing with highly relatedness gamergates. Pc decreases when the working rate w increases. Being a hopeful reproductive has little cost since they still work at a high rate, and it is thus beneficial to become a hopeful reproductive even at low benefits (Fig. 3b left, dashed line). Finally, if the number of gamergates G increases Pc increases, that is less workers become hopeful reproductives. This is because the more gamergates there are the smaller the fraction of egg production $1/G$ a worker becoming a gamergate would get. Other factors such as mortalities of gamergates and hopeful reproductives (g and h, respectively) have no effect on Pc (Fig. 3c–d left, dashed line).

Actual probability of becoming gamergate, P

The actual probability of becoming gamergate, P, depends largely on the relationship between hopeful reproductives. When there is no dominance hierarchy all hopeful reproductives have the same probability of becoming gamergate, and P essentially depends on the number of individuals competing for the breeding vacancy. When hopeful reproductives are ordered in a dominance hierarchy each individual has a
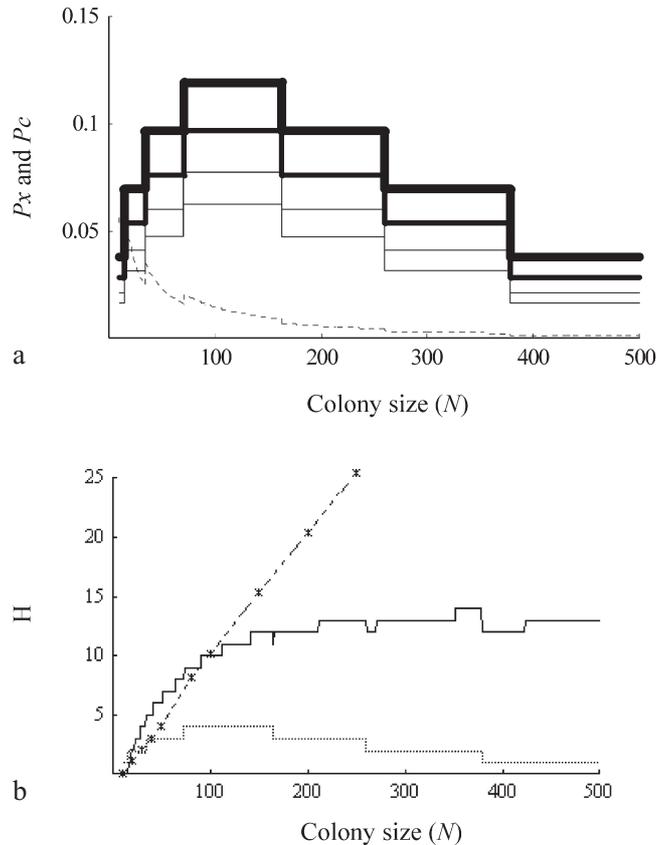

Figure 2. Calculation of the hierarchy length and effect of gamergate number. (a) Critical probability Pc (dashed line) and probability Px that the worker ranked x in a linear hierarchy becomes gamergate (full lines, the broader the line the higher the rank x). Pc is a decreasing function of N. Px is discontinuous because when mortalities are held constant it only depends on the number of gamergates G, which is discontinuous as it is an integer (Methods). The pattern of P is thus similar to that of G (in (b), dotted line). Individuals for which $P > Pc$ enter the hierarchy, so that the number of P curves above the Pc curve gives the hierarchy length. (b) The model of linear hierarchy (full line) predicts that in small colonies the hierarchy length increases as colony size N increases, and reaches a plateau and remains constant for larger colonies. In contrast, the model without hierarchy (dashed line, stars are computed values) predicts a linear increase of the number of competing individuals. Thus, in small colonies the predictions of the models are close, whereas in large colonies the occurrence of a hierarchy dramatically decreases the number of individuals competing for direct reproduction

different probability of becoming gamergate, depending on its rank and on the degree of linearity of the hierarchy.

Let Px be the actual probability of becoming gamergate for hopeful reproductive x. When $Px \geq Pc$ she obtains a higher payoff as a hopeful reproductive than as a labour worker, whereas when $Px < Pc$ she increases her payoff by being a labour worker. Therefore, the optimal number of hopeful reproductives we seek to determine under each scenario is the number H for which $P_{H+1} < Pc \leq P_H$.

Model a: no dominance hierarchy

In this model (Fig. 1a) hopeful reproductives form a group of H individuals with equal probability Px of becoming gamergate (for comparison with the following model of a linear dominance hierarchy one can see this model as a hierarchy where all hopeful reproductives have the same rank). H is the highest value for which $Px \geq Pc$. If i gamergates die, each hopeful reproductive has a probability i/H of becoming gamergate
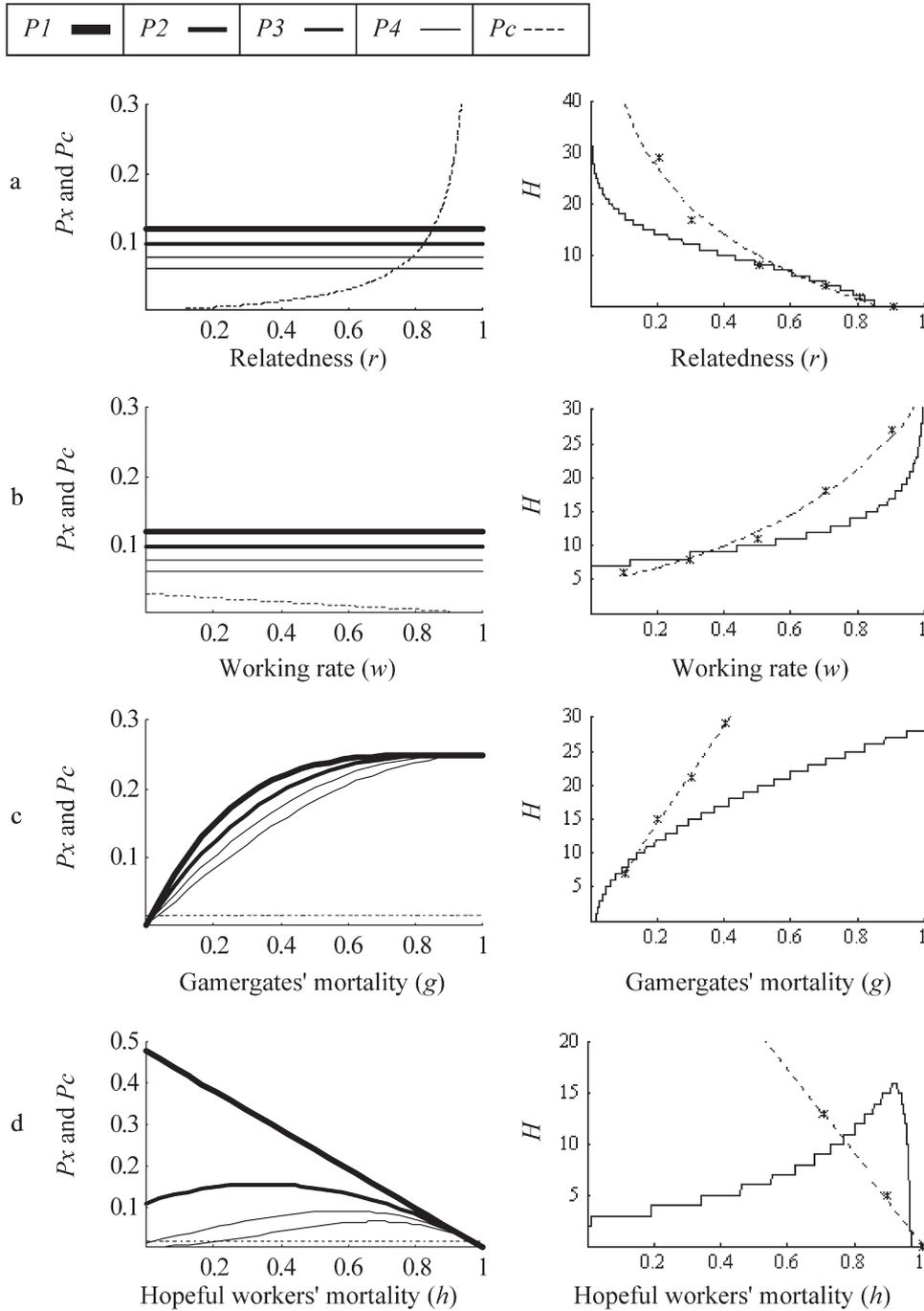
Figure 3. Critical probability, probability of becoming a gamergate and hierarchy length. Figures (a) to (d) show the effect of the variation of parameters r, w, g, and h when other parameters are held constant, respectively. The figures on the left show the critical probability Pc above which joining is beneficial (dashed line), and the actual probabilities Px that the worker ranked x in a linear hierarchy has to become gamergate (the thicker the line the higher the rank). The figures on the right show the resulting hierarchy length with a linear hierarchy (full line) and without hierarchy (dashed line). The defaults values of the parameters are $r = f(G)$ (Methods), $w = 0.5$, $g = 0.15$, $h = 0.75$ and $N = 100$

if $i \leq H$ (there are less breeding vacancies than hopeful reproductives), or a probability 1 if $i > H$ (there are more breeding vacancies than hopeful reproductives and $i/H > 1$). Two cases arise, depending on whether there are more gamergates than hopeful reproductives or less.

When there are more gamergates than hopeful reproductives ($G > H$) the probability of becoming gamergate is

$$Px = (1 - h) \left[\sum_{i=1}^{H} C_G^i\, g^i (1-g)^{G-i} \cdot \frac{i}{H} + \sum_{i=H+1}^{G} C_G^i\, g^i (1-g)^{G-i} \cdot 1 \right], \text{ where:}$$

– 1 − h is the probability that the focal worker survives
– the first sum is the probability that the focal worker becomes gamergate when less gamergates die than there are hopeful reproductives

($i \leq H$). The probability that i out of G gamergates die (with probability g for each) while $G - i$ gamergates survive (with probability $1 - g$ for each) is $\sum_{i=1}^{H} C_G^i\, g^i (1-g)^{G-i}$, and the probability that the focal worker obtains each breeding vacancy is i/H.

– the second sum is the probability that the focal worker becomes gamergate when more gamergates die than there are hopeful reproductives ($H + 1 \leq i \leq G$). The probability that i out of G gamergates die while $G - i$ gamergates survive is $\sum_{i=H+1}^{G} C_G^i\, g^i (1-g)^{G-i}$, and the probability that the focal worker obtains a breeding vacancy is 1 since there are more vacancies than hopeful reproductives.

When there are no more gamergates than hopeful reproductives ($G \leq H$) the probability of becoming gamergate is simply

$$Px = (1-h) \sum_{i=1}^{G} C_G^i g^i (1-g)^{G-i} \cdot \frac{i}{H}$$, because there cannot be more vacancies than hopeful reproductives.

Model b: linear dominance hierarchy
In this model (Fig. 1b) hopeful reproductives are ranked in a strictly linear dominance hierarchy, which means that if i gamergates die the i highest ranked hopeful reproductives become gamergate provided that they survive.

If the number of gamergates is higher than the rank of the focal worker ($G \geq x$, i.e. there are more gamergates than hopeful reproductives better-ranked than the focal worker) the probability that this worker becomes gamergate is $Px = (1-h) \sum_{k=1}^{x-1} \sum_{i=x-k}^{G} C_{x-1}^k h^k (1-h)^{x-1-k} C_G^i g^i (1-g)^{G-i}$, where:

- $1-h$ is the probability that the focal worker survives
- some of the $x-1$ better-ranked hopeful reproductives die, from none ($k=0$) to all of them ($k = x-1$). The probability that k out of $x-1$ hopeful reproductives die is $C_{x-1}^k h^k (1-h)^{x-1-k}$
- some of the gamergates die. If k of the $x-1$ hopeful reproductives with a better rank died, then $x-1-k$ survived. So the hopeful reproductive x becomes a gamergate only if at least $(x-1-k)+1 = x-k$ gamergates die. Thus the number of gamergates that died is i, varying from $x-k$ to G. The probability that i out of G gamergates die is $C_G^i g^i (1-g)^{G-i}$.

When the number of gamergates is lower than the rank of the focal worker ($G < x$, i.e. there are less gamergates than hopeful reproductives better-ranked than the focal worker), the probability that the focal worker becomes gamergate is

$$Px = (1-h) \sum_{k=1}^{x-1} \sum_{i=x-k}^{G} C_{x-1}^k h^k (1-h)^{x-1-k} C_G^i g^i (1-g)^{G-i}.$$

If all the gamergates die (G) but all the hopeful reproductives better-ranked than the focal worker survive ($x-1$) the latter does not become gamergate, because all the vacancies left by the G gamergates are filled by better-ranked individuals. The focal worker becomes gamergate if at most $G-1$ better-ranked hopeful reproductives survive, that is at least $x-G$ die.

Results

Comparison of the models

When there is no dominance hierarchy the number of hopeful reproductives increases linearly as colony size increases (Fig. 2b, dashed line). In contrast, when there is a linear dominance hierarchy the number of hopeful reproductives increases until it reaches a plateau, for colonies with 150–200 workers or more (Fig. 2b, solid line). Counter intuitively, for colonies with less than 100 workers the model with a dominance hierarchy predicts more hopeful reproductives than the model without hierarchy. The difference is small in absolute number (2–3 additional hopeful reproductives) but large in proportion (c.a. 40% hopeful reproductives more). For colonies with 100 workers both models predict the same number of hopeful reproductives, and for colonies with over 100 workers the model with hierarchy predicts less hopeful reproductives. Because this model reaches a plateau while the model without hierarchy does not the difference in the number of hopeful reproductive predicted by both models increases as colony size increases. For instance, for a colony of 300 individuals the model without hierarchy predicts 30 hopeful reproductives whereas the model of linear hierarchy predicts only 13.

Relatedness, working rate and gamergate mortality affect both models in the same way, although the difference can be quantitatively large (Fig. 3a–c), whereas the mortality of hopeful reproductives has opposite effects on the models (Fig. 3d). For most values of the parameters the model with dominance hierarchy predicts less hopeful reproductives than the model without hierarchy.

Both models predict an exponential shortening of the number of hopeful reproductives when relatedness increases (Fig. 3a). No hopeful reproductives are expected when $r > 0.85$ but this is an unrealistic value as daughter-mother relatedness is 0.5. When r is low a labour worker benefits a lot from competing with other workers because she can significantly increase her relatedness to the offspring reared by the colony. Conversely, when r is high the benefit is small as the brood is already highly related. Because $0.375 < r \leq 0.5$ (Methods) it has a moderate effect on the number of hopeful reproductives. Taking into account the relationship between r and G (Methods) shows that $r = 0.5$ when $G = 1$, and r decreases as G increases. Therefore, the number of hopeful reproductives increases when there are more gamergates in the colony, not only because the relatedness decreases, but also because the probability that some breeding positions become vacant is higher since there are more breeding positions, even if gamergate mortality g remains constant.

The number of hopeful reproductives increases exponentially when working rate w increases, in both models (Fig. 3b). When $w = 0$ hopeful reproductives do not work and suffer a large cost from reduced colony productivity (Pc is maximal). Conversely, when $w = 1$ hopeful reproductives work as much as labour workers and suffer no cost, so that all workers are hopeful reproductives. These two extreme values are biologically unrealistic. With more realistic values w has a smaller effect, in particular with a dominance hierarchy (e.g. $0.1 < w < 0.9$, Fig. 3b).

Hierarchy length increases when mortality of gamergates g increases, whether there is a hierarchy or not (Fig. 3c). The increase is linear without hierarchy and logarithmic with a linear hierarchy. It stems from the fact that higher gamergate mortality results in more breeding vacancies, and hence in increased probability for a hopeful reproductive to become gamergate.

The mortality of hopeful reproductives has opposite effects on the models. When there is a dominance hierarchy the number of hopeful reproductive increases as mortality h increases, and then decreases until zero when h is very high (Fig. 3d). This is because a higher turnover of hopeful reproductives increases the probability that lower-ranked workers become gamergates. When h increases the survival $1-h$ of all hopeful reproductives is equally affected, whereas the probability $C_{x-1}^k h^k (1-h)^{x-1-k}$ that workers better ranked than the focal worker die and leave a vacancy increases more for lower- than for higher-ranked workers. However, when mortality is very high workers seldom become gamergates before dying (or giving up and becoming labour workers). In contrast,

when there is no hierarchy the number of hopeful reproductives decreases linearly as their mortality h increases (Fig. 3d, dashed line). This is because all workers have equal "rank" so that there are no benefits of increased mortality of higher-ranked competitors, but only costs of increased own mortality.

Application and test of the model with Rhytidoponera confusa

The models were tested with *Rhytidoponera confusa*, an Ectatomminae ant (Bolton, 2003, previously belonging to the paraphyletic subfamily Ponerinae) living in Australian rainforests and wet sclerophyll forests. This species has two types of colonies (Ward, 1981): type A colonies have one mated queen and unmated workers, whereas type B colonies are queenless and reproduce by several gamergates.

The variables of the models were estimated as follows. The respective mortalities of gamergates and hopeful reproductives, g and h, have been estimated in two queenless ants. The ratio h/g is approximately 3 in *Diacamma* cf. *rugosum* (Tsuji et al., 1996) and 1 to 5 in *D. cyaneiventre* (André et al., 2001). In our model h also includes the probability that the hopeful reproductive gives up the fight and becomes a labour worker. Therefore, h and h/g are higher than the above estimated values, and we set $h/g = 5$ with $h = 0.75$ and $g = 0.15$ as default values. Nevertheless, we also investigate the effects of various values of h and g. The working rate of hopeful reproductives and of gamergates, w, is set to 0.5 by default, which means that hopeful reproductives and gamergates work half as much as labour workers. The number of gamergates, G, is estimated from 39 *R. confusa* type B colonies collected by Ward between 1975 and 1978 (pers. comm.) and 9 type B colonies collected by Peeters between 1986 and 2003 (pers. comm.). G correlates well with colony size, N, with $G = N.e^{-0.009N - 2.527}$ (non-parametric linear correlation test between N and $\ln(G/N)$, Spearman R = –0.70, p = 10^{-6}, N = 48 colonies). Our calculations with C_n^p require the use of integers, so we round up G to the nearest integer, with G tending towards 1 when N increases (Fig. 2b, dotted line). When colony size increases, the number of gamergates increases, reaches a maximum, and then decreases. Relatedness between

gamergates and workers does the exact opposite. In *R. confusa* the mean workers-gamergates relatedness is somewhere between 0.375 and 0.5 (for 100 and 1 gamergate respectively, see definition of parameter r). At these values Pc is low and does not vary much, thus relatedness has little effect on the number of hopeful reproductives (Fig. 3a). Pc depends on the number of hopeful reproductives, H, which the comparison of Pc and Px aims to determine. For simplification we initially set $H = 0$ to calculate Pc, and show in the discussion that this simplification has no effect.

The predictions of the models were tested using 7 colonies of *R. confusa* with 127 ± 111 individuals (mean $\pm$ SD, Table 2). Two colonies were of type B, with no queen and 1 or 5 gamergates. Two colonies were of type A, with one queen and no gamergate. The queen was removed in order to trigger aggressive interactions among workers and investigate hierarchy length in orphaned colonies. Three colonies had no queen and no gamergate. They were either naturally orphaned when collected, or the reproductive(s) were not collected or died during transportation. In either case, their colony type could not be determined. One of these colonies was large and was split into two groups of equal size. Therefore, of the eight colonies studied two had gamergates and six were orphaned. In order to identify the hopeful reproductives and determine the dominance relationships colonies were observed by bouts of approximately 15 min, totalising 5h04 $\pm$ 1h42 of observations per colony (mean $\pm$ SD, Table 2). Agonistic interactions are "antennal boxing", which consists in a dominant worker repetitively hitting with her antennae the head of a subordinate (e.g. *Rhytidoponera confusa* and *chalybaea*, Ward, 1983). After these observations colonies were dissected to determine ovarian development and gamergate number (i.e. workers with filled spermatheca).

We define hopeful reproductives as workers involved in at least 2% of the aggressive interactions. This excludes workers who interacted only once or a very few times, and are thus more likely to be labour workers than hopeful reproductives. Indeed, labour workers can occasionally be harassed as a way to increase their work rate (Hölldobler and Wilson, 1990), and they may occasionally aggressively test hopeful reproductives to assess their strength and social status. Additionally, misreading or mistyping the colour code of an ant

Table 2. Colony composition. Seven colonies of *Rhytidoponera metallica* were observed for a total of 5h04 $\pm$ 1h42 each (mean $\pm$ SD) *

colony name	collection date	queen?	colony size in the laboratory (N)	number of gamergates (G)	number of observed hopeful reproductives (H)	observation (hours)
1	25 Jan 2003	no	285	0	15	5h40
2	17 Feb 2003	yes	40	0	5	3h05
3	17 Feb 2003	no	291	–	–	
3a	–	–	135	0	18	6h25
3b	–	–	135	0	11	5h40
4	17 Feb 2003	no	74	0	10	3h00
5	17 Feb 2003	no	61	1	16	6h05
6	12 Mar 2003	no	47	5	12	7h20
7	12 Mar 2003	yes	90	0	10	3h15

* Colony 3 was split into two colonies 3a and 3b.
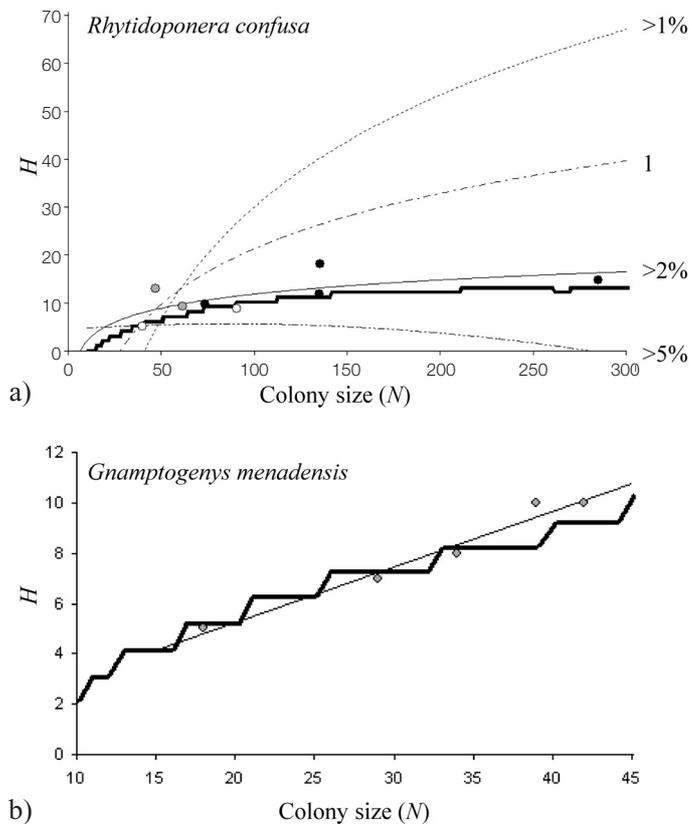
Figure 4. Predictions of the linear model and observed hierarchy length in (a) *Rhytidoponera confusa* and (b) *Gnamptogenys menadensis*. (a) Bold lines: prediction of the linear model; dotted and dashed lines: hierarchy lengths observed when defining hopeful reproductives as individuals performing more than one aggression or more than 1%, 2% or 5 % of all aggressions (curves are logarithmic regressions of eight data points, except 5% curve: second order polynomial regression). Circles are the data points for line 2%: empty circles = colonies orphaned by removal of the queen (type A), grey circles = colonies with gamergates (type B), black circles = orphaned colonies of undetermined type. (b) Observed hierarchy length using data from Gobin et al. 2001. All colonies are gamergates colonies. $h = 0.75$ and $g = 0.15$

could result in an individual being attributed an interaction that did not occur, so that being involved in very few interactions is not meaningful. $89 \pm 11\%$ (mean $\pm$ SD) of workers with developed ovaries were hopeful reproductives, and they were involved in $74 \pm 33\%$ of the interactions. Using a higher threshold (e.g. 5% as in *D. quadriceps*, Monnin and Ratnieks, 1999) would have resulted in more workers with developed ovaries being misclassified as labour workers. Moreover, the hierarchies based on the 2% threshold include $67 \pm 33\%$ of the workers who interacted more than once. This suggests that this 2% criterion is well suited to identify hopeful reproductives in *R. confusa*. The number of hopeful reproductives increases with colony size, and fits well the predictions of the model with a linear hierarchy (Fig. 4a). Similar-sized colonies have hierarchies of comparable lengths, whether they have gamergates or are orphaned (Fig. 4a).

Hopeful reproductives were ordered using the BBS method (Jameson et al., 1999), which takes into account the number of aggressions performed and received by each individual. Then we transformed the interaction matrix obtained into a dominance matrix, following De Vries' method (De Vries, 1995). There was no correlation between the degree of ovarian development and the rank of hopeful reproductives. Although the matrices of interactions show that the hierarchies are more or less linear, De Vries' linearity index is not significant ($h' = 0.38 \pm 0.25$, $p = 0.30 \pm 0.15$SD for all 8 colonies, De Vries, 1995). This is because workers do not interact with all the other workers of the colony, so that many dominance relationships are unknown (often more than 50%). With so many unknown dominance relationships both Landau's and De Vries' linearity indices are known to fail to detect linearity, even when all known relationships allow rearranging the hierarchy linearly with zero inconsistency (De Vries, 1998). Therefore, these indices are not well suited to estimate the degree of linearity of hierarchies in queenless ants. This is in part because these indices have been primarily designed to study vertebrates, whose groups are typically much smaller than queenless ant colonies.

Discussion

Both models predict that the number of hopeful reproductives increases when colony size, work rate, and gamergate mortality are higher, and decreases when relatedness is higher (as in Wenseleers et al., 2004). For most parameter values the model without hierarchy predicts more hopeful reproductives than the model with a linear dominance hierarchy. A model of near-linear hierarchy (unpublished) predicts an intermediate number of hopeful reproductives, showing that the more linear the hierarchy the less hopeful reproductives there is. This is because a higher degree of linearity restricts the benefits of being a hopeful reproductive to higher-ranked individuals only. Therefore, dominance hierarchies are selected for, provided that the proximate mechanisms allowing for the sorting of individuals exist. This is strongly supported by the fact that dominance hierarchies are common in social insects where totipotent individuals compete for direct reproduction (e.g. queenless ants, polistine wasps, Halictid and Allodapine bees). However, this does not hold for small colonies (less than 100 workers) where more workers compete if there is a linear hierarchy than if there is no hierarchy (Fig. 2b). In small colonies the critical probability above which it is beneficial to be a hopeful reproductive is very high. There are few gamergates and thus few breeding vacancies, and the cost of not working is high (each hopeful reproductive represents a high proportion of the work force). Without hierarchy all hopeful reproductives have the same probability of becoming gamergate, and it cannot exceeds the critical probability. In contrast, when there is a dominance hierarchy this probability remains comparatively high for higher-ranked individuals, even in small colonies.

Our models are based on several assumptions. We assume that breeding vacancies are always immediately filled by a

hopeful reproductive who becomes gamergate. This supposes that mating can occur at any time of the year, and hence that males are present and active all year. This is supported by the data available for *Rhytidoponera confusa* (Ward, 1981). Would there be more hopeful reproductives if mating were seasonal? If workers were unable to predict the onset of the mating season the number of hopeful reproductives would be constant throughout the year, but it would be lower. This is because there would be no benefit of being a hopeful reproductive outside of the mating season. However, it is unlikely that workers cannot predict the forthcoming reproductive season since they rear male brood to adulthood (Ward, 1981). If workers could predict the onset of the mating season the number of hopeful reproductives would be lower outside of the mating season and higher during the mating season. We also assumed that all males are produced by gamergates. Male production by hopeful reproductives would increase the benefits of being a hopeful reproductive and thus increase their number. This assumption is reasonable in *R. confusa*. Only 5.8% of individuals with developed ovaries are not gamergates but uninseminated workers, and such workers with developed ovaries occur in only 1/4 of colonies (Ward, 1983). Additionally, we assume that all gamergates are equally fertile, so that each gamergate produces a fraction $1/G$ of the eggs. This is true in *R. confusa* (Ward, 1983) and in *Pachycondyla berthoudi* (Sledge et al., 1996). As we assume a constant colony size this implies that the number of eggs produced does not increase with gamergate number, and thus that gamergate fertility declines when gamergate number increases. This is the case in *Pachycondyla berthoudi* (Sledge et al., 1996). We further consider that gamergates are full-sisters, which is usually true in the related *Rhytidoponera* sp. 12 (Tay and Crozier, 2000). For simplification we set $H = 0$ to calculate Pc. With this assumption the linear model predicts that the longest possible hierarchy is 14 workers in a colony of 100 workers. To estimate the effect of this approximation we calculated Pc using $H = 14$ (i.e. $H = Hmax$) and re-run the linear model. The effect of the approximation is low: for almost all values of N the hierarchy length is identical when using $H = 14$ or $H = 0$. It is longer by one worker, seldom by two, for only few values of N.

We do not take into account colony fission. Queenless ant colonies reproduce by fission, with part of the colony leaving the nest to establish a new, independent, colony. Colony fission represents an additional benefit of becoming a hopeful reproductive, because it increases breeding opportunities (Peeters and Ito, 2001). For example, empirical data show that colonies with 100 workers have 4 gamergates, whereas colonies with 50 workers have 3 gamergates. Therefore, the fission of one colony of 100 workers in two colonies of 50 workers results in 2 additional breeding positions. This increased number of breeding vacancies results in more hopeful reproductives. However, the effect is likely to be small because fissions are not common (C. Peeters, unpublished). If workers are unable to predict a forthcoming fission the number of hopeful reproductives remains constant over time. Conversely, if workers can predict the imminence of fission the number of hopeful reproductives should increase before

the fission occurs. The linear hierarchy model predicts 10 hopeful reproductives in a colony of 100 individuals without fission containing 4 gamergate positions, and 12 hopeful reproductives in a colony splitting in two colonies of 50 ants with 3 gamergates positions each.

One major problem for studying dominance hierarchies is to objectively determine which workers are competing in the hierarchy. We defined hopeful reproductives as workers involved in at least 2% of the aggressive interactions. Another possibility is to determine the skew in aggressions (Kokko and Lindström, 1997; Kokko et al., 1999; Tsuji and Kazuya, 2001), which allows comparing relative hierarchy lengths: the shorter the hierarchy the larger the skew, as fewer individuals monopolise aggressions (Monnin et al., 2003). However, skews in aggressiveness do not allow determining absolute hierarchy length. This lack of objective ways to unambiguously determine where the hierarchy stops needs to be addressed, and suitable mathematical tools needs to be developed.

The smallest *R. confusa* type B colony collected in the field had 21 workers and 2 gamergates (collected by C. Peeters in August 1983, pers. comm.). We do not know if smaller type B colonies occur in nature. Small colonies are difficult to detect because they have few foragers returning to the nest and an inconspicuous nest entrance. However, because type B colonies reproduce by fission it is probable that there is a minimum size for the group starting a new colony, because smaller groups would be less efficient or not viable. The linear model predicts a hierarchy of 2 workers for a colony with 21 workers and 2 gamergates. It also predicts that no hierarchy can exist in colonies with less than 20 workers: the probability of a breeding vacancy is too low (one or two breeding positions at most) and the cost of lazy hopeful reproductives is too high (each worker represents about 5% of the colony work force) for joining to be profitable. Such small colonies resemble colonies of *Dinoponera australis*, with a single gamergate and in average 14 workers. As predicted by the models, the gamergate performs most aggressions, that is there is no hopeful reproductive (Monnin et al., 2003).

In *R. confusa* gamergate number, G, depends on colony size, N. However, this correlation is not absolute and colonies of similar size can have different number of gamergates. Our observations reveal no differences in hierarchy lengths between similar-sized colonies with or without gamergates (Fig. 4a). That orphanage does not lengthen the hierarchy in our *R. confusa* colonies is surprising given that it does in other species. In *Platythyrea conradti* the experimental removal of the single queen results in increased aggressions among workers during a few days (Molet et al., in prep). Similarly, in several queenless ants the death or removal of the gamergate results in high aggressiveness during a few days, until a worker establishes her dominance (e.g. *D. quadriceps*: Monnin and Peeters, 1999; *Diacamma ceylonense*: Cuvillier-Hot et al., 2002). This suggests that hierarchy length does not depend on gamergate number. However, it is likely that colonies adjust the number of gamergates to colony size, so as to optimise colony efficiency. Colonies with many for-

agers but few gamergates would have a surplus of resources and could recruit additional gamergates. Ecological conditions are thus likely to affect hierarchy length. For instance, colonies living in a rich environment may have more gamergates because foragers are more successful so that fewer are required to sustain the colony.

The models can be applied to other polygynous species (or monogynous species using $G = 1$) where reproduction is regulated by a dominance hierarchy. In *Gnamptogenys menadensis* most colonies have no queen and several gamergates (Gobin et al., 1999). The gamergate number depends on colony size ($G = 0.0027N + 2.4594$, Spearman R = 0.45; p = 0.018, 27 colonies from Gobin et al., 2001) and the hierarchy length is known in various-sized experimental colonies (Gobin et al., 2001). These observed hierarchy lengths fit well the prediction of the linear model (Fig. 4b). The models could include additional factors, such as male production by hopeful reproductives, and possibly colony fission. It would be especially interesting to include morphological castes with caste-specific working rate and egg laying efficiency, and to model the costs and benefits of joining the hierarchy for the queen and for gamergates. This could help understanding the existence of type A and type B colonies, the loss of the queen caste in some species, and the loss of worker totipotency in others. For example, the high lifespan and fertility of queens in higher ants might make it unprofitable for workers to become hopeful reproductives, therefore precluding the existence of a dominance hierarchy, whereas the low queen-worker dimorphism characteristic of lower ants might favour queen replacement by workers. Species such as *Rhytidoponera confusa*, with two types of colonies (type A with one queen and no gamergate versus type B with no queen and gamergates), are ideal for such a study.

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