

Shift in Colonial Reproductive Strategy Associated with a Tropical-Temperate Gradient in *Rhytidoponera* Ants

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ABSTRACT: Offspring quality and quantity are subject to a trade-off. Depending on species, ant colonies can produce either numerous winged queens that start new colonies alone (independent colony foundation [ICF]) or one propagule consisting of reproductives helped by workers (fission). Some species do both. In the *Rhytidoponera impressa* group, colonies with winged queens use ICF, whereas colonies with mated workers use fission. We assessed the effect of latitude and environment on colonial reproduction by collecting 79 colonies along the Australian east coast. A population dynamical model predicted that from tropical north to temperate south, seasonal fluctuations and harsher conditions should lead to a decrease in ICF success (−48%), making fission a suitable alternative. Yet, our empirical data showed that ICF persists at a higher rate than expected, presumably because it allows aerial dispersal, unlike fission. Investigation of colony demography and measurement of lean and fat weights in virgin winged queens and workers showed that, from north to south, colonies increase quality of queens relative to workers (+50%) at the cost of quantity (−86%). This modification limits the decrease in ICF success (−34%). A tremendous range of offspring phenotypes associated with quality-quantity trade-offs make ants competitive in diverse habitats.

Keywords: independent colony foundation, colony fission, gamergate, quality-quantity trade-off, *r*-/*K*-selection.

The choice between offspring quality and quantity is a widespread dilemma faced by parents in both animals and plants. It has been the subject of extensive theoretical work

and empirical testing (see reviews by Roff 1992, chap. 10; Stearns 1992, chap. 7). Typically, however, only small shifts in the body size of offspring are possible (e.g., in solitary arthropods; Fox and Czesak 2000). In contrast, if we consider colonies of social insects, not only can the size and number of gynes (i.e., young virgin winged queens) produced annually be adjusted, but it is possible to produce additional workers that help queens (e.g., swarms of honeybees). Thus, the investment strategy in offspring has an extra dimension, allowing a much wider range of options, from producing many small and independent gynes to one single dispersing unit composed of one or a few reproductives and many workers.

This wide range of offspring phenotypes is especially conspicuous in ants, because the workers are wingless. During independent colony foundation (ICF), the gynes disperse by flight, excavate their nests, and live like solitary insects until the first generation of offspring workers become adults. Mortality is high, and as a consequence, numerous gynes have to be produced each year (e.g., up to 54 gynes in a colony of *Harpegnathos saltator* with 60 workers; Peeters et al. 2000). In species that exhibit “nonclaustral” ICF, a foundress needs to forage outside the nest to feed her first brood; this is risky and carries a high probability of failure (Wilson 1971; Peeters 1997; Brown and Bonhoeffer 2003). The success of gynes can be increased by provisioning them with larger metabolic reserves (fat: Passera and Keller 1990; proteins: Wheeler and Martínez 1995; wing muscles reviewed in solitary insects: Roff 1990) that limit the frequency of foraging during this vulnerable period. The evolution of gynes that have enough reserves to found their colony in complete isolation (“claustral” ICF) probably led to a dramatic increase in success, although mortality remains high during nuptial flight and nest excavation (Hölldobler and Wilson 1977; Peeters and Ito 2001). In the few species where both claustral and nonclaustral ICF are possible, the production of gynes faces a quantity-quality trade-off (e.g., Johnson 2006). The other alternative to decrease the mortality of queens is through colony fission, where a gyne leaves the mother colony with a group of workers that help her throughout colony founding. Fission does not require ex-

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pensive gynes, but it does require an additional investment in workers (Pamilo 1991). This is a strategy in which the quality of propagules is extremely high but the quantity is dramatically reduced, often to one.

Importantly, whereas nonclaustral and claustral ICF are two ends of a continuum, fission is a very distinct strategy in ants, causing dramatic differences with respect to dispersal. Indeed, ICF allows for long-range dispersal by flight, but ant workers are always wingless, so fission results in only limited dispersal on the ground. Nevertheless, transitions from ICF to fission occurred repeatedly and independently in ants (Rüppell and Heinze 1999). Given that the strategies of ICF and fission have such different consequences, it remains an open question how selection can favor such transitions and how they originate. In this article, we investigate under what conditions one strategy is favored over the other. Previous studies on the correlation between these two strategies and the characteristics of colonies and habitats yielded inconsistent results. It seems that habitat patchiness, food and nesting sites limitation, and nesting site instability favor fission over ICF (Heinze and Tsuji 1995). Polygyny, the occurrence of several queens per colony, is also thought to be linked with colony fission (Hölldobler and Wilson 1977), although many species that perform fission are monogynous (e.g., André et al. 2001). Nevertheless, we do not know how species adapt to increasing difficulty in succeeding with ICF. Do they immediately switch to fission or do they keep on producing gynes that can offer the benefits of long-range dispersal? In that case, do they alter the quantity or quality of gynes so that individual gynes remain sufficiently successful to be a strategy worth investing in? Genera and species exhibiting alternative colonial reproductive strategies are ideal models to answer such questions.

Ants of the *Rhytidoponera impressa* group (subfamily Ectatomminae) are carnivorous and occur in forests of the Australian east coast, in a wide range of latitude (about 3,000 km) from the tropical north, in subtropical rain forests, to the temperate south, in dry rain forests and wet sclerophyll forests (Ward 1981a). Most species of the genus *Rhytidoponera* lack winged queens but have mated egg-laying workers called gamergates, and colonies reproduce exclusively by fission (Haskins and Whelden 1965). Yet winged queens still occur in the basal *R. impressa* group (unpublished phylogeny by H. Reichel), thus allowing the option of colonial reproduction by ICF. Founding queens raise offspring almost as large as themselves (fig. 1), hence ICF is always nonclaustral; that is, queens need to hunt insects aboveground (Ward 1981b). Queenright colonies produce a large number of gynes annually. Following queen death, a few workers can mate and reproduce. Gamergate colonies reproduce by fission (Ward 1981b). The *R. impressa* group consists of five sibling species (Ward 1980b). Three

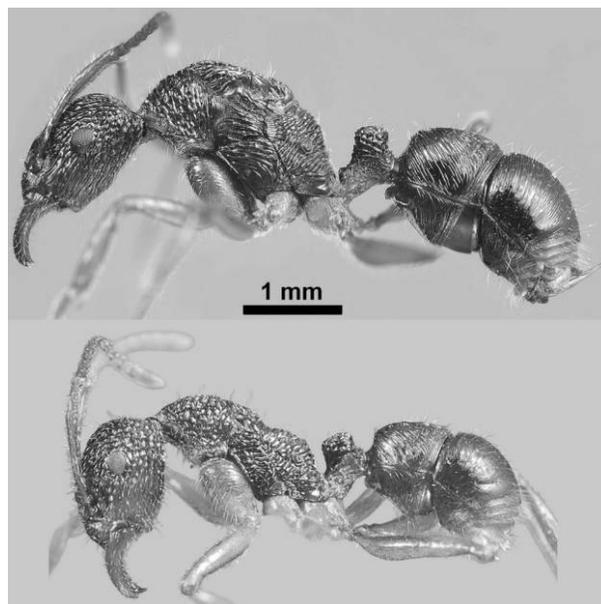


Figure 1: Small size difference between a queen (*top*; here after having shed her wings) and a worker (*bottom*) of *Rhytidoponera confusa*. Such a queen cannot produce workers solely with her metabolic reserves and must forage during the founding phase. Photographs copyright Derek Smith.

of them, *R. impressa*, *R. chalybaea*, and *R. confusa*, exhibit both nonclaustral ICF and fission. Interestingly, in the northern species *R. purpurea*, only queenright colonies are known, suggesting that colonies reproduce only by ICF, whereas in the southern species *R. enigmatica*, winged queens have never been reported, suggesting that colonies reproduce only by fission (Ward 1981b, 1983a).

The biology and distribution of the *R. impressa* group provides a rare opportunity to investigate the mechanisms of the transition from ICF to fission. Indeed, being nonclaustral, founding queens are directly exposed to the environmental changes that occur in the large latitudinal range. We empirically assessed the effect of latitude on colonial demography and colonial reproductive strategies, that is, quality (lean and fat weight) and quantity of gynes. Their subsequent success at ICF was estimated using both field data (the proportion of queenright and gamergate colonies in the populations) and modeling approaches. Importantly, our population dynamical model allows the assessment of the likely outcome of plausible cause-consequence relationships between environmental parameters and colonial reproductive strategies. Indeed, the empirical approach only correlates latitude with colonial reproductive strategies, which does not give much insight without assessing which environmental parameters are responsible. However, the latter are very difficult to measure

in the field, and their effect is difficult to test without modeling. We studied whether the transition from ICF to fission occurs gradually or suddenly, and we discuss this transition in relation to r - and K -selection. We also discuss the generality of our model, which is valid for any ant taxa having ICF and fission as alternative colonial strategies.

Material and Methods

Colonies

We collected 79 complete colonies (49 queenright and 30 gamergate) of four species from the *Rhytidoponera impressa* group, that is, *R. purpurea*, *R. impressa*, *R. chalybaea*, and *R. confusa*, in rain forests along the Australian east coast (Lake Eacham National Park: 17.28°S, 145.60°E; Paluma Range National Park: 19.01°S, 146.21°E; Mary Cairncross Park: 26.78°S, 152.88°E; Bruxner Park: 30.25°S, 153.11°E; Pearl Beach: 33.55°S, 151.30°E; Ku-Ring-Gai Chase: 33.75°S, 151.15°E; Royal National Park: 34.14°S, 151.03°E; Cataract: 34.33°S, 151.00°E; Bateman Bay: 36.25°S, 150.50°E) in different months between 1985 and 2005. These ants nest in rotten logs or under stones on the ground (Ward 1981a). All workers, gynes, males, and pupae were counted in each colony. We also used data on 129 colonies (73 queenright and 56 gamergate) collected by P. Ward between 1974 and 1980 at 34 different localities from latitude 17.28°S to 37.38°S (Ward 1978; P. S. Ward, personal communication).

Determination of Dry, Lean, and Fat Weights

In the 18 gyne-producing colonies collected in September 2005, 30 workers and up to 30 gynes per colony were stored in a 5% formaldehyde solution, a preservative that does not solubilize fat (D. Reznick, personal communication). Since colonies were collected just before mating flights (Ward 1981b), gynes were already almost fully provisioned (see Keller and Passera 1989). Fat content was estimated using an extraction procedure similar to that of Peakin (1972). Specimens were dried for 24 h at 70°C and weighed (dry weight). Fat was then extracted with petroleum ether (boiling point 40°–60°C) in a Soxhlet extractor, with the following schedule: 6 h extraction, 18 h soaking, and 6 h extraction. Preliminary tests showed that 6 h were enough to extract all the fat from gynes. Specimens were dried again for 24 h at 70°C and weighed (lean weight). The difference between dry and lean weights is fat weight.

Data Analysis

The *R. impressa* group has been divided into five sibling species by Ward (1980b), but it consists of a series of quasi-

isolated populations. The species overlap only slightly. Within *R. impressa*, differences in gene frequencies as well as allelic substitutions suggest reproductive isolation between populations (Ward 1980a). Moreover, hybridization leads to genic introgression between *R. impressa* and *R. chalybaea*. Because the boundaries between species are unclear and the isolation between populations is important (e.g., recent destruction of forest habitats), we treated the whole group as a single unit. This allows us to cover a wide range of latitude from the north to the south of the Australian east coast, thus maximizing changes in environmental conditions and their potential impact on ants' life history. Although only queenright colonies of *R. purpurea* have been reported, no mating experiments or extensive dissections have been performed to test whether workers of this species can mate and reproduce like other workers in the genus *Rhytidoponera*. Accordingly, we cannot exclude the ability of this species to produce new colonies by fission. The lack of gamergate colonies may just be an answer to selective pressures in the northern latitudes. Hence, *R. purpurea* must be included in the analysis.

We assessed the effect of latitude on ants by performing linear regressions of each trait against latitude. When there was a single value of the trait per latitude, standard linear regressions were performed (Sokal and Rohlf 1995, box 14.3). However, when there were multiple values of the trait per latitude, linear regressions were performed using the mean value of the trait at each latitude (Sokal and Rohlf 1995, box 14.4). The significance of the regression coefficient was tested over the mean squares of the deviations from the regression line, but when possible, it was tested over the pooled within-group mean squares and deviations-from-regression-line mean squares in order to increase the power of the test (Sokal and Rohlf 1995, box 10.3). We used Statistica 7.1 for all other analyses.

Modeling the Effect of Latitude on the Proportion of Queenright Colonies

The empirical data link latitude with colonial reproductive strategies, and data available in the literature link latitude with environmental parameters. However, this gives no indication about which of these environmental parameters the correlation results from. As the causal effect cannot be easily measured empirically, we needed another approach to assess the effect of these parameters on colonial reproductive strategies. Consequently, we developed a simple population dynamical model in order to predict the effect of different parameters on the coexistence between queenright and gamergate colonies (q and g) in a population. The dynamics of the system is governed by the following equations:

$$\frac{dq}{dt} = \left[i \frac{R}{1+q+g} \left(1 - \frac{q+g}{c \max} \right) - m - d \right] q,$$

$$\frac{dg}{dt} = dq + \left[f \frac{R}{1+q+g} \left(1 - \frac{q+g}{c \max} \right) - m \right] g.$$

Queenright colonies disappear either because of accidental destruction (with rate m) or because only the queen dies (with rate d), which results in a gamergate colony (orphanage). Indeed, queen adoption (e.g., Stuart et al. 1993) is not an option in such monogynous colonies. Queenright colonies start by ICF with a success of i . However, i is the maximum possible success for independent foundation, and it is reduced by competition for both resources (R) and nesting sites (carrying capacity: $c \max$).

Gamergate colonies end only through extinction m ; they result either from orphanage of queenright colonies (with rate d) or from fission (with success f) of another gamergate colony. The subsequent success of colony establishment is dependent on competition for resources R and nesting sites $c \max$ in the same way as queenright colonies.

Environmental factors such as latitude probably influence all these parameters. Our assumption is that going from tropical to temperate environments, resources R and success of ICF i decrease while colony extinction m and orphanage following queen death d increase (we return to these hypotheses in "Discussion"). Importantly, these parameters may not be constant in time because of seasonality, and moreover, there is likely to be a latitudinal gradient in the amplitude of fluctuations, from low in the north to high in the south.

For simplicity, colony size and colony growth are not explicitly taken into account, which allows us to limit the variables of the model to the number of colonies of each type. This approach is justified if colonies grow quickly to an equilibrium colony size and there are no other systematic differences between the two types of colonies. Differences regarding colony size and growth are implicitly included in the values of i and f . These two parameters combine colonial growth rate, number of propagules produced, and density-independent success rate of foundation. The model is sufficiently simple to allow a mathematical analysis of the equilibrium in a constant environment. Here, we present a numerical analysis of the equilibrium densities of queenright and gamergate colonies predicted by the model.

Modeling the Effect of Latitude on Gyne Success

Our aim was to understand how latitude affects the success of ICF by gynes, through changes in both environmental conditions and gyne/worker dry weight ratio, and to assess

these two effects individually. Wiernasz and Cole (2003) estimated the effect of gyne weight on success of ICF in one population of the harvester ant *Pogonomyrmex occidentalis* as $\text{survival} = -0.0874 + 0.0419 \times \text{dry weight}$. Only one population was studied, so environment was constant. We adapted this function to compute the expected effect of *Rhytidoponera* gyne/worker dry weight ratio on gyne success at the different latitudes. We compared this with the empirical gyne success at each latitude, estimated from the proportion of queenright colonies in the population, and we predicted the effect of the environment on gyne success independently of gyne/worker dry weight ratio.

Results

Colony Demography

Queenright colonies consisted of one dealate queen, 337 ± 43 (mean \pm SE, $N = 49$) workers, 37 ± 11 gynes ($N = 39$), and 46 ± 20 males ($N = 39$), while gamergate colonies consisted of 101 ± 14 workers ($N = 30$), 0.04 ± 0.04 gynes ($N = 23$), and 2 ± 1 males ($N = 23$) but no dealate queen. When adding Ward's data (129 colonies), queenright colonies consisted of one dealate queen, 330 ± 25 workers ($N = 122$), 41 ± 6 gynes ($N = 112$), and 35 ± 8 males ($N = 112$), while gamergate colonies consisted of 159 ± 28 workers ($N = 86$), 0.08 ± 0.07 gynes ($N = 76$), and 16 ± 4 males ($N = 76$) and no dealate queen. Thus, queenright colonies had significantly more workers (t -test: $t = 4.53$, $df = 206$, $P < 10^{-5}$) and more males ($t = 1.85$, $df = 186$, $P = .07$) than gamergate colonies, regardless of the data set used. Gamergate colonies produced almost no gynes, that is, many fewer than queenright colonies ($t = 5.52$, $df = 186$, $P < 10^{-6}$).

Effect of Latitude on the Proportion of Queenright Colonies

Our population dynamical model was used to predict the effects of the parameters on the numbers of queenright and gamergate colonies when both are at equilibrium. A little algebra shows that under equilibrium, the overall density of colonies is

$$\bar{q} + \bar{g} = c \max \frac{[Ri/(m+d)] - 1}{[Ri/(m+d)] + c \max},$$

with a proportion

$$\frac{\bar{q}}{\bar{q} + \bar{g}} = 1 - \frac{di}{(m+d)(i-f)}$$

of queenright colonies (provided that ICF is efficient

enough, $i > f[m + d]/m$; otherwise, the gamergate colonies will outcompete the queenright colonies, resulting in the equilibrium $\bar{q} = 0$, $\bar{g} = c \max [Rf/m - 1]/[Rf/m + c \max]$. Given coexistence, resources R and nesting sites $c \max$ have no effect on the proportion of queenright colonies (see also fig. 2), which is not a surprise because these factors equally affect the foundation success of both types of colonies. The proportion of queenright colonies increase with success of ICF i and colony extinction m and decrease with increasing orphanage following queen death d and success of fission f (fig. 2). Going from north to south along the Australian east coast probably increases m and d and decreases i and R because of the harsher environmental conditions (see “Discussion”). If we simulate a latitudinal shift that would cause a 10% change in each parameter (10% increase for m and d and 10% decrease for i and R), this would lead to a 2.4% decrease in the proportion of queenright colonies. Moreover, the temperate southern climate yields more seasonal and inter-annual variations in these parameters than the tropical

northern climate (see “Discussion”). Thus, we included temporal variability in our model, with oscillating parameters; for example, $R(t) = R_0 \times (1 + \sin(t))$. Note that these oscillations do not alter the mean value of the parameters over time. Although the overall effect of the oscillations was small, a sensitivity analysis (fig. 3) showed that an oscillating R leads to a 3% decrease in the proportion of queenright colonies and an oscillating i to a 6% decrease. Thus, when modifying its parameters to mimic a shift from north to south, the model predicts a decrease in the proportion of queenright colonies. Note that a change in R does not change the equilibrium proportion; the effect of fluctuations in R is therefore entirely due to its destabilizing effect on the dynamics of queenright and gamergate colonies. Such destabilization can result because R directly affects the number of new queenright colonies, whereas changes in the number of new gamergate colonies follow later because they are buffered by the dynamics of queenright colonies. That mean densities may diverge from equilibrium densities is a well-

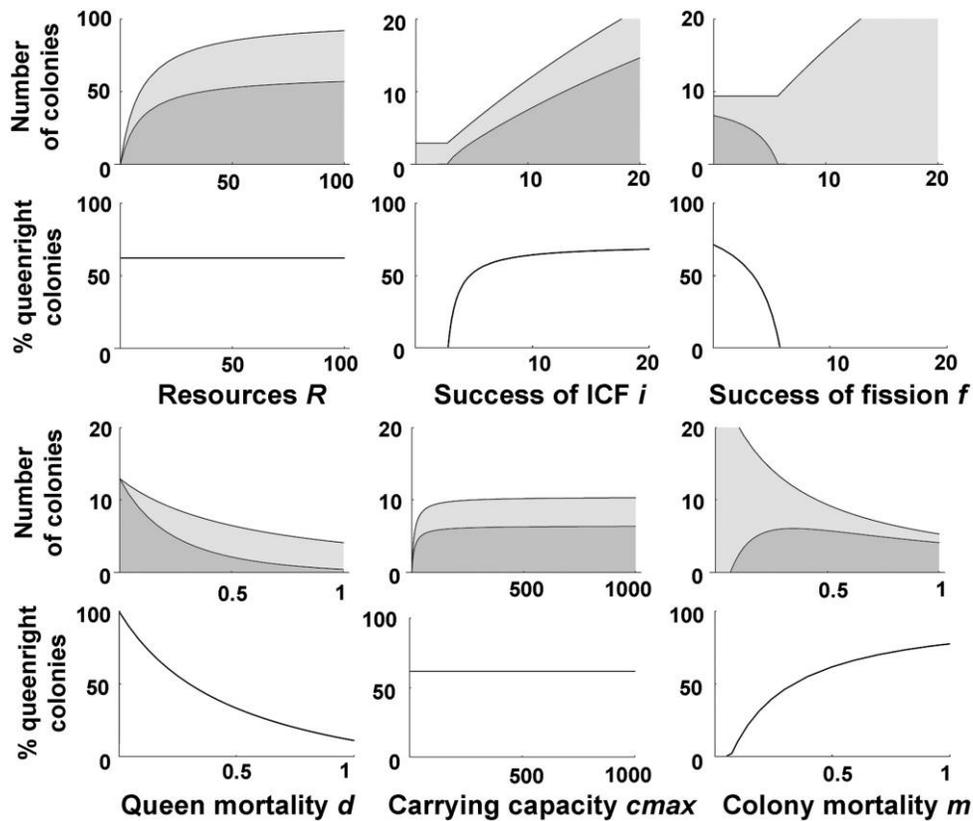


Figure 2: Densities of queenright and gamergate colonies as a function of model parameters. Dark gray = queenright colonies, light gray = gamergate colonies. Default values of parameters were chosen so that queenright and gamergate colonies coexist at the equilibrium, that is, resources $R = 1$, success of independent colony foundation $i = 8$, success of fission $f = 2$, queen death $d = 0.2$, carrying capacity $c \max = 100$, colony mortality $m = 0.5$.

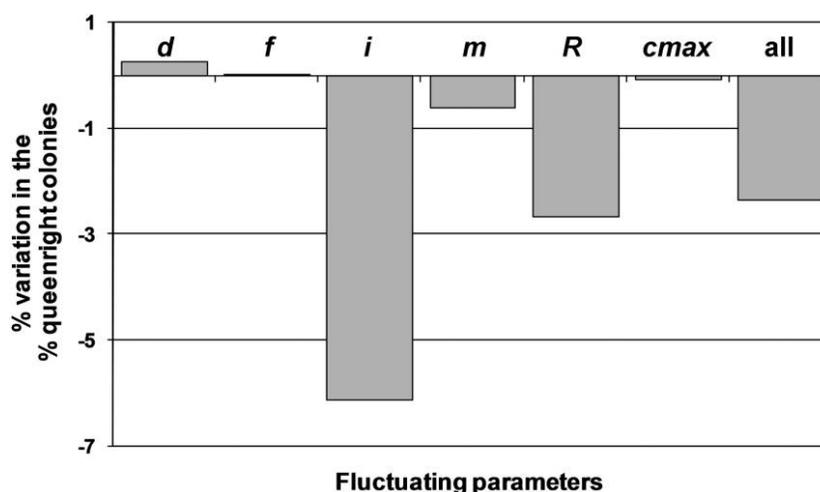


Figure 3: Sensitivity analysis of the proportion of queenright colonies to fluctuations in model parameters. Default values of parameters are the same as in figure 2.

known effect but unfortunately very difficult to assess mathematically (Hofbauer and Sigmund 1988).

This prediction was tested by assessing empirically the effect of latitude on colonial reproductive strategy. Contrary to the model, this approach directly connected latitude and colonial reproductive strategies without involving the different parameters that are influenced by latitude and that in turn influence colonial reproductive strategy. For each latitude of collection, we computed the proportion of queenright colonies in the population. The proportion of queenright colonies decreased when latitude increased (weighted linear regression, table 1; fig. 4), although this became not significant when pooling our data with those obtained by Ward (detailed statistics in table 1). Thus, queenright colonies are more frequent in the north than in the south. This is obvious at the species level because *Rhytidoponera purpurea* from the north does not have gamergate colonies, so only queenright colonies occur, while *Rhytidoponera enigmatica* from the south only has gamergate colonies. The three species in between have both types. Adding Ward's data to ours led to a decrease in the significance of the test. Indeed, his data alone yielded no significant linear regression (table 1) because all his collection sites except one were located in the south. Moreover, only 10 colonies were collected at the north locality (vs. 119 in the south), thus lowering the weight of this population in the linear regression. In contrast, our collection sites are more evenly distributed from north to south (fig. 4), and the number of colonies collected per population is more similar. Thus, each population contributes importantly to the regression line. For these rea-

sons, the linear regression based on our results alone is more likely to reflect reality.

Effect of Latitude on Colony Demography

Empirical data showed that the size of queenright colonies (i.e., number of workers) decreased when latitude increased, but latitude had no effect on the size of gamergate colonies (linear regressions, table 1). These results remained the same when we added Ward's data. The number of gynes in queenright colonies decreased with latitude. However, this effect disappeared when we removed the positive effect of colony size on the number of gynes; it became significant again when increasing our sample size with Ward's data.

Effect of Latitude on Gyne Weight

The data obtained from fat extractions showed that gyne dry weight, lean weight, and fat weight did not change with latitude (table 1; fig. 5a). In contrast, worker dry weight and lean weight decreased with latitude, but latitude had no effect on worker fat weight (fig. 5b). Gyne and worker fat percent also did not change with latitude (fig. 5c). However, gyne/worker dry weight, lean weight, and fat weight ratios increased with latitude (fig. 5d). Total colonial investments in gyne dry weight, lean weight, and fat weight corrected for colony size and male production were not influenced by latitude (regression of latitude on residuals of the multiple regression between colony size/number of males and investment in gynes).

Table 1: Linear regression of latitude on different parameters, using our data alone (79 colonies), our data and Ward’s data combined, and Ward’s data alone (129 colonies)

Effect of latitude on	Statistics				Regression line $y = A \times \text{latitude} + B$	
	<i>F</i>	df	<i>P</i>	<i>R</i> ²	A (slope)	B (intercept)
% of queenright colonies:						
Our data only	10.72	1, 6	.02	.64	-1.75	116.15
Combined data	1.51	1, 31	.23	.05
Ward’s data only	.09	1, 25	.77	.004
Size of queenright colonies:						
Our data only	184.60	1, 47	<10 ⁻⁶	.8	-25.53	1103.44
Combined data	477.36	1, 120	<10 ⁻⁶	.8	-29.54	1241.14
Size of gamergate colonies:						
Our data only	.31	1, 29	.58	.01
Combined data	.84	1, 84	.36	.01
Number of gynes in queenright colonies:						
Our data only	23.70	1, 37	<10 ⁻⁴	.39	-4.30	161.63
Combined data	303.86	1, 110	<10 ⁻⁶	.73	-6.23	231.04
Effect of colony size on number of gynes:						
Our data only	28.47	1, 37	<10 ⁻⁵	.43	.14	-17.41
Combined data	104.60	1, 110	<10 ⁻⁶	.49	.16	-14.26
Number of gynes in queenright colonies after correcting for colony size:						
Our data only	1.44	1, 37	.24	.04
Combined data	21.52	1, 110	<10 ⁻⁵	.16
Gyne dry weight	.52	1, 3	.52	.08
Gyne lean weight	.49	1, 3	.53	.07
Pooled ^a	.95	1, 16	.34
Gyne fat weight	1.46	1, 3	.31	.22
Worker dry weight	44.92	1, 3	.01	.83	-.05	3.22
Pooled ^a	51.44	1, 16	<10 ⁻⁴
Worker lean weight	13.11	1, 3	.04	.71	-.04	2.88
Pooled ^a	26.15	1, 16	<10 ⁻³
Worker fat weight	.50	1, 3	.53	.09
Gyne fat %	2.11	1, 3	.24	.29
Worker fat %	.02	1, 3	.90	.004
Gyne/worker dry weight	11.79	1, 3	.04	.7	.05	1.78
Pooled ^a	24.80	1, 16	<10 ⁻³
Gyne/worker lean weight	10.22	1, 3	.05	.57	.03	1.42
Gyne/worker fat weight	4.60	1, 3	.12	.46	.23	4.64
Pooled ^a	9.21	1, 16	.01
Colonial investment in gyne dry weight after correcting for colony size and male production						
Our data only	.96	1, 3	.40	.12
Pooled ^a	1.90	1, 16	.19
Colonial investment in gyne lean weight after correcting for colony size and male production						
Our data only	.66	1, 3	.47	.08
Pooled ^a	1.11	1, 16	.31
Colonial investment in gyne fat weight after correcting for colony size and male production						
Our data only	.67	1, 3	.47	.12

^a See “Data Analysis” in “Material and Methods.”

Data about gyne and worker dry weight in populations of species from the *Rhytidoponera impressa* group are available (Ward 1983b). However, these colonies were collected throughout the year, generally long before the mating flights, so gyne provisioning was not always complete. In-

deed, Ward’s gyne dry weights are lower than ours (*t*-test: *t* = 2.65, *df* = 34, *P* = .012), while worker dry weights are similar (*t*-test: *t* = 2.02, *df* = 23, *P* = .055). Thus, we could not pool these data with ours. These differences imply a significant provisioning of gynes at the adult stage,

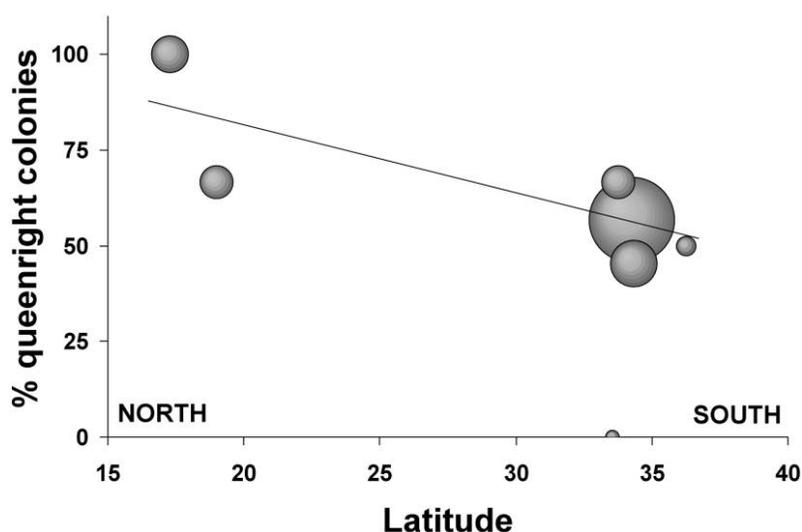


Figure 4: Effect of latitude on the proportion of queenright colonies (our data only—Ward’s data excluded). The surface of data points is proportional to the number of colonies collected at this locality, and the linear regression is weighted accordingly. 17.28°S: six *Rhytidoponera purpurea* and one *Rhytidoponera impressa*; 19.01°S: six *R. impressa*; 33.55°S: one *Rhytidoponera confusa*; 33.75°S: six *R. confusa*; 34.25°S: 37 *R. confusa*; 34.33°S: 11 *R. confusa*; 36.25°S: two *R. confusa*. Detailed statistics in table 1.

making timing of collection a crucial point in studies that estimate investment in sexuals. Larval feeding is not the sole provisioning stage. For instance, Keller and Passera (1988) found that in *Iridomyrmex humilis*, gyne dry weight increases by 46% between emergence and time of mating.

Effect of Latitude on Gyne Success

We wanted to disentangle the effects of gyne/worker dry weight ratio and environment on gyne success by combining theoretical and empirical approaches. Wiernasz and Cole’s (2003) equation is based on empirical data and describes the success of gyne as a function of gyne weight. We modified it to take into account gyne/worker dry weight ratio (relative measure) instead of gyne dry weight (absolute measure), so that the equation could also be applied to our taxa. The new slope thus became $0.0419 \times Pogonomyrmex occidentalis$ worker dry weight = 0.100 (dry weight = 2.376 ± 0.588 ; B. Cole, personal communication). We set the northernmost locality as reference, which means that we considered gyne success to depend only on the environment and that gyne/worker dry weight ratio does not bring extra success at this latitude: $\text{success}_{\text{reference}} = \text{intercept} + 0.100 \times \text{gyne/worker dry weight ratio}_{\text{reference}}$, with $\text{success}_{\text{reference}} = 0$ and $\text{gyne/worker dry weight ratio}_{\text{reference}} = 1.997$. Thus, our function was $\text{success} = -0.200 + 0.100 \times \text{gyne/worker dry weight ratio}$. We used it to predict the theoretical increase in gyne success in our taxa due to an increase in gyne weight at each locality from

north to south. We subtracted this success from the empirical success estimated from the proportion of queenright colonies in the populations, to obtain the theoretical effect of the environment on gyne success. When latitude increases by 1°, the success of gynes decreases by 2.80% because of the environment (linear regression: $F = 182.13$, $df = 1, 3$, $P = .001$, $R^2 = 0.98$) and increases by 0.76% because of the increased gyne/worker dry weight ratio (linear regression: $F = 13.45$, $df = 1, 3$, $P = .035$, $R^2 = 0.82$). Thus, throughout our sample from north to south, the success of gynes decreases by 34.43%, which can be seen as a 47.83% decrease due to the harsher environment and a 13.40% increase due to heavier gynes relative to workers (fig. 6).

Discussion

Our study suggests that the latitudinal gradient from tropical north to temperate south has a large impact on the reproductive strategy of the *Rhytidoponera impressa* group. Both modeling and empirical approaches show that the proportion of queenright colonies in the populations decreases from north to south, indicating that environmental changes make fission more successful than nonclaustral ICF by winged queens. This is confirmed empirically by the decrease in size of queenright colonies but not gamergate colonies. Our empirical data also show that gynes are produced in smaller quantity, but they are heavier relative to workers in both lean weight and fat weight

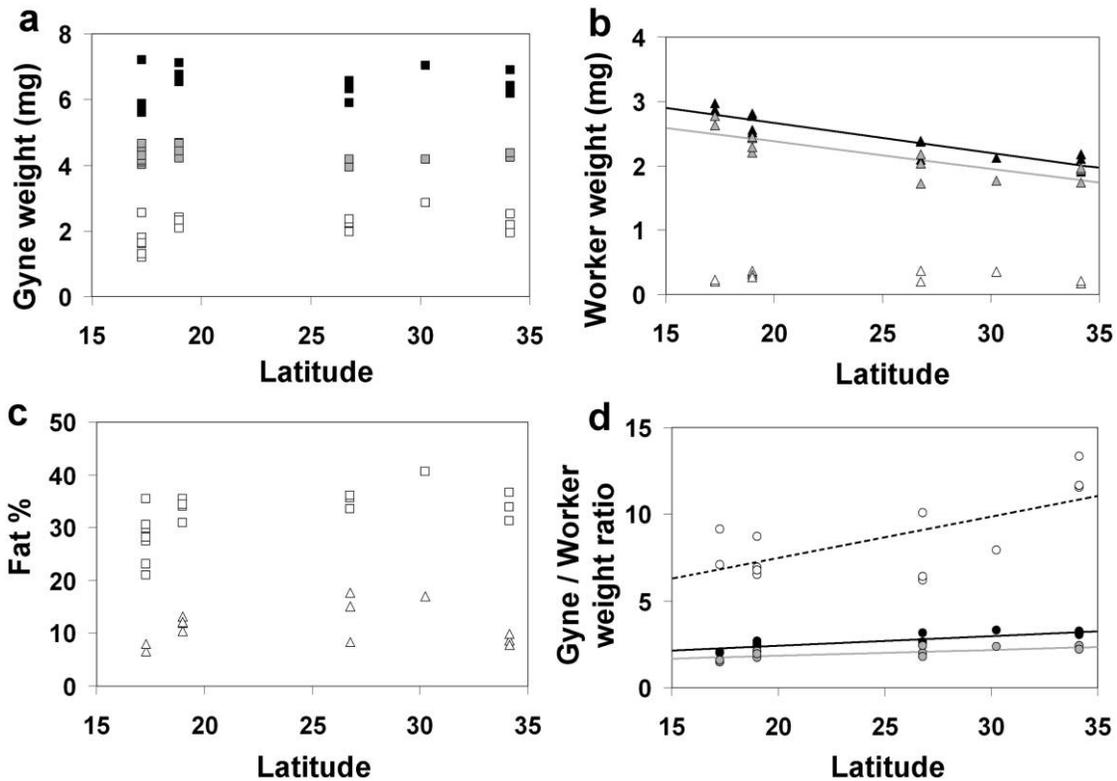


Figure 5: Effect of latitude on dry weight (*black*), lean weight (*gray*), and fat weight (*white*) of gynes (*squares* in *a*) and workers (*triangles* in *b*). *c*, Fat percentages; *d*, queen/worker weight ratios. Only significant regression lines are shown. Detailed statistics in table 1.

(queen/worker weight ratios increase by 50% in the latitudinal range of our study). Thus, their individual success in raising the first generation of workers would be expected to increase, were it not that the environment deteriorates even faster. The improvement in gyne quality at the cost of quantity aims at limiting the decrease in colonial reproductive success. Considering gyne/worker weight ratios instead of absolute values is essential, because founding queens have to produce a certain number of workers during ICF before colonies become established. These ratios are therefore indices of gyne quality, whereas gyne and worker absolute weights may vary for other reasons, including changes in prey preference and consequences of Bergmann's rule (Bergmann 1947; Mayr 1956) or converse Bergmann's rule (Mousseau 1997). Bergmann's rule states that the size of organisms increases with latitude. In endothermic organisms, bigger size is indeed linked with lower surface/volume ratio and accordingly lower heat loss, which is useful at higher latitudes. However, Bergmann's rule also applies to ectothermic organisms (e.g., Kaspari and Vargo 1995; Blanckenhorn and Demont 2004; in ants: Kaspari 2005) because low temperatures at higher latitudes delay maturity and cause a longer growth period.

In order to understand why the environmental changes from north to south do not affect queenright and gamergate colonies to the same degree, one must consider their respective life-history traits, which differ dramatically. First, during nonclaustral ICF, queens have to forage on their own and face high mortality, whereas several workers carry out this task during colony fission. Second, incipient colonies founded by ICF remain small for quite a long time. This is especially true in ants with low queen/worker dimorphism, where incipient colonies grow very slowly. For instance, founding queens of *Rhytidoponera confusa* need 2 months to produce the first six workers (C. Peeters, unpublished data on one incipient colony with a queen fed ad lib.). In contrast, fission propagules initially have a much larger size. Last, contrary to gamergate colonies, queenright colonies are monogynous, which makes orphanage more likely. In addition, the consequences of orphanage are not the same in the two colony types, because orphaned queenright colonies become gamergate colonies, while the gamergate state is irreversible.

For all these reasons, incipient queenright colonies are more susceptible to stress imposed by the environment than gamergate colonies. Several facts indicate that tem-

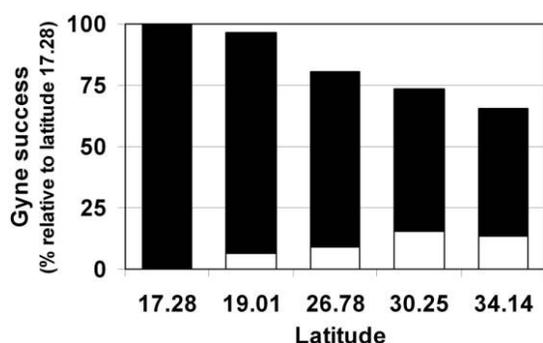


Figure 6: Effect of latitude on the success of colony founding by gynes, divided into two components as predicted by the model. Total bar area represents success measured empirically. The area in white represents success due to gyne quality, estimated from Wiernasz and Cole's (2003) equation (dry weight increases from north to south). The area in black represents success due to environment, computed as the difference between total and white (conditions become harsher from north to south).

perate environments impose a disadvantage on lone foundresses and incipient queenright colonies, and this may eventually tip the balance in favor of fission. First, annual net primary productivity (and by extension available insect prey) decreases from tropical to temperate forests (Begon et al. 1996). Second, activity remains high year-round in tropical environments, but it decreases during winter in temperate environments, notably because temperatures and humidity drop below the critical thresholds for many arthropods (Janzen and Schoener 1968; Wolda 1988). For instance, monthly mean temperatures never drop below 16°C in Cairns (latitude 16.87°S) but they reach 7°C in Sydney (33.94°S; data collected since 1945: <http://www.apsru.gov.au>). In species of the *R. impressa* group, foraging activity decreases during winter (Ward 1981a) and very few prey are available, so inter- and intraspecific competition for resources must be high. Last, small colonies are not buffered as efficiently as large colonies against food shortages (e.g., in *Solenopsis invicta*; Kaspari and Vargo 1995). These factors may also explain why queenright colonies never grow as large in the south as in the north. In our population dynamical model, this corresponds to decreased resources R , increased mortality m of colonies and mortality d of queens in queenright colonies, and decreased success i of ICF. Seasonal fluctuations in environmental parameters are also more pronounced in the south. For instance, between-months coefficient of variation of mean daily minimum temperatures is two times higher in Sydney than at Lake Eacham (0.16 vs. 0.07), and so is the coefficient of variation of mean daily evaporation is (0.35 vs. 0.18).

Although our population dynamical model is based purely on demography, additional evolutionary predic-

tions are straightforward. Indeed, any genetic change that modifies the pattern of investment in gynes (quality vs. quantity) would undergo the strong environmental pressures that we brought to light and would become selected for or against. A change in the genetically determined threshold at which larvae develop into gyne or worker (Wheeler 1986) would be sufficient to produce such an effect. The strong isolation between populations of the *R. impressa* group and their genetic differences (Ward 1980a) suggest that each population is adapted to its local habitat. In order to further study the conditions of coexistence between two alternative strategies, one relying on propagules of low quality but high quantity and the other relying on the opposite pattern, adaptive dynamical models would be useful. The i and f parameters of our population dynamical model are "growth rates" that can be seen as the product of two components, the quantity of propagules (gynes or fission units) produced per unit of time and their quality (establishment success). Quantity and quality are fixed in our population dynamical model, but with an adaptive dynamical model, they can be allowed to vary. Under certain environmental conditions, a population that relies on a single strategy could branch into two alternative strategies that coexist durably.

The model that we developed is not restricted to the *R. impressa* group. It can be used for any ant taxa exhibiting both ICF and fission. This is the case in species that have both winged queens and wingless reproductives (Peeters and Ito 2001) but also in species in which winged queens are involved in both modes of colony founding (Rüppell et al. 1998). Our model can also deal with other types of gradients, as long as they differentially affect the success of ICF and fission. Environmental gradients have important consequences on ant activity (e.g., moisture gradient: Kaspari and Weiser 2000), and ecological pressure is probably even higher during colony founding. For instance, altitudinal gradient is suspected to select for different colonial reproductive strategies in a *Monomorium* species group in Arizona (Marie-Julie Favé, personal communication). Colonies at lower elevations produce winged queens, whereas those at higher elevations produce wingless reproductives. At intermediate altitudes, colonies produce both types. The link between environmental gradients and colonial reproductive strategies remains to be explored in many ants.

Aerial Dispersal Is a Crucial Life-History Trait

Based on our model, a sudden loss of winged queens at a critical latitude could have been expected, once non-claustral ICF becomes less successful than fission. However, we observed a gradual shift, suggesting that selection favors the retention of a low rate of aerial dispersal, even

though fission allows for better local reproduction. The *R. impressa* group is not an isolated example of taxa where fission is more efficient locally than ICF and yet winged queens are retained. For instance, in *Harpagoxenus sublaevis*, wingless queens reproduce and winged gynes are rare (Bourke 1987), but they offer an opportunity for dispersal by flight in a patchy environment. In order to maintain a reasonable success rate of ICF in environments that are seasonally harsh and offer fewer resources, and where fission is more successful than ICF, colonies of the *R. impressa* group increase gyne/worker weight ratios. The increased lean and fat weights reflect respectively larger proteic and lipidic reserves (Keller and Passera 1989; Wheeler and Martínez 1995). First, these limit the number of foraging events during lone foundation and thus decrease queen mortality (Wiernasz and Cole 2003). Second, we hypothesize that the first brood of workers can be produced earlier or can consist of either more or larger workers, any of which increases the survival of incipient colonies (see Johnson 2002). The ecological success of ant species that perform claustral ICF is probably linked to the higher survival of gynes with large metabolic reserves. The trade-off between quality and quantity of gynes could be dissociated from the benefits of fission by studying *Harpegnathos saltator*, another species in which either winged queens or gamergates reproduce. In this species, gamergate colonies do not fission because nests are complex constructions that represent large investments (Peeters et al. 2000).

Different Ways to Increase the Success of ICF

Ant colonies have two options to improve the success rate of ICF. First, they can retain gynes of the same size but produce more of them, although this does not benefit individual gynes. Second, they can alter the phenotype of gynes. In the *R. impressa* group, individual gyne quality (relative to workers) is increased at the expense of quantity. In that case, the interests of colonies and gynes are similar. Wiernasz and Cole (2003) argued that in *Pogonomyrmex occidentalis*, colonies should produce gynes that are as fat as possible because gyne success increases linearly with gyne weight, but they supposed that gyne weight is limited by biomechanical constraints. In the *R. impressa* group, gynes' weight relative to workers increased dramatically toward the south, so if gynes are light in the north, it is not because of biomechanical constraints but because they represent the optimal phenotype. This means that producing bigger gynes in the north would not benefit the colony and that it is better to invest in additional gynes.

Another strategy to increase success of ICF is by modifying foundress behavior. By associating with other queens (pleometrosis), foundresses decrease their foraging fre-

quency, and they produce the first workers earlier and in larger quantity (Bernasconi and Strassmann 1999). In *R. confusa*, this was found only in two instances by Ward (1981b). Foundresses can also change their nesting site preferences. From north to south, *Rhytidoponera* colonies are found more often under stone than in rotten logs (Ward 1981a). Thus, they can bury deeper in the ground during the dry winter, which is not possible in rotten logs.

Optimizing both ICF and Fission through Alternative Reproductive Phenotypes

The evolution of higher-quality winged queens is not possible in all ant species that exhibit both fission and ICF. Indeed, workers cannot mate in most species, so it is the queens that are involved in fission as well as ICF. Selection for such alternative reproductive strategies imposes conflicting pressures on queen size. With respect to colonial economy, queen size is selected to decrease with colony fission (the limit to smaller size being the retention of a sufficient fertility), while queens should be as large as possible for ICF. Thus, monomorphic queens cannot be fully optimal for both ICF and fission. This led to the evolution of small and large winged queens in various species in which the cheap phenotype is dedicated to fission, whereas the expensive one specializes in ICF (Rüppell and Heinze 1999). However, either wingless queens or gamergates have replaced winged queens in some taxa (Peeters and Ito 2001; Molet et al. 2007).

Small Queens, Large Queens, and Fission: r-Selection or K-Selection

The evolution of the size of organisms has been the subject of extensive theoretical and empirical research. MacArthur (1962) proposed that selection on organisms differs depending on the degree of density dependence or resource limitation that they experience. Pianka (1970) made explicit predictions about the subsequent evolution of life-history traits. In populations close to the carrying capacity, *K*-selection favors individual persistence and delayed reproduction. As a consequence, few but high-quality offspring (i.e., good competitors) are produced. In populations expanding in resource-rich habitats, *r*-selection favors early reproduction and high fecundity. This can be achieved by producing many cheap offspring to colonize the habitat quickly. The *r*- and *K*-selected populations can thus be distinguished by their pattern of investment in offspring quality versus quantity. When compared with other insect species, especially semelparous social wasps and bumble bees with annual colonies, ants are *K*-strategists (Bourke and Franks 1995): they delay reproduction and produce high-quality offspring (expensive gynes or

fission propagules) that are efficient competitors for the few available nesting sites or resources. However, analyses at such a high taxonomic level are problematic, notably because comparisons of different strategies are meaningful only if the organisms involved have the ability to use all these strategies. Since in our study alternative options are available at the species-group level, this gives a rare opportunity to examine the type of selection that favors ICF with either small or large gynes and fission.

On one hand, in the *R. impressa* group, the trade-off between offspring quality and quantity supports the proposition that populations are *r*-selected in the north and *K*-selected in the south. Indeed, from north to south, the quality of propagules increases while their quantity decreases (from small to bigger gynes in queenright colonies and fission in gamergate colonies), making them more fit to compete in a harsher environment. Considering the pattern of investment in offspring by mother colonies, queenright colonies are *r*-strategists, whereas gamergate colonies are *K*-strategists.

On the other hand, when looking at the phenotype of the mother colonies themselves, the pattern is reversed. First, queenright colonies grow for several years and reach a large colony size before becoming mature and starting to produce gynes and males (Ward 1980a). In contrast, gamergate colonies reach maturity (i.e., ability to produce males and to fission) earlier and at a smaller size. Second, queenright colonies invest more in maintenance than gamergate colonies. Indeed, workers in queenright colonies are restricted to nonreproductive tasks, while in gamergate colonies they contribute to the success of fission. Finally, fission is a strategy that allows for quick colonization of habitats. For instance, fission can facilitate invasion by introduced species (Hee et al. 2000). Considering these arguments then, queenright colonies are *K*-strategists while gamergate colonies are *r*-strategists.

Hence, the two reproductive strategies exhibited in the *R. impressa* group are not consistent with discrete *r*- and *K*-selection, because they show a combination of traits from both syndromes. This provides an additional argument for the cautious use of this concept (Stearns 1992), especially in social insects, where both individual and colonial traits must be considered. Environmental conditions do not act directly on every life-history trait of the colonies, but they mainly affect mortality during the founding stage. Therefore, only life-history traits associated with colony founding, that is, quality and quantity of the offspring, are modified initially. Eventually this can lead to a complete change in all other colonial traits—demography, seasonality in the production of sexuals, or evolution of novel reproductive phenotypes (Peeters and Ito 2001). Social insects are an interesting model for investigation of the evolution of reproductive strategies since they exhibit mul-

iple imbricated levels of selection (individual, caste, and colony).

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