Benefits and Costs of Secondary Polygyny in the Dampwood Termite *Zootermopsis angusticollis*

COLIN S. BRENT,[1] JAMES F. A. TRANIELLO,[2] AND EDWARD L. VARGO[3]

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ABSTRACT Newly molted female neotenic reproductives of the dampwood termite *Zootermopsis angusticollis* Hagen were allowed to mature in the presence of a neotenic male, a fixed number of larval helpers, and varying numbers of sibling neotenic queens to assess the impact of secondary polygyny to the individual and colony. Under monogyne conditions, neotenics developed more ovarioles per ovary and had higher individual fecundities after 60 d compared with females under polygyne conditions. Queens in groups of three females were able to gain more body mass than those in groups of five. Although the division of resources provided by helpers reduced individual female development and fecundity under polygyne conditions, it resulted in an overall increase in colony fecundity. In addition, neotenic females in polygynous colonies did not differ significantly in reproductive competence. There was no evidence that neotenics were attacked or injured by other reproductives or larval helpers, suggesting little if any reproductive competition among sibling queens. The physiological responses of neotenics to the increasing queen/worker ratio may have the benefit of enhancing the colony growth at the cost of the fecundity of individual queens.

KEY WORDS reproductive skew, neotenic reproductives, inclusive fitness, reproductive plasticity, inbreeding

In social insects, a division of labor between reproductive and worker castes enables a queen to direct nutritional resources toward oogenesis, facilitating rapid colony growth (Oster and Wilson 1978, Porter and Tschinkel 1986, Tschinkel 1988, Keller and Vargo 1993). As colony size increases, a reproductive female will eventually become saturated with help, and the rate at which she lays eggs will be determined by her physiological limitations (Oster and Wilson 1978, Tschinkel 1988). Secondary polygyny (Hölldobler and Wilson 1977), which regularly occurs in many species of the lower termites (reviewed in Miller 1969, Myles and Nutting 1988, Roisin 1993, Myles 1999), may allow colony growth to exceed the physiological limitation of individual queen fecundity (Darlington 1985, Roisin 1993). However, colony fecundity is still constrained by nutritive resources, particularly nitrogen, made available to queens (reviewed in LaFage and Nutting, 1978, Nalepa 1994). Some species balance resource limitations and egg production by regulating queen number, either through neglect or the aggression of workers (Ruppli 1969, Mensa-Bonsu 1976, Lenz 1985, Sieber 1985, Roisin and Pasteels 1986, Miyata et al. 2004) or by intragroup competition between reproductives (Thorne 1985, Noirot 1990, Roisin 1993). For species in which the long-term coexistence of multiple queens is common, the fecundity of each queen may be reduced (Thorne 1982, 1984, 1985, Keller and Vargo 1993, Kaib et al. 2001). In this case, a decline in the per capita rate of egg production may occur through equal reductions in all queens, lowering the variance in their fecundities. Alternatively, a dominant queen might inhibit oogenesis in subordinates, thereby creating high variance in queen fecundities, as occurs in some wasps (Gibo 1978, West-Eberhard 1969), ants (Ross 1988, Hölldobler and Wilson 1990), and possibly the termite *Nasutitermes princeps* (Roisin and Pasteels 1985).

Although several studies using natural populations of termites have shown a negative correlation between queen number and individual fecundity as measured from oviposition rates (Roisin and Pasteels 1985, 1986, Kaib et al. 2001) or queen weight (an indicator of potential fecundity; Thorne 1982, 1984, 1985, Darlington 1985, Lenz 1985, Roisin and Pasteels 1985, 1986, Kaib et al. 2001), there have been no controlled experiments that directly measure the extent that termite reproductives are affected by increasing resource partitioning. To examine the relationship of queen number and individual queen fecundity, the reproductive development of newly molted neotenic females of *Zootermopsis angusticollis* Hagen was examined under monogynous and increasingly polygynous colony conditions. Dampwood termites are single-piece nesters (Abe 1987), and long-lived polygynous associations of secondary (neotenic) reproductives are common in older colonies (Heath 1903, Castle

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[1] Corresponding author: School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501 (e-mail: colin.brent@asu.edu).

[2] Department of Biology, Boston University, Boston, MA 02215.

[3] Department of Entomology, North Carolina State University, Raleigh, NC 27695.

1934, Light and Illg 1945, unpublished data). The rate of ovarian maturation and oocyte production of *Z. angusticollis* neotenics has been shown to be influenced by the availability of larval helpers that supply the reproductives with nutrients (Greenberg and Stuart 1979; Brent and Traniello 2001b). Increasing the proportion of queens relative to helpers should therefore affect reproductive development. Here we examined how queen number influences individual and colony fecundity, assessing whether direct or indirect competition occurs among reproductive females as colony resources become increasingly divided.

Materials and Methods

Termites originated from stock colonies of *Z. angusticollis* collected in 1998 from the Redwood East Bay Regional Park, near Oakland, CA, and in 2004 from the Del Monte Forest in Pebble Beach, CA. Secondary reproductives (neotenics) were generated from fourth- to seventh-instar larvae that were removed from five stock colonies and isolated in 14 groups of 50–60 individuals that were all from the same colony. These termites were placed in clear covered plastic boxes (17 by 12 by 6 cm) containing moistened filter paper and small pieces of wood from their natal nest. The sex ratio of larvae is roughly equal for this species (unpublished data), and it was assumed the ratio was maintained for each isolated group. Containers were visually surveyed on an approximately daily basis to detect neotenics, which were collected within 1–2 d of their adult molt. Three groups of experimental colonies were established, containing either 1 ($n = 24$), 3 ($n = 23$), or 5 female neotenics ($n = 14$), in addition to 10 larvae (randomly mixed sexes, third or fourth instar) and 1 male neotenic. Before being placed in a colony, each female neotenic was weighed to determine initial mass and given an identifying mark on the abdomen with enamel paint (Testor's). Ten larvae are adequate to ensure reproductive maturation in a monogynous pair of secondary reproductives (Brent and Traniello 2001b), but there are sufficiently few so that adding neotenics produces a marked skew in such a queen/worker ratio. All colonies nested in covered plastic petri dishes (100 by 15 mm) containing ≈5 g (dry weight) of moistened birch wood. The dishes were placed in large covered plastic boxes with paper towel liners moistened regularly to maintain humidity. Colonies were maintained under a 14 L: 10 D light cycle at 23°C. A subset of 10 colonies was randomly selected from each treatment group for behavioral analysis. During two 1-h long sessions for each of the first 10 d after colony founding, all instances of agonistic interaction (i.e., biting, lunging) between both reproductive and nonreproductive nestmates were recorded. During the observation period, the termites were left under the same housing conditions as the unobserved termites to ensure similar development environments.

Termites were sampled 60 d after the colonies were initiated. This is an adequate time period for neotenics to mature reproductively and begin ovipositing (Brent and Traniello 2001a, b). Neotenics were checked for evidence of agonistic interactions (bite marks and missing or damaged legs and antennal segments) and weighed to determine change in body mass. The percent change in mass was used as an estimate of the availability of endogenous resources above what is used toward ovarian development and activity. Because it is a relative measure, it is not influenced by differences in initial mass caused by colony of origin. Termites were preserved individually in labeled 0.5-ml Eppendorf tubes containing 70% ethanol until dissection. Both ovaries were removed, and the total number of functional ovarioles in each ovary was recorded. The number of vitellogenic oocytes and corpora lutea was also noted to estimate of fecundity. Oocytes were considered vitellogenic if their volume was $\geq 0.01\ \text{mm}^3$ (Brent and Traniello 2001a). In a number of colonies, neotenic mortality led to the differentiation of new neotenics from helper larvae. Monogynous colonies in which these changes occurred were not used, but data were collected from polygynous colonies that did not deviate from the original number of neotenic females by more than one individual.

Statistical analysis was performed using JMP v. 5.1 (SAS Institute 2002). Normally distributed data allowed the use of analysis of variance (ANOVA) to determine whether there were significant ($\alpha_{\text{critical}} = 0.05$) differences between treatment groups on individual days. Probability values were adjusted for multiple tests using Scheffé correction (Sokal and Rohlf 1995). A two-tailed Student's *t*-test was used to compare the frequency of interactions of each female with the male, larvae, and the other females.

Results

The first neotenics began to differentiate within isolated groups of larvae 1 wk after isolation from the inhibitory stimuli of reproductives, but the majority of adult molts occurred after 4 wk. Across the isolated groups of larvae, females developed into neotenics 2.7 times more frequently than males, although groups varied (0.9–4.7), perhaps because of differences in the initial sex ratio in the isolated groups.

There were significant developmental differences among neotenics maturing in monogynous and polygynous colonies. Females maturing in polygynous colonies of three queens had a significantly higher percent mass gain (Fig. 1; 44.77 ± 1.90; $n = 57$) than females in monogynous colonies (35.04 ± 2.54; $n = 24$; ANOVA, $F = 6.686$, df = 1, $P = 0.012$) or polygynous colonies of five queens (38.25 ± 1.83; $n = 61$; ANOVA, $F = 5.999$, df = 1, $P = 0.016$). There was no significant difference in the mass gained by the reproductive females from the latter two groups (ANOVA, $F = 1.151$, df = 1, $P = 0.286$). However, the number of ovarioles per ovary in females from monogynous colonies (32.04 ± 0.83, $n = 24$; Fig. 1) was significantly greater than that observed in females developing in polygynous colonies with three (27.95 ± 0.51, $n = 57$; ANOVA, $F = 19.251$, df = 1, $P < 0.0001$) or five queens (27.99 ± 0.52, $n = 61$; ANOVA, $F = 17.031$, df = 1, $P <$

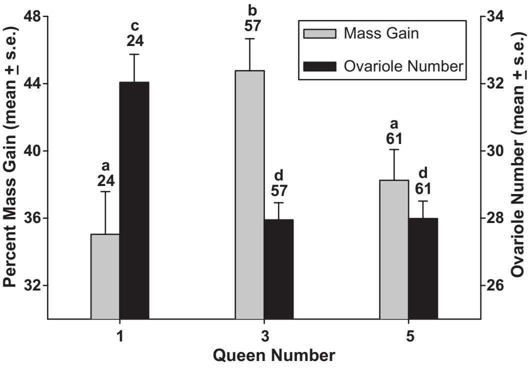

Fig. 1. Mean (±SE) percent mass gain (gray bars) and number of functional ovarioles per ovary (black bars) for neotenic females in colonies with one, three, or five queens. Sample sizes are provided. Bars having the same letter are not significantly different ($P > 0.05$, one-way ANOVA with Scheffé correction).

0.001). Similarly, individual fecundity was significantly higher in females from monogynous colonies (Fig. 2; 4.13 ± 0.46, $n = 24$) compared with that of females from polygynous colonies of three (1.70 ± 0.36, $n = 57$; ANOVA, $F = 14.199$, df = 1, $P < 0.001$) or five queens (1.69 ± 0.33, $n = 61$; ANOVA, $F = 16.150$, df = 1, $P < 0.001$). Females from the two polygynous groups did not differ significantly in either ovariole number (ANOVA, $F = 0.004$, df = 1, $P = 0.948$) or fecundity (ANOVA, $F = 0.008$, df = 1, $P = 0.960$). Total colony fecundity varied among groups (Fig. 2). Colonies with five female neotenics had the highest cumulative fecundity (7.34 ± 0.84, $n = 14$), which was significantly greater than that observed in colonies with one (4.13 ± 0.46, $n = 24$; ANOVA, $F = 5.683$, df = 1, $P = 0.023$) or three (4.22 ± 0.89, $n = 23$; ANOVA, $F = 4.627$, df = 1, $P = 0.039$) female neotenics. There was no statistical difference in total fecundity for colonies with one or three queens (ANOVA, $F = 0.006$, df = 1, $P = 0.940$).

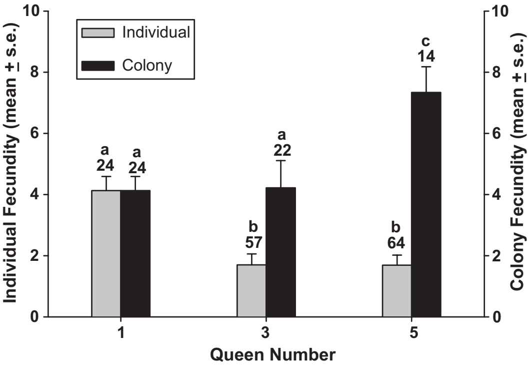

Fig. 2. Mean (±SE) individual (gray bars) and collective colony (black bars) fecundities for neotenic females in colonies with one, three, or five queens. Sample sizes are provided. Bars having the same letter are not significantly different ($P > 0.05$, one-way ANOVA with Scheffé correction).

Despite the physiological differences among females maturing under different social conditions, there seemed to be little developmental difference between nestmate females maturing under the same colony conditions. In colonies of three females, the most fecund individuals did not significantly differ from the overall average for percent mass gain (45.79 ± 3.48 versus 44.77 ± 1.90 ANOVA, $F = 0.061$, df = 1, $P = 0.805$), ovariole number (29.07 ± 0.72 versus 27.95 ± 0.51; ANOVA, $F = 1.740$, df = 1, $P = 0.191$), or fecundity (2.54 ± 0.38 versus 1.70 ± 0.36; ANOVA, $F = 3.27$, df = 1, $P = 0.074$). Similar results were found in colonies with five neotenics; females selected for having the highest fecundities did not differ from the remaining neotenics in percent mass gain (38.07 ± 3.25 versus 38.25 ± 1.56; ANOVA, $F = 0.003$, df = 1, $P = 0.959$) and ovariole number (29.25 ± 1.01 versus 27.99 ± 0.49; ANOVA, $F = 1.250$, df = 1, $P = 0.267$). Fecundity was significantly greater for the females selected on this attribute (3.46 ± 0.44 versus 1.69 ± 0.33; ANOVA, $F = 13.016$, df = 1, $P < 0.001$), but when 100 replicates of the data set were run using randomized assortment of the fecundity values, similarly significant differences were found 16% of the time. This indicates there was no real difference among neotenic fecundities within polygynous colonies beyond what might occur by chance.

There was no physical or behavioral evidence of aggression directed toward neotenics by other reproductives or their larval helpers. Rather, neotenics were occasionally observed allogrooming and spent most of their time in close proximity. Larvae appeared to provision and groom each reproductive to a similar extent. Together with the developmental data, these observations suggest that there is little if any direct or indirect competition between reproductives at this stage in their maturation.

Discussion

The tendency for *Z. angusticollis* colonies with replacement reproductives to be polygynous seems to be the result of two factors. First, the rate of differentiation of larvae into neotenics is skewed, favoring females over males. Similar data have previously been reported for this species (Heath 1903, Castle 1934, Greenberg and Stuart 1982). Second, behavioral observations suggest that there is no immediate culling of supernumerary reproductives, by other reproductives or larval helpers, as has been observed in other termite species (reviewed in Roisin 1993, 2000, Myles 1999. It is possible that secondary culling occurs under natural conditions or at some point later in the development of neotenics, but there is little supporting evidence. Although other basal termites tend toward parity in sex ratios of secondary reproductives, these species normally have fewer reproductives in general (Myles 1999). *Z. angusticollis* seems to have a much higher tolerance for multiple neotenics, sometimes having dozens of neotenics in a single colony (Heath 1903, Castle 1934, Greenberg and Stuart 1982, unpublished data). Although selection might favor a larger number of coexisting females to increase colony growth, superfluous males should be selected against because only one or a few males are needed to provide adequate sperm, the remainder adding only a metabolic cost to the colony (Myles 1999).

Behavioral and developmental data for neotenic females maturing within the same colony indicate that there is also little if any indirect competition between secondaries to monopolize limited resources necessary for reproduction. There were no differences in the reproductive capabilities of neotenic nestmates, which is likely the result of each female being cared for by their larval helpers to the same extent. Termite reproductives, and neotenics in particular, are highly dependent on larvae, which can increase the energetic reserves of a female by transferring nutrients or by relieving the female of performing colony tasks (Rosengaus and Traniello 1993, Nalepa 1994, Brent and Traniello 2001b). However, there seemed to be a cost to sharing resources. Because the number of larvae was held constant, increasing the number of neotenic females resulted in fewer resources available to each reproductive. This resulted in monogynous females developing more ovarioles and having higher fecundities than individual polygynous females, and females in groups of three acquiring more body mass than those in groups of five, despite similar resources expenditures on ovarioles and oocytes.

It is possible that the reduced development of polygynous females was not the result of partitioning colony nutritional resources, but may instead have been caused by a subtle form of nestmate manipulation. Polygynous reproductives of the ant *Solenopsis invicta* use recognition cues to modulate each other's development, causing an increasing degree of suppression with increasing queen number (Vargo 1992). Pheromones probably trigger a neurohormonal cascade resulting in a decreased ovarian activity in *S. invicta* (Brent and Vargo 2003); a similar mechanism has been proposed for alates of this species (Brent et al. 2007). However, this seems an unlikely explanation for *Z. angusticollis* neotenics given that pairing two female neotenics does not have an effect on their ovarian maturation and egg production that is discernibly different from pairing them with a male neotenic (Brent and Traniello 2001a). In this case, resource partition seems to be a more probable explanation than mutual inhibition.

The indirect fitness gains from cooperative brood production may have reduced direct and indirect competition among *Z. angusticollis* female neotenics. Although individual fecundity decreased as the number of female neotenics increased, total colony fecundity increased. As neotenics mature and become more fecund, such differences in reproductive potential likely become more pronounced. Additionally, because of haplometrotic colony foundation (Heath 1903, Castle 1934, Light 1934, Shellman-Reeve 1999, Thorne et al. 2002), neotenics would normally be siblings and thus would mate with either a parent or sibling, producing highly related offspring (Calleri et al. 2006). The increased inclusive fitness gained in the production of a greater number of highly related nieces and nephews could compensate for a reduction of direct fitness caused by sharing nutritional resources (Darlington 1985, Crozier and Pamilo 1996). The added benefits would decrease the likelihood of competition among the females. The high relatedness of resulting offspring would also decrease selection in larvae to provision any given reproductive. However, the pattern we observed was for newly molted neotenics only, and individual reproductive capability could become increasingly skewed among queens as reproductives and the colony mature.

For *Z. angusticollis,* in which the growth and maximum fecundity of a single primary female is physiologically limited relative to the more advanced termite queens (Nutting 1969), secondary polygyny could be an important adaptation to increase the rate at which colonies mature and exploit patchily distributed resources (Darlington 1985, Roisin 1993). However, the rate of colony growth could be constrained by the number of neotenics that develop and the number of larvae available to support them. The results of our studies, which are the first to control for the ages and ratios of queens and workers and colony conditions, suggest that newly differentiated *Z. angusticollis* neotenics adjust their individual reproductive development and fecundity to match the colony conditions in which they develop. Reproductives limited by the presence of few helpers or numerous neotenics compensate by producing fewer eggs. As the colony grows, the fecundity of each neotenic can be commensurately increased. Although we examined only the earliest stage of neotenic development, it is likely that this responsiveness to colony conditions is retained throughout the life of the reproductives. It remains to be determined whether the adjustments in individual fecundity are the result of decreased care from larvae or mutual inhibition between neotenics.

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