Offspring Size and Reproductive Allocation in Harvester Ants

Diane C. Wiernasz* and Blaine J. Cole*,†

Department of Biology and Biochemistry, University of Houston, Houston, Texas 77204 Submitted March 16, 2017; Accepted July 24, 2017; Electronically published November 17, 2017 Online enhancements: supplemental material. Dryad data: http://dx.doi.org/10.5061/dryad.h4953.

ABSTRACT: A fundamental decision that an organism must make is how to allocate resources to offspring, with respect to both size and number. The two major theoretical approaches to this problem, optimal offspring size and optimistic brood size models, make different predictions that may be reconciled by including how offspring fitness is related to size. We extended the reasoning of Trivers and Willard (1973) to derive a general model of how parents should allocate additional resources with respect to the number of males and females produced, and among individuals of each sex, based on the fitness payoffs of each. We then predicted how harvester ant colonies should invest additional resources and tested three hypotheses derived from our model, using data from 3 years of food supplementation bracketed by 6 years without food addition. All major results were predicted by our model: food supplementation increased the number of reproductives produced. Male, but not female, size increased with food addition; the greatest increases in male size occurred in colonies that made small females. We discuss how use of a fitness landscape improves quantitative predictions about allocation decisions. When parents can invest differentially in offspring of different types, the best strategy will depend on parental state as well as the effect of investment on offspring fitness.

Keywords: parental investment, life history, *Pogonomyrmex*, fitness, fitness functions, Trivers-Willard.

Introduction

One of the most widespread and robust patterns in life history is the size-number trade-off among offspring (Stearns 1992; Messina and Fox 2001; Roff 2003). Any organism with a limited amount of resources for reproduction must invest along a continuum from a greater number of small offspring to fewer, larger offspring. Negative correlations between the size and number of offspring have been observed among species (fish [Elgar 1990]; insects [Fox and Czesak 2000]; plants [Jakobsson and Eriksson 2000]; mammals [Charnov and Ernest 2006]), as well as among or within populations of a single species for a variety of plants, insects, and vertebrates (Sinervo and Licht 1991; Carrière and Roff 1995; Jonsson

* The authors contributed equally to the work.

[†] Corresponding author; e-mail: bcole@uh.edu.

and Jonsson 1999; Bleu et al. 2013). The most convincing studies are experimental manipulations where offspring size or number is artificially increased or decreased (Sinervo 1990, 1998; Ji et al. 2006) or selection studies that show a correlated response to selection on either offspring size or offspring number (see Roff 2003 for discussion; Czesak and Fox 2003; but see Fischer et al. 2006 for a complex reaction).

Any intrinsic trade-off between size and the number of offspring can be modified by variation in the size or condition of females (Hendry et al. 2001), their age (Derocher and Stirling 1998; Fischer et al. 2006; Plaistow et al. 2007; Gonzalez et al. 2012), or their location (McGinley et al. 1987; see Bernardo 1996 for a general review of maternal effects). For example, when there is variation in the total quantity of resources available, those females who can produce the largest offspring might be able to produce the most offspring as well (van Noordwijk and de Jong 1986; Venable 1992). However, we can use the idea of this underlying trade-off to help understand the consequences of environmental variation for the size-number allocation problem.

If resources are added in a system that is completely defined by a trade-off between size and number, the female can make either larger offspring, more offspring, or some combination of the two. Additional resources are expected to increase the total number of offspring when offspring size cannot change (e.g., because of a strict constraint on the relationship between offspring size and maternal size; Shine 2005). Early theoretical models showed that in a stable environment, parental fitness is maximized by investing equally in all offspring, with the optimum determined by the relationship between offspring size and offspring fitness (Smith and Fretwell 1974). In these optimal offspring size models, increased resources for reproduction are expected to increase clutch size rather than offspring size. This results in minimal variation in the size of offspring and may be characteristic of many organisms (Fox and Czesak 2000; Christians 2002).

Alternatively, it may be impossible to change the number of offspring. When females can produce a limited number of eggs, then the only response to a food surplus is to increase the size of the offspring (egg limitation models; Mangel 1987; Rosenheim et al. 1996, 2008). As offspring size increases, the variance in offspring size may also increase if not all parents

Am. Nat. 2018. Vol. 191, pp. 000–000. © 2017 by The University of Chicago. 0003-0147/2018/19101-57617\$15.00. All rights reserved. DOI: 10.1086/694903

or offspring are affected equally. Egg limitation may arise if extended egg maturation must begin seasonally before the resources available for offspring rearing are determined (Rosenheim et al. 2008, 2011). Encompassing both investment in eggs and subsequent parental investment in offspring (e.g., provisioning) is the multifaceted parental investment hypothesis (Rosenheim et al. 1996; Gilboa and Nonacs 2006). Egg limitation may influence investment, but so does the possibility that brood size can be reduced in the face of resource limitation.

Offspring size and number may both increase if extra resources become available unpredictably. In many species, females produce a larger number of eggs or offspring than can complete development (reviewed in Mock and Forbes 1995). Brood size represents an optimistic estimate of the number of offspring that typically will survive. Excess offspring production leads to brood reduction in many taxa (reviewed in Mock and Parker 1997, 1998). Although many species undergo actual brood reduction, that is, some offspring survive and some are eliminated, sublethal competition among young may produce stunted offspring, increasing the variance in the size distribution of offspring. Whether offspring are eliminated or reduced in size may depend on how fitness is related to offspring size (Bonabeau et al. 1998). In these optimistic brood size models, more eggs than offspring are produced unless the female encounters favorable conditions. Optimal offspring size and optimistic brood size formulations represent two different approaches to the size-number problem in life history, so we expect that each approach will be more predictive in certain circumstances. We argue below that the expected outcome depends on the form of the fitness function.

The strategies of income and capital breeders provide an alternative conceptual framework for the evolution of reproductive investment (Jönsson 1997; Johnson 2006; Houston et al. 2007). Income breeders adjust reproductive effort based on resources that are acquired during offspring production, while capital breeders use stored resources acquired before the offspring are produced. Although it is possible to consider optimal offspring, most studies of income and capital breeding address the determinants of the amount of reproductive output. We find the framework of optimal offspring size, optimistic clutch size, and egg limitation to be the more useful in this study because we focus on the relationship between the number and the size of offspring produced.

Many species of social insects meet some of the conditions of the optimistic brood size models (Mock and Parker 1997). Production of males and females occurs annually at a specific season, and the commitment to reproduction may occur before the extent of resources for reproduction are known. In addition, because the destiny of female eggs (queens vs. workers) is frequently determined primarily by nutrition (reviewed in Wheeler 1986), brood reduction may be asymmetrically distributed between the sexes. Others have argued that social insects may fail to conform to simple models of optimal offspring size due to egg limitation (Rosenheim et al. 1996; Gilboa and Nonacs 2006). Because reproductive (as opposed to worker) eggs are produced in only one season, exploitation of unpredictable resource excess may manifest as an increase in offspring size and variance rather than an increase in number. Finally, there is some evidence to suggest that fitness of offspring is a function of investment in them (Nonacs 1990; Wiernasz et al. 1995, 2001; Rüppell et al. 1998; Abell et al. 1999; Kikuchi et al. 1999; Wiernasz and Cole 2003; Cahan and Rissing 2005; Enzmann and Nonacs 2010), a key assumption of optimal offspring size models.

Studies of reproductive allocation in social insects have focused most intensively on the problem of how investment is divided between males and females (reviewed in Nonacs 1986a, 1986b; Bourke and Franks 1995; Crozier and Pamilo 1996); an exception is Herbers' (1990) comprehensive study of reproductive allocation components in Temnothorax. However, many species of social insects, especially ants, are known to display within-colony variation in reproductive size (Hölldobler and Wilson 1990; Buschinger and Heinze 1992; Backus 1993; Fjerdingstad and Boomsma 1997; Wagner and Gordon 1999; Ode and Rissing 2002; Bono and Herbers 2003; Fjerdingstad 2005; Gilboa and Nonacs 2006). The consequences of this variation are unknown for most species, although they have been considered theoretically (MacNair 1978; Frank 1987a, 1987b). Size is likely to affect multiple components of individual fitness (e.g., Davidson 1982; Wiernasz et al. 1995, 2001; Abell et al. 1999; Wiernasz and Cole 2003; Fjerdingstad and Keller 2004; Clemencet et al. 2010; Courvillon et al. 2010).

We examine the allocation of resources among offspring in the western harvester ant, *Pogonomyrmex occidentalis* Cresson. We combine data on variation in offspring size from a long-term field study of reproduction in a large population with analyses of selection on size variation in both sexes to argue that sex-specific differences in variation in offspring size reflect the sex-specific differences in selection on body size. We use food supplementation to probe the behavioral decisions about allocation that a colony may make when forced to balance changes in offspring size and offspring number.

Selection on Body Size in Harvester Ants

In *P. occidentalis*, reproductives of both sexes are subject to strong selection favoring large body size. In males, fitness is a linear function of size. Intense competition in the mating swarms results in strong sexual selection on size and shape: mating males are significantly larger than randomly collected ones (Wiernasz et al. 1995; Abell et al. 1999). Large males transfer more sperm than small males (Wiernasz et al. 2001),

which also increases individual fitness. However, at least some small males mate and transfer sperm, leading to lower, but not zero, reproductive success. We have no evidence for alternative male mating strategies, but small males have lower wing loading than large males (D. Wiernasz and B. Cole, unpublished data) and may be better at dispersal.

Body size affects the probability that a female successfully founds a new colony (Wiernasz and Cole 2003; in the remainder of this article, "female" refers to investment decisions about reproductive offspring that the parental colonies make, and "queen" refers to the mother of a colony). Queens that survived the initial period of colony founding were significantly larger than those that died. The fitness function for size based on queen survival is nonlinear—queens that are larger than a threshold size have a significantly higher probability of colony initiation. Overall selection on individual queens may be stabilizing rather than directional; queens have significantly higher wing loading than males (D. Wiernasz and B. Cole, unpublished data), which may constrain maximum queen size.

To visualize how selection should modify colony-investment patterns in terms of male and female size, we graph the fitness of each sex in comparable units of overall size (the standard deviates from the first principal component of multiple size measures; fig. 1). For both males and females, we quantify the effect that investment by the colony of origin has on the fitness of individual reproductives. For male fitness, we



Figure 1: Fitness functions of male and female reproductives as a function of body size (units of principal component 1 for multivariate size). The fitness of queens of mean size is 0.295, and therefore we fix the fitness of mean size males at 0.295. This value is arbitrary; it is important only that mean male fitness equal mean female fitness. Male fitness increases linearly with size, while female fitness has a marked threshold. The dashed line represents the logistic function $(0.2 + [.8/\{1 + \exp(-1.9 \times (x - .9))\}])$ that is the best fit to the female fitness function.

use the size-specific number of sperm transferred (Wiernasz et al. 2001), a combination of mating probability and sperm transferred per mating. For female fitness, we use size-specific survival (Wiernasz and Cole 2003). Although lifetime queen fitness can be a function of nest site, neighborhood density, and many other factors, the effect of parental investment on queen fitness is likely to be greatest during colony initiation, while she is raising the first brood of workers. Resources invested in building large queens lead to a greater payoff to a colony than resources invested in building large males (fig. 1). Queens smaller than the threshold size (which corresponds to approximately 11 mg dry mass) are extremely unlikely to survive through the first year of colony founding. A strategy that pushes females over the threshold for survival will often result in the greatest fitness payoff. However, if colony investment is limited to small reproductives, investing in small males will give a greater payoff than investing in small females, because the male fitness does not decline as rapidly with size. Sex-specific selection on body size should have substantial consequences for patterns of reproductive allocation. These empirically derived relationships between size and fitness suggest that size should be more tightly controlled in females than it is in males.

Determinants of Reproductive Allocation and Fitness

Trivers and Willard (1973) were the first to predict how differences in investment between the sexes are shaped by selection on offspring size. We build on this approach to develop a model to predict how changes in resource abundance will influence strategies for investment in males and females, using the fitness functions presented earlier.

Total colony fitness will be a function of both number and size of reproductives produced. It is the sum of the fitness acquired through each male, M_i , or female, F_j , quantities that may vary with body size. We can write colony fitness as

$$\sum_{i=1}^{N_m} M_i + \sum_{j=1}^{N_j} F_j = W = (N_m + N_f)(r_m \overline{M} + r_f \overline{F}).$$
 (1)

The fitness of each of the N_m males and the N_f females is a function of their size, \overline{M} and \overline{F} are the fitness of males and females of mean size, and the numerical sex ratio of males and females are $r_m(=N_m/(N_m + N_f))$ and r_f . Increasing $N_m + N_f$, the total reproductive output, yields substantial increases in fitness. Because males are smaller than females, requiring smaller absolute investment to produce, it will often be easier for colonies to increase the numerical output of males more significantly than that of females.

Increasing the average size of reproductives will increase colony fitness in a more complicated fashion. Increased investment in males will change fitness differently from increased investment in females if payoffs for increased size differ between the sexes (i.e., fig. 1). Colony fitness is a function of the mean size of male and female reproductives:

$$W_t \propto W_m(\overline{M}) + W_f(\overline{F}), \tag{2}$$

where the fitness functions are linear for males and logistic for females. From our previous data we can construct the fitness landscape of possible male and female sizes (fig. 2). The numerical sex ratio influences the payoffs for changing the size of either sex. For ease of presentation, we discuss what happens when males and females are equally common, later taking the numerical sex ratio into account (fig. 3).

In this fitness landscape, the gradient is the path that has the highest slope from a particular point and forms a vector field that varies with both male and female size. The gradient of this fitness surface represents the simultaneous change in male and female size that produces the highest fitness returns given the current investment conditions. Each vector on this landscape represents an investment strategy. We are not using the fitness landscape to predict how the sizes of reproductives in a population may evolve but rather to solve for the allocation decision of a colony by taking the directional derivative of equation (2) along a vector *e* at an angle θ in the male-female size plane (see fig. 2, *inset*). This angle describes a strategy of investment in males and females for colonies with a given starting position. When $\theta = 0^\circ$, the vector is parallel to the *X*-axis, and all additional investment is directed to increasing the size of males. When $\theta = 90^\circ$, the vector is vertical, and all additional investment is di-



Figure 2: Fitness landscape for investment in males and females of different sizes. We graph total fitness of a colony only as a function of male and female size (fitness functions as in fig. 1). The fitness payoffs are calculated from the point of view of the colony queen who values fitness through male and female function equally. The axes show the size of males and females in standard deviation units of the first principal component of multivariate size for each sex. Increasing fitness is shown by increasing contours. An investment strategy is the proportional investment in male versus female size, represented by a direction θ in this plot. A colony producing average-sized males and females is located at the plus sign (size = 0 for both males and females). If the average colony gains more resources, allowing it to increase the size of the reproductives, it should follow the trajectory given by the red line. For colonies that produce both males and females of average size, increasing female size results in higher fitness returns than increasing male size. Attenuation of gains through female fitness eventually leads to a switch favoring investment in males.



Figure 3: Optimal investment strategy in males and females. The strategy is the angle of a vector reflecting investment in males versus females. The *Y*-axis is plotted in degrees; 45° indicates equal investment in males and females, with angles greater than 45° showing increasing bias toward female investment. The *X*-axis shows the size of females plotted in principal component 1 units (these are SD units of the principal component). The broken line represents the strategy based only on reproductive size (as shown in fig. 2). The solid line incorporates the numerical sex ratio (male bias of 2:1), the difference in the relative size and therefore cost of the sexes (the standard deviation of female size is ~1.6 that of males), and expresses the strategy in terms of worker interests (multiple mating [mean = 6.3 mates/queen] makes the average worker value queens by a factor of 1.3 over males). Overall, workers receive a greater payoff to investment in males by a factor of about 2.46 over females. If a colony makes females that are larger than about 0.2 SD units above the population mean, then greater payoff is obtained by disproportionate investment in female size. If female size is smaller than this value, then greater payoff is obtained by a greater increase in male size. The lower portion of the figure shows the distribution of colony mean size of females to give a context for the predictions about changing investment.

rected to increasing the size of females; intermediate θ values are a mixture of male and female investment:

$$\frac{dW}{d(F, M \to e)} = \frac{\partial W}{\partial M} \cos \theta + \frac{\partial W}{\partial F} \sin \theta = K(\theta, F, M). \quad (3)$$

The combination of investment in males and females that maximizes the rate of fitness return is given by the θ that maximizes the function *K*. By taking the derivative and setting it equal to 0, we find:

$$\hat{\theta} = \tan^{-1} \frac{\frac{\partial W}{\partial F}}{\frac{\partial W}{\partial M}}.$$
(4)

Taking the second derivative confirms that this is always a maximum when $0^{\circ} \le \theta \le 90^{\circ}$ (for $\partial W/\partial M$, $\partial W/\partial F \ge 0^{\circ}$). (It will also usually be a maximum when θ has other values.) In other words, when resources are added, allowing the size of males and/or females to increase ($0^{\circ} \le \theta \le 90^{\circ}$), equation (4) gives the investment strategy that results in the greatest return in fitness.

Using the previously estimated fitness functions for male and female size, we solved for θ using equation (4) (fig. 3). Because fitness through male function changes linearly with male size, the denominator of equation (4) is a constant, and the investment strategy depends only on the size of females. In *P. occidentalis*, the observed distribution of female sizes (fig. 3, *bottom*) falls on the ascending side of the optimal investment strategy. Therefore, the smaller the size of females, the larger the investment by a colony to increase male size. Only in colonies that already produce very large females should investment of additional resources be used to increase female size. Colonies that produce the smallest females will gain the greatest fitness by using additional resources to increase male size. Thus, we predict a negative correlation between the magnitude of any male size increase and the initial size of females.

Our model allows for the possibility that an organism may receive different fitness payoffs from changing the size of different categories of offspring depending on the current size of offspring. For harvester ants, the fitness return from males is proportional to investment, while the fitness return from females is disproportionately greater with larger body size. While this adds complexity to the predictions about the consequences of food supplements, we can predict the following: (1) the fitness response will be greatest when increasing numbers of either males or females, (2) male size will be more likely to change with food supplements than female size, and (3) there will be a negative relationship between the size of females before food supplementation and the increase in male size after supplementation.

Material and Methods

The Study System

Pogonomyrmex occidentalis is extremely common in the arid grasslands and cool deserts of western North America. Populations reproduce annually in hilltop mating swarms that are triggered by midsummer rains (Nagel and Rettenmeyer 1973; Cole and Wiernasz 2002). Colonies are founded by single queens, although queens mate multiply (Cole and Wiernasz 1999; Wiernasz et al. 2004). Reproduction in this species is a function of size rather than age; large colonies are significantly more likely to reproduce than small ones, although there is no colony size where the probability of reproduction becomes 1 (Cole and Wiernasz 2000). However, among colonies that reproduce, colony size is not correlated with the amount of reproductive biomass or number of reproductives.

Reproductive brood are the first offspring of the year; presumably reproductive eggs are laid soon after the colony becomes active in late March or early April. Colonies appear to produce either workers or reproductives—we have not observed both types of brood in excavated nests. It is not known whether more than one batch of reproductive eggs are laid. The rate at which reproductive broods develop depends on temperature, but they probably require at least 2 months before they are capable of flight (from pupation to eclosion requires about 1 week, and completion of cuticle tanning in eclosed alates also requires approximately 1 week; D. Wiernasz and B. Cole, unpublished data). Production of the first brood of workers in the lab requires 25–50 days (Johnson 1998; D. Wiernasz and B. Cole, unpublished data), but these nanitic workers are much smaller than reproductives.

Our study was performed on Bureau of Land Management land approximately 15 km northwest of Fruita (Mesa County), Colorado, at 1,470 m elevation (see Wiernasz and Cole 1995 for a detailed description). The land is a mixture of adobe hills, dry washes, and flat areas, with a mixture of largely native vegetation and a few disturbed areas.

We examined patterns of reproduction allocation in 160 colonies initially chosen in March 1994. We selected colonies based on the size of the nest cone, which we have previously shown is highly correlated with the size of the forager force (Wiernasz and Cole 1995). Nest size is calculated as (length of the north/south axis) × (length of the east/west axis) × (height of the nest cone + 1 cm). We present the size of colonies as the natural log-transformed nest volume because the product of these measurements is strongly lognormal. We initially chose nests in two size classes. The size classes that comprise large nests have an estimated probability of reproduction of \geq 60% in a given year (Cole and Wiernasz 2000). Small nests were size classes estimated to be between 5 and 10 years old and nearing the size of first reproduction. Four subareas (A–D) were used, producing groups of 32, 56, 40, and 32 colonies (see fig. S1; figs S1, S2 are available online). Equal numbers of large and small nests were chosen from each subarea. Colonies were tagged and mapped to facilitate recovery in later years. In 1996, we added 16 nests to the study to replace nests that had died since 1994 and 40 additional large nests in two additional subareas (E and F; see fig. S1). The size of all experimental nests was measured each year in early July, before experimental watering began.

To quantify reproduction in experimental colonies, we simulated rainfall by watering colonies and collected reproductive offspring (see Cole and Wiernasz 2000 for details of the experimental method). Reproductive males and females were collected from colonies between 1600 and 1800 hours, the normal time of the reproductive flight, and stored at 5°C. Within 48 h, we sorted each day's collections to separate reproductives from any workers. Workers were returned to their colony between 0700 and 0800 hours, a time when the colonies are beginning to forage. Workers were always accepted by their nest mates. Alates were freeze-killed at -20° C, sorted by sex into 96-well tissue culture plates, shipped by overnight airfreight to the University of Houston, and held at -20° C until weighing.

We collected from experimental nests on July 12–19, 1994; July 13–21, 1995; July 7–17, 1996; July 6–17, 1997; July 7–18, 1998; July 8–17, 2001; July 11–21, 2003; July 7–16, 2004; and July 6–13, 2007. In 1999, early rainfall on July 8 resulted in an early flight of the population, and no data were obtained. In 2000, early rainfall on June 25 resulted in an early flight; however, low spring rainfall had greatly lowered reproduction in this population. In 2002, a severe drought resulted in the absence of reproduction in nearly all of the study colonies. In 1996, the study site received approximately 4 mm of rain on June 28, and a small partial flight occurred the next day between 1300 and 1800 hours. The major flight occurred on July 19, 1996. In 2005–2006, early rainfall caused reproductive flights before any measurement of reproductive output could be made.

To quantify intra- and intercolony variation in the size of reproductives, we measured the dry weight of individual males and females from each colony that reproduced. The tissue culture plates were placed uncovered in a drying oven at 65°C for 5 days (Wiernasz et al. 1995). For 1994-1999, we weighed 30 randomly chosen individuals of each sex (or all individuals if a colony produced fewer than 30). Ants were selected using random draws of the 96 wells on the plate; for colonies that occupied multiple plates, the draws were allocated proportionately among up to three plates. In subsequent years, all collected reproductives were weighed. Ants were weighed individually to the nearest 0.1 mg using a Sartorius 2000AS analytical balance in 1994 and to the nearest 0.01 mg using a Mettler AT20 analytical balance in 1995-2007. Repeatability (r^2) of dry weights, based on a sample of 30 individuals, was 0.96 for females and 0.98 for males. We obtained the mean and standard deviation of dry body weight for all colonies.

During 1996–1998, we performed a two-way food supplementation experiment to assess the effects of resource availability on the size and number of reproductive males and females. Previous studies on ants (e.g., DeSlippe and Savoleinen 1994; Herbers and Bansbach 1998) had supplemented using protein, sugar, or both. The diet of P. occidentalis is primarily seeds, with opportunistic foraging on dead arthropods. Because we wanted to manipulate carbohydrate independently of protein-lipid, nests were given either 50 g of cracked wheat (primarily carbohydrate), 5 g of mealworms (primarily protein-lipid), both types of food, or neither type in a balanced design across blocks and colony size categories. Food supplements were put out weekly (beginning on June 1, 1996; March 25, 1997; April 10, 1998) and terminated with the start of experimental watering. Cracked wheat was scattered evenly over the nest cone surface to reduce the likelihood that birds or rodents would collect the food; mealworms were chopped and placed near the nest entrance, where they were immediately dragged inside. Colonies did not receive food supplements after 1998 so that data from 2001-2007 are treated as though no food supplements had been administered.

Statistical Analysis

The data for this study were complex. There were 2 years of baseline data, followed by a 3-year food supplement experiment, which was followed by 4 years of postsupplement measurements. Environmental conditions were extremely variable across years-rainfall dictates the abundance of resources and may have influenced many of the attributes of colony reproduction. Analyses must account for annual variation as well as the issue of repeated measures of parameters. For example, the sexual investment ratio of a colony tends to remain constant over long periods (Wiernasz and Cole 2009). Colonies did not reproduce in every year, resulting in uncontrolled amounts of missing data. We measured nine parameters: the number of males and females produced; the mean, standard deviation, and coefficient of variation of individual dry mass of males and females; and the investment ratio (biomass of males/total reproductive biomass).

We have addressed this complexity by dividing the data into two sets. First, we used two-way ANOVA to ask: how does food supplementation influence the parameters of allocation? Second, we compared the parameters of allocation for each colony before, during, and after food supplementation to address how the parameters of allocation changed during food supplementation and after food supplementation was removed. These analyses were not independent since they use some of the same data, but employing both can give complementary pictures of the response of the parameters of allocation to food supplementation.

The data for the analyses were processed in the following manner. For the number of males or females produced, we used data from all colonies. For the average size of males or females, we used the data from colonies that produced a minimum of 10 males or females (to obtain a valid average). For the investment ratio, we used colonies that produced a total of at least 20 males and females. This was in keeping with past analyses (Wiernasz and Cole 2009) and reduced the chance of obtaining extreme allocation ratios when reproduction was very low. For the standard deviation in body size, we used the standard deviation of dry mass for colonies that produced a minimum of 20 males or females. Although more reliable estimates of the variance would be obtained with larger samples, a higher cutoff leads to a substantial reduction in sample size. Because males and females differ in size, we also calculated the coefficient of variation in body size. After transforming variables (the number of reproductives was log transformed, and the investment ratio was arcsine transformed; there was no need to transform the size of the reproductives), we performed an ANOVA with year and colony identity as classification variables. (The results of these ANOVAs are given in table S1A-S1C; tables S1, S2 are available online.) We calculated the least-squares estimate of the colony effect for each colony. This measure statistically removed the effect of annual differences and accounted for among-colony variation in the number of reproductive events. Colony estimates were obtained for three periods: before food supplementation (1994-1995), during supplementation (1996–1998), and after the experiment (2001–2007).

The colony estimates of the allocation parameters were then used as the dependent variables in a two-way ANOVA using the levels of the food supplements as classification variables. Because colony size is known to influence reproduction (Cole and Wiernasz 2000), we included colony size as a covariate. This procedure had the advantage of preserving degrees of freedom by allowing colonies that do not reproduce each year to contribute to the analysis. However, we did not inflate degrees of freedom by considering the repeated measures from a colony to be independent.

To compare colonies before, during, and after food supplementation, we used an analogous procedure. We analyzed reproductive output prior to food supplementation to verify that assignment to food treatment categories was independent of past reproductive performance. To explore persistent effects of food supplementation, we looked at the effect of food addition on total reproduction separately in the years 2001, 2003, 2004, and 2007. For each year, we measured the effect of colony size and the type of food supplementation that the colonies received in 1995–1997. We expressed the experimental effects with respect to the performance of control colonies.

We tested the prediction that the change in male size will be inversely related to the initial size of the females in two ways. Initially, we regressed the size change of males during food supplementation (male size after - male size before) on the size of females that the colony produced before the food supplement. However, because the size of males and females is correlated across colonies (D. Wiernasz and B. Cole, unpublished data), the X- and Y-axes are not independent. To alleviate this effect, we calculated the partial correlation of the difference in male size and the original female size while holding the original male size constant; our model predicts a significant negative partial correlation coefficient. The second approach tested the prediction that the relationship between male size and female size will be influenced by food supplementation. Our model predicts that colonies that produce small females will maximize fitness increase by allocating additional investment to males when supplemented with food. This will lead to a lower slope when male size is regressed on female size (i.e., a significant interaction effect between food supplementation and female size on male size). We tested for an interaction effect using a one-tailed test, because we predicted the direction of the interaction.

Results

Colonies varied in most aspects of their reproductive allocation. When we limited the analysis to only those colonies that never received any food supplements (to eliminate the effects of food supplementation on any response variables), we found that colonies differed in the size of male and female reproductives that they produced, the variance in these sizes, and their sexual allocation (all P < .01; D. Wiernasz and B. Cole, unpublished data). Colonies also differed in reproductive output, but this was strongly influenced by colony size (see below). Data supporting this article have been deposited in the Dryad Digital Repository: http://dx.doi.org /10.5061/dryad.h4953 (Wiernasz and Cole 2017).

Food supplementation had the greatest influence on reproductive output (fig. 4; results summarized in table 1; full results are part of table S2). Wheat addition strongly increased the number of both males and females; mealworm addition had no significant effect. Supplementation had the smallest effect on reproductive output in 1996, when food addition was started later, in June rather than late Marchearly April. Colonies may also differ in their response to supplementation because they may be at different stages in their reproductive cycle on the same calendar date. While colonies may differ, we do not know whether this difference is consistent from year to year. Male, but not female, size responded to food addition. Colonies that received mealworms produced significantly larger males. During the period of food supplementation, female size was modestly influenced by colony size. Neither the standard deviation nor the coefficient of variation in male or female body size was influenced by food addition or related to colony size. The sexual investment ratio was not directly altered by food addition, but during the experiment the investment ratio was positively related to colony size, indicating greater investment in males by larger colonies.

None of the food supplement treatments was significant before the experiment (P > .2 for all variables), indicating that variation in the allocation parameters among colonies was not correlated with the food treatment that they would receive (see table S2). As expected, colony size was positively correlated with reproductive output both before (P < .025for both sexes), during (P < .0001 for both sexes), and after (P < .0001 for both sexes) the food supplements. Colonies that received wheat substantially increased the number of males and females, but this effect declined after supplementation ceased (fig. 5). However, the reproductive output of colonies that had received wheat supplements in 1996-1998 was significantly higher than expected from their colony size (P < .001 for both male and female reproductive output), largely as a consequence of their having a higher probability of reproduction. Examining each year after the food supplement (table S1C) showed that there was a significant effect of wheat supplement (in 1996-1998) on reproduction in 2001 and 2004 (P < .006 for both cases) but not in 2003 (P > .4), with a marginally significant result in 2007 (see table 2; fig. S2B). Male size increased during food supplementation with mealworms (fig. 6) but returned to values similar to those of males in control colonies after supplementation ceased. No other reproductive allocation parameter displayed any evidence of a persistent effect of supplementation by either type of food (P > .1 in all cases).

The change in male size was significantly related to the original size of the females. The regression of the change of male size on the original size of females was highly significant (standardized regression coefficient r = -0.577, N = 46, df = 44, t = -4.68, P < .001; fig. 7). The partial correlation of the change in male size with female size is -0.327 (N = 46, t = -2.18, df = 43, P = .017), which supports the prediction of a negative relationship between the change of male size and the original female size. Food supplement altered this relationship, as colonies that had made small females prior to supplementation produced substantially larger males than those that had made large females (significant female size \times food supplement interaction term; $F_{1,127} = 5.14$, one-tailed P = .0125).

Discussion

As predicted, the primary effect of food supplementation was to increase production of both sexes; this is the most efficient way to increase colony fitness. Past studies of food supple-



Figure 4: Effects of food supplementation on the number of males and females produced and the size of males and females. B = colonies that received both cracked wheat and mealworms; C = control colonies that received no food supplements; M = colonies that received mealworms only; W = colonies that received cracked wheat only. The bars show the standard error of the mean. For both male and female number, colonies that received cracked wheat (W or B) were higher than other treatments (P < .0001). For male size, colonies that received mealworms (M or B) were larger (P < .01), while there were no effects of food treatment on female size. There were no interaction effects.

mentation in ants typically recorded increased reproductive output (of both males and females: Backus and Herbers 1992; Backus 1993, 1995; DeSlippe and Savolainen 1994, 1995; Herbers and Banschbach 1998; Aron et al. 2001; Ode and Rissing 2002; Bono and Herbers 2003; Foitzik et al. 2004; Smith 2007; of males only: Backus and Herbers 1992; of females only: Morales and Heithaus 1998), although in several studies there was no effect (Munger 1992; DeHeer et al. 2001; Brown and Keller 2006). These previous studies varied substantially in the type of food provided and how the experiment was conducted. The robustness of the result, despite the wide variety of experimental formats, suggests that the egg limitation hypothesis will not apply to ant species unless the food supplements are given so late in offspring development that changes are not possible (e.g., Ode and Rissing 2002).

Our prediction that differences in the form of selection on males and females would shape investment of additional re-

sources was also upheld. For colonies, the payoff depends on the size of individual reproductives and favors building large females over large males (figs. 2-4). For most colonies, the average female is smaller (11.9–13.3 mg dry mass) than the threshold size that leads to higher survival; approximately 25% of colonies make females as large or larger than the threshold size (13.3 mg). This difference may be due in part to irreducible error in building reproductive females (and in colonies with lower average size, some females will be larger than the threshold size). But it may also result from the high mortality of founding queens (>97%; D. Wiernasz and B. Cole, unpublished data; Wiernasz and Cole 2003), favoring increases in female number. This strategy of investing in females first was supported by the results of this study. Food supplementation increased only female number, not female size, indicating that investment in new females conforms broadly to the predictions of the optimal offspring size hypothesis.

000 The American Naturalist

Allocation parameter	During food supplement			Before food supplement			After food supplement		
	Seeds	Mealworms	Size	Seeds	Mealworms	Size	Seeds	Mealworms	Size
Male no.	<.0001	>.5	<.001	>.9	>.8	<.0001	<.001	>.6	<.00001
Female no.	<.0001	>.3	<.025	>.9	>.6	<.0001	<.001	>.3	<.0001
Male size	>.7	<.01	>.6	>.4	>.9	>.7	>.15	>.1	>.9
Female size	>.1	>.15	<.025	>.3	>.7	>.5	>.8	>.3	>.2
Male SD size	>.05	>.1	>.8	>.7	>.2	>.8	>.7	>.7	>.3
Female SD size	>.05	>.7	>.1	>.5	>.4	>.5	>.3	>.3	>.9
Male CV size	>.5	>.9	>.9	>.8	>.4	>.9	>.9	>.5	>.4
Female CV size	>.1	>.5	>.3	>.2	>.4	>.1	>.1	>.9	>.5
Investment ratio	>.2	>.7	<.001	>.4	>.3	>.9	>.3	>.2	>.8

Table 1: Summary of experimental effects on reproductive characters

Note: The experimental treatments are addition of seeds and/or mealworms. Size refers to the effect of colony size as a covariate. Before and after food supplement columns show the data from the same colonies that would or did receive the experimental treatments. CV = coefficient of variation.

Our model predicted that male size should be more responsive to food addition than female size. Male size increased with mealworm addition but was not affected by wheat. Unlike wheat, mealworms cannot be stored by the colony, suggesting that the different responses were a function of whether the food can be stored (to increase reproductive output; e.g., Smith 2007) or must be used immediately (and invested in current reproductives). The production of males broadly conformed to the predictions of the optimistic brood size hypothesis. Colonies that produce an excess of males, some of which will be small if resources are relatively limited, experience costs that are much lower than they would be for a similar overproduction of females. Finally, we predicted that colonies that had been producing small females should invest additional resources disproportionately in males. The negative correlation between the size of females at the onset of the experiment and the amount of size change in males supported this prediction.

Most studies have not measured the effect of food supplementation on the size of reproductives. Smith (2007) found that fed colonies produced larger males than starved colonies, although the difference was not significant. Brown and Keller (2006) found a similar pattern of male size change and female size stability with food supplementation in the polygynous *Formica exsecta*. They suggested that, like *Pogonomyrmex occidentalis* males, larger males of *F. exsecta* may have higher fertilization success, although unfortunately they lacked direct fitness measures. Aron et al. (2001) showed that protein supplements in artificial nests increased the size of both males and females in *Linepithema humile*. Backus (1995) found that males increased in size with food supplements in *Temnothorax longispinosus*. Although the data are



Figure 5: Reproductive output of colonies as a function of food addition (males [*A*] and females [*B*]). After = the output of colonies in the years after the experiment; before = the output of colonies that would subsequently receive food; during = colonies that received either wheat (filled circles) or mealworms (filled triangles) during food supplementation. The reproductive output is the difference between the log-transformed mean output for colonies with a particular food treatment and those without the food treatment. We estimate the 95% confidence limit of the difference as $2 \times s \times (1/n_1 + 1/n_2)^{1/2}$, where *s* is the average, standard error = $(s_1n_1 + s_2n_2)/(n_1 + n_2)$, and *n* is the sample size (Rosner 2006).

Year	Male no.				Female no.		Wilk's λ		
	df	F	Р	df	F	Р	df	F	Р
2001	1, 164	7.58	.0066	1,164	9.2	.0028	2, 163	4.807	.009
2003	1,157	.65	.42	1,157	.16	.68	2,156	.4	.67
2004	1,144	11.82	.0008	1,144	9.05	.0031	2, 143	6.17	.0027
2007	1,111	3.75	.055	1,111	6.35	.013	2,110	3.30	.041

Table 2: Effect that food supplement had during the years after the food supplement

Note: Reproduction for the years after the food supplement in relation to seed supplement received during the food supplement. These are the results of an analysis of variance with mealworm supplement (during the food supplement) as the other food treatment and colony size as a covariate. In all cases the mealworm treatment was not significant, while in all cases the colony size treatment was significant for both the univariate and the multivariate (simultaneous male and female) tests.

sparse, these results suggest that sexual selection on male size may be widespread in ants.

Many previous food addition experiments in ants changed sex allocation (Deslippe and Savolainen 1995; Herbers and Banschbach 1998; Morales and Hiethaus 1998; Ode and Rissing 2002; Bono and Herbers 2003; certain blocks in Foitzik et al. 2004; Brown and Keller 2006; and in food addition relative to starved colonies in Smith 2007), while other studies did not show a change (Backus and Herbers 1992; Munger 1992; Aron et al. 2001; overall treatment effect in Foitzik et al. 2004). However, in all but one of these (i.e., Brown and Keller 2006), the effect was caused by increasing both male and female reproductive output, with a disproportionate increase in females. The disproportionate increase in female production can be interpreted as diverting resources to convert diploid females into reproductives when there is a food bonanza rather than an adaptive adjustment to sex ratio.

The correlation of sexual investment ratio with colony size during the years of food supplementation appears to be a function of the differential response of colonies to the production of new males compared to new females. During food supplementation, the number of both sexes increased, but larger colonies produced disproportionately more males. This result is consistent with resource tracking (Temme and Charnov 1987), where colonies with a larger workforce were better able to convert a food windfall into increased reproduction. The cost of overproducing haploid (male) eggs may be modest because they do not require use of the queen's finite number of sperm. In years with a glut of resources, more males survive as well as grow to a larger average size, leading to increased male production in larger colonies.

The persistent effect of food addition on colony reproduction was unexpected. The robustness of the result is uncertain, because data were unavailable for some years (1999, 2000, 2002, 2005–2006) and because the magnitude of the effect varied (strong in 2001, 2004; weak in 2007; absent in 2003). Our analyses accounted for effects of colony size, indicating that the probability of reproduction for a colony changed as a consequence of its supplementation history. The simplest explanation is that food supplementation advanced the onset of reproduction, which then occurred at lower size thresholds in subsequent years, although the mechanism for this change is unknown.

Long-lived ant colonies share many features with perennial plants, including iteroparity, size-based demography, and sessility (Cole 2009). The problem of investing in reproduc-



Figure 6: Change in size of males (*A*) and females (*B*) with respect to food supplements. The symbols and time periods are the same as in figure 4. The difference in size is the difference in the mean size in food supplemented compared to control colonies and is calculated as in figure 4.



Figure 7: Change in male size during food supplementation as a function of the presupplement size of the females produced by the colony. The correlation is still highly significant (r = 0.50, N = 38 colonies, P = .0014) if the colony with the smallest female size is removed.

tion through male and female production has been extensively studied in flowering plants. Although it is possible to measure investment in male and female function in perfect flowers (e.g., Campbell 1989, 1998; Arista and Ortiz 2007), a more appropriate parallel to our study is the investment patterns in imperfect flowers of monoecious or dioecious species. The dominant result of these studies is that large male flowers are more effective at attracting pollinators and deliver greater fitness through male function than smaller male flowers (Ågren and Schemske 1995; Schemske and Ågren 1995; Burd and Callahan 2000; Worley et al. 2000; Parachnowitsch and Elle 2004; Arista and Ortiz 2007). One could hypothesize that fitness increases, perhaps nonlinearly, with increasing male size, while female fitness is relatively insensitive to flower size (Worley et al. 2000; Arista and Ortiz 2007). However, because male flowers, large or small, are displayed on the parent plant, the fitness achieved through each genetically identical male flower may depend on the phenotypes of all other male flowers. Male (or female) ants produced by a single ant colony leave the colony to mate and achieve fitness through male or female function independently of their sibling reproductives.

Trivers and Willard (1973) modeled sex allocation strategies based on both a female's condition, which affected the quality of offspring that she could produce, and how the condition of the offspring affected its fitness. Their prediction, that the more costly sex will be produced by the females in better condition, has been tested hundreds of times (reviewed in Cameron 2004; Sheldon and West 2004). Although the results are complex, the overall support for this hypothesis in mammals is very strong. Our model is a generalization of the Trivers-Willard hypothesis: the sex of offspring with the larger slope on the fitness surface may differ depending on the starting location of the parent. This generalization (eq. [1]) can encompass diverse investment strategies. Importantly, the model incorporates the possibility that many offspring can be produced by a single mother, while the Trivers-Willard hypothesis is generally applied to a mother that produces one or a few offspring.

We have shown how the sex-specific fitness functions inform the calculation of the reproductive payoff when organisms vary in the investment they may provide to different categories of offspring. The power of this approach was demonstrated by a study on maternal investment in *Anolis sagrei* (Cox and Calsbeek 2010). A male's size has a nonlinear effect on the fitness of his sons but a linear effect on the fitness of his daughters. The disproportionate effect of sire size on male offspring fitness accounts for the male bias of offspring sex ratio among females that mated with larger males. Male quality is now known to influence investment in offspring by females in many species (see reviews by Røed et al. 2007; Horváthová et al. 2011; Prokop et al. 2012), suggesting that maternal investment may be quite plastic.

Reproductive success is maximized when the rate of return on reproductive investment is also maximized (Charnov 1982). This will be straightforward when considering investment in a single trait that has similar effects on the fitness of all offspring. When the fitness of different kinds of offspring (males vs. females or one sex with alternate morphologies) responds differently to similar levels of investment, then the effects can be visualized using a fitness landscape. Individuals maximize the rate of return on their investment by allocating resources among offspring in such a way as to generate the greatest rate of increase on the fitness landscape. Parents will vary in age, available resources, or environmental conditions and are likely to begin at many different positions on this fitness landscape. Consequently, two individuals that acquire an identical increase in resources will not always change investment identically.

Acknowledgments

We thank J. Villinski, I. Billick, B. Mallberg, J. Yencharis, K. Haight, C. Kracht, M. Hayden, T. Holbrook, L. Holm, J. Heyward, and K. Miller for help with the fieldwork and J. Yencharis, J. Coombs, K. Miller, B. Tao, F. Trampus, C. Perroni, A. Zarrabi, M. Bosley, S. Turner, D. David, and T. Nguyen for help with weighing ants. We thank I. Billick, B. Dertien. L. Appleby, D. Lubertazzi, C. Baer, and two anonymous reviewers for comments on earlier versions of the article. This work was supported by grant 003652-0014 from the Texas Coordinating Board Norman Hackerman Advanced Research Program to D.C.W.; National Science Foundation grant BSR-910834 to D.C.W. and grants DEB-9509312, IBN-9507470, IOS-0344896, and IOS-1147418 to B.J.C. and D.C.W.; and grants from the University of Houston Coastal Center to D.C.W. and B.J.C.

Literature Cited

- Abell, A., B. J. Cole, R. Reyes-Garcia, and D. C. Wiernasz. 1999. Sexual selection on body size and shape in the western harvester ant, *Pogonomyrmex occidentalis*. Evolution 53:535–545.
- Ågren, J., and D. W. Schemske. 1995. Sex allocation in the monoecious herb *Begonia semiovata*. Evolution 49:121–130.
- Arista, M., and P. L. Ortiz. 2007. Differential gender selection on floral size: an experimental approach using *Cistus salvifolius*. Journal of Ecology 95:973–982.
- Aron, S., L. Keller, and L. Passera. 2001. Role of resource availability on sex, caste and reproductive allocation ratios in the Argentine ant *Linepithema humile*. Journal of Animal Ecology 70:831–839.
- Backus, V. L. 1993. Packaging of offspring by nests of the ant, *Lep-tothorax longispinosus*: parent-offspring conflict and queen-worker conflict. Oecologia 95:283–289.
- . 1995. Rules for allocation in a temperate forest ant: demography, natural selection, and queen-worker conflict. American Naturalist 145:775–796.
- Backus, V. L., and J. M. Herbers. 1992. Sexual allocation ratios in forest ants: food limitation does not explain observed patterns. Behavioural Ecology and Sociobiology 30:425–429.
- Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. American Zoologist 36:216–236.
- Bleu, J., J. Le Galliard, P. S. Fitze, S. Meylan, J. Clobert, and M. Massot. 2013. Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard. Oecologia 171:141–151.
- Bonabeau, E., J. L. Deneubourg, and G. Theraulaz. 1998. Withinbrood competition and the optimal partitioning of parental investment. American Naturalist 152:419–427.
- Bono, J. M., and J. M. Herbers. 2003. Proximate and ultimate control of sex ratios in *Myrmica brevispinosa* colonies. Proceedings of the Royal Society B 270:811–817.
- Bourke, A. F. G., and N. R. Franks. 1995. Social evolution in ants. Princeton University Press, Princeton, NJ.
- Brown, W. D., and L. Keller. 2006. Resource supplements cause a change in colony sex-ratio specialization in the mound-building ant, *Formica exsecta*. Behavioral Ecology and Sociobiology 60:612–618.
- Burd, M., and H. S. Callahan. 2000. What does the male function hypothesis claim? Journal of Evolutionary Biology 13:735–742.
- Büschinger, A., and J. Heinze. 1992. Polymorphism of female reproductives in ants. Pages 11–23 *in* J. Billen, ed. Biology and evolution of social insects. Leuven University Press, Leuven.
- Cahan, S. H., and S. W. Rissing. 2005. Variation in queen size across a behavioral transition zone in the ant *Messor pergandei*. Insectes Sociaux 52:84–88.
- Cameron, E. Z. 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism. Proceedings of the Royal Society B 271:1723–1728.

- Campbell, D. R. 1989. Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. Evolution 43:318–334.
- . 1998. Variation in lifetime male fitness in *Ipomopsis aggregata*: tests of sex allocation theory. American Naturalist 152:338–353.
- Carrière, Y., and D. A. Roff. 1995. The evolution of offspring size and number: a test of the Smith-Fretwell model in three species of crickets. Oecologia 102:389–396.
- Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.
- Charnov, E. L., and S. K. Morgan Ernest. 2006. The offspring-size/ clutch-size trade-off in mammals. American Naturalist 167:578–582.
- Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews 77:1–26.
- Clemencet, J., L. Cournault, A. Odent, and C. Doums. 2010. Worker thermal tolerance in the thermophilic ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Insectes Sociaux 57:11–15.
- Cole, B. J. 2009. The ecological setting of social evolution: the demography of ant populations. Pages 74–104 *in* J. Fewell and J. Gadau, eds. New frontiers in behavioral ecology—from gene to society. Harvard University Press, Cambridge, MA.
- Cole, B. J., and D. C. Wiernasz. 1999. The selective advantage of low relatedness. Science 285:491–493.
- ———. 2000. Size and reproduction in the western harvester ant, *Pogonomyrmex occidentalis*. Insectes Sociaux 47:249–255.
- 2002. Recruitment limitation and population density in the harvester ant, *Pogonomyrmex occidentalis*. Ecology 83:1433–1442.
- Courvillon, M. J., W. O. H. Hughes, J. A. Perez-Sato, S. J. Martin, G. G. F. Roy, and F. L. W. Ratnieks. 2010. Sexual selection in honey bees: colony variation and the importance of size in male mating success. Behavioral Ecology 21:520–525.
- Cox, R. M., and R. Calsbeek. 2010. Cryptic sex-ratio bias provides indirect genetic benefits despite sexual conflict. Science 328:92–94.
- Crozier, R. H., and P. Pamilo. 1996. Evolution of social insect colonies. Oxford University Press, Oxford.
- Czesak, M. E., and C. W. Fox. 2003. Evolutionary ecology of egg size and number in a seed beetle: genetic trade-off differs between environments. Evolution 57:1121–1132.
- Davidson, D. W. 1982. Sexual selection in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). Behavioural Ecology and Sociobiology 10:245–250.
- DeHeer, C. J., V. L. Backus, and J. M. Herbers. 2001. Sociogenetic responses to ecological variation in the ant *Myrmica punctiventris* are context dependent. Behavioural Ecology and Sociobiology 49:375–386.
- Derocher, A. E., and I. Stirling. 1998. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). Journal of Zoology 245:253–260.
- Deslippe, R. J., and R. Savolainen. 1994. Role of food supply in structuring a population of *Formica* ants. Journal of Animal Ecology 63:756– 764.
- ———. 1995. Sex investment in a social insect: the proximate role of food. Ecology 76:375–382.
- Elgar, M. A. 1990. Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. Oikos 59: 283–287.
- Enzmann, B. L., and P. Nonacs. 2010. Digging beneath the surface: incipient nest characteristics across three species of harvester ants that differ in colony founding strategy. Insectes Sociaux 57:115–123.
- Fischer, K., A. N. M. Bot, M. Brakefield, and B. J. Zwaan. 2006. Do mothers producing large offspring have to sacrifice fecundity? Journal of Evolutionary Biology 19:380–391.

000 The American Naturalist

- Fjerdingstad, E. J. 2005. Control of body size in *Lasius niger* ant sexuals—worker interests, gynes and environment. Molecular Ecology 14:3123–3132.
- Fjerdingstad, E. J., and J. J. Boomsma. 1997. Variation in size and sperm content of sexuals in the leaf cutter ant *Atta columbica*. Insectes Sociaux 44:209–218.
- Fjerdingstad, E. J., and L. Keller. 2004. Relationships between phenotype, mating behavior and fitness of queens in the ant, *Lasius niger*. Evolution 58:1056–1063.
- Foitzik, S., V. L. Backus, A. Trindl, and J. M. Herbers. 2004. Ecology of *Leptothorax* ants: impact of food, nest sites, and social parasites. Behavioral Ecology and Sociobiology 55:484–493.
- Fox, C. W., and M. E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45:341–369.
- Frank, S. A. 1987*a*. Individual and population sex allocation patterns. Theoretical Population Biology 31:47–74.
- ———. 1987b. Variable sex ratio among colonies of ants. Behavioural Ecology and Sociobiology 20:195–201.
- Gilboa, S., and P. Nonacs. 2006. Testing models of parental investment strategy and offspring size in ants. Oecologia 146:667–674.
- Gonzalez, O., A. Zedrosser, F. Pelletier, J. E. Swenson, and M. Festa-Bianchet. 2012. Litter reductions reveal a trade-off between offspring size and number in brown bears. Behavioural Ecology and Sociobiology 66:1025–1032.
- Hendry, A. P., T. Day, and A. B. Cooper. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. American Naturalist 157:387–407.
- Herbers, J. M. 1990. Reproductive investment and allocation ratios for the ant *Leptothorax longispinosus*: sorting out the variation. American Naturalist 136:178–208.
- Herbers, J. M., and V. S. Banschbach. 1998. Food supply and reproductive allocation in forest ants: repeated experiments give different results. Oikos 83:145–151.
- Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap, Cambridge, MA.
- Horváthová, T., S. Nakagawa, and T. Uller. 2011. Strategic female reproductive investment in response to male attractiveness in birds. Proceedings of the Royal Society B 279:163–170.
- Houston, A. I., P. A. Stephens, I. L. Boyd, K. C. Harding, and J. M. McNamara. 2007. Capital or income breeding? a theoretical model of female reproductive strategies. Behavioral Ecology 18:241–250.
- Jakobsson, A., and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88:494–502.
- Ji, J. X., W.-G. Du, H. Li, and L.-H. Lin. 2006. Experimentally reducing clutch size reveals a fixed upper limit to egg size in snakes, evidence from the king ratsnake, *Elaphe carinata*. Comparative Biochemistry and Physiology A 144:474–478.
- Johnson, R. A. 1998. Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae). Insectes Sociaux 45:255–266.
- 2006. Capital and income breeding and the evolution of colony founding strategies in ants. Insectes Sociaux 53:316–322.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66.
- Jonsson, N., and B. Jonsson. 1999. Trade-off between egg mass and egg number in brown trout. Journal of Fish Biology 55:767–783.
- Kikuchi, T., S. Higashi, and T. Murakami. 1999. A morphological comparison of alates between monogynous and polygynous colo-

nies of *Myrmica kotokui* in northernmost Japan. Insectes Sociaux 46:250–255.

- MacNair, M. R. 1978. An ESS for the sex ratio in animals, with particular reference to the social hymenoptera. Journal of Theoretical Biology 70:449–459.
- Mangel, M. 1987. Oviposition site selection and clutch size in insects. Journal of Mathematical Biology 25:1–22.
- McGinley, M. A., D. H. Temme, and M. A. Geber. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. American Naturalist 130:370–398.
- Messina, F. J., and C. W. Fox. 2001. Offspring size and number. Pages 113–127 in C. W. Fox, D. A. Roff, and D. J. Fairbairn, eds. Evolutionary ecology: concepts and case studies. Oxford University Press, New York.
- Mock, D. W., and L. S. Forbes. 1995. Parent-offspring conflict: a case of arrested development. Trends in Ecology and Evolution 18:88–93.
- Mock, D. W., and G. A. Parker. 1997. The evolution of sibling rivalry. Oxford University Press, New York.
- . 1998. Siblicide, family conflict, and the evolutionary limits of selfishness. Animal Behaviour 56:1–10.
- Morales, M. A., and E. R. Heithaus. 1998. Food from seed dispersal mutualism shifts sex ratios in colonies of the ant *Aphaenogaster rudis*. Ecology 79:734–739.
- Munger, J. C. 1992. Reproductive potential of colonies of desert harvester ants (*Pogonomyrmex desertorum*): effects of predation and food. Oecologia 90:276–282.
- Nagel, H. G., and C. W. Rettenmeyer. 1973. Nuptial flights, reproductive behavior and colony founding of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 46:82–101.
- Nonacs, P. 1986*a*. Ant reproductive strategies and sex allocation theory. Quarterly Review of Biology 61:1–21.
- ——. 1986b. Sex-ratio determination within colonies of ants. Evolution 40:199–204.
- ———. 1990. Size and kinship affect success of co-founding *Lasius pallitarsis* queens. Psyche 97:217–228.
- Ode, P. J., and S. W. Rissing. 2002. Resource abundance and sex allocation by queen and workers in the harvester ant, *Messor pergandei*. Behavioural Ecology and Sociobiology 51:548–556.
- Parachnowitsch, A. L., and E. Elle. 2004. Variation in sex allocation and male-female trade-offs in six populations of *Collinsia parviflora* (Scrophulariaceae sl.). American Journal of Botany 91:1200– 1207.
- Plaistow, S. J., J. J. H. St. Clair, J. Grant, and T. G. Benton. 2007. How to put all your eggs in one basket: empirical patterns of offspring provisioning throughout a mother's lifetime. American Naturalist 170:520–529.
- Prokop, Z. M., Ł. Michalczyk, S. M. Drobniak, M. Herdegen, and J. Radwan. 2012. Meta analysis suggests choosy females get sexy sons more than "good genes." Evolution 66:2665–2673.
- Røed, K. H., Ø. Holand, A. Mysterud, A. Tverdal, J. Kumpula, and M. Nieminen. 2007. Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. Proceedings of the Royal Society B 274:727–733.
- Roff, D. A. 2003. Life history evolution. Sinauer, Sunderland, MA.
- Rosenheim, J. A. 2011. Stochasticity in reproductive opportunity and the evolution of egg limitation in insects. Evolution 65:2300– 2312.
- Rosenheim, J. A., S. J. Jepson, C. E. Matthews, D. S. Smith, and M. R. Rosenheim. 2008. Time limitation, egg limitation, the cost of ovi-

Reproductive Allocation and Fitness 000

position and lifetime reproduction by an insect in nature. American Naturalist 172:486-496.

Rosenheim, J. A., P. Nonacs, and M. Mangel. 1996. Sex ratios and multifaceted parental investment. American Naturalist 148:501– 535.

Rosner, B. 2006. Fundamentals of biostatistics. Thomson, New York.

- Rüppell, O., J. Heinze, and B. Hölldobler. 1998. Size-dimorphism in the queens of the North American ant *Leptothorax rugatulus* (Emery). Insectes Sociaux 45:67–77.
- Schemske, D. W., and J. Ågren. 1995. Deceit pollination and selection on female flower size in *Begonia involucrata*: an experimental approach. Evolution 49:207–214.
- Sheldon, B. C., and S. A. West. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. American Naturalist 163:40–54.
- Shine, R. 2005. Life history evolution in reptiles. Annual Review of Ecology, Evolution, and Systematics 36:23–46.
- Sinervo, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution 44:279–294.
- . 1998. Adaptation of maternal effects in the wild: path analysis of natural variation and experimental tests of causation. Pages 288– 306 *in* T. A. Mousseau and C. W. Fox, eds. Maternal effects as adaptations. Oxford University Press, Oxford.
- Sinervo, B., and P. Licht. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. Science 252:1300–1302.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.
- Smith, C. R. 2007. Energy use and allocation in the Florida harvester ant, *Pogonomyrmex badius*: are stored seeds a buffer? Behavioural Ecology and Sociobiology 61:1479–1487.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Temme, D. H., and E. L. Charnov. 1987. Brood size adjustment in birds: economical tracking in a temporally varying environment. Journal of Theoretical Biology 126:137–147.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.
- Venable, D. L. 1992. Size-number trade-offs and the variation of seed size with plant resource status. American Naturalist 140:287–304.
- Wagner, D., and D. M. Gordon. 1999. Colony age, neighborhood density and reproductive potential in harvester ants. Oecologia 119:175–182.
- Wheeler, D. E. 1986. Developmental and physiological determinants of caste in social hymenoptera: evolutionary implications. American Naturalist 128:13–34.
- Wiernasz, D. C., and B. J. Cole. 1995. Spatial distribution of *Pogono-myrmex occidentalis*: recruitment mortality and overdispersion. Journal of Animal Ecology 64:519–527.
- ——. 2003. Queen size mediates queen survival and colony fitness in harvester ants. Evolution 57:2179–2183.
- 2009. Dioecy and the evolution of sex ratios in ants: evidence from harvester ants. Proceedings of the Royal Society B 209:2125– 2132.
- 2017. Data from: Offspring size and reproductive allocation in harvester ants. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.h4953.
- Wiernasz, D. C., C. Perroni, and B. J. Cole. 2004. Polyandry and fitness in the western harvester ant, *Pogonomyrmex occidentalis*. Molecular Ecology 13:1601–1606.
- Wiernasz, D. C., A. K. Sater, A. J. Abell, and B. J. Cole. 2001. Male size, sperm transfer and colony fitness in the western harvester ant, *Pogonomyrmex occidentalis*. Evolution 55:324–329.
- Wiernasz, D. C., J. Yencharis, and B. J. Cole. 1995. Size and mating success in males of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). Journal of Insect Behavior 8:523–531.
- Worley, A. C., A. M. Baker, J. D. Thompson, and S. C. Barrett. 2000. Floral display in *Narcissus*: variation in flower size and number at the species, population, and individual levels. International Journal of Plant Sciences 161:69–79.

Associate Editor: Charles F. Baer Editor: Judith L. Bronstein