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The ecological setting of social evolution: the demography of ant populations.

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This chapter is centered on the demography of ant populations: the growth, reproduction and mortality of colonies. I have chosen to focus on this rather specific set of topics in the ecology of ants because they are a central feature of life history that is a prerequisite for understanding social evolution. I will first describe the utility of demographic data and its analysis and then review information on the demography of ant populations. More detailed descriptions of some of the demographic methods are given in the appendix.

Age-specific mortality, age-specific fecundity and population growth rate interact to influence the fitness of an organism. For ants, when we say that strategies concerning communication, recognition, division of labor, foraging or sex allocation, are selectively advantageous, we are making a statement about the fitness consequences of a behavioral tactic or syndrome. What we often measure, however, are the functional consequences of a trait: how does a particular change in behavior influence the efficiency of communication or division of labor. We then use the functional differences to infer the direction of selection by a logical argument. This approach is probably correct in a qualitative sense: a difference in behavior that increases the efficiency of communication or division of labor probably is selectively advantageous. However, it is nearly impossible to say how significant even a major change in behavior will be without considering the evolutionary ecology of the organism. It is even less likely that we can fruitfully argue about the relative importance of one behavioral change (e.g., sex allocation) over another (e.g., division of labor) without understanding the ecological setting of the trait. To make significant progress in understanding the evolution of any trait, including social behavior, we must place our evolutionary, genetic and behavioral studies in a demographic context. The state of this information in ants is not very satisfactory, but there is some information, and the hope is that a review of techniques and data will stimulate the collection of more information.

The demographic literature on natural populations of ants is incomplete and often sketchy. There are a number of reasons for the lack of information, but to some degree we can blame the ants. Ant colonies are long-lived, iteroparous organisms who place their nests where workers cannot be easily seen. Colonies may move frequently or have cryptic locations often making them impossible to follow. If one cannot identify individual colonies, determine their ages, follow their survival, measure their reproduction or be able to carry out the study for long enough, it is difficult to gather demographic data. An ideal study for obtaining demographic data would be a detailed longitudinal study, but even when the study does not have the most desirable properties, it can be possible to extract useful information. For example, when we do not have direct information on the age of colonies, it can be possible to infer their age-specific mortality and fecundity.

One of the main techniques used in this chapter is manipulation of demographic matrices. The (online supplementary material?) appendix shows how to extract a variety of information from the age and stage-based data that can be collected from ant populations. Essentially we will work with two types of data: age or stage-specific survival and reproduction. The survival data are encapsulated by the transition matrix, **T**, that measures the probability of making a transition from one age or stage to another. The reproductive data are given by the fecundity matrix, **F**, measuring the reproductive contribution of one age or stage to another. When the data are age-specific, then the sum of the two matrices is the familiar Leslie matrix, **L**, and when the data are stage-specific we refer to this matrix as **S**. By manipulating these matrices a variety of information about life expectancy, population growth rate, age distribution, and reproductive value can be obtained. The appendix relies heavily on Cochran and Ellner (1992) and especially

Caswell (2002), the definitive source for demographic analysis of populations using the matrix methods described below. Age within stage distributions are discussed by Boucher (1997).

Demography of ant populations

This part of the chapter is divided into components that reflect life cycle stages and the type of data: age or stage-based. Queens produce colonies, colonies grow and eventually reproduce and finally they die. There is some information on the probability that queens will successfully found a colony and about growth and mortality of colonies and somewhat more on the reproduction of colonies. It is fair to say that there has been more of a focus on gathering data on reproduction rather than growth and survival.

Queen survival during colony founding. The demography of queens, the least conspicuous stage in the life cycle of the colony, is often poorly known. Although we all assume that colony founding is the most dangerous portion of the life cycle, the probability that a queen will survive to found a colony is known for few species. Laboratory studies have shown that under appropriate conditions the probability of successful colony founding can be quite high (Johnson 1998), so the observed high mortality must be due to a combination of parasites, predators, pathogens, competitors, environmental stress and the physiological cost of producing the first workers that is expressed in the field.

When queens disappear into the soil or wood during claustral colony founding, it may be impossible to associate a queen with a specific colony. If queens are only observable for a matter of hours, then it is difficult even to measure the density of queens and the density of incipient colonies. This latter measure may provide a possible way to assay the success of colony founding, but estimates of the density of founding queens are rare. Colony founding by non-independent means, such as colony fission or by temporary social parasitism or through readoption of queens into natal nests, yield higher values for queen survival, but these types of colony founding will not be discussed.

There are published data for colony founding success by queens in *Pogonomyrmex occidentalis*, *Crematogaster ashmeadi*, *Solenopsis invicta* and *Atta bisphaerica* (Table 1). The probabilities range from 0.001 - 0.076 that a queen produces colonies through the incipient stage. Indirect data would be a welcome addition to these scanty direct measurements. One approach would be to relate the density of queens to the density of colonies. In a population, the number of queens that land on a particular area should be related to the number of colonies in that area. The form of the relationship is a function of the survival of queens to the colony stage and colony lifespan. Figure 1 shows the correlation between the number of queens of a variety of species and the density of colonies (Table 1). As expected, the number of queens is substantially more than the number of colonies. For two species that have been measured repeatedly, *P. occidentalis* and *Lasius flavus*, the density of queens and colonies fall roughly on a line, indicating a relatively constant relation of queen and colony density. Because *P. occidentalis* colonies cluster around the line indicating about ten times as many queens as colonies, it would require at least 90% mortality (10% survival), for the entire population to be replaced in one year. Since we know that survival is actually closer to 1%, we estimate that about 10 years are required for population replacement. This rough method gives an estimate of colony survival that is rather accurate. It estimates approximately 1 year for *S. invicta*, and 3.3 years for *C. ashmeadi,* consistent with direct measures. Remembering that these are not longevities (which can be at least 45 years in the case of *P. occidentalis*), but life expectancies at the smallest colony size, estimates are probably consistent to within a factor of two or three.

For species that cluster in the vicinity of the 100 isocline, with a life expectancy (after colony founding) of approximately 10 years, we would predict that queen survival must be approximately 0.001. For *Atta bisphaerica*, the estimate of founding success is 0.002 and while there is an estimate of queen density, there is no estimate of colony density at that location. After colony founding in *A. capiguara*, the survival of incipient colonies is again 0.001 over the first three months (Fowler, et al. 1976; this is a time period after colony founding has occurred). Comparing queen and colony density for two other species of *Atta* suggests that the probability of founding a colony should be as low as 0.0001 - 0.00001. Whether this estimate is off by a factor of two or three, it seems clear that survival of queens in many species must be less than 1 per thousand and for certain species may be far less than that.

For two species, *S. invicta* and *P. occidentalis*, there is information about survival at more than one time point during colony founding. The survival of *S. invicta* queens was followed daily during the formation of incipient colonies and high mortality rates of 5-6% per day were followed by a period of declining mortality (0.6-2% per day) as incipient colonies formed. *P. occidentalis* has a similar pattern with a mortality of 7% per day falling to 5.5% per day at the time when incipient colonies are produced. The concordance of the two measures suggests qualitative generality if not quantitative congruence. These mortality rates mean that the life expectancy of a queen after a mating flight is 14 - 18 days. This is a rather amazing value for an insect that, in the case of *P. occidentalis*, can live for 45 years (Keeler 1988, 1993). It seems likely that the life expectancy of an *Atta* queen must be measured in hours.

Survival of colonies. For colonies with a single queen, the survival of the queen and the colony coincide. For many of the best studied species, the survival of colonies is another life-cycle stage in the survival of queens. In these cases the demography of colonies cannot be separated from the demography of queens.

Age-related mortality. Age-specific mortality of colonies has been measured in several species. One might predict that mortality would be higher among young colonies and lower among older colonies, if for no other reason than the increased size of the colony. In *S. invicta* survival increases with colony size (Adams & Tschinkel 2001), colony size increases with age (Tschinkel 1993) and survivorship is particularly low in young colonies (Adams and Tschinkel 1995).

Age-specific mortality rates decline in *P. occidentalis* (unpubl. data) initially, as expected, but they increase in *P. barbatus* (Gordon & Kulig 1998). Both species are seed harvesting ants in arid environments, with relatively large adult colony sizes and single queens. It seems unlikely that the increase in mortality reflects senescence. It is not clear why these two species, with superficially similar ecologies are different. These data are collected by direct observations of the survival of individual colonies for at least 10 years. Figure 2 shows the age-specific survival for *P. barbatus* colonies together with *P. occidentalis*. There are substantial differences in the pattern of survival between *P. occidentalis* and *P. barbatus*. Although survival is fairly consistent later in life with annual survival being ~ 0.8 in *P. occidentalis* and ~ 0.9 in *P. barbatus*, there is a ten-fold greater mortality among first year *P. occidentalis* young colonies (0.4) compared to *P. barbatus* (0.04).

Survival of queens during colony founding is 1.8% for *P. occidentalis*. This means that when we imagine the colony from 0 to 1 year, the curve would climb to 56 times the starting value shown in Fig 2. The survival of *P. barbatus* queens is unknown, but presumed to be similarly low. All evidence suggests that queens have an extreme Type III survivorship

Table 1–Queen and Population Density

Species	Queen Density [a]	Colony Density [a]	Notes	Reference
Acromyrmex landolti fracticornis	4500	2400	Paraguay[b]	Data cited in Fowler, et al. 1986
Acromyrmex muticonodis	200	2.5	Sao Paulo, Brazil[b]	Data cited in Fowler, et al. 1986
Atta capiguara	300	2.3	Sao Paulo, Brazil[b]	Data cited in Fowler, et al. 1986
Atta capiguara	450	8	Paraguay[b]	Data cited in Fowler, et al. 1986
Atta capiguara	8000	.	Sao Paolo, Brazil[b]	Data cited in Fowler, et al. 1986
Atta cephalotes	6000	0.5	Guatemala[b]	Data cited in Fowler, et al. 1986
Atta sexdens rubropilosa	500	3	Sao Paulo, Brazil[b]	Data cited in Fowler, et al. 1986
Atta vollenweideri	1800	0.9	Paraguay[b]	Data cited in Fowler, et al. 1986
Atta bisphaerica	900		Sao Paulo, Brazil[b] Survival of queens 0.0009	Fowler 1987. Data cited in Fowler, et al. 1986
Pogonomyrmex occidentalis	112 - 1104	20 -96	20 plots, Colorado, USA survival of queens 0.013	Cole & Wiernasz 2002

Pogonomyrmex occidentalis	671	81	Colorado, USA	Cole & Wiernasz, unpubl.
Crematogaster ashmeadi	197	49	Florida, USA, survival of queens 0.076	Hahn & Tschinkel 1997
Solenopsis invicta	3000	40	Florida, USA, Survival of queens 0.002 - 0.04	Tschinkel 1992
Lasius flavus	10000	2600	England[c]	Elmes
Lasius niger	12000	100	England[c]	Elmes
Lasius niger	55173	392	Denmark[c]	Boomsma, et al. 1982
Lasius niger	5699	181	Denmark[c]	Boomsma, et al. 1982
Lasius niger	1092	16	Denmark[c]	Boomsma, et al. 1982
Lasius niger	23360	800	Poland[c]	Pętal 1980
Myrmica spp.	67100	1100	Poland[c]	Pętal 1980

[a] Except for *C. ashmeadi* density ha^{-1}. Where multiple values given by source, the midpoint of range.

[b] Data for queen density and colony density come from same location, but not necessarily the same population.

[c] Data calculated from queen production per colony, colony density and, where applicable, proportion of colonies that produce queens.

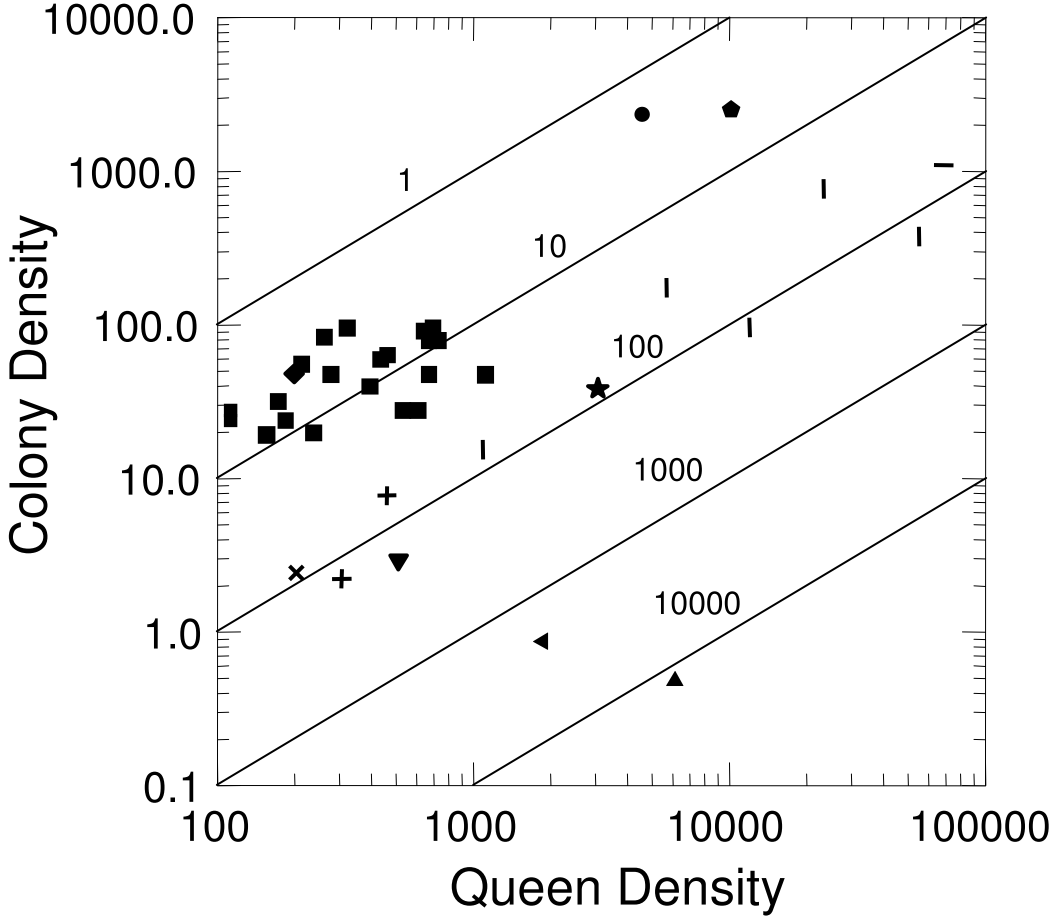

Figure 1. Density of colonies and queens at a site. Densities are given in colonies or queens per hectare (except for *Crematogaster ashmeadi*). Data are given in Table 1. Symbols represent different species: Circles-*Acromyrmex landolti*; squares-*Pogonomyrmex occidentalis*; diamond-*Crematogaster ashmeadi*; x-*Acromyrmex multiconodis*; + *Atta capiguara*; upright triangle - *Atta cephalotes*; downward pointing triangle - *Atta sexdens*; left-pointing triangle - *Atta vollenweideri*; vertical line - *Lasius niger*; pentagon - *Lasius flavus*; horizontal line - *Myrmica*; star - *Solenopsis invicta*. The diagonal lines indicate equal ratios of queens to colonies at a location.

curve–most mortality occurring early in life, with a very small fraction of the population reaching reproductive maturity. While many insects are known to have extreme Type III survivorship, most do not combine it with extreme longevity. In this way ant colonies are most similar in their patterns of mortality to trees, cod fish and corals. They do not have many similarities, apart from longevity, to the survival patterns of the social vertebrates with which they are often compared.

The data points that produce Fig. 2 constitute the entries in the transition matrix, **T** (see Appendix). From the transition matrix we can obtain an estimate of the amount of time that a colony can be expected to spend in each subsequent age category as a function of age (= $(\mathbf{I}\text{-}\mathbf{T})^{-1}$, where **I** is the identity matrix-ones on the diagonal and zeros elsewhere). The sum of these estimates are the colony life expectancy which for *P. occidentalis* rises to a maximum of about 10 years at the age of 4-5 years.

Stage-related patterns of mortality. For ants it is often far easier to obtain information about stage or size related patterns of mortality than about age-related patterns of mortality. It may be easier to obtain survival information about incipient colonies, young colonies, and mature colonies, for example, than to follow individual colonies for long enough to obtain age information. Size information, as one specific type of stage information, is particularly informative. Data must be collected in at least two time intervals and individuals of known stage or size must be classed as surviving (to a size class) or dying. Because individuals are assessed after a time interval, there is temporal information implicit in the data set, and it is possible to extract a considerable amount of age-related information from the size or stage related data.

The size of an ant colony is usually given as the number of workers, often a difficult measurement to make. Little is known about architecture of subterranean colonies (but see

Tschinkel 2004, 2005 for some recent counter-examples) so that it can be difficult even to know how to excavate a nest. One alternative is to measure the sizes of ant mounds or other colony constructions. The question is whether these external nest measurements are good indicators of colony size. The good news is that in many cases the number of workers correlates well with the size of the nest structure (Table 2). The bad news is that most species do not make conspicuous colony constructions.

If we use stage-based data, the basic tool is again the transition matrix, **T**. Scherba (1963) presented information on the transition of colonies of *Formica opaciventris* between 5 colony categories based on mound structure and colony activity levels. He calculated mortality rates for each of his colony categories. This is important information for understanding the dynamics of a population, however, with the category transition data that he also collected, it is possible to infer life expectancy and age-specific survival. The data were from censuses in 1957-1959. These data can be used to construct a transition matrix between categories for each year (1957-58 and 1958-59). In this case the entries refer to the probability that a colony will make a transition from one stage to another. Calculating life expectancy yields (2.7 3.3 5.2 4.2 7.0 years) for colonies that are found in each of his categories. Additionally, one can obtain an estimate of the age-specific survival, based on stage-specific data. One obtains this result by iterating the transition matrix (see appendix), obtaining the result shown in Fig 2. It is not generally appreciated that this sort of information can be extracted from stage-classified data.

For harvester ants we have obtained size based transition matrices, an example of which is shown in the appendix. This matrix was obtained by measuring the size of nests in two consecutive years. In this case the transition matrix is between colonies of different sizes. Finding the life expectancy as above yields an estimate of life expectancy for the largest colonies

Table 2–Colony Size and Nest Sizes

Species	Pattern of colony growth	Sample sizes	Notes	References
Pogonomyrmex occidentalis	r = 0.88	31	log Mound volume with log foragers from mark/recapture	Wiernasz & Cole 1995
Pogonomyrmex occidentalis	r = 0.7	33	Mound area with worker number	Lavigne 1969
Solenopsis invicta	$r^2 = 0.9$	55	Mound volume with worker biomass/numbers	Tschinkel et al. 1995
Solenopsis invicta	$r^2 = 0.85$	89	Mound volume with worker biomass/numbers	Tschinkel 1993
Pogonomyrmex badius	$r^2 = 0.73 - 0.93$	31	Various measure of (subterranean) nest architecture	Tschinkel 1999
Pogonomyrmex barbatus	nest mound area directly related to colony number		Mound area with worker number	Gordon 1992
Trachmyrmex septentrionalis	r = 0.57	55	Surface area of craters and worker number	Beshers & Traniello 1994
Formica exsecta	r = 0.77	59	Nest surface area and mark-recapture of workers.	Liautard, et al. 2003
Pogonomyrmex salinus	No relation of nest characters to colony size	25	Excavation of nests	Gaglio et al 1998
Lasius flavus	Strongly correlated, r not given	10	Excavation	Nielsen, et al. 1976

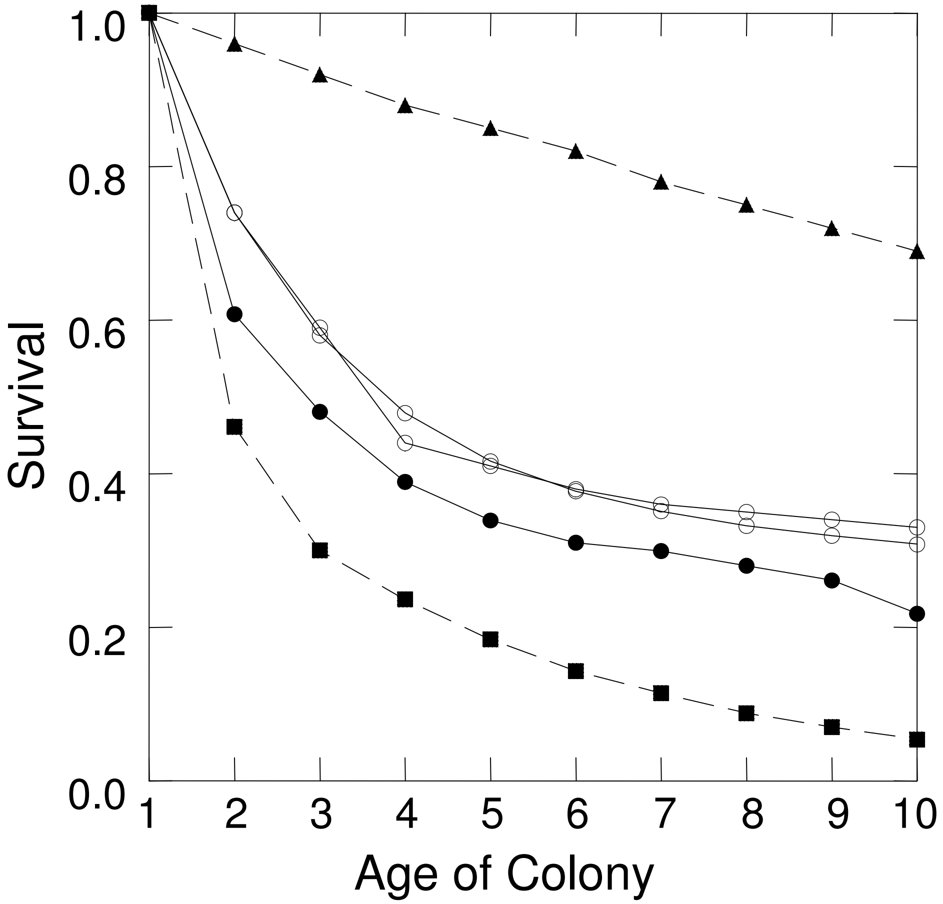

Figure 2. Survival curves of colonies from approximately one year of age. The three solid lines are *P. occidentalis* colony survival. The line with solid circles is the survival curve from agebased data. The two curves with hollow circles are the survival curves for colonies based on stage-based data. The upper line with solid triangles is from age-based data for *P. barbatus*. The lower dashed line, with solid squares, is the estimated survival curve based on the stagespecific survival probabilities for *Formica opaciventris* from Scherba's (1963) data.

of about 35 years. This is not unexpected, given other estimates of longevity, based on 25 years of observation of *P. occidentalis* (Keeler 1988, 1993) of about 45 years. This latter estimate is based on regressing survivorship on age and assuming constant mortality.

Estimates of longevity based on size transitions may be better for this long-lived organism than estimates based on age itself, even when the data set is more than ten years in duration. The age-specific survival derived from stage-based data for colonies starting in either of the two smallest size categories is shown in Fig 2 along with the measured age-specific survival for the first 10 years of this study. The size-based estimates are always somewhat higher and begin to deviate from the age-based data in later years, but the overall agreement between two methods based on completely different data sets lends confidence in the utility of this approach. It is important to emphasize that the stage-specific survival curves based on size are data that were collected over two years, while the data from colonies of known age required 10 years to assemble.

For other species (Table 3), investigators have provided a simple measure of the proportion of colonies remaining alive after a time interval. In the terms of a stage-based transition model, the transition matrix becomes the single probability of survival. The life expectancy is estimated as the reciprocal of the mortality rate. It is natural that investigators are more likely to measure survival of larger colonies and in many cases the authors recognize this bias in their calculation (e.g., Jonkman 1979, Fowler 1984 were particularly aware of this because their data are from colonies visible in areal photographs). Because mortality usually declines with colony size, data from larger colonies will overestimate life expectancy for the population as a whole, though of course will be accurate for the subset of colonies observed. If there has been a thorough search for all colonies, large and small, and the data are aggregated across those size categories, then the mortality rates represent an average of the population. The only data set where a single estimate of survival can be compared to the survival spectrum for age or stage-based data is in *P. occidentalis*. In this case the data present a point estimate that yields a life expectancy of 13.3 years, while the life expectancy ranges from 11 to 35 yrs for the smallest to largest colonies. These values must agree with one another and therefore reflect the higher size-specific mortality of small colonies as well as the size distribution in the population. From Table 3 we see that averaged life expectancy varies over a relatively small range, compared to other life history measures. In part, this is probably due to the fact that when one measures life expectancy based on the entire population of colonies one obtains an aggregate measure reflecting the size/age distribution in a population, colony growth rates and size-specific survival. All of the data from *Atta* seem lower than expected for reasons that are not clear. The survival of *Paraponera clavata* is the outlier among species, although the figures may reflect movement of nests as well as mortality.

Reproduction of Colonies. The second main ingredient of population demography is reproduction. As with mortality, we can look at reproduction as either age-related or size/stage related. Ideally, we want to know the age-specific pattern of reproduction so that we can calculate reproductive values, and interpret selection operating at various life-cycle stages. However, if there was little information on age-related patterns of mortality among ants, there is virtually nothing on age-related patterns of reproduction. Data from *P. barbatus* are the only published information that directly touch on this point (Gordon 1995, Wagner & Gordon 1999). They reported that the number of reproductive colonies increased from 3 to 5 years of age (Gordon 1995), but it was not clear how many colonies of each age were observed.

Table 3–Annual Mortality Rates

Species	Gross Annual Mortality Rate (extrapolated life expectancy)	Notes	References
Paraponera clavata	0.36, 0.23 (2.8, 4.3)	Survivorship for 3 three yrs at one site, 2 at another, N = 217 colonies	Thurber, et al. 1993
Formica exsecta	0.049 (20.4)	Censuses at intervals of 1-3 yrs for 10 years. Average over time span N = 57 colonies	Pamilo 1991
Atta cephalotes	0.26 (3.8)	Mortality rates 0.14 - 0.57, across sites combined, mortality measured over two yr interval; N = 74 colonies.	Perfecto & Vandermeer 1993
Pogonomyrmex owyheei	0.07 (14.3)	Mortality from annual censuses, 3 yrs, 2 sites N = 88 colonies	Porter & Jorgensen 1988
Pogonomyrmex owyheei	0.05 (20)	Mortality from 2 yrs, 3 sites, N = 201 colonies	Sharp & Barr 1960 reported in Porter and Jorgensen 1988
Pogonomyrmex occidentalis	0.028 (35.7)	Mortality from 14 yrs, N = 107 colonies. Concordant with previous report (Keeler 1988). Longevity est. 45 yr.	Keeler 1993
Atta vollenweideri	0.14 (7.1)	Mortality estimated from aerial photos 30 yrs apart. Only colonies > 3 yrs	Jonkman 1979
Atta capiguara	0.15 (6.7)	Survival estimated from photos 10 yr interval. Survival of large nests estimated from table as 0.2 for 10 yrs	Fowler 1984

Atta columbica	0.095 (10.5)	Survival from multiple censuses. N = 92 colonies, 2 years.	Wirth, et al. 2003
Myrmecocystus depilis	0.075 (13.3)	Mortality from 5 time intervals. Weighted average by sample size, N = 133 colonies – 1958-1993	Chew 1995
Myrmecocystus mexicanus	0.053 (18.9)	Mortality from 5 time intervals. 4 cohorts from Chew 1993 one from Chew 1987. Weighted average by sample size, N = 82 colonies	Chew 1987, 1995
Aphaenogaster cockerelli	0.15 (6.7)	Mortality from 3 time intervals. Weighted average by sample size N = 32 colonies, 1958-1976	Chew 1987
Pogonomyrmex barbatus[1]	0.048 (20.8)	Estimate derived from deaths of all ages, N = 250 colonies, 13 yrs	Gordon & Kulig 1998
Pogonomyrmex occidentalis[1]	0.075 (13.3)	Estimate for one year derived from deaths of all ages/sizes, N = 1121 colonies.	Cole & Wiernasz, unpubl data

[1] Overall mortality rate included for comparison purposes. Age and/or size based mortality functions are available

Reproductive output increased slightly with age ($r^2 = 0.03 - 0.06$, Wagner & Gordon 1999), but unfortunately the number of queens produced could not be measured. While the regression of reproductive output on colony age was significant for those colonies that produced reproductives, it was not significant when all colonies, even those that did not reproduce, were included in the analysis. Since colony size presumably increases with age, it is difficult to conclude that there is any direct effect of colony age.

Size related reproduction. Apart from the importance of size to survival, size is most often linked to reproduction. There are at least two ways in which colony size can be related to reproductive output. The first is that there may simply be a positive correlation between the number of workers and the number of queens that the colony produces. Another relationship between colony size and reproduction also recurs–a threshold size for reproduction. Among those colonies that reproduce there may be no relationship between colony size and reproductive output, instead there is a relationship between colony size and the probability that a colony reproduces. Both patterns have been observed (Table 4). In a few species or populations, the number of queens produced and colony size are correlated (e.g. *Myrmica sulcinodis*, Elmes & Wardlaw 1982) . However, it occurs far less commonly than expected. A much more common pattern is that there is essentially a size threshold for reproduction (e.g. *Camponotus*, Fowler 1986, *Pogonomyrmex*, Cole and Wiernasz 2000). It is nearly universal that the size of a colony affects the probability that a colony will reproduce. The number of queens that are produced is much less strongly (and frequently not) related to colony size. Interestingly, there is usually a stronger relationship between colony size and the production of males (e.g. *Myrmica*, Elmes & Wardlaw 1982). Given the complex interactions between local food abundance, within-colony demography and differing queen and worker interests (Herbers 1990), perhaps it should not

Table 4–Size/Age and Reproductive output

Species	Method	Result	Notes	Reference
Pogonomyrmex occidentalis	logistic regression, correlation	threshold for reproduction (N=89-324 colonies, 9 years)	Reproduction does not increase for colonies that reproduce (N=37-61 colonies, 9 years)	Cole and Wiernasz 2000 unpubl. data
Pogonomyrmex barbatus	correlation	begin to reproduce at 3 yrs. Apparently increasing probability with age, but size versus age unclear	Increasing # of reproductive colonies with age but unknown total # of colonies of given age (Gordon 1995). Queen production itself not measured by Wagner & Gordon	Gordon 1995; Wagner & Gordon 1999
Tetramorium caespitum	correlation	no correlation	N = 49 colonies from 2 years	Brian, et al. 1967
Lasius niger	correlation	1 positive, 1 non-significant, 1 significant for total reproduction but not for queens	three populations	Boomsma, et al. 1982
Lasius niger	correlation	no correlation	2.7% of variation in sexual numbers explained by worker #. Presumed non-significant	Pętal 1980
Myrmica spp.	correlation	see Notes	9.9 % of variation in total sexual reproduction explained by worker #. Unknown significance	Pętal 1980

Camponotus pennsylvanicus	correlation	from graph a clear threshold for reproduction. N unknown.	For colonies that reproduce apparent increase of reproduction with size. Some possible lab colonies	Fowler 1986
Camponotus ferrugineus	correlation	A clear threshold from graph	No relation to size above threshold for reproduction. Some possible lab colonies	Fowler 1986
Myrmica sabuleti	correlation and categorical analysis of reproducing and non-reproducing colonies	Threshold (?) at Site X (reproductive nests bigger, but no correlation of size and gyne output) ; positive correlation at Stonehill.	Site X, N = 64 nests, two years Stonehill, N = 99 nests, two years	Elmes & Wardlaw 1982
Myrmica sulcinodis	As for *M. sabuleti*	Reproductive colonies are bigger, R^2 =0.27 for reproductive colonies only	two sites, 7 years. All nests, N = 224; all gyne producing nests N = 44.	Elmes & Wardlaw 1982
Myrmica sulcinodis	As for *M. sabuleti*	Threshold (?) at site X (reproductive nests bigger, but no correlation of size and gyne output)	N = 49, two years	Elmes & Wardlaw 1982
Solenopsis invicta	correlation	Small size class with much less reproduction, apparent increase in reproduction with increasing size classes.	Analysis based on size classes and reproduction assayed throughout a season.	Tschinkel 1993

Leptothorax longispinosus	correlation, path analysis	1. No pattern in path analysis when other variables considered 2. Smaller colonies more likely to be non-reproductive	Small correlations of variable directions depending on queens and other factors. N = 7 years, 2 popls, 679 colonies	Herbers 1990
Trachymyrmex septentrionalis	correlation	alate biomass correlates with worker popl at one site.	FL correlation with all alate biomass; Long Island no correlation. For large colonies, no relation of size to reproduction, N = 55 colonies.	Beshers and Traniello 1994

surprise us that new queen production bears a complicated relationship to colony size. However, a long-standing assumption about colony demography that bigger colonies have greater reproduction, which may form the basis of ideas about topics as diverse as population dynamics and reproductive conflict does not deserve the status of generalization.

The age/size frequency distribution. In a stable age distribution the proportion of individuals of a given age must decline with age. The few non-invading populations for which we have age distributions show this pattern (*P. barbatus, P. occidentalis*). This is not a proof that the populations are at a stable age distribution, but it is necessary prerequisite. For species that may be invading a new habitat, such as *Diacamma ceylonense* (Karpakakunjaram et al. 2003), there is no expectation that the age distribution will have any particular form. If numerous colonies invade over a short time, then the age distribution will initially contain a few cohorts. Invasion of a new habitat by one or a few colonies will produce an age distribution that is characteristic of an expanding population. The age distribution may indicate more about the progress of the invasion than about demographic processes within the population.

The size distribution of colonies reflects the convolution of colony growth and survival. Unlike age distributions, for size distribution a variety of patterns are possible. If colony growth and mortality rates are declining functions of colony size, colony size distributions may have a peak. If colonies grow rapidly through small sizes, and survive for a long time at large sizes they will accumulate in the larger size classes. The size distribution will thus be affected by the patterns of colony growth. Some have suggested that colony growth patterns should follow a logistic function (Brian 1965, Wilson 1971, Oster and Wilson 1978), by analogy with simple models of population growth. The often cited example of honeybee colony growth (Figure in Wilson 1971, p. 431) is a spectacular fit to a logistic function; however, there are few data from ants to allow us to conclude that logistic colony growth in nature is common (Table 5). Tschinkel (1993) showed that a logistic function with overlaid periodicity fit the colony size data that he and co-workers collected. While logistic colony growth is generated by a negative linear function between growth rate and colony size, virtually any sort of negative relationship between growth rate and colony size will result in an upper limit to colony size especially when combined with mortality.

There are more data on the size distributions of colonies than age distributions in nature (Fig 3). Size information from sufficient numbers of colonies to generate a distribution limits the number of studies that can be included. Additionally, it is important that the data be comprehensive and not restricted to mature or representative colonies, as this biases data to larger colonies. I have standardized the presentation of the data so that the frequency distribution is divided into 10 size categories with a maximum relative frequency near one. Species may have a declining distribution (Fig 3a), a right skewed distribution (Fig 3b) or a left skewed distribution (Fig 3c).

The differences in size distribution reflect differences in colony growth and survival, but we cannot completely disentangle their relative contributions. Declining distributions are most likely to be associated with very high mortality rates relative to colony growth. A fairly short lifespan or tremendous differences among colonies in growth rate may also contribute to this pattern. While we do not have information about demographic properties from these species, they represent a suite of covarying characters that are required to produce the observed distributions. Distributions that are skewed left may indicate that those colonies which achieve a maximum size have a long lifespan. There has been no systematic investigation of the life

Table 5–Colony age and Colony size

Species	Pattern	Notes	Reference
Oecophylla smaragdina	Linear or logistic increase	# nests increases; 5 colonies	Gupta 1968
Solenopsis invicta	Logistic growth with variation or logistic growth with overlying cycles. Colony growth declines with size	Multiple colonies of known age fit to function. Field measurements of growth rate	Adams &Tschinkel 2001; Tschinkel 1993.
Pogonomyrmex barbatus	Colonies increase in size over 4 years	N = 12 colonies	Gordon 1992
Atta vollenweideri	Logistic growth and/or maximum size reached with decline	From aerial photographs 15 years apart,	Jonkman 1980
Lasius flavus	Linear increase	Correlate 3 nest dimensions to age for 8 years. N = 8 colonies	Waloff and Blackith 1962
Pogonomyrmex occidentalis	Growth rate declines with colony size	Can fit linear function to data (i.e. logistic) but huge scatter in data means other declining functions fit equally well.	Wiernasz and Cole 1995, unpubl. data.

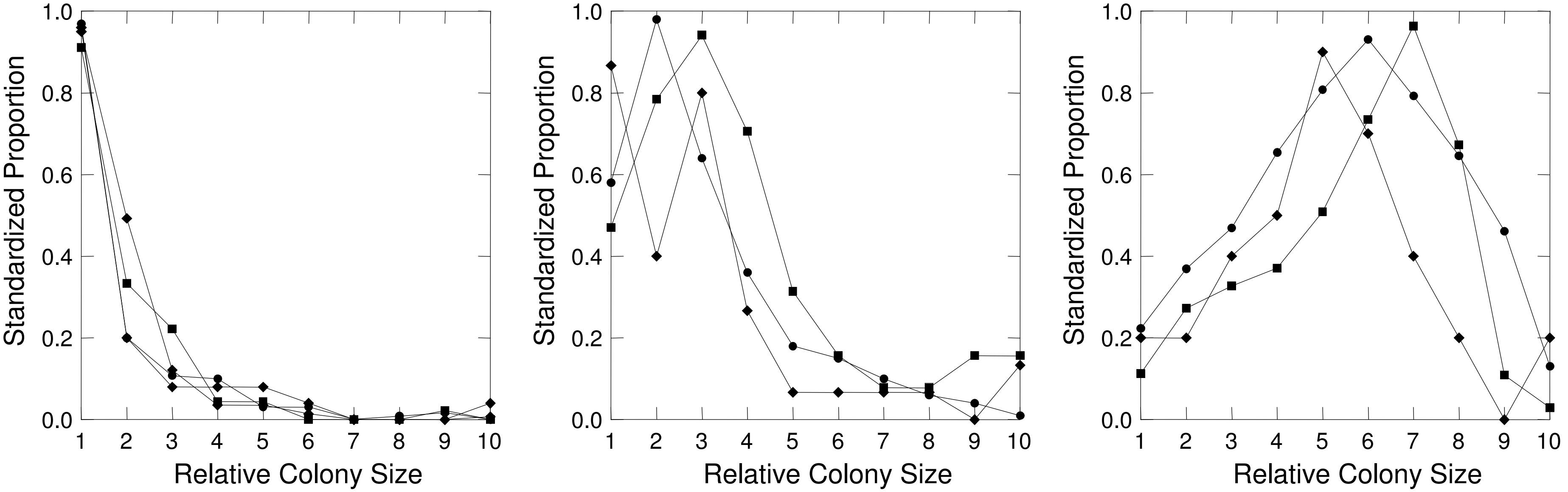

Figure 3. Several representative colony size distributions. Species do not fall into three categories, they are just shown that way for presentation. 4A: *Formica japonica*– Yasuno 1964; *Aphaenogaster rudis*–Talbot 1951; *Polyrhachis dives*–Yamauchi, et al. 1987; *Dolichoderus quadripunctatus*–Torossian 1967. 4B: *Tetramorium caespitum* Brian, et al.1967; *Myrmica rubra* Elmes 1973; *Dolichoderus pustulosus*–Kannowski 1967. 4C: *Myrmica schencki* Talbot 1945; *Pogonomyrmex occidentalis* Wiernasz & Cole unpubl.; *Odontomachus haematodes*–Colombel 1970. The range of colony sizes is divided into ten categories and the most abundant size class is set to near one.

history correlates of colony size distributions, but the fact that there is considerable variation suggests that it may prove profitable to explore them.

It can be useful to determine the age distribution to associate with a particular stage (e.g. colony size). That there is an age-distribution rather than a particular age is due to the fact that not all colonies of the same size will be the same age. To determine the distribution of ages within stages requires information that can be obtained from the **S** matrix: the population growth rate and the stable stage distribution, stage-based fecundity, and stage-based survival. For *P. occidentalis* the distribution of ages within a stage (see appendix) is shown in Fig 4. Because colonies can increase or decrease in size, the age distribution of larger colonies is flatter, with long tails. The distribution gives an estimate of the ages of colonies that occur in a population with the stage transition matrix **S**.

Life History Evolution

We have been trying to assemble data on the demography of ant species so that we can make inferences about the age or stage-based survival and age or stage-based reproduction of the species. With this information we obtain several derived parameters such as life expectancy, population growth rates and stable age or stage distributions. The goal of obtaining these data is to use the information to make inferences about the strength of selection operating on supposed adaptations. For that we need to use a different tool.

Reproductive Value. A population that has a consistent pattern of age related mortality and reproduction will eventually attain a stable age distribution. Fisher (1930) introduced the concept of the reproductive value of an individual of age x in a population that has reached a

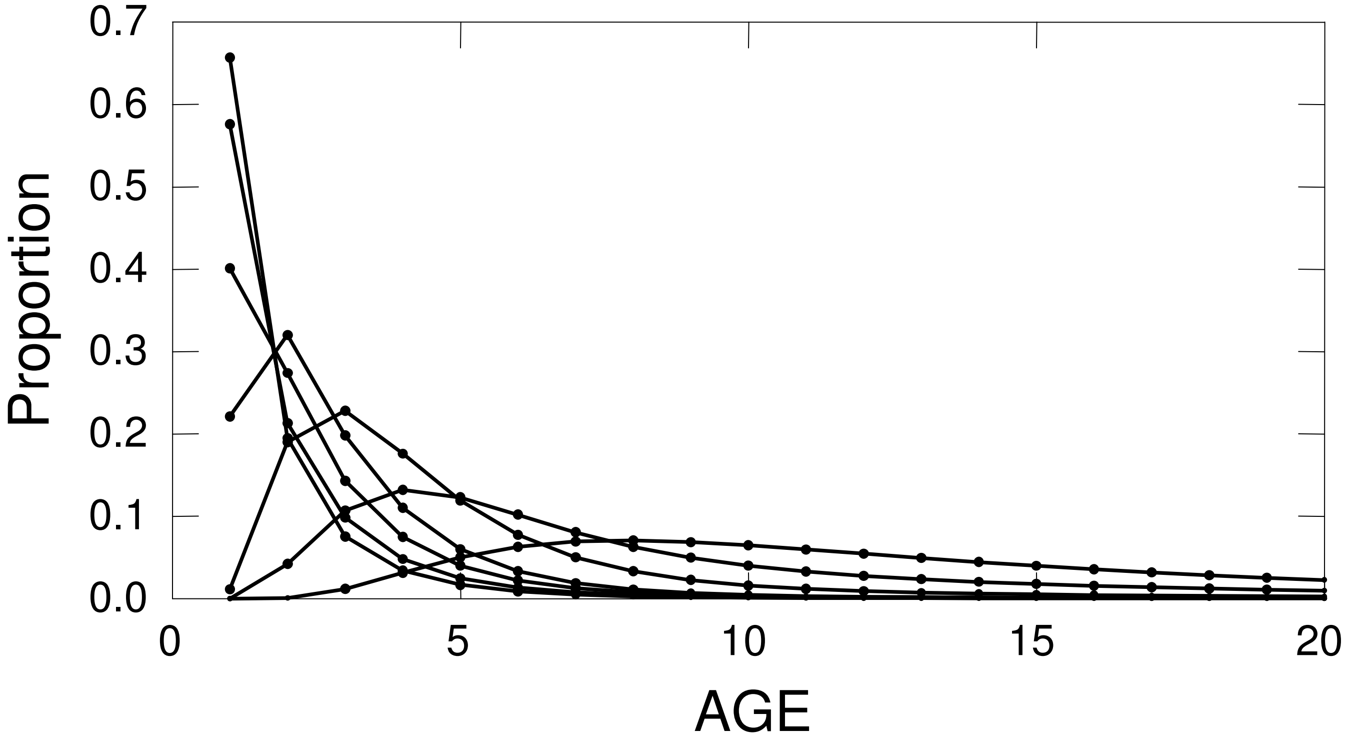

Figure 4. The age-within-stage frequency distributions for the seven size classes of *P. occidentalis* used in this paper. Very small colonies are very likely to be young, while size class 6 shows much greater variation in size. Some colonies reached this size while young and others are declining to this size after being much older.

stable age distribution: $V(x) = \frac{e^{r(x-1)}}{l(x)} \sum_{i=x}^{\infty} e^{-ri} l(x) m(x)$, where *l(x)* is the probability of surviving to age x, *m(x)* reproductive output at age x, that is the schedules of mortality and fecundity that we have been discussing and *r* is the rate of population increase (Roff 2002). If the population size is not changing (r = 0), the reproductive value (of a female) at age x is the expectation of future reproductive success. Additional mortality (i.e. selection) will have a disproportionate effect when it operates on individuals with higher reproductive value. Reproductive value rises to a maximum at about the age of first reproduction and then declines independently of senescence, simply due to the greater cumulative probability of mortality. To understand the operation of natural selection in a population, it is necessary to understand the age-specific schedules of mortality and fecundity and the growth of the population. To determine whether a change in life history is at a selective advantage, we can examine the change in the reproductive value function.

The age-specific reproductive value is the dominant eigenvector of the transposed Leslie matrix (see Figure 5 for the *P. occidentalis* data set). By estimating the age-specific survival to be 0.9 after the age of ten years, this function has been extrapolated beyond the actual duration of this study. There are not, to my knowledge, other comparable data for ants. Reproductive value reaches a peak at age 6-7 years and then declines, but the value of future reproduction is usually greater than that of current reproduction. For example, if a colony is more than 7 years old, the value of current reproduction is about 0.6 (the probability of reproducing), while that of reproduction next year is: 0.8 x 0.6 = (survival times reproduction) = 0.48 and in two years is: 0.8^2 x 0.6 = .38. The value over the next two years of reproduction (0.86) outweighs the value of

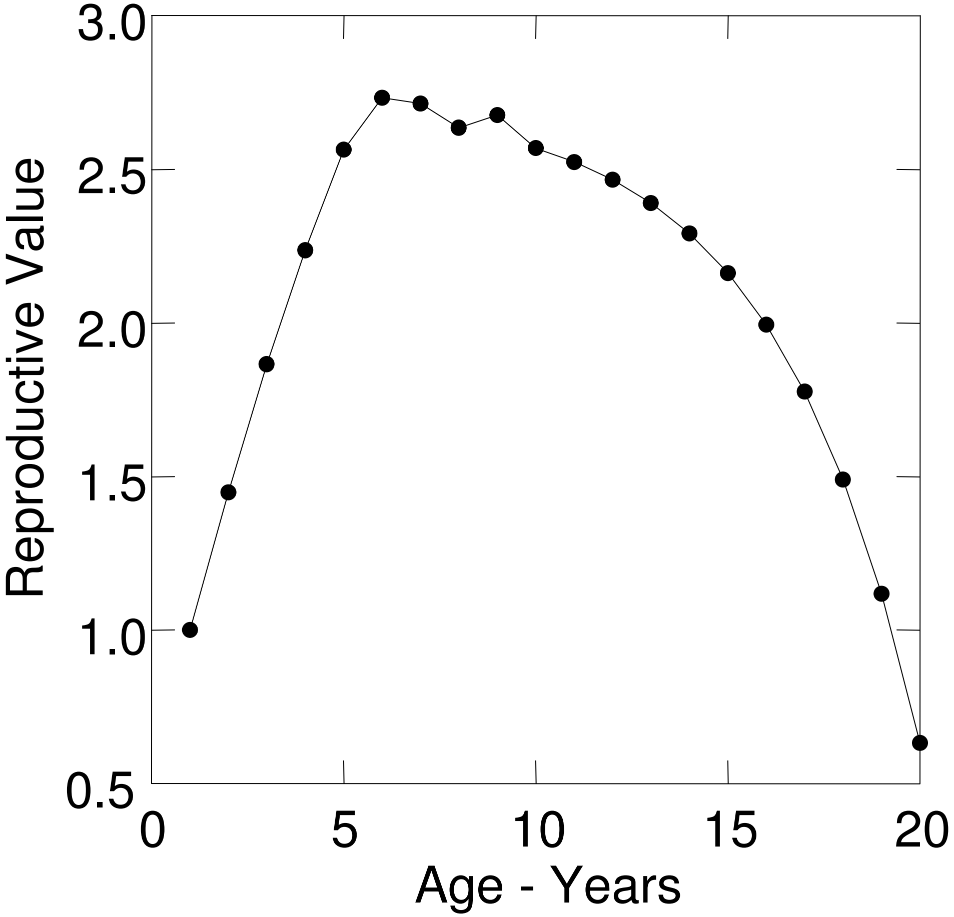

Figure 5. The reproductive value function for the harvester ant *P. occidentalis*. Reproductive value is standardized so that it is one in the earliest age category– reproductive value is measured with respect to this. Reproduction does not begin until age 5-6, so that the increase in reproductive value before that is a function of survival to greater ages. The decrease in reproductive value after age 10 reflects accumulating mortality rather than a decline in reproduction.

reproduction this year. This means that it is difficult for any strategy that increases current reproduction at the expense of future reproduction to be advantageous. Because survival is rather high from year to year, reproduction to exhaustion is not expected. Bang-bang control strategies, in which colonies invest all resources in colony growth until a critical moment when they switch all resources to reproduction have been elegantly analyzed in annually reproducing vespids (Macevicz & Oster 1976). Such a life history is not expected in this long-lived ant species, but until we have information that is obtainable only from the demographic data that allows us to calculate reproductive values, can we estimate how valuable future reproduction may be.

With the distribution of ages within stages, it is possible to compute the mean age (and the confidence intervals) of colonies of a given size. In Fig 6 I show the reproductive value function calculated for the age-based demography for *P. occidentalis* (circles). The reproductive value of the oldest age category includes the reproductive value of individuals that are $\geq$ 10 years old. The squares show the function derived from the reproductive value of each size category of the population and the mean age of colonies that are in that size category. Inferences made using measures of reproductive value obtained from age-based and size-based survival and reproduction, would probably be the same. It is not possible currently to know whether other species will give similar results and therefore how broadly this can be applied.

Investigating Adaptation. It is a rather simple matter to investigate the selective advantage or disadvantage of a particular change to a life history by altering the terms of the age or stage-based matrix. For example, suppose we wanted to determine whether a strategy that resulted in increased probability of reproduction in one year and decreased probability of reproduction and survival in the following year was advantageous. Within a demographic context, we could

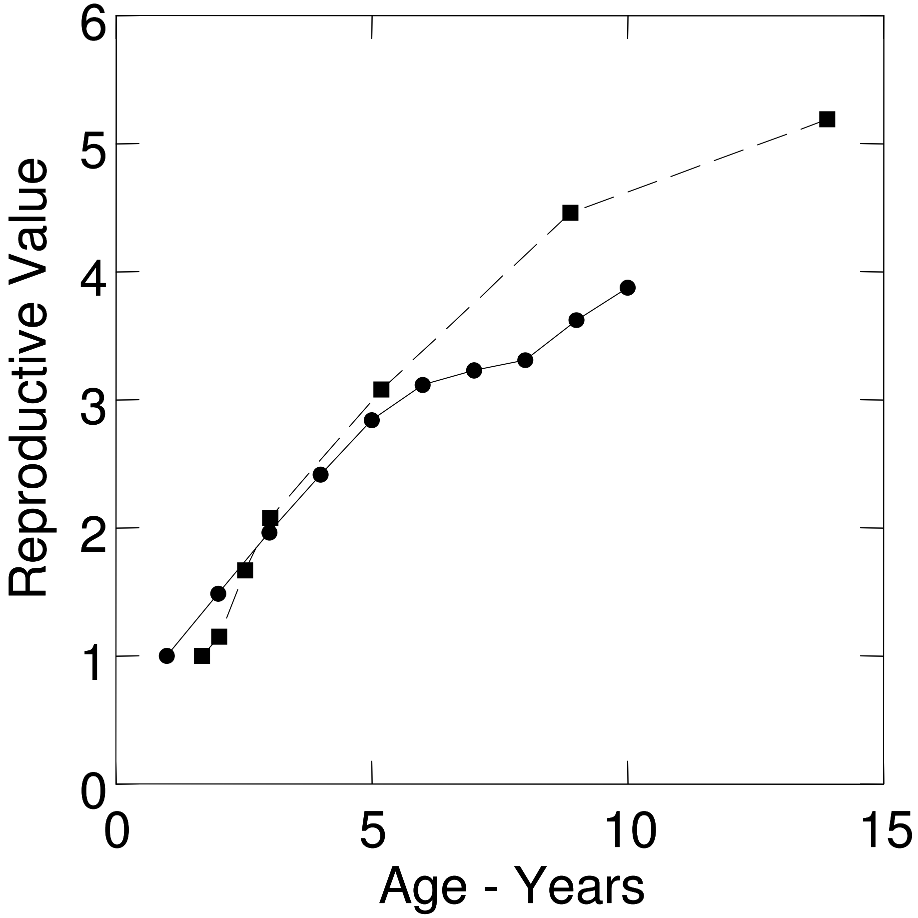

Figure 6. The reproductive value function calculated in the standard way (circles) and using size based data (squares). The reproductive value of the oldest colonies includes the summed reproductive value for the rest of their life. The size based reproductive value calculates the reproductive value of a size category and associates a particular age by calculating the mean of the age-within-stage distribution given in Figure 6.

quantitatively ask the question. For combinations of the size of an effect and stage of effect, we can determine whether the eigenvalue of **S** had increased or decreased, that is whether an individual with this life history would have greater or lower intrinsic growth rate–whether the trait was selectively advantageous or disadvantageous. The reproductive value function, calculated from the same matrix, is also changed and the magnitude of the change of alternative life history or behavioral strategies could be measured. We have the opportunity to quantify the magnitude of selection on life history differences, but only with information on the age/stage-specific mortality and reproduction. This takes us into a more analytic stage in the behavioral ecology of social insects.

The size distribution of colonies should be the result of the size transition matrix, **S** (contingent on the assumption that the population approximates the stable size distribution). This matrix condenses information on survival, growth and reproduction of colonies. Size distributions of colonies in nature could not be more varied (Fig 3). The conclusion that one is forced into is that the **S** matrix of populations, the patterns of survival, growth and reproduction vary enormously. This is another way of emphasizing that understanding the variety of demography in ant populations is guaranteed to generate interesting and surprising results.

Conclusion

Tschinkel (1991) called for the development of a sub-field within social insect biology that he called "Sociometry". He made the point that in studying the biology of social insects, we have skipped over the step of gathering basic information on the colonies and life cycles of social insects. The situation in ants has improved somewhat, in no small part due to Tschinkel's work. However, we are still lacking most quantitative information on demography.

This chapter emphasizes both the utility of demography in social insect evolutionary biology, and the lack of data for most species. It is not very likely that the species that have received the most attention are in any way representative of ants in general. *Pogonomyrmex* ants, which have the best demographic information, form large colonies with very long-lived queens. They produce colonies that are genetically diverse, due to multiply mated queens, and the colonies gather seeds as a main food source. This deviates in every way from more "typical" ants. Leaf-cutter ants, which also have substantial demographic data, have the same list of oddities only perhaps more extreme–they also have multiply mated queens, huge colonies and have the most intricate caste system specialized for processing vegetation and cultivating fungi. The demography of fire ants is known primarily from its introduced range (Tschinkel 2006). The list of species that are well-known are those that have advantages for collecting demographic data. It is important to remember that we are not in a position to make generalizations about ant demography. However, it is becoming clearer that these data are necessary for understanding the dynamics of evolutionary change.

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Appendix

In an age-based demography, the information about the life cycle can be represented by a Leslie matrix such as:

$$\left|\begin{array}{ccccc} 0 & F_2 & F_3 & F_4 & F_5 \\ p_1 & 0 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 & 0 \\ 0 & 0 & p_3 & 0 & 0 \\ 0 & 0 & 0 & p_4 & 0 \end{array}\right| = \mathbf{L}.$$

The entries refer to transitions between one state (the columns) and another state (the rows). The F values are the age-specific fecundity of the population, while the p's are the age specific probability of survival to the next age class. Individuals of age 1 have a probability of p_1 of surviving to age 2. An individual of age 4 will produce F_4 individuals of age 1. The number of individuals, at some time t, in each of the year cohorts is: $(N_0\ N_1\ N_2\ N_3\ N_4)^{\mathsf{T}}$,= $\mathbf{n}_t$. {Note: This is actually a column vector, but representing the column vector takes a lot of space. Instead I will use T to indicate the transpose.} Post-multiplying the Leslie matrix by the population vector gives the number of individuals in each of the age groups in the next year $\mathbf{n}_2 = \mathbf{L}\mathbf{n}_1$. If this process is repeated the age distribution is $\mathbf{n}_3 = \mathbf{L}\mathbf{n}_2$. If this process continues to be repeated (using the assumption that the age related patterns of mortality and fecundity are consistent) it will rapidly converge on the stable age distribution. There is a scalar value, λ, for which the following is true: $\boldsymbol{\lambda}\mathbf{n} = \mathbf{L}\mathbf{n}$. Multiplying the Leslie matrix by a particular vector is equal to multiplying the same vector by a constant. The vector is the stable age distribution of the population represented by the Leslie matrix and the λ is the growth 'rate' of the population (it is actually a multiplicative constant). These values are the dominant eigenvector and eigenvalue of the Leslie matrix and can be obtained from standard mathematical packages.

This procedure is easily generalized to size or stage-based demography. These life cycles are more flexible. As for age, it may be impossible for stages to reverse. For example, stages may be queen, incipient colony, immature colony, mature colony. However, colonies that are categorized by size can become larger, smaller or remain the same size. In the matrix below colonies can stay the same size (the entries on the diagonal), increase in size (below the diagonal) or contribute to size categories that are smaller (above the diagonal).

$$\begin{vmatrix} p_{11} & F_1 & F_2 & F_3 & F_4 \\ p_{21} & p_{22} & p_{23} & 0 & 0 \\ 0 & p_{32} & p_{33} & p_{34} & 0 \\ 0 & 0 & p_{43} & p_{44} & p_{45} \\ 0 & 0 & 0 & p_{54} & p_{55} \end{vmatrix} = \mathbf{S}.$$

There is a corresponding vector for the size or stage distribution, which we can still call **n**. Either by repeatedly post-multiplying the stage transition matrix until it reaches stable values, or by extracting the dominant eigenvalues and eigenvectors of the matrix **S** we can again find the growth ‘rate’ of the population and the stable size or stage distribution. A major difference between the stable age and size distribution is that the entries of the stable age distribution are a non-increasing function of age. The proportion of the population in successively older age categories must decline. If the age distribution is not declining, then the stable age distribution has not been achieved. The same is not true for the stable size distribution. If colonies rapidly grow to a mature size and then remain at that size for a relatively long time, they will build up in this category which will be the most common size. This means that it is possible for there to be a modal size or stage in a population.

Getting age information from stage-based data. It is often very useful to obtain information about age-related patterns of demography from data that are not based on age. For example, a study may have information about the size distribution of colonies or the distribution of life cycle stages (e.g. queens, incipient colonies, reproductive colonies, etc.) and not have information about the age of the colonies. It is still possible to extract certain age-related information from these data (see Cochran & Ellner 1992 and Caswell 2002 for description). If we are using age or stage-based transition matrices to represent the demography this is the same as the assumption that the life cycle of an organism can be represented as a Markov chain with an absorbing state (death). The reason that I say “we can often make this assumption,” is because colonies that bud or swarm (hesmosis) can potentially be of unlimited lifespan. In this case we must limit our consideration to the identity of a subunit. Making the Markov assumption is saying that all colonies, or units, in one time interval end up in some state in the next time unit (the sum of the probabilities of transition is one) and where they end up depends on their current state rather than on their past states. This assumption is the same that allows us to construct the population projection matrices in the first place. If one examines the Leslie matrix, or the size-based projection matrix, there are entries that refer to the survival of individuals and entries that refer to the reproduction of individuals (they are represented as p’s versus F’s in the matrices above). The Leslie matrix (or the a stage based matrix) can be decomposed: $\mathbf{L} = \mathbf{T} + \mathbf{F}$, where the **T** matrix is the transition matrix–the probabilities of transition between states, and the **F** matrix is the reproduction matrix. The number of times that an individual will spend in each of the states of the matrix before it reaches the absorbing state is given by $\mathbf{N} = (\mathbf{I}\text{-}\mathbf{T})^{-1}$, where **I** is the identity matrix (ones on the diagonal and zeros elsewhere). Since the **T** matrix is formed by transitions occurring in known time units, the units of the **N** matrix are the same. If the transition probabilities are the probability of surviving from one year class to the next, the time units will be years. If the transition probabilities are calculated based on survival of size categories in censuses with an interval of ten years, then the time units in the **N** matrix will be in 10-yr units. The sum of the entries in a column are the expected time spent in each state, in other words, the life expectancy of an individual in a given state. This applies to age-based as well as stage or size based demography. When the only information available is a yearly survival rate, s, then this yields life expectancy of 1/(1-s). {Published results vary depending on whether survival is considered to be from one time unit to the next or to be from the mean time of successive censuses, but these are minor points.}

As an example, we can consider the age based transition matrix for *P. occidentalis* shown here. The matrix represents the probability that a colony survives from one age to the next. The only difference is the last entry in the matrix which gives the probability that a colony in the largest age class will continue to survive. This is the solution to the problem that the maximum lifespan of the colonies is not just 10 years, even if the data do not extend beyond 10 years, but it makes the matrix a hybrid of strictly age-related terms and stage-related terms (the last value in the analysis will then refer to colonies of ten or more years of age). If we find $(\mathbf{I}\text{-}\mathbf{T})^{-1}$, then we obtain the number of time units, years in this case, that a colony is expected to spend in each age category j, given it is currently in age category i.

$$\begin{vmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.72 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.81 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.87 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.91 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.96 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.94 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.93 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.84 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.83 & 0.9
\end{vmatrix}$$

$$\begin{vmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.72 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.58 & 0.81 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.51 & 0.71 & 0.87 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.46 & 0.64 & 0.79 & 0.91 & 1 & 0 & 0 & 0 & 0 & 0 \\
0.44 & 0.62 & 0.76 & 0.87 & 0.96 & 1 & 0 & 0 & 0 & 0 \\
0.42 & 0.58 & 0.71 & 0.82 & 0.90 & 0.94 & 1 & 0 & 0 & 0 \\
0.39 & 0.54 & 0.66 & 0.76 & 0.84 & 0.87 & 0.93 & 1 & 0 & 0
\end{vmatrix}$$

$$\left|\begin{array}{cccccccccc} 0.33 & 0.45 & 0.56 & 0.64 & 0.71 & 0.73 & 0.78 & 0.84 & 1 & 0 \\ 2.7 & 3.75 & 4.63 & 5.32 & 5.85 & 6.09 & 6.48 & 6.97 & 8.3 & 10 \end{array}\right|$$

For this matrix the entries refer to the amount of time that a colony of a given age is expected to spend in each subsequent age. For example, colonies spend 1 year in each age that they are in, while colonies of age 10 or more, which are given a probability of death of 0.1, spend 10 years in the last stage. Colonies that are currently 5 years old are expected to spend 0.84 years as 8 year old colonies. The expectation is less than one year because some of the colonies will die before reaching their eighth year. The sum across rows is the life expectancy, (7.6 9.1 10.0 10.3 10.3 9.6 9.2 8.8 9.3 10).

In addition to the life expectancy, one can obtain an estimate of the age-specific survival to time t, given a particular starting stage by finding $\mathbf{T}^t$. This is done by iteratively multiplying the matrix. The sum across rows is the probability that the colony is in one of the activity/size stages and therefore not dead. Scherba's data (1963) can be used to form this transition matrix where the entries refer to his activity categories 0-4. Calculating $(\mathbf{I}\text{-}\mathbf{T})^{-1}$ gives the life expectancy for a colony, given that it is currently in a particular stage shown in the text. By finding $\mathbf{T}^t$ for increasing t, we get the age-specific survival, conditioned on the assumption that colonies start in category 1 shown in Figure 2.

$$\left|\begin{array}{ccccc} 0.16 & 0.131 & 0.018 & 0 & 0 \\ 0.16 & 0.278 & 0.16 & 0.034 & 0 \\ 0.15 & 0.16 & 0.51 & 0.21 & 0.022 \\ 0 & 0.045 & 0.21 & 0.29 & 0.34 \\ 0 & 0 & 0.012 & 0.11 & 0.64 \end{array}\right|$$

For harvester ants a size specific transition matrix for one year showing the probability of a colony changing from one size to another is given below:

$$\begin{array}{ccccccc} \text{Size} = 5 & 6 & 7 & 8 & 9 & 10 & 11+ \\ 0.18 & 0.07 & 0.04 & 0.01 & 0 & 0 & 0 \\ 0.18 & 0.18 & 0.12 & 0.05 & 0 & 0 & 0.003 \\ 0.2 & 0.24 & 0.13 & 0.14 & 0.02 & 0.004 & 0.003 \\ 0.18 & 0.19 & 0.26 & 0.21 & 0.05 & 0.004 & 0 \\ 0 & 0.06 & 0.19 & 0.28 & 0.34 & 0.07 & 0.003 \\ 0 & 0 & 0.07 & 0.14 & 0.41 & 0.53 & 0.07 \\ 0 & 0 & 0 & 0.01 & 0.07 & 0.39 & 0.9 \end{array}$$

One obtains the size-specific life expectancy, as above (= $(\mathbf{I}\text{-}\mathbf{T})^{-1}$): (10.9 12.1 16.4 19.4 26.2 33.1 34.8), and an estimate of the age-specific survival by iterating the matrix (Figure 2).

The fertility matrix for the age-based survival of *P. occidentalis* is just a matrix with (0 0 0 0 .05 .3 .38 .5 .66 .66) in the top row and zeroes in all other cells. This gives the probability that a colony reproduces as a function of age. The amount of reproduction per reproductive event is unrelated to age or size. To change the total number of offspring per event requires that these values are all multiplied by a constant. Including this constant does not have an effect on the analyses of age/stage structure, ages-within stage or reproductive value (see below). The Leslie matrix is simply the sum of the **F** and the **T** matrix Similarly the **F** matrix for sizes is:

$$\left|\begin{matrix} 0 & 0 & 0 & 0 & 0 & 0.05 & 0.125 \\ 0 & 0 & 0 & 0 & 0 & 0.072 & 0.18 \\ 0 & 0 & 0 & 0 & 0 & 0.05 & 0.125 \\ 0 & 0 & 0 & 0 & 0 & 0.026 & 0.065 \\ 0 & 0 & 0 & 0 & 0 & 0.001 & 0.003 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{matrix}\right|$$

This is the probability that colonies of a given size (row) will be produced by the reproductive colonies (the columns). Remember that it is possible for colonies to enter the population at sizes that are larger than the smallest size.

The age-specific reproductive value, **v**, can be calculated directly from the Leslie matrix as the dominant eigenvector of $\mathbf{L}^{\mathrm{T}}$ (Caswell 2002). We can obtain the stage-specific ‘reproductive value’ by finding the dominant eigenvector of the transpose of the stage transition matrix. It is difficult to say what relationship this value has to reproductive value in the sense of Fisher. We could convert this to age specific reproductive value if we could associate an age with a particular stage. However, colonies of many different ages can be in a particular size class–they may have grown directly to this size or they may have once been larger and have decreased to this size class. We can determine the distribution of ages within any particular stage and thus the mean age of individuals within a given stage.

To compute the age within-stage distribution relies on manipulating the stable stage distribution (see Boucher 1997 and, again Caswell 2002 for a discussion). The number of new colonies at a given time is proportional to the stage distribution (the dominant eigenvector of the **S** matrix) times **F**, the fertility matrix. The number of new colonies last year is proportional to this product divided by the growth rate of the population, the dominant eigenvalue of the **S** matrix. They are currently in stages that are determined by the transition matrix, **T**. To determine the current fate of individuals born two years ago requires dividing by growth rate of the population squared and requires two passages through the transition matrix to determine the current stage. Similar reasoning applies for times into the past, with the result that it is possible to estimate the frequency distribution of ages in a given stage and compute the mean age of individuals in any stage.