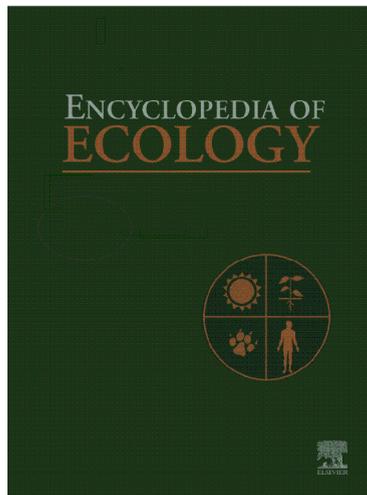


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Fecundity

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Introduction

Organisms exist to reproduce and fecundity is the measure of an individual's (or population's) reproductive performance. As such, fecundity (in combination with its sister concepts – see below) can be viewed as one of the two cornerstones of population biology, the other being the ability of an individual to survive in order to reproduce. Mortality (proportion of surviving individuals) expresses the proportion of a population that dies within a defined period of time and fecundity quantifies the new individuals added to the population. A population remains stable when the number of individuals dying is equivalent to the number of new individuals added, and it decreases when mortality exceeds replacement (births and immigration). Although these themes may appear straightforward, the relationships between reproduction, age, population density, and environmental stochasticity (random variation due to environmental changes) are complex and not fully understood. Furthermore, these relationships must be contextualized within the major reproductive strategies that have evolved as a result of different selective pressures, and they must be examined while taking into account the multitude of tradeoffs that occur between reproduction and individual survival.

In ecology, 'fecundity' can be described simply as the physiological maximum potential reproductive output of an individual over its lifetime, and it is usually applied to the female's (rather than a male's) output, although there

is no inherent reason why fecundity should be restricted to females. Regardless, ecologists have defaulted to using the gender-general term of 'reproductive success' to describe the reproductive output of both males and females. We adhere to these traditions and restrict our definition of fecundity to apply to females only. However, reproductive success is not equivalent to fecundity because the former is a measure of an individual's genetic contribution to subsequent generations. As such, reproductive success can vary among individuals due to the effects of maternal age, fitness of progeny from clutches of different size, and other life-history characteristics. Fecundity is therefore a genetical and developmental trait that evolves within a particular selective framework. The term 'fertility' differs from fecundity in that it describes the actual (or current) reproductive performance of (typically) a female, and it is a generalization of the terms 'maternity', 'birth rate' and 'natality' which refer to the average number of offspring produced by an individual female of a particular age per unit time. 'Net reproductive rate' is defined as the average number of daughters produced by mothers over a lifetime. Fertility varies primarily as a function of environmental stochasticity and demography, and generally fluctuates temporally and spatially among individuals and populations.

In this article we have chosen to discuss both fecundity and fertility given their obvious connection and importance to the discipline of ecology. Henceforth the usage of each term relates specifically to the developmental and

evolutionary (fecundity) or environmental (fertility) contexts shaping these fundamental parameters of population biology.

Sexual and Asexual Reproduction

The concept of fecundity should, in practice, be applied equally to the two major modes of reproduction – sexual and asexual. Discussions centered on the evolution of sexual reproduction must reconcile the theoretical advantage asexual reproduction presents to an individual – the possibility of a twofold fitness (fecundity) advantage over their sexual counterparts. The relatively higher cost of sexual reproduction arises from anisogamy (gamete dimorphism), but sexual selection can reduce or even eliminate this cost. Although there is no difference in the fecundity of sexual females and asexuals of the same genotype, the equilibrium frequency of deleterious mutations is lower in sexual populations, usually giving rise to higher fitness in sexual females.

Despite the advantages of sexual reproduction, the prevalence of clonal or asexual reproduction in the life histories of many plant and animal species suggests that this strategy does indeed provide advantages at least in some circumstances. For example, clonal reproduction may allow the clone to survive many reproductive events by reducing a potentially catastrophic local extinction associated with a restricted distribution. A large number of clone-mates may also increase the number of bodies producing gametes and improve the probability of them finding mates once sexual reproduction is invoked. Thus, variation in the costs and benefits of clones should depend on an individual's sexual neighborhood (relative abundance of potential mates) and the degree of competitive stress induced by the environment.

Inclusive Fitness

The concept of inclusive fitness has become the foundation of modern biology and may be one of the most important advances in evolutionary biology since Darwin introduced the theory of natural selection. If natural selection occurs at the individual level (i.e., individuals with higher reproductive success have the greatest genetic representation in future generations), how do cooperative breeding systems evolve? The apparent paradox of some individuals within a population foregoing the opportunity to breed can be explained if some individuals help their close relatives reproduce. By assisting close relatives, altruists still manage to pass on their genes indirectly. This behavior can arise when the genetic relatedness between an altruist and beneficiary (r) multiplied by the fitness gain to the beneficiary (b) minus the

fitness cost to the altruist (c) is greater than zero; that is, $(rb - c) > 0$.

Consequently, the degree of relatedness between the altruist and the beneficiary determines the probability that they share a particular gene, and therefore, the probability that the altruistic gene will be passed on to the next generation. Sterile castes in social insects are an extreme case of quasi-altruism (worker females give up reproduction and raise their mother's offspring). This occurs most commonly in the Hymenoptera (bees, wasps, ants), and is probably the result of their haplodiploid chromosomal organization where males have single chromosome copies and develop parthenogenetically from unfertilized eggs and females have two copies of each chromosome. Because males are haploid, there is no meiosis and all daughters of a particular male have identical paternal genes. Nonreproductive females have a greater chance of passing on their own alleles via their reproductive sisters than they do by reproducing themselves, so zero direct fecundity for these individuals results in the highest indirect lifetime reproductive success.

Eusocial Systems

Eusocial systems are an evolutionarily advanced level of colonial existence in which adult colonial members (1) belong to two or more overlapping generations, (2) care cooperatively for the offspring, and (3) are divided into either reproductive and nonreproductive (or less-reproductive) castes. The presence of castes is an integral requirement of eusociality, and it is most commonly found in social insects, especially ants, bees, wasps, and termites. As a reproductive strategy it is rarely observed in nature, but it appears to be an important mode of reproduction nonetheless. Although eusocial ants comprise only 2% of the $c. 900\,000$ insect species known globally, this taxon comprises more than half of the global insect biomass. The strategy is obviously successful in evolutionary terms, so why then, despite this apparent success, has eusociality rarely evolved? It is generally thought that eusociality is the result of some extraordinary environmental circumstances that existed in the evolutionary past when a particular genome coding for group breeding and subordinate reproductive suppression was selected. Selection of this genome consequently led to a cooperative breeding system and was maintained not by the inability of individuals to breed, but because individuals are outcompeted by breeding conspecifics in well-integrated communal colonies.

Implicit in understanding fecundity patterns in eusocial systems is recognizing the factors that regulate body size and growth. The eusocial female that does all or most of the breeding is usually the biggest and most dominant. As such, in species of cooperative insects living in large groups,

selection for increased fecundity has repeatedly resulted in the evolution of an increased body size for females. Whether this is also true of cooperative vertebrates is currently debatable; however, increased size of dominant breeding females has been documented in naked mole rats (*Heterocephalus glaber*) and meerkats (*Suricata suricatta*). Eusociality and the resultant reduction or eradication of fecundity in some individuals among diploid animals is rare and appears to occur only when (1) species live in burrows, (2) food is abundant, (3) parents care for offspring, and (4) mechanisms exist for mothers to manipulate other females, such as pheromones that inhibit their breeding.

Fecundity Patterns

The term 'parity' is used to describe a breeding event, and species can assume various modes of reproductive timing and frequency depending on their evolutionary past and the constraints of their current environment. There are too many variants of life-history strategies to describe succinctly given the large number of possible combinations of longevity, breeding frequency, and offspring number, but there are some major groups of strategies that have evolved. The two major fecundity patterns are semelparous and iteroparous reproduction.

Semelparity

Semelparous organisms reproduce only once during their lifetime. This may occur at the age of only 20 min in certain bacteria, a few hours in many protozoa, or up to a few weeks or months in some insects and mammals. Many semelparous species are annuals (live only one year), but some reproduce only after several years of maturation. Early work predicted that greater temporal variation in adult survival relative to juvenile survival favored the evolution of semelparity, although more recently it has been demonstrated that this also depends on the age structure of the population under selection. Semelparity may also provide other advantages over iteroparity in terms of offspring body size, leading possibly to increased juvenile growth rates and survival.

Semelparity in mammals is restricted to two marsupial families (Didelphidae and Dasyuridae), where all species demonstrate high post-reproductive senescence, but not all are semelparous. In some of the semelparous species, only the males die after the short, highly synchronous mating season, whereas in others, male die-offs are facultative. Some have argued that because the interval between conception and weaning is short and that these marsupials tend to live in highly predictable seasonal environments, there should be selection for a monoestrous reproductive pattern, high estrus synchrony, and a short mating season. These factors should therefore induce intense male–male

competition and a low probability of multiseason male survival giving rise to the evolution of male semelparity. Additionally, the high rate of female mortality resulting from long lactation periods in some species also demonstrating female semelparity selects for a bet-hedging strategy by males and the evolution of male semelparity.

Iteroparity

Species that reproduce more than once during their lifetime are iteroparous. The time of maturation preceding first reproduction may vary from a few days in small crustaceans to greater than 100 years in some trees. The frequency of reproduction can also vary markedly – daily (e.g., some tapeworms), semiannually, annually, biennially, or irregularly (e.g., humans). Some have argued that iteroparity is favored over semelparity when high environmental variability induces large variation in offspring production and offspring survival. However, it has been demonstrated more recently that the evolution of either strategy does not depend on environmental variability alone, but also on the strength of intrinsic regulation (a tradeoff between fertility and survival – see below) operating on a population and the demographic rates most affected by extrinsic variation.

In many iteroparous species there are a certain proportion of individuals that reproduce only in alternate seasons (or less often), thereby foregoing a proportion of their potential lifetime reproductive success. Known formally as 'low frequency of reproduction', this phenomenon is most common among vertebrate ectotherms, but it has also been documented in endotherms (e.g., willow tits (*Parus montanus*); kittiwakes (*Rissa tridactyla*); fat dormice (*Myoxus glis*)). There is also considerable phenotypic variation within a species, with some individuals opting for lower-frequency reproduction than others. Ectothermic species employing this strategy appear to have accessory activity associated with reproduction (but independent of fecundity) such as breeding migrations, egg brooding through incubation, and live bearing. With its apparent ubiquity, low-frequency reproduction appears to offer some selective advantage in certain systems. It has been suggested that the strategy could evolve only under two scenarios: (1) when reproduction does occur, it confers a much higher fecundity benefit than would a regular-frequency breeding event; or (2) the probability of surviving the interval between reproduction is much higher than it would be during the same interval of regular-frequency breeding. Thus, lower-frequency reproduction may actually result in higher average fecundity over the individual's lifetime when at least one of the two previous conditions is met. There also appears to be a relationship between the occurrence of low-frequency breeding with habitat quality. Here, regular reproduction may become less favorable as the habitat becomes less suitable because

resource availability declines and accessory activity cannot decrease to the same extent.

Age Specificity

In iteroparous organisms, fecundity often increases with age following reproductive maturity and then can decline at older ages. As such, age specificity of reproduction is an essential element for understanding the evolution of life-history strategies. Reproductive rate may increase with age when an individual devotes relatively more resources to reproduction with increasing age. For example, growth rate often declines after reproductive maturity is achieved, so more resources can thereafter be directed to reproduction, thereby increasing age-specific fecundity. This introduces the concept of 'primiparity', which is generally defined as the age of first reproduction. In some species, this age is rather constant suggesting genetic control. However, in other species (especially ectothermic organisms), it is environmentally mediated and may demonstrate high phenotypic plasticity. The extent to which primiparity is delayed (i.e., the length of the pre-reproductive period) also depends on type of niche exploited by a species and the particular demographic configuration of a population.

Increasing fecundity is also observed in many organisms that do not grow following maturity, giving rise to three hypotheses to explain the pattern: (1) less-fit individuals are constantly eliminated from a population so that the average fecundity of surviving individuals increases; (2) increasing fecundity is a reflection of the gradual improvement in the competence of older, more experienced, and often higher-ranking individuals; and (3) as life expectancy decreases with age, individuals allocate more and more resources to reproduction at the expense of survival. The decline in fecundity with age is often referred to as 'reproductive senescence'. One hypothesis to explain this pattern is as an individual ages its resource acquisition rate deteriorates due to physiological ageing.

Recent work has attempted to combine the various hypotheses for age specificity in fecundity into a single conceptual model that incorporates the other key life-history parameter – age-specific survival. When extrinsic mortality is high, early maturity is favored allowing for high reproductive investment and fecundity early in life (Figure 1). Under this scenario, allocating resources to repair cumulative somatic damage is not beneficial when life expectancy is already low, and fecundity will still diminish with time due to physiological ageing. When extrinsic mortality is low, investing in somatic repair at the cost of reduced fecundity is beneficial because it increases life expectancy. Thus, reproductive rate is low early in life, but gradually increases toward a late-life maximum, and then inevitably declines again due to physiological deterioration late in life (Figure 1).

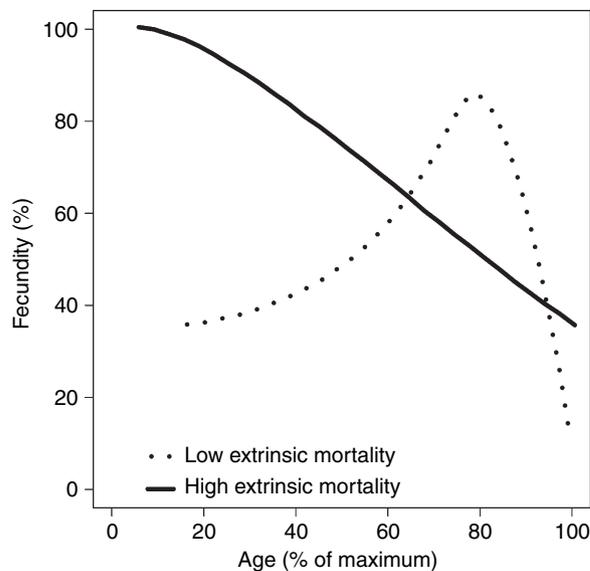


Figure 1 Patterns of age-specific fertility fecundity expressed as a percentage of maximum age under two different rates of extrinsic mortality. Reproduced from Cichoń M (2001) Diversity of age-specific reproductive rates may result from ageing and optimal resource allocation. *Journal of Evolutionary Biology* 14: 180–185.

Allometric Scaling

Allometry is the relation between the size of an organism and aspects of its physiology, morphology, and life history. Typically, variation in body mass among individuals or species can be used to predict traits such as metabolic rate, dispersal capacity, survival probability, and fecundity. The ratio of combined offspring mass to maternal mass tends to remain approximately constant over a broad range of maternal sizes within a species. As such the ratio of offspring mass at independence to average adult body mass remains stable within major taxonomic groups. In other words, larger females tend to have more or larger offspring, especially among invertebrates and ectothermic vertebrates. An increase in fecundity with increasing female body size may constitute a selective advantage toward large female body size (the so-called 'fecundity advantage' model) in some taxa, especially in those for which energy is not limiting. However, this does not necessarily mean that larger females will always have higher reproductive success because of the increased risks due to predation, limited resources, and environmental uncertainty.

Density Dependence

It is in every individual's interest to maximize its reproductive output without compromising its own survival prospects; however, the production of too many individuals can lead to overcrowding and a reduction in

per capita resources such as food availability, breeding sites, and territories. Under such circumstances, it is clearly unprofitable for individuals to engage in potentially wasteful energy expenditure associated with fertility if the probability of their progeny surviving to breeding age is low. This observation is supported by the ample evidence that population density affects fertility negatively. In general, as population size increases, either the average number of offspring produced per female decreases (in litter or clutch sizes greater than one), or average offspring size decreases. However, the relationship between density and fertility is not necessarily linear. For example, for many long-lived, iteroparous species, the negative effects of population density are not expressed in average fertility until the population approaches its environmentally mediated carrying capacity. In many semelparous species with short life expectancies the opposite is true – fertility declines rapidly as soon as the population begins to grow. **Figure 2** shows examples of fertility patterns relative to population density in different species.

Increasing density does not always result in depressed fertility. In many species, fertility is relatively invariant over the range of population densities experienced so that intrinsic regulation operates almost exclusively through the modification of age-specific survival rates. Some species do not appear to respond to density by adjusting fertility *per se*; rather, the age of first reproduction (primiparity) may change according to the per capita resources available. In other species, high-density living can actually stimulate production of offspring (known as inverse density dependence; e.g., **Figure 2c**). For example, many plant species require high population densities to attract grazers or pollinators that assist in cross-pollination and propagule dispersal. This Allee effect (a term used to describe a reduction in reproductive output with decreasing population density, thus affecting population growth rate) is another example of inverse density dependence that occurs when populations existing at low densities suffer from stochastic demographic events that, for example, skew the tertiary sex ratio (the ratio of the rarer sex to the total number of breeding adults). In these cases, the availability of potential mates for the more common sex is reduced so that not all reproductively capable individuals succeed in fertilization and the production of offspring. The type and strength of density dependence operating on a population also have implications for the patterns of age-specific fecundity. A reduction in extrinsic mortality favoring the evolution of reduced reproductive senescence is predicted only when density dependence acts principally on fertility and without differentially decreasing late-age fecundity. Alternatively, a reduction in extrinsic mortality can favor the evolution of faster senescence if density dependence acts mainly on the survival of older age classes.

Tradeoffs

A particular fecundity pattern evolves as an adaptation to the specific constraints imposed by the niche exploited by a species. For example, the high fecundity of parasites and many marine organisms is thought to have evolved because the probability that any particular individual will establish itself and reproduce successfully is low. As such, life-history theory predicts that the degree to which parents place themselves or their offspring at risk of mortality when threatened with predation depends on the offspring number and survival probability of parents. This type of tradeoff will also vary between the sexes in relation to the degree of investment in the offspring. A species with low adult survival and high fecundity should tolerate greater risk from predation given the low probability of surviving to reproduce in the future. In contrast, species with high adult survival and lower fecundity should tolerate less risk even at a cost to their offspring. This fundamental tradeoff essentially expresses an organism's capacity to maximize its potential lifetime reproductive success by assessing the best strategy to achieve the highest potential fecundity. Thus, tradeoffs are the benefits accrued from one life-history process that are purchased at the expense of another. For example, pre-breeding migrations requiring the use of stored resources can result in less energy available for the production of offspring. Other processes that present an individual with additional energy costs can also affect reproductive output, including exposure to antigens or parasites that increase the costs associated with mounting an immune reaction.

This introduces the concept of 'reproductive allocation' (or 'reproductive effort') which is the proportion of an individual's acquired resources that is allocated to reproduction over a defined interval of time. Because resources are finite, reproduction itself can incur a cost in that it can reduce the survival probability or growth rate of the individual. As such, the rules governing reproductive allocation are viewed in a benefit–cost framework. Dimensionless ratios of the benefits and costs of reproduction, such as the ratio of the life span spent in reproduction (E) to the length of the pre-reproductive period (α), and the ratio of the fraction of adult mass (m) devoted to reproduction (R/m) to the inverse of the life span spent in reproduction (E^{-1}), provide useful indices to classify life histories because they tend to be invariant within major taxonomic groups.

Environmental Stochasticity

Climate change is perhaps the most pressing and urgent environmental issue facing the world today. Despite the

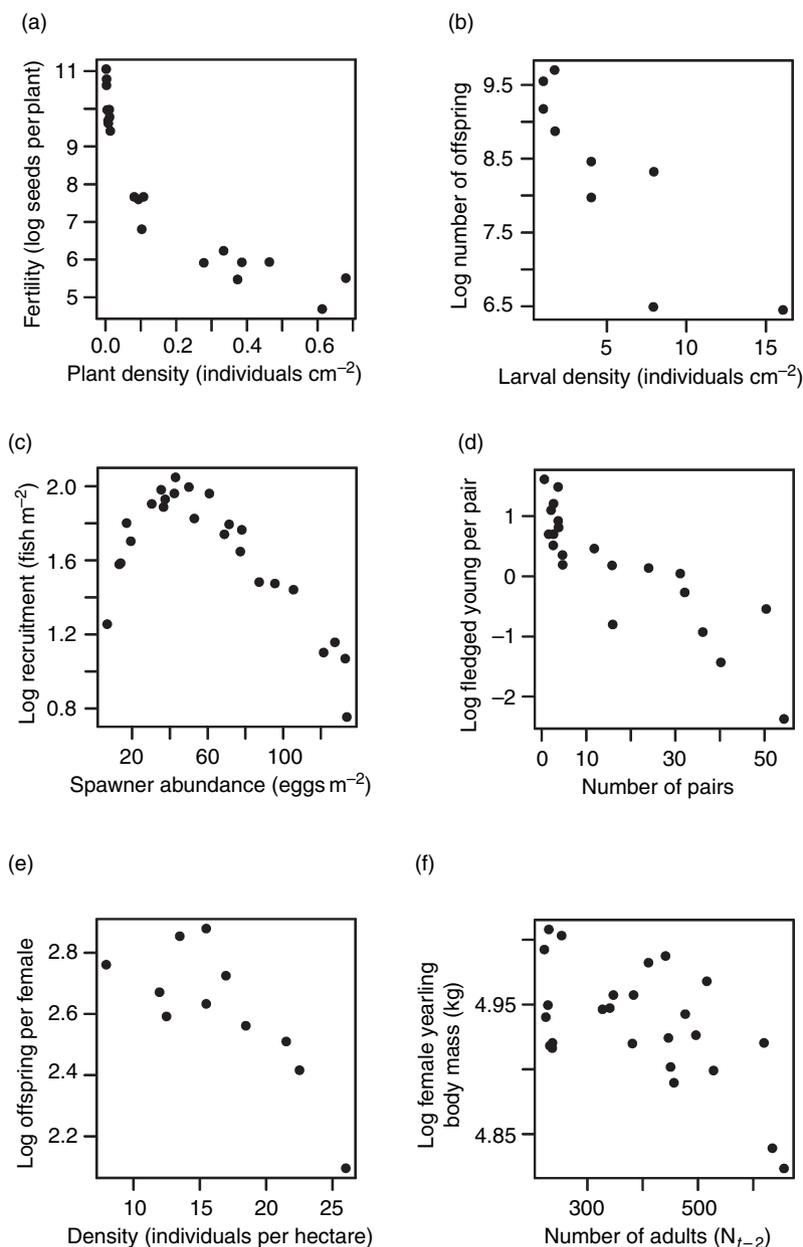


Figure 2 Example patterns of fecundity fertility with changes in population density for (a) scentless chamomile (*Tripleurospermum perforatum*); (b) midge (*Chironomus riparius*); (c) brown trout (*Salmo trutta*); (d) muted swan (*Cygnus olor*); (e) European rabbit (*Oryctolagus cuniculus*); and (f) moose (*Alces alces*). (a) Reproduced from Buckley YM, Hinz HL, Matthies D, and Rees M (2001) Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecology Letters* 4: 551–558. (b) Reproduced from Hooper HL, Sibly RM, Hutchinson TH, and Maund SJ. (2003) The influence of larval density, food availability and habitat longevity on the life history and population growth rate of the midge *Chironomus riparius*. *Oikos* 102(3): 515–524. (c) Reproduced from Myers RA (2001) ICES *Journal of Marine Science* 58: 937–951. (d) Reproduced from Nummi P and Saari L (2003) Density-dependent decline of breeding success in an introduced, increasing mute swan *Cygnus olor* population. *Journal of Avian Biology* 34 (1): 105–111. (e) Reproduced from Rödel H, Bora A, Kaiser J, et al. (2004) Density-dependent reproduction in the European rabbit: A consequence of individual response and age-dependent reproductive performance. *Oikos* 104 (3): 529–539. (f) Reproduced from Solberg EJ, Saether B-E, Strand O, Loison A (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* 68 (1): 186–204.

limitations in our ability to predict and quantify the consequences of this change, there is ample evidence that changes in climate have profound effects on the bios. Indeed, given that fertility is one of the key life-history

parameters determining population abundance and persistence, it is important to understand how it responds to environmental stochasticity. Prevailing environmental conditions can affect fertility in four principal ways by

altering (1) maternal body condition, (2) maternal survival, (3) offspring body condition, and (4) offspring survival. However, quantifying these effects can be challenging. The usual way of collecting such information on vital rate variability is to census a population in different age classes or stages over time and to compare measured vital rates (e.g., fertility) against some environmental variable (see Figure 3 for examples). Although repeated measures provide estimates of temporal variance in vital rates, this total variance also includes two other sources: demographic stochasticity and measurement/sampling error. The true variance due to environmental stochasticity must be isolated from other sources of variability or risks of decline and extinction may be biased. Several methods exist for partitioning these variances for fertility to examine the role of environmental stochasticity on this life-history parameter within population models (see also the section titled 'Fecundity and fertility in population dynamical models').

Sex-Allocation Theory

Although sex ratios are discussed elsewhere in this encyclopedia, it is important to understand the basics of sex-allocation theory with respect to fecundity. The discussions centered on the allocation of resources toward reproduction have thus far ignored the notion that the long-term value of producing offspring of one sex versus another depends on the complex relationship between current and future reproduction. Just as various life-history strategies have evolved with respect to the timing, frequency, and magnitude of reproductive effort, there are various optimality models that exist to explain sex ratio variation. Early theoretical work argued that equal sex ratios are evolutionarily stable because parental investment in sons and daughters should be identical under stable environmental conditions and population-wide random mating. However, skewed sex ratios are commonly observed due to factors such as nutritional

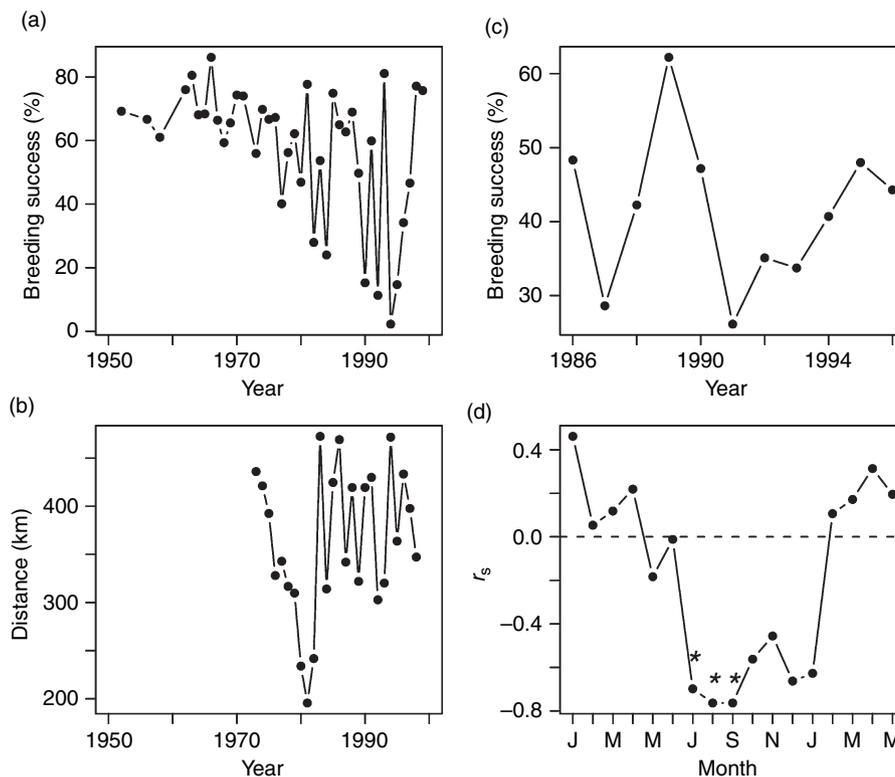


Figure 3 Examples of fecundity fertility measures fluctuating with environmental stochasticity. (a) Breeding success (% chicks fledged of eggs laid) of emperor penguin (*Aptenodytes forsteri*) pairs from 1952 to 1999. Variation in breeding success increased progressively since the 1970s resulting from complete or extensive breeding failures in some years due to early breakout of the sea ice (b) or from prolonged blizzards during the early chick-rearing period. (c) Breeding success (% chicks fledged of eggs laid) of blue petrel (*Halobaena caerulea*) pairs from 1985 to 1996. (d) Spearman's rank correlation coefficients between sea surface temperature (SST) anomalies and blue petrel breeding success for the period ranging from February preceding the reproductive period until May the following year. Months where the correlation was nonzero are indicated by an asterisk (*). (a) Reproduced from Barbraud C and Weimerskirch H (2001) Emperor penguins and climate change. *Nature* 411: 183–186. (c) From Inchausti P, Guinet C, Koudil M, Durbec J-P, et al. (2003) Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology* 34(2): 170–176.

stress, age, condition, and social rank of mothers, litter size, population density, and changes in resource availability. Optimality models focus on the idea that parents should adjust the sex ratio of their offspring in response to factors affecting their own and their offspring's future reproductive success. For example, one highly cited model used to explain sex ratio variation in mammals predicts that in polygynous species with marked sexual dimorphism, good-condition mothers should invest in the sex showing the highest variation in reproductive success because investment in that sex can potentially provide a better lifetime return on maternal investment. The apparent contradiction to the evolutionary stability of equal sex ratios invoked by adaptive sex ratio manipulation models may be explained by the existence of negative temporal autocorrelation in sex ratios between breeding events over the lifetime of the individual. In other words, equal investment in the sexes may only operate when taking total lifetime reproductive output into consideration.

Mate Choice

In the case of sexual reproduction, the optimal allocation of resources to reproduction actually begins prior to fertilization itself. The theory of mate selection by females is usually described in the context of sexual selection so that the evolution of female mating preferences centers on the genetic consequences of gamete union. Hypotheses to explain the patterns range from females seeking to improve the genetic quality of their offspring by choosing genetically superior male mates to the existence of genetic correlations between female preference and male traits. Indeed, the direct benefits of female choice can be expressed in terms of increased fertility during a breeding season, or the evolution toward selecting particular mate characteristics to increase fecundity. Mate choice is therefore seen as an important component in the evolution of particular life-history strategies.

Models constructed to investigate mate choice can be complicated by the existence of multiple mating. In many species (e.g., the majority of insects), females permit or actively seek multiple mating with different males, even though several female fitness costs of excess mating are known (e.g., additional time and energy devoted to mating, increased predation risk, higher chance of injury, higher probability of disease or parasite transmission, male-originating chemicals reducing female longevity or female fecundity). Nonetheless, the ubiquity and magnitude of this trait suggest large positive effects on female fitness. For example, a fresh supply of sperm can maintain egg fertility, accessory substances can increase egg production rate, and the mating act itself can stimulate egg production.

However, the most studied component of multiple mating concerns sperm competition. This widespread phenomenon occurs when sperm from two or more males compete for a female's ova. Relative sperm numbers are important for sperm competitive success, so that species experiencing higher rates of sperm competition have males with larger testes that produce more sperm. Sperm competition is therefore a selective force shaping optimal ejaculate structure, although spermatogenesis is not unlimited. While males usually possess a greater reproductive potential than females, males have evolved mechanisms for the optimal allocation of finite sperm among females to maximize lifetime reproductive success.

Fecundity and Fertility in Population Dynamical Models

Being a cornerstone of population biology, quantifying fecundity and fertility patterns is a central component of models that attempt to describe complex population dynamics and structure. Many models exist exclusively to provide direction in the understanding of the evolution of life-history strategies, while others have a more utilitarian function such as the estimation of a population's future status for conservation purposes. One of the most common methods used to summarize population behavior mathematically is the stage-structured matrix population model that provides a link between the individual (and its selective pressures) and the population using stage-specific estimates of vital rates (rates of birth, growth, maturation, fertility, and mortality). A more detailed description of matrix models is provided in this encyclopedia; however, there are some important aspects of these models that deal with fecundity and fertility specifically.

Stage-structured models provide an estimate of the stable stage distribution, which is the theoretical proportional allocation of individuals within the population to the defined stages (e.g., age groups, size classes, developmental stages) resulting from constant demographic rates. The stable stage distribution is a useful metric because it provides the theoretical composition of a population exhibiting a fixed birth rate, so factors such as environmental variation or intrinsic regulation that alter this theoretical distribution can be ranked for their effects on the future composition of a population. This introduces the concept of 'reproductive value' – a measure of the combined effects of fecundity, fertility, and survival that takes an individual's proportional contribution to the future status of its population into account. It is formally expressed as the sum of the current and future reproductive values, and is considered the currency used by natural selection to produce a particular life-history strategy.

Because life histories evolve to maximize reproductive success, fecundity is linked formally to population models by using the measure of reproductive value. In matrix models the relative effects of proportional changes in fertility (and survival) to population growth provide a sensitivity analysis for stage-specific terms. Here, the reproductive value for a particular stage is calculated as the product of the sensitivity of all matrix elements that contain that stage and the stable stage proportion. For example, short-lived species tend to demonstrate a relatively higher sensitivity for fertility than survival, while the reverse is often true for long-lived organisms. Thus, sensitivity analysis can be used in combination with observed variation in demographic rates to determine which factors have the largest impact on population growth and thus, the future composition of the population. Lifetime reproduction patterns expressed as reproductive allocation and ranked relative to other demographic rates therefore provide a means to compare the evolution of life-history strategies.

Genetic Considerations

An important consideration for population studies is the effect of inbreeding on reproductive fitness (the combination of fecundity, fertility, and survival). There is strong evidence to demonstrate that inbreeding reduces reproduction and survival in naturally outbreeding species and to a lesser extent in self-fertilization species, whereas increasing the incidence of outbreeding can reverse these deleterious effects. Not only does inbreeding reduce individual reproductive fitness, a population of inbred individuals often results in a declining population and an increased rate of inbreeding. As such, inbreeding is also expected to increase the risk of population extinction. This process begs the question: how much inbreeding can be tolerated without inbreeding depression? All finite closed populations will eventually become inbred without outbreeding, and even a low frequency of inbreeding is expected to result in some inbreeding depression. Effective population sizes of 50 or greater have been suggested as sufficient to avoid inbreeding depression, although it is generally unknown how large populations must be to avoid inbreeding depression in the long term. This number will also be highly variable among populations as a result of local dynamical processes and extrinsic forces.

See also: Age Structure and Population Dynamics; Demography; Matrix Models; Parasites; Population Viability Analysis; Recruitment; Sex Ratio; Visualization

and Interaction Design for Ecosystem Modeling; r-Strategist/K-Strategists.

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