



Clutch Size

Author(s): H. C. J. Godfray, L. Partridge, P. H. Harvey

Reviewed work(s):

Source: *Annual Review of Ecology and Systematics*, Vol. 22 (1991), pp. 409-429

Published by: [Annual Reviews](#)

Stable URL: <http://www.jstor.org/stable/2097268>

Accessed: 15/02/2012 07:31

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Annual Reviews is collaborating with JSTOR to digitize, preserve and extend access to *Annual Review of Ecology and Systematics*.

<http://www.jstor.org>

CLUTCH SIZE

H. C. J. Godfray

Department of Biology and Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, United Kingdom

L. Partridge

Division of Biological Science, University of Edinburgh, Ashworth Building, West Mains Road, Edinburgh EH9 3JT, United Kingdom

P. H. Harvey

Department of Zoology, University of Oxford, South Parks Rd., Oxford, OX1 3PS, United Kingdom

KEY WORDS: Clutch size, life history theory, behavioral ecology

INTRODUCTION

In recent years, problems associated with the evolution of clutch size have evoked continued interest. Although it can claim to be one of the oldest topics in life history theory, a variety of new mechanisms have been proposed that may influence selection on clutch size. Notable advances have also occurred in the sophistication of the experimental (79, 104) and comparative techniques available for testing theory (60). In addition, the taxonomic scope of clutch size studies has widened appreciably: Clutch size theory was invented by ornithologists to help explain the reproductive behavior of birds and was largely developed by vertebrate biologists. Today, the theory is widely applied to invertebrates and even to plants (84, 151).

Many animals lay eggs or produce young in discrete groups or clutches. The relationship between per capita offspring fitness and clutch size (we shall refer to this as the offspring fitness curve) is of crucial importance in de-

termining the evolution of clutch size. Here, we review the selective processes that have been proposed to influence clutch size in animals and how these hypotheses may be tested. Our intention is not to provide an exhaustive review of experimental studies on clutch size (recent reviews for birds include 79, 83, 103, and for invertebrates 49), but to concentrate on conceptual issues and controversies. We also adopt a wide taxonomic perspective and discuss how theory may be applied to disparate animal groups—in particular, we make no special distinction between groups with and without parental care.

Two broad approaches to the study of adaptation can be distinguished. The behavioral ecological approach uses optimality models to predict phenotypes and tests the models using a combination of observation, manipulative experiments, and comparative studies. The assumption is made that the population will evolve to the optimum phenotype unhindered by genetic constraints. Here, we concentrate on the application of this approach to clutch size evolution. However, an important and complementary method of studying clutch size evolution is through the use of quantitative genetics which we briefly outline here. Additive genetic variation is usually detectable for both litter size in mammals (39) and for clutch size in birds (17). Clutch size is an important determinant of the fecundity component of fitness, and a number of workers have estimated selection differentials for clutch size in birds. Most studies have found large, consistent and positive selection differentials (18, 44, 116; but see 153) which at first sight suggest the presence of directional selection for larger clutch size. If the environment has recently changed, then it is possible that the species is not at evolutionary equilibrium (116) or that it lacks sufficient heritable variation (44, 116). However, the frequency with which positive selection differentials have been found has prompted the search for other explanations. One possibility is that there is negative genetic covariance between clutch size and other components of fitness (see the discussion on trade-offs below). Alternatively, Price & Liou (113) have shown that positive selection differentials can be maintained by selection acting on nonheritable traits which covary with clutch size, such a nutritional state, while Cooke et al (27) have shown that the same result can arise through a gene-environment interaction caused by antagonistic selection through competitive abilities—a Red Queen effect. A more prosaic explanation is that ornithologists tend to study birds in good habitats where gene flow from poor habitats may lead to the appearance of selection differentials.

We begin by discussing clutch size in circumstances in which the female is selected to maximize her gain in fitness from a single clutch and where what has become known as Lack's hypothesis applies. We then examine trade-offs between clutch size and future reproductive success and go on to discuss the influence of different forms of environmental variability. Finally, we explore conflicts of interest over clutch size, both between relatives and between nonrelatives.

LACK'S HYPOTHESIS

The modern study of the evolution of clutch size began with the work of the ornithologist David Lack in the 1940s (74–76). Lack provided an explanation of clutch size in terms of individual selection at a time when many (perhaps most) biologists considered that clutch size evolved to allow a population or species to persist without overexploiting limiting resources (e.g. 162, see also 158, 159). Lack saw that selection acting on the individual would normally outweigh selection acting on the population and argued that a bird would lay the number of eggs that resulted in the maximum number of fledged young. He argued further that, in altricial birds, the main factor limiting the number of fledged young was the ability of the parents to feed their offspring.

Lack's hypothesis applies when maximizing the fitness gain per clutch is equivalent to maximizing lifetime fitness. This is true when the animal produces a single clutch in a lifetime, but it will also be true if reproductive success is severely limited by opportunities to reproduce. A number of biological mechanisms can lead to limited opportunities for reproduction. In birds and mammals, as well as in other groups with extensive parental care, the physiological requirements for reproduction limit the opportunities to breed. Many invertebrates lay eggs in resource patches that are rare or difficult to find in the environment. Lack's hypothesis will not apply if there is a trade-off between the number of offspring in a clutch and future reproductive success; we discuss such trade-offs in the following section.

In a slightly modified form, Lack's hypothesis is at the core of modern clutch size theory, and the clutch size that maximizes the gain in parental fitness is sometimes called the "Lack clutch size" (22). Lack measured parental fitness using the number of fledged young as a currency. However, as Lack was aware, clutch size may affect the fitness of young after fledging; for example, poorly fed birds from large clutches may have low overwinter survival (83). Today it is normal to use a better measure of parental fitness, for example, the number of young surviving to breed or the number of grandchildren (54). In discussing clutch size in altricial birds, Lack suggested that offspring fitness would decline monotonically with increasing clutch size because of increased competition for food. However, other factors may cause a decreasing offspring fitness curve, and it may be domed or even monotonically increasing. We refer to the Lack clutch size as the clutch size that leads to the greatest gain in parental fitness, irrespective of the biological mechanisms relating clutch size to offspring fitness.

Other factors apart from food may influence clutch size in birds. Skutch (128) argued that the fitness of offspring in large clutches would decline because of an increased incidence of predation. Comparative work on New World passerine species has supported this idea: There is an association between the size of clutch laid and the probability of loss of offspring to

predators (73). The risk of predation may increase with clutch size because large broods make more noise and attract predators (106, 128, 129, 134) or because they take longer to fledge (this assumes chicks in the nest are more susceptible to predation than recent fledglings) (9, 81). There is also evidence that the costs of incubation are related to clutch size (15, 56). Increasing clutch size may thus increase the risk of improper incubation or so weaken the parent that the quality of parental care is reduced.

In species where there is no parental care after the eggs hatch and where individuals from the same clutch do not compete, offspring fitness may still decline with clutch size if the resources used to provision eggs are limiting. In other words there is a trade-off between egg size and clutch size. The first analysis of this problem was by Smith & Fretwell (131) who assumed the parent had a fixed pool of resources (perhaps yolk) that is distributed among an indeterminate number of young. Offspring fitness is assumed to increase with greater parental investment, though with diminishing returns. Smith & Fretwell calculated the optimum egg size that maximized the parental fitness returns from the clutch. Two rather separate literatures have developed, one devoted to calculating optimum clutch size and the other to calculating optimum egg size (or equivalently optimum parental investment) (e.g. 26, 84, 98, 161). In fact, when the parent is selected to maximize the gain in fitness from a single clutch, the two approaches are often identical: The Smith & Fretwell result is obtained when the variable chosen for optimization is parental investment, while the Lack result is obtained when clutch size is the chosen variable. Complications arise when there are trade-offs between parental investment early in the life of the offspring (for example, investment in egg size) and subsequent competition between offspring for parental care or other resources (98).

A domed offspring fitness curve may be found in cases where small clutches are penalized. Again, this may be caused by a variety of biological processes. In birds, single chicks in a nest may be unable to thermoregulate efficiently (90). It has been suggested that large clutches of mollusc eggs gain protection from desiccation (11) and that large clutches of lepidopteran caterpillars are able to protect themselves from environmental extremes by constructing shelters (135, 150). Individual larvae of some herbivorous insects are unable to initiate feeding in the absence of conspecifics (43). Small clutches of some gregarious parasitoid species fail as, unless all the host tissue is consumed, the larvae drown when they attempt to pupate (146). A variety of other mechanisms that may give rise to domed offspring fitness curves in invertebrates are discussed in Ref. 49.

While predation tends to penalize large clutches of birds, the reverse is often true for invertebrate clutches. If a predator becomes satiated before it consumes a whole clutch, or a parasitoid runs out of eggs, predation or parasitism will be inversely density dependent and the probability of an

individual escaping attack will increase with clutch size. The effect of predator satiation will be accentuated if predator efficiency declines when attacking large broods. There is evidence that swarms of prey may confuse predators, lessening their attack rate (89). Large clutches may also lead to more efficient predator defense, by either physical or passive means. For example, in the presence of predators, clutches of newly hatched ascalaphid larvae (*Acaloptynx furciger*) aggregate, turn to the attacker, and rapidly and repeatedly snap their ferocious jaws (62). Individual females of some moths lay irregular piles of eggs, the interior eggs protected from parasitism by the eggs on the outside (36). The egg masses of other moths are arranged to mimic the tendrils of plants (25). Large clutches of lepidopteran larvae are able physically to conceal themselves from parasitism by building large communal webs (135). Large clutch size may also improve the efficiency of aposematic coloration or lead to its evolution because predators cease attack after experiencing one or few brightly colored, distasteful food items (45). In butterflies, at least in cross-species comparisons, there appears to be a clear correlation between aposematism, distastefulness, and gregarious oviposition (25, 28).

The Lack clutch size can still be calculated if per capita offspring fitness initially increases with clutch size, as long as offspring fitness ultimately declines. However, in some organisms, the advantages of producing large clutches may be so great that the Lack clutch size exceeds the egg capacity of the organism. The animal will then be selected to lay its complete complement of eggs as a single clutch. Observed clutch sizes in such species will be determined by the factors that limit total reproductive effort and by the dynamics of egg production. The evolution of reproductive effort is a classic problem of life history theory (41, 63, 148) though the evolutionary dynamics of egg production have been little studied. Begon & Parker (12) investigated clutch size theoretically in an organism that mated eggs while foraging and where parental fitness increased monotonically with clutch size. The optimum clutch size was determined by the trade-off between the advantages of laying a large clutch and the risk of dying before reproduction. In a number of species, several females tend to deposit their eggs in the same place despite an abundance of potential oviposition sites. For example, butterflies that lay large clutches of eggs are not infrequently observed to lay next to, or even on top of, clutches laid by other females (49). This provides strong though circumstantial evidence that the optimum clutch size exceeds that that can be laid by an individual. Brood fusion in precocial birds may also have a similar explanation (37).

The majority of clutch size models do not distinguish between the sex of the offspring. However, in circumstances where sibling competition is affected by sex, sex ratio and clutch size evolve together. Depending on the exact form of the competition, all clutches may be of the same size and uniformly biased

toward the sex with least competition between siblings (40, 47, 144). Alternatively, where intersexual competition is greater than intrasexual competition, single sex clutches may be produced. The size of the separate clutches will be the "within-sex" Lack clutch size, and the overall sex ratio will be determined by the ratio of the two expected clutch sizes. Single sex clutches of different sizes are known in some parasitoid wasps (53). In lions an association exists between large litter size and a male-biased sex ratio (97). The functional explanation may be that the fitness of male, but not female, offspring increases sharply with the size of the same-sex cohort of relatives in which they are reared.

In some cases, the clutch size strategies available to a female may be severely constrained by the organism's breeding biology. Long-tailed skuas (jaegers) never lay a clutch size greater than two, evidently because they do not build a nest and instead incubate their eggs on their feet. This habit is apparently an evolutionary response to high rates of egg-predation; experimentally introduced nests greatly increased predation on eggs (4). A rather different constraint operates in the greater rhea. The environment deteriorates strongly during the breeding season, favoring the immediate incubation of eggs. Synchronous hatching is also selectively favored so that all the young in a clutch can be kept together to protect them from predators. However, females cannot lay all their eggs at once because it takes time to produce such large eggs. The evolutionary resolution to this conflict is for each female in a local geographical area to mate with and lay their eggs in the nests of different males, starting with the top dominant and working down the hierarchy. As a consequence each female lays a clutch of one egg that contributes to a much larger clutch of male eggs (19). Some butterflies lay their eggs in crevices, and clutch size is simply the number of eggs needed to fill the crevice (28).

The standard experimental technique for investigating the Lack clutch size is to manipulate brood size and then measure offspring and parental fitness. Such experiments have now been carried out on a wide variety of birds (surveys in 78, 79). Overall, most studies have shown that the observed clutch size is either equal to or a little smaller than the most productive clutch size. Relatively few manipulative studies have been performed on clutch size in invertebrates, but the available evidence (35, 142, 143) suggests that clutch size in these groups is considerably smaller than the Lack clutch size. While manipulation is a powerful experimental technique, care must be taken to avoid several potential problems. The female must respond to the manipulation which must not result in very high or very low clutch sizes, outside the range of a realistic phenotypic response. Costs of reproduction associated with the production of eggs are unaffected by the manipulation of brood size. Lindén & Møller (83) discuss some particularly ornithological problems: Manipulations are frequently carried out on hole-nesting birds in nest boxes

where unnaturally high population densities, reduced predation, and reduced ectoparasitoid load may all influence clutch size dynamics.

Until recently, it has not been practical to manipulate egg size to investigate the relationship between egg size and fitness. However, Sinervo & Huey (125, 126) have demonstrated that it is possible to remove yolk from lizard eggs which go on to produce small, but entirely viable hatchlings. Small hatchlings had lower sprint speeds which probably increases their vulnerability to predation.

Comparisons among taxa in clutch size have often been reported, but making sense of them has led to several controversies. The main problem is that species differences in clutch size may be correlated with several ecological, morphological, and life-history variables, any number of which may be causal (60). The task is to distinguish confounding from causal associations. For example, Lack (76) suggested that individual birds might allocate finite resources into producing larger clutches of smaller eggs or smaller clutches of larger eggs. He considered that the idea was likely to apply most forcefully to precocial taxa in which the mother feeds the offspring little, if at all. Accordingly he compared waterfowl (Anatidae) species and found the predicted negative correlation between egg size and clutch size. Rohwer (117) argued that females from larger species, which are known to have smaller clutches, are likely to have more resources to invest in their offspring and would therefore produce larger eggs. He thus attempted to control statistically for body size in his analysis and found that the residual variance in clutch size accounted for only 13% of the variance in egg weight. However, Rohwer's study did not properly control for body size (he used deviations from a major axis rather than a Model I regression line), for phylogenetic association, or for species differences in life history and habitat utilization. Blackburn's (16) reanalysis of Rohwer's data controlled for these factors and found that clutch size accounted for at least 29% of the variance in egg weight after controlling body weight. Similar negative relationships have been revealed, using varying degrees of statistical sophistication, in several other taxa, including salamanders (122), chelonians (38), other birds (14) and mammals (114).

The same problems in inferring mechanisms from the cross-species comparison of clutch sizes also occur in cross-population studies within a species (105), although in such cases differences in clutch size correlated with environmental variation are much more likely to indicate causality (e.g. 71).

TRADE-OFFS BETWEEN CLUTCH SIZE AND FUTURE REPRODUCTIVE SUCCESS

A number of reasons may suggest why the production of a Lack clutch size might lead to a reduction in future reproductive success. The presence of trade-offs will lead to selection for clutches smaller than the Lack clutch size.

Much recent work on clutch size has involved the theoretical investigation and experimental measurement of trade-offs.

The first trade-off implicated in clutch size evolution was that between clutch size and the probability of surviving to breed again (21, 158). It was suggested that birds that *reared* large clutches would be so physically exhausted by the end of the breeding season that their probability of surviving to breed again would be reduced. This trade-off is an example of a cost of reproduction (13, 105) and will lead to selection for reduced clutch size. Large clutches may not only increase the risks of overwinter mortality but may also lead to loss of condition and reduced fecundity the following year. A related trade-off occurs if the production and rearing of a large clutch precludes a bird from breeding a second time in the same breeding season.

A slightly different trade-off has been discussed by Sibly & Calow (123). Suppose that laying a large clutch has no effect on the instantaneous risk of mortality but delays the next breeding attempt. This may have two effects on lifetime reproductive success. First, if the instantaneous risk of mortality is constant, delaying breeding increases the chances of dying prior to breeding again. Second, in an age-structured population with overlapping generations, there may be an advantage to breeding early so that the young reach maturity and themselves reproduce as quickly as possible. This advantage only occurs in increasing populations and is analogous to compound interest on a financial investment. It is therefore most likely to operate in organisms that reproduce several times within a breeding season or that are multivoltine. Delayed reproduction may also be important in birds that breed once a year if the production of a large clutch results in a delayed start to breeding in the next year because there is frequently a strong correlation between reproductive success and the date that nesting commences (e.g. 112).

A number of workers have attempted to detect these trade-offs in birds by manipulating clutch size (surveys in 79, 83, 103). Some studies have demonstrated impaired overwinter survival of birds with experimentally enlarged broods (34, 115), while other studies have found evidence for reduced fecundity in the subsequent breeding season (54, 55, 119). A delay in the time of breeding may also occur in the following year (78). Brood enlargement has been shown to reduce the probability of producing a second brood in the same season (82, 132) as well as the size and success of the second brood (61, 129). Overall, manipulative studies have usually found evidence of trade-offs, while nonmanipulative ones generally have not (103).

In species without parental care, other trade-offs will be more important. Perhaps the most fundamental trade-off involves egg limitation. Consider a species with a monotonic decreasing offspring fitness curve. Note that as each egg is added to make up the Lack clutch size, the fitness gain per egg for the parent decreases. Now compare an animal whose lifetime reproductive suc-

cess is limited by opportunities to reproduce with an animal limited by the number of eggs it has to lay. The first animal should maximize its fitness gain per clutch while the second animal should maximize its fitness gain per egg. While the first animal should produce a Lack clutch size, the second animal should, in this case, lay a single egg in each clutch. Often, reproductive success will be partially limited both by the opportunities to produce clutches and by egg supply. The predicted clutch size will then be determined by the balance between the immediate gain in fitness from increasing the size of the current clutch and the potential loss in fitness through running out of eggs (22, 99, 155). Any factor that increases the likelihood of running out of eggs, for example, an increase in the opportunities to produce clutches or a decrease in the risk of mortality, will lead to selection for smaller clutch sizes. When the risk of mortality is independent of age, the optimum clutch size clearly should decrease through life as egg reserves are used up and the risk of egg exhaustion increases (68, 85). If, however, mortality increases with age, the optimum clutch size may increase in old animals with a short life expectancy, an example of terminal investment (109, 145). A final complication is found in animals which mature eggs throughout their life. In these animals, the optimum clutch size will be inversely related to the current egg reserves (85, 86).

Where the offspring fitness curve is domed, the parent achieves the maximum fitness gain per egg with a clutch size greater than one. Domed offspring fitness curves thus lead to selection for clutches greater than one, even when the parent is egg limited but has abundant opportunities to produce clutches. This may explain why animals such as folivorous insects, which often appear to have unlimited sites to lay eggs, choose to lay their eggs in clutches (46, 156).

Few manipulative experiments have attempted to test the idea that clutch size is related to egg supply. Rosenheim & Rosen (118) recently studied the influence of the size of egg reserves on the clutch of a parasitoid wasp. Egg reserves were manipulated by storing wasps at different temperatures prior to experimentation; egg reserves also varied in wasps of different sizes. Clutch size was found to be inversely related to egg supply, which, in a multiple regression analysis, was the most important factor influencing clutch size.

A third way in which the production of large clutches may reduce future reproductive success is by wasting time. Consider again the case of a monotonic decreasing offspring fitness curve and suppose that the oviposition of each egg takes an appreciable period of time. As each egg is added to the clutch, the fitness increment per egg declines, and a point may be reached when the female is selected not to "waste" time adding more eggs to create the Lack clutch size, but to begin searching for a site to lay a new clutch. This assumes that the female is under selection to maximize her rate of gain of

fitness over time, just as classical foraging theory assumes an animal is selected to maximize its rate of gain of food. In fact, there is a very close parallel between foraging in a patchy environment and clutch size with time limitation. For example, the marginal value theorem (20) is used to calculate the optimum behavior in both cases. In foraging theory, longer patch residence is predicted in high quality patches or when travel time between patches is high (136). In contrast, larger clutch sizes are predicted on good oviposition sites or when travel time between oviposition sites is high (22, 23, 68, 99, 127). If the production of clutches involves time-consuming activities that do not depend on clutch size (for example, nest construction), then these will also lead to selection for increased clutch size (127). Models of time limitation are relatively simple and popular with theoreticians. In particular, complexities such as state-dependent decisions arise less readily (24, 86). However, there are probably relatively few cases when the time spent in oviposition is a substantial fraction of time available for reproduction.

THE EFFECT OF A VARIABLE ENVIRONMENT

The Lack clutch size is not constant for a species or a population. In species with parental care, different individuals will vary in their ability to feed their young and will thus have personal Lack clutch sizes. For all species, there is likely to be both temporal and spatial variation in the factors that affect offspring fitness leading to temporal and spatial variation in the Lack clutch size. This variation is likely to contain both predictable and unpredictable components. Another possible source of variability is in the production of the clutch itself: Some organisms may not be able to lay a precise number of eggs. Finally, there may be variation among the young themselves, for example, the youngest offspring is frequently a runt in birds and mammals. All these sources of variability may influence the evolution of clutch size.

The study of individual variation in optimum clutch size has largely concerned birds. There is normally considerable within-population variation in clutch size in birds. An individual's clutch size is likely to be influenced by proximate factors such as the physiological condition of the bird (either directly—7, 152, 160—or because birds in better condition obtain better territories—64). A bird's condition may act simply as a constraint, preventing the individual from producing its optimum clutch size (70), or natural selection may mould the behavior of the bird so that it produces the optimum clutch size appropriate to its condition. Proximate and ultimate factors thus interact in a complex manner, and physiological constraints and individual optima should not be treated as alternative hypotheses. A number of workers have suggested that individual adjustment in clutch size might explain the observation that the most productive clutch size is higher than the mean clutch size

(76, 107). This idea can be tested by manipulating brood size, both up and down, to see whether parents are able to rear more young than they lay and whether their survival to breed again is affected by the manipulation. The results from such experiments are mixed: Nur (94), reviewing a number of studies, concluded that while some results are consistent with the individual optimization hypothesis, there is no firm evidence in its support. However, more recent studies (55, 108) do provide better evidence for individual optimization though there is still much controversy. For example, Nur (94) and Pettifor et al (108) analyzed the same data on Great Tits and concluded respectively that individual optimization is absent and present. The difference of opinion arises from the use of different statistical techniques, and the question cannot be resolved without further analysis. Finally, it should be noted that experiments to manipulate brood size do not exclude all aspects of individual optimization. For example, birds may adjust their clutch size with respect to their ability to incubate eggs or to the ability of their mate to feed them while incubating (94).

Individual optimization may also be important when there is a cost to reproduction. Nur & Hansson (95) have modelled optimal reproductive effort when birds vary in their abilities to overwinter. They predict a positive correlation between clutch size and female weight (after controlling for body size, a measure of condition) *after* breeding. There is evidence of this from a number of bird species (94).

In the face of environmental variability, either spatial or temporal, an animal may evolve a single response to an "average" environment or may evolve phenotypic plasticity. Obviously, for plasticity to evolve, the environmental variability must be measurable or predictable. The average response will be a genetically determined compromise and subject to temporal and spatial variation in natural selection (33). Plastic responses, if perfect, will lead to optimal behavior at all times.

Consider first unpredictable spatial variability, for example, an insect ovipositing clutches of eggs in patches of unknown quality or a bird nesting in a heterogeneous habitat in which food quality varies. The optimum clutch size is determined simply by calculating the arithmetic mean fitness of different strategies over the range of environmental variability. It has been suggested (121) that when there is a high, clutch size-independent probability that some clutches will be completely destroyed, an organism will be selected to lay many small clutches instead of few large clutches. Although the mean fitness of the two strategies may not differ, producing many small clutches increases the likelihood of at least some young surviving and thus reduces the variance in fitness. *Prima facie*, this argument is incorrect as selection will not distinguish among strategies with the same within-generation arithmetic fitness. However, in finite populations with density-dependent mortality, within-

generation variance in reproductive success may lead to variation between generations, in which case the strategy with the highest temporal geometric mean fitness will be selected.

Temporal variability occurs if, for example, conditions vary unpredictably between breeding seasons. In species with non-overlapping generations, the appropriate measure of the fitness of a trait is its geometric mean fitness across generations. The geometric mean is more sensitive to low values of fitness than the arithmetic mean and is zero overall if the fitness in any one year is zero. Temporal variability thus tends to select for more conservative traits than does spatial variability. Boyce & Perrins (18) have suggested that temporal variability may explain why the mean clutch size of birds is frequently less than the most productive. If large clutches are more productive but have a greater variance in fitness than small clutches, then the clutch size that results in the highest geometric mean fitness will be less than the clutch size that results in the highest arithmetic mean fitness. Their results can explain the difference between the mean and most productive clutch sizes in Great Tits. However, the problem of defining fitness in an age-structured population with temporal variability is poorly explored, and their definition of fitness and application of the geometric mean needs further study. Note that different patterns have also been claimed for the same data (108).

Many examples of phenotypic plasticity appear in conditions where environmental variability can be measured or predicted. There is evidence that birds lay small clutches in years where food supply is poor (8, 66, 106) or in areas where food is scarce (69). Supplying birds with additional food can lead to both an advance in laying date and larger clutch size (65, 72). However, it is often difficult to distinguish between whether the bird lays a small clutch because it is weakened by lack of food or as a strategy to anticipate future food shortages while rearing young. Phenotypic plasticity is easier to demonstrate in species without parental care. Several herbivores are known to lay clutches of different sizes on different host plants (46, 110). In both cases small clutches are laid on the plant species providing fewer resources for the developing young. Some of the best examples of phenotypic plasticity come from parasitoid wasps that lay clutches of eggs on the bodies of parasitized insects (hosts). The host provides the only sustenance for the developing young and thus the size of the host is crucial in determining the fitness of the clutch. It has been repeatedly shown that female wasps modulate their clutch size in response to both interspecific and intraspecific size variation in the host (reviews in 49, 154).

One strategy of coping with uncertain environmental conditions is always to produce the same size clutch but subsequently to reduce the size of the brood in poor years or in poor localities. In species where the parent remains with the brood, this could be done through direct intervention. Burying

beetles (*Nicrophorus*) lay clutches of eggs on dead mice and remain with their brood while they develop. They lay a fixed clutch size over a range of mouse sizes and then reduce their first instar brood by cannibalism to match the food reserves provided by the mouse (10). Direct intervention by the parent may not be necessary if the parent controls the food supply, as in altricial birds. An alternative strategy is thus to create a hierarchy in offspring size and allow smaller offspring to die when conditions are bad (75). Hierarchies in offspring size are common in birds and are produced by the parent commencing incubation before completing the clutch. Brood reduction occurs either because the smallest young are outcompeted by their nest mates or through sibling aggression. The evolution of asynchronous brooding has been a major preoccupation of modern experimental ornithology, and recent reviews list no less than eight competing explanations (80, 130). A number of studies have examined the effects of artificial synchrony on the fate of nestlings under different circumstances. Many of these found that synchrony did not reduce nestling survival or growth, and that the effect of asynchrony was to impose a cost in the form of the death of the youngest nestling without any clear compensating advantage (138). One study (87) did find a reduction in nestling survival and growth with imposed synchrony, but only under poor feeding conditions; the study did not demonstrate that this would compensate the costs of asynchrony under good feeding conditions.

The ability of a female's mate to provide resources for the growing brood provides another source of environmental variability. There is evidence that secondary female Pied Flycatchers that share a male's territory with a primary female and have to rear their clutch alone, lay comparatively small clutches (1). In contrast, facultatively polygamous female dunnocks lay larger clutches if they are tended by two males than do birds tended by a single male (30).

The optimum clutch size may also be affected by the inability of a female to produce a clutch of a precise size (18, 51, 92). The effect of this imprecision can be seen by weighing the penalties of overshooting and undershooting the deterministic optimum clutch size. To take an extreme example, if the most productive clutch size is x but if all members of a clutch of $x + 1$ died, the female may be selected to lay a clutch smaller than x to avoid the risk of a costly overshoot. Imprecise clutch sizes may arise if the parent is unable to gauge exactly the size of the clutch: This is very likely in invertebrates with large clutches—for example, some parasitoids oviposit 400 eggs in under ten seconds. A second cause of imprecision is egg infertility. Offspring hierarchies leading to brood reduction may also be an adaptation to cope with infertile eggs (3). For example, several eagle species almost invariably lay a clutch of two eggs but never, or very seldom, rear both young (42, 88). Where both eggs hatch, the larger chick kills its sibling in its first few days of life. In eagles, egg infertility can be as high as 10%, and laying an extra egg substantially lessens the risk of wasting a whole breeding season.

CONFLICT OVER CLUTCH SIZE

At least three potential sources of conflict exist over clutch size. First, natural selection operating on genes expressed in the young may have different results than natural selection operating on genes expressed in the parent: In other words there may be parent-offspring conflict in the sense of Hamilton (58) & Trivers (149). Second, the females of many organisms, especially invertebrates, lay clutches together on a single resource patch. The offspring compete together for resources, and the optimum clutch size for an individual depends on the strategy adopted by the rest of the population—an example of a classical evolutionary game. Finally, although it is not discussed here, there may also be conflicts of interest between the mother and the father over clutch size.

The most obvious way for an offspring to influence clutch size is by killing one or more siblings. While not common, siblicide is widespread in birds, especially in large raptors, herons and allies, gannets and skuas (3, 90, 91, 93, 124). An offspring may be selected to destroy a sibling if the fitness advantages to itself and to its surviving siblings compensate for the death of a relative (50, 58, 96, 101, 137). Conditions such as food shortage that favor parental brood reduction also favor brood reduction by siblings, though theory suggests that siblings will be more willing to reduce the size of the brood than is optimal for the parent. As mentioned above, where brood reduction does occur, it is normally the young and not the parents that cause the death of the runt. This suggests that the extent of brood reduction may be determined by selection acting on the offspring rather than the parent, but as yet no experimental study has succeeded in disentangling the two processes.

Brood reduction is found in a variety of invertebrate groups where it is often associated with cannibalism. It has been suggested (2) that some beetles lay large clutches of eggs that hatch over several days so that the larvae that hatch first are able to obtain their first meal by feeding on their unhatched siblings. A number of spiders and marine invertebrates lay large clutches of eggs, many of which are infertile (nurse eggs), and their only apparent function is to provide nourishment for the eggs that hatch (111, 147). The production of nurse eggs is an alternative strategy to increasing the yolk content of the egg. The larvae of many parasitoid wasp species kill all conspecifics in the same host, and this has a major influence on the possible clutch size that can be produced by the female (48).

Offspring may also have a more subtle, indirect influence on clutch size. In sexual species, offspring differ genetically and will compete among themselves for resources. For example, nestling birds compete with each other when begging food from their parents, while gregarious insect larvae may compete for food resources at the oviposition site. Sibling competition will

entail costs to the participants; for example, begging may use up energy and attract predators while a caterpillar might sacrifice assimilation efficiency for speed of ingestion. The fitness gain to the parent may thus be reduced by sibling competition, and the parent may be selected to reduce clutch size to lessen sibling conflict (52). It has been suggested that the production of an offspring hierarchy is a mechanism to reduce sibling competition (57, 58) though it is unclear how this may evolve (53, 102). Where the parent remains with the brood, sibling conflict may be reduced by direct parental intervention, an imposition of the parental optimum (2), though it is unlikely that the parent always "wins" (32, 59, 100). Direct intervention is, of course, not possible in species where the parent abandons her eggs.

In some species of parasitoid wasp, clutch size is under the control of the offspring. Polyembryonic wasps inject a single egg into the body of their host. The egg then divides asexually to produce a large number, sometimes several thousand, of genetically identical offspring (139). Because of the genetic identity, there is no sibling conflict among the larvae, and some species even have fighting larval morphs that protect their siblings but fail to mature sexually (29). As the clutch size is determined by the mass of larvae and there is no question of parental trade-offs, the species should evolve to the Lack clutch size. It is interesting that this group of parasitoids, where a strong a priori argument can be made for the Lack clutch size, has the largest clutch size of any parasitoid.

Conflict over clutch size among nonrelatives occurs if more than one female lays clutches of eggs in the same site. In species that feed their young, this phenomenon is known as brood parasitism. Intraspecific brood parasitism occurs when one female clandestinely lays an egg in another female's nest, and this is known to occur in many bird species (5, 120). With the occurrence of intraspecific brood parasitism, selection may occur for hosts to drop their clutch size, and some evidence suggests that this occurs in birds (6, though see 77). The well-known interspecific brood parasite, the European cuckoo, has a simple strategy for manipulating host clutch size: The young cuckoo ejects all the host offspring from the nest (31).

Many invertebrates lay several clutches of eggs in the same place. This behavior has been particularly studied in parasitoid wasps (where it is termed superparasitism) and more recently in other groups such as herbivorous and carrion insects (superoviposition) (49). If a resource patch already contains eggs laid by another female, then the value of the resource will normally be reduced and a second female may be expected to ignore the patch or to lay a reduced clutch size (22, 127). In parasitoid wasps, the clutch of eggs laid by a superparasitizing female is normally smaller than a primary clutch (154, 157). The calculation of optimum clutch sizes is complicated as, if superparasitism is common, females laying eggs on unexploited patches may experience

selection to lay smaller clutches because of the high risk that the patch will be subsequently discovered by another female. This question has been investigated using game theoretic models (47, 67, 99, 133, 141, 157). Other complications arise when superparasitizing females destroy the eggs of previous females (133, 140) or adopt different sex ratio strategies (141, 157).

CONCLUSION

The behavioral ecological theory of the evolution of clutch size is well developed and rich in predictions. The pioneering work of field ornithologists in testing these predictions using field manipulations continues to provide remarkable insights into life history theory. The experimental approach to the study of clutch size is now being applied to novel taxonomic groups while recent developments in manipulating egg size allow the experimental investigation of new sets of questions. Recent advances in the comparative method offer the prospect of a far more rigorous approach to cross-species comparisons. Though only briefly considered here, the renaissance of quantitative genetics has provided a variety of new techniques for the study of clutch size, and while they complement the methods of behavioral ecology, greater integration of the two approaches is desirable. It thus seems likely that the modern study of clutch size, initiated by David Lack over 40 years ago, will continue at the forefront of the investigation of adaptation.

Literature Cited

1. Alatalo, R., Carlson, A., Lundberg, A., Ulfstran, S. 1981. The conflict between male polygamy and female monogamy: the case of the pied flycatcher *Ficedula hypoleuca*. *Am. Nat.* 117:738-53
2. Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5:325-83
3. Anderson, D. J. 1990. Evolution of obligate siblicide in boobies. I. A test of the insurance-egg hypothesis. *Am. Nat.* 135:334-50
4. Andersson, M. 1976. Clutch size in the Long-tailed Skua *Stercorarius longicaudus*: some field experiments. *Ibis* 118:586-88
5. Andersson, M. 1984. Brood parasitism within species. In *Producers and Scroungers*, ed. C. Barnard, pp. 195-228. London: Croom Helm
6. Andersson, M., Eriksson, M. O. G. 1982. Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. *Am. Nat.* 120:1-16
7. Ankney, C. D., MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-71
8. Arcese, O., Smith J. N. M. 1988. Effects of population density and supplemental food on reproduction in song sparrows. *J. Anim. Ecol.* 57:119-36
9. Arnold, T. W., Rohwer, F. C., Armstrong, T. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* 130:643-53
10. Bartlett, J. 1987. Filial cannibalism in burying beetles. *Behav. Ecol. Sociobiol.* 21:179-83
11. Bayne, C. J. 1969. Survival of the embryos of the grey field slug *Agrioclimax reticulatus* following desiccation of the egg. *Malacologia* 9:391-401
12. Begon, M., Parker, G. A. 1986. Should egg size and clutch size decrease with age? *Oikos* 47:293-302
13. Bell, G., Koufopanou, V. 1986. The costs of reproduction. In *Oxford Surveys of Evolutionary Biology*, ed. R. Dawkins, M. Ridley, 3:83-131. Oxford: Oxford Univ. Press

14. Bennett, P. M. 1986. *Comparative studies of morphology, life history and ecology among birds*. PhD thesis. Univ. Sussex, England
15. Biebach, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating starlings (*Sternus vulgaris*). *Phys. Zool.* 57:26–31
16. Blackburn, T. 1991. The interspecific relationship between egg size and clutch size in waterfowl—a reply to Rohwer. *Auk*. In press
17. Boag, P. T., van Noordwijk, A. J. 1987. Quantitative genetics. In *Avian Genetics: A Population and Ecological Approach*, pp. 45–78. London: Academic
18. Boyce, M. S., Perrins, C. M. 1988. Optimizing great tit clutch size in a fluctuating environment. *Ecology* 68: 142–53
19. Bruning, D. F. 1973. The greater rhea chick and egg delivery route. *Nat. Hist.* 82:68–75
20. Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9:129–36
21. Charnov, E. L., Krebs, J. R. 1974. On clutch size and fitness. *Ibis* 116:217–19
22. Charnov, E. L., Skinner, S. W. 1984. Evolution of host selection and clutch size in parasitoid wasps. *Fla. Entomol.* 67:5–21
23. Charnov, E. L., Skinner, S. W. 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. *Environ. Entomol.* 14:383–91
24. Charnov, E. L., Stephens, D. W. 1988. On the evolution of host selection in solitary parasitoids. *Am. Nat.* 132:707–22
25. Chew, F. S., Robbins, R. K. 1984. Egg-laying in butterflies. In *The Biology of Butterflies*, ed. R. I. Vane-Wright, P. R. Ackery, pp. 65–80. London: Academic
26. Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton: Princeton Univ. Press
27. Cooke, F., Taylor, P. D., Francis, C. M., Rockwell, R. F. 1990. Directional selection and clutch size in birds. *Am. Nat.* 136:261–67
28. Courtney, S. P. 1984. The evolution of batch oviposition by Lepidoptera and other insects. *Am. Nat.* 123:276–81
29. Cruz, Y. P. 1981. A sterile defender morph in a polyembryonic hymenopterous parasite. *Nature* 289:27–33
30. Davies, N. B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Anim. Behav.* 33:628–48
31. Davies, N. B. 1988. Cuckoos versus reed warblers: adaptations and counter-adaptations. *Anim. Behav.* 36:262–84
32. Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford Univ. Press
33. Dhondt, A. A., Adriansen, F., Matthyssen, E., Kempenaers, B. 1990. Non-adaptive clutch size in tits. *Nature* 348:723–25
34. Dijkstra, C. 1988. *Reproductive tactics in the Kestrel*. PhD thesis. Univ. Groningen, The Netherlands
35. Dijkstra, L. J. 1986. Optimal selection and exploitation of hosts in the parasitic wasp *Colpoclypeus florus* (Hym., Eulophidae). PhD Thesis. Univ. Leiden, The Netherlands
36. Dowden, P. B. 1961. The gypsy moth egg parasite, *Ooencyrtus kuwanai*, in Southern Connecticut in 1960. *J. Econ. Entomol.* 54:876–78
37. Eadie, J. McA., Kehoe, F. P., Nudds, T. D. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: A review of hypotheses. *Can. J. Zool.* 66:1709–21
38. Elgar, M. A., Heaphy, L. J. 1989. Covariation between clutch size, egg weight and egg shape: comparative evidence from chelonians. *J. Zool. Lond.* 219:137–52
39. Falconer, D. S. 1981. *Introduction to Quantitative Genetics*. London: Longman
40. Frank, S. A. 1990. Sex allocation theory for birds and mammals. *Annu. Rev. Ecol. Syst.* 21:13–55
41. Gadgil, M., Bossert, W. H. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1–24
42. Gargett, V. 1978. Sibling aggression in the Black Eagle in the Matapos, Rhodesia. *Ostrich* 49:57–63
43. Ghent, A. W. 1960. A study of the group feeding behavior of larvae of the jack-pine sawfly, *Neodiprion pratti bankstanae* Rao. *Behaviour* 16:110–48
44. Gibbs, H. L. 1988. Heritability and selection on clutch size in Darwin's medium ground finches (*Geospiza fortis*). *Evolution* 42:750–62
45. Gittleman, J. L., Harvey, P. H. 1980. Why are distasteful prey not cryptic? *Nature* 286:149–50
46. Godfray, H. C. J. 1986. Clutch size in a leaf-mining fly (*Pegomya nigratarsis*: Anthomyiidae). *Ecol. Entomol.* 11:75–81
47. Godfray, H. C. J. 1986. Models for clutch size and sex ratio with sibling interaction. *Theor. Popul. Biol.* 30:215–31
48. Godfray, H. C. J. 1987. The evolution

- of clutch size in parasitic wasps. *Am. Nat.* 129:221–33
49. Godfray, H. C. J. 1987. The evolution of invertebrate clutch size. In *Oxford Surveys of Evolutionary Biology*, ed. P. H. Harvey, L. Partridge, 4:117–54. Oxford: Oxford Univ. Press
 50. Godfray, H. C. J., Harper, A. B. 1990. The evolution of brood reduction by siblicide in birds. *J. Theor. Biol.* 145:163–75
 51. Godfray, H. C. J., Ives, A. R. 1987. Stochastic models of invertebrate clutch size. *Theor. Popul. Biol.* 33:79–101
 52. Godfray, H. C. J., Parker, G. A. 1991. Sibling competition, parent-offspring conflict and clutch size. *Anim. Behav.* In press
 53. Godfray, H. C. J., Parker, G. A. 1991. Clutch size, fecundity and parent-offspring conflict. *Philos. Trans. R. Soc. Lond. B* 332:67–79
 54. Gustaffson, L., Part, T. 1990. Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347:279–81
 55. Gustaffson, L., Sutherland, W. J. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature* 335:813–15
 56. Haftorn, S., Reinertsen, R. E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* 102:470–78
 57. Hahn, D. C. 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. *Anim. Behav.* 29:421–27
 58. Hamilton, W. D. 1964. The genetical theory of social behaviour. I & II. *J. Theor. Biol.* 7:1–16, 17–51
 59. Harper, A. B. 1986. The evolution of begging: sibling competition and parent-offspring conflict. *Am. Nat.* 128:99–114
 60. Harvey, P. H., Pagel, M. D. 1991. *The Comparative Method*. Oxford: Oxford Univ. Press
 61. Hegner, R. E., Wingfield, J. C. 1987. Effects of brood size manipulations on parental investment, breeding success, and reproductive endocrinology. *Auk* 104:470–80
 62. Henry, C. S. 1972. Eggs and repagula of *Ululodes* and *Ascaloptynx* (Neuroptera: Ascalaphidae): a comparative study. *Psyche (Cambridge)* 79:1–22
 63. Hirshfield, M. F., Tinkle, D. W. 1975. Natural selection and the evolution of reproductive effort. *Proc. Natl. Acad. Sci. USA* 72:2227–31
 64. Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210:1148–50
 65. Hogstedt, G. 1981. Effect of additional food on reproductive success in the Magpie *Pica pica*. *J. Anim. Ecol.* 50:219–90
 66. Hornfeldt, B., Eklund, U. 1990. The effect of food on laying date and clutch-size in Tengmalm's Owl *Aegiolus funereus*. *Ibis* 132:395–406
 67. Ives, A. R. 1989. The optimal clutch size of insects when many females oviposit per patch. *Am. Nat.* 133:671–87
 68. Iwasa, Y., Suzuki, Y., Matsuda, H. 1984. Theory of oviposition of parasitoids. I. Effect of mortality and limited egg number. *Theor. Popul. Biol.* 26:205–27
 69. Jarvinen, A. 1989. Clutch-size variation in the pied flycatcher *Ficedula hypoleuca*. *Ibis* 131:572–77
 70. Jones, P. J., Ward, P. 1976. The level of reserve protein as the proximate factor controlling the timing of clutch size in the red-billed quelea. *J. Zool. (Lond.)* 189:1–19
 71. Klomp, H. 1970. The determination of clutch size in birds, a review. *Ardea* 58:1–124
 72. Korpimäki, E. 1989. Breeding performance of Tengmalm's owl *Aegiolus funereus*: effects of supplementary feeding in a peak vole year. *Ibis* 131:51–56
 73. Kuleza, G. 1990. An analysis of clutch size in New World passerine birds. *Ibis* 132:407–22
 74. Lack, D. 1947. The significance of clutch size. *Ibis* 89:309–52, 90:25–45
 75. Lack, D. 1954. *Natural Regulation of Animal Numbers*. Oxford: Clarendon
 76. Lack, D. 1966. *Population Studies of Birds*. Oxford: Oxford Univ. Press
 77. Lank, D. B., Rockwell, R. F., Cooke, F. 1990. Frequency-dependent fitness consequences of intraspecific nest parasitism in snow geese. *Evolution* 44:1436–53
 78. Lessells, C. M. 1986. Brood size in Canada geese: a manipulation experiment. *J. Anim. Ecol.* 55:669–89
 79. Lessells, C. M. 1991. The evolution of life histories. In *Behavioral Ecology: an Evolutionary Approach*, ed. J. R. Krebs, N. B. Davies pp. 32–68. Oxford: Blackwell Sci. 3rd ed.
 80. Lessells, C. M., Avery, M. I. 1989. Hatching asynchrony in European Bee-eaters *Merops apiastor*. *J. Anim. Ecol.* 58:815–35
 81. Lima, S. L. 1987. Clutch size in birds: a predation perspective. *Ecology* 68:1062–70

82. Lindén, M. 1988. Reproductive trade-offs between first and second clutches in the Great Tit *Parus major*: an experimental study. *Oikos* 51:285-90
83. Lindén, M., Möller, A. P. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* 4:367-71
84. Lloyd, D. 1987. Selection of offspring size at independence and other size versus number strategies. *Am. Nat.* 129: 800-17
85. Mangel, M. 1987. Oviposition site selection and clutch size in insects. *J. Meth. Biol.* 25:1-22
86. Mangel, M. 1989. Evolution of host selection in parasitoids: does the state of the parasitoid matter. *Am. Nat.* 133: 688-705
87. Magrath, R. D. 1989. Hatching asynchrony and reproductive success in the Blackbird. *Nature* 339:536-38
88. Meyburg, B.-U. 1974. Sibling aggression and mortality among nestling eagles. *Ibis* 116:224-28
89. Milinski, M. 1977. Do all members of a swarm suffer the same predation? *Z. Tierpsychol.* 45:373-88
90. Mock, D. W., Parker, G. A. 1986. Advantages and disadvantages of brood reduction in egrets and herons. *Evolution* 40:459-70
91. Mock, D. W., Ploger, B. J. 1987. Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. *Anim. Behav.* 35:150-60
92. Mountford, M. D. 1968. The significance of litter size. *J. Anim. Ecol.* 37:363-67
93. Nelson, B. 1989. Cainism in the Sulidae. *Ibis* 131:609
94. Nur, N. 1986. Is clutch size variation in the blue tit (*Parus caeruleus*) adaptive? An experimental study. *J. Anim. Ecol.* 55:983-99
95. Nur, N., Hansson, O. 1984. Phenotypic plasticity and the handicap principle. *J. Theor. Biol.* 110:275-97
96. O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim. Behav.* 26:79-96
97. Packer, C., Pusey, A. E. 1987. Intrasexual cooperation and the sex ratio in African lions. *Am. Nat.* 130:636-42
98. Parker, G. A., Begon, M. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* 128:573-92
99. Parker, G. A., Courtney, S. P. 1984. Models of clutch size in insect oviposition. *Theor. Popul. Biol.* 26:27-48
100. Parker, G. A., Macnair, M. R. 1979. Models of parent-offspring conflict. IV. Suppression: Evolutionary retaliation by the parent. *Anim. Behav.* 27:1210-35
101. Parker, G. A., Mock, D. W. 1987. Parent-offspring conflict over clutch size. *Evol. Ecol.* 1:161-74
102. Parker, G. A., Mock, D. W., Lamey, T. C. 1989. How selfish should stronger sibs be? *Am. Nat.* 133:846-68
103. Partridge, L. 1989. Lifetime reproductive success and life history evolution. In *Lifetime Reproduction in Birds*, ed. I. Newton, pp. 421-40. London: Academic
104. Partridge, L. 1989. An experimentalist's approach to the role of costs of reproduction in the evolution of life histories. In *Toward a More Exact Ecology*, ed. P. J. Grubb, J. B. Whittaker, pp. 231-46. Oxford: Blackwell Sci.
105. Partridge, L., Harvey, P. H. 1988. The ecological context of life history evolution. *Science* 241:1449-55
106. Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit *Parus major* L. *J. Anim. Ecol.* 34:601-47
107. Perrins, C. M., Moss, D. 1975. Reproductive rates in the great tit. *J. Anim. Ecol.* 44:695-706
108. Pettifor, R. A., Perrins, C. M., McCleery, R. H. 1988. Individual optimization of clutch size in great tits. *Nature* 336:160-62
109. Pianka, E. R., Parker, W. S. 1975. Age-specific reproductive tactics. *Am. Nat.* 109:453-64
110. Pilson, D., Rausher, M. D. 1988. Clutch size adjustment by a swallowtail butterfly. *Nature* 333:361-63
111. Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* 12:225-51
112. Price, T., Kirkpatrick, M., Arnold, S. J. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240:798-800
113. Price, T., Liou, L. 1989. Selection of clutch size in birds. *Am. Nat.* 134:950-59
114. Read, A. F., Harvey, P. H. 1989. Life history differences among the eutherian radiations. *J. Zool. (Lond.)* 219:329-53
115. Reid, W. V. 1987. The cost of reproduction in the glaucous-winged gull. *Oecologia* 74:458-67
116. Rockwell, R. F., Findlay, C. S., Cooke, F. 1987. Is there an optimal clutch size in snow geese. *Am. Nat.* 130:839-63
117. Rohwer, F. C. 1988. Inter- and intraspecific relationships between egg

- size and clutch size in waterfowl. *Auk* 105:161-76
118. Rosenheim, J. A., Rosen, D. 1991. Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: distinguishing the influences of egg load and experience. *J. Anim. Ecol.* In press
 119. Røskaft, E. 1985. The effect of enlarged brood size on the future reproductive potential of the rook. *J. Anim. Ecol.* 54:255-60
 120. Rothstein, S. I. 1990. Brood parasitism and clutch-size determination in birds. *Trends Ecol. Evol.* 5:101-2
 121. Rubenstein, D. I. 1982. Risk, uncertainty, and evolutionary strategies. In *Current Problems in Sociobiology*, ed. King's College Sociobiol. Group, pp. 91-111. Cambridge: Cambridge Univ. Press
 122. Salthe, S. N. 1969. Reproductive modes and the number and sizes of ova in urodeles. *Am. Midl. Nat.* 81:467-90
 123. Sibly, R., Calow, P. 1983. An integrated approach to life-cycle evolution using selective landscapes. *J. Theor. Biol.* 102:527-47
 124. Simmons, R. 1988. Offspring quality and the evolution of cainism. *Ibis* 130:339-57
 125. Sinervo, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279-94
 126. Sinervo, B., Huey, R. B. 1990. Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science* 248:1106-09
 127. Skinner, S. W. 1985. Clutch size as an optimal foraging problem for insects. *Behav. Ecol. Sociobiol.* 17:231-38
 128. Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430-55
 129. Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *J. Anim. Ecol.* 53:945-53
 130. Slagsvold, T., Lijfield, J. T. 1989. Constraints on hatching asynchrony and egg size in pied flycatchers. *J. Anim. Ecol.* 58:837-50
 131. Smith, C. C., Fretwell, S. D. 1974. The optimal balance between the size and number of offspring. *Am. Nat.* 108:499-506
 132. Smith, H., Källänder, H., Nilsson, J-Å. 1989. The trade-off between offspring number and quality in the great tit *Parus major*. *J. Anim. Ecol.* 58:383-401
 133. Smith, R. H., Lessells, C. M. 1985. Oviposition, ovicide and larval competition in granivorous insects. In *Behavioural Ecology*, ed. R. M. Sibly, R. H. Smith, pp. 423-48. Oxford: Blackwell Sci.
 134. Snow, B. K. 1970. A field study of the bearded bellbird in Trinidad. *Ibis* 112: 299-329
 135. Stamp, N. E. 1980. Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly. *Am. Nat.* 115:367-80
 136. Stephens, D. W., Krebs, J. R. 1986. *Foraging Theory*. Princeton: Princeton Univ. Press
 137. Stinson, C. H. 1979. On the selective advantage of fratricide in raptors. *Evolution* 33:1219-25
 138. Stouffer, P. C., Power, H. W. 1990. Density effects on asynchronous hatching and brood reduction in European Starlings. *Auk* 107:359-66
 139. Strand, M. R. 1989. Clutch size, sex ratio and mating by the polyembryonic encyrtid *Copidosoma floridanum* (Hymenoptera: Encyrtidae). *Fla Entomol.* 72:32-42
 140. Strand, M. R., Godfray, H. C. J. 1989. Superparasitism and ovicide in parasitic Hymenoptera: theory and a case study of the ectoparasitoid *Bracon hebetor*. *Behav. Ecol. Sociobiol.* 24:421-32
 141. Suzuki, Y. & Iwasa, Y. 1980. A sex ratio theory of gregarious parasitoids. *Res. Popul. Ecol.* 22:366-82
 142. Takagi, M. 1985. The reproductive strategy of the gregarious parasitoid *Pteromalus puparum* (Hymenoptera: Pteromalidae). I. Optimal number of eggs in a single host. *Oecologia* 68:1-6
 143. Taylor, A. D. 1988. Host effects on larval competition in the gregarious parasitoid *Bracon hebetor*. *J. Anim. Ecol.* 57:163-72
 144. Taylor, P. D. 1981. Intra-sex and inter-sex sibling interaction as sex ratio determinants. *Nature* 291:64-66
 145. Taylor, P. D. 1990. Optimal life histories with age-dependent trade-off curves. *J. Theor. Biol.* 148:33-48
 146. Taylor, T. H. C. 1937. *The Biological Control of an Insect in Fiji*. London: Imperial Inst. Entomol.
 147. Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25:1-45
 148. Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Am. Nat.* 103:501-16
 149. Trivers, R. L. 1974. Parent-offspring conflict. *Am. Zool.* 14:249-64
 150. Tsubaki, Y. 1981. Some beneficial

- effects of aggregation in young larvae of *Pryeria sinica* Moore (Lepidoptera: Zygaenidae). *Res. Pop. Ecol.* 23:156-67
151. Uma Shaanker, R. U., Ganeshiah, K. N., Bawa, K. S. 1988. Parent-offspring conflict, sibling rivalry, and brood-size patterns in plants. *Annu. Rev. Ecol. Syst.* 19:177-205
 152. van Noordwijk, A. J., de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128:137-42
 153. van Noordwijk, A. J., van Balen, J. H., Scharloo, W. 1981. Genetic and environmental variation in clutch size of the great tit *Parus major*. *Neth. J. Zool.* 31:342-72
 154. Waage, J. K. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In *Insect Parasitoids*, ed. J. K. Waage, D. J. Greathead, pp. 449-70. London: Academic
 155. Waage, J. K., Godfray, H. C. J. 1985. Reproductive strategies and population ecology of insect parasitoids. See Ref. 133, pp. 449-70
 156. Weis, A. E., Price, P. W., Lynch, M. 1983. Selective pressures on the clutch size of the gall maker *Asteromyia carbonifera*. *Ecology* 64:688-95
 157. Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* 208:1157-59
 158. Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton: Princeton Univ. Press
 159. Williams, G. C. 1971. *Group Selection*. Chicago: Aldine Atherton
 160. Winkler, D. W. 1985. Factors determining a clutch size reduction in California gulls (*Larus californicus*): a multi-hypothesis approach. *Evolution* 39:667-677
 161. Winkler, D. W., Wallin, K. 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *Am. Nat.* 129:708-20
 162. Wynne-Edwards, V. C. 1962. *Animal Dispersion in Relation to Social Behaviour*, Edinburgh: Oliver & Boyd