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Parental effort in birds and mammals: theory and measurement

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1. INTRODUCTION

Parental care is the most apparent and variable aspect of the reproductive effort of birds and mammals. To give an example, individuals of the Australian brush turkey, *Megapodius freycinet*, differ dramatically in the effort expended in nest-building. Some females merely lay their eggs in rock crevices warmed by the sun, whereas others lay in enormous nesting mounds of earth and vegetation. These mounds, which are built by several pairs of birds, can reach 11 m in diameter and 5 m in height (Frith 1985). Similar examples could be given for many other bird and mammal species. Although numerous attempts have been made to characterize and explain qualitative differences in parental care patterns between major taxa in fishes, birds, and mammals (e.g. Kendeigh 1952; Low 1978; Silver *et al.* 1985; Gross and Sargent 1985), the causes and consequences of quantitative variation in parental care are just beginning to be explored. In this review we argue that our understanding of intraspecific variation in parental care can best be advanced by developing and testing models that relate components of fitness to quantitative variation in parental care.

Parental care is merely any behaviour that increases offspring survival rates, and we use the term parental effort to designate specific measures of time, energy, or risk expended in parental care. Increasing parental effort will usually yield benefits in the form of increased offspring survival rates, and it will often result in parental costs in the form of reduced reproductive potential of the parents. Other authors (e.g. Rose and Charlesworth 1981; Reznick 1985; Reznick *et al.* 1986) have argued that such 'costs of reproduction' must be measured in genetic, rather than phenotypic terms. This insistence on genetic trade-offs between parental effort and reproductive potential springs from the assumption that adaptive models for reproductive traits necessarily describe only their response to selection over generations. If one's goal, instead, is to understand the determinants of quantitative variation in parental behaviour within a generation, then adaptive models can yield valuable predictions for behavioural responses of individuals irrespective of the genetic details underlying those behaviours. This view rests

on two assumptions: (1) that current variation in parental effort has effects on components of fitness and (2) that parents can be thought of as 'decision-making machines' that have been moulded by selection to make adaptive behavioural responses to changes in their environments. Long-lived, iteroparous vertebrates that provide parental care, such as most birds and mammals, must constantly make choices about how to allocate resources into maintenance versus reproduction.

We limit our attention in this review to birds and mammals because their iteroparity makes it possible to monitor multiple breeding episodes and survival between them for single individuals, because their extensive quantitative variation in parental effort is often easier to measure than in other taxa, because their biologies are generally better known than are those of other animal groups, and because they have the most extensive parental care of any vertebrate group. Contrasts between these two principal groups of endothermic vertebrates are made all the more interesting by their different modes of reproduction (i.e. oviparity versus viviparity). They thus provide interesting alternative solutions to similar problems of parental care evolution.

We will now review the kinds of adaptive models that can be applied to parental effort, turning thereafter to methodological and empirical issues germane to their application to nature.

2. ADAPTIVE MODELS APPROPRIATE FOR PARENTAL EFFORT

A considerable number of adaptive approaches have been used to model parental effort. Some of these have taken the form of verbal arguments (e.g. von Haartman 1954; Royama 1966; Barash 1975; Kleiman and Malcolm 1981), whereas others have included explicit maximization or optimization models (e.g. Trivers 1974; Andersson *et al.* 1980; Nur 1984a; Gross and Sargent 1985; Sargent and Gross 1986; Winkler 1987).

The more recent of these models have built upon the framework of life history theory, in which fitness or reproductive value is maximized subject to two assumed constraint functions: a decrease in parental survival rate and an increase in offspring survival rate with an increase in parental effort (Fig. 1). The optimal effort is then often at an intermediate level (see Schaffer 1974), because the rate of increase in benefits from increasing effort (increased survival and production of offspring) are countered by increases in the rate of cost (decreased parental survival probability). Sargent and Gross (1986) have adopted this model for the specific case of parental effort. Winkler (1987) explored the effect of environmental variables on the relations between effort and parental and offspring survival and presented general equations for the resulting changes in optimal parental effort.

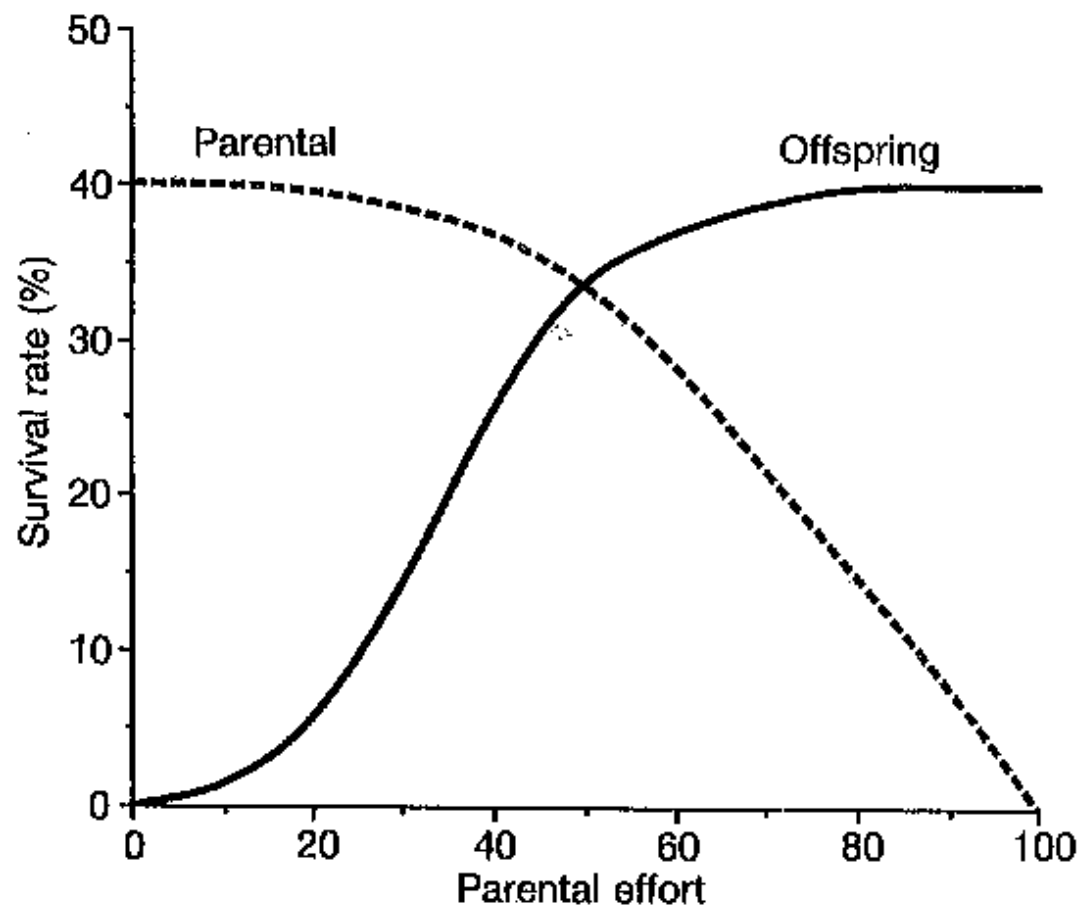


Fig. 1. This figure illustrates the central trade-off in a life-history approach to parental care: as parental effort increases, parental survival rate decreases and offspring survival rate increases. The shapes and axis values of these curves are hypothetical, because they have not yet been measured for any bird or mammal.

These models are well suited to analyses of parental effort in which the adaptive problem is the most efficient allocation of scarce resources, energy, or time, especially when the benefits and costs of allocation 'decisions' remain stable over time. The models require knowing or assuming the shapes of the functions relating offspring and parental survival to variation in effort. The various optimization models have produced remarkably similar predictions in the areas of parental effort that they have in common, and the data available appear consistent with those predictions. Predictions of models are supported by the available data in birds for: an increase in effort with increasing offspring age (Andersson *et al.* 1980; Patterson *et al.* 1980) and brood size (Sibly and Calow 1983; Nur 1984*a,b*; Houston and Davies 1985), and with decreasing effort of the mate (Chase 1980; Houston and Davies 1985). Similar predictions (Winkler 1987) and tests could be made on a large number of other variables affecting parental effort; the initial successes of the method suggest optimism for further developments of this sort.

If one assumes that parental effort is to be optimized over a single breeding attempt with offspring independence as the far horizon of this interval, then parental effort is a natural candidate for application of the technique of dynamic optimization (see e.g. Mangel and Clark 1986; McNamara and Houston 1986). In the context of parental care, the technique would embody changes in costs and benefits as offspring independence is approached, and it would yield predictions sensitive to that change. The approach would require only: (1) that a parent's fitness at the time of offspring independence could be expressed as a function of its own state (e.g. weight) and that of its

offspring and (if needed) its mate, and (2) that equations for the changes in state of the parent, offspring, and mate could be written as consequences of each of a number of possible parental strategies. Although this technique is only now being applied to parental effort (e.g. Mangel and Clark, in press; Adler and Winkler, unpublished), it holds great potential.

In species in which more than one individual provides parental effort, the optimization approach probably needs to be supplemented or replaced with a game-theoretic approach, because the parental expenditures of any given individual are then expected to depend critically on the expenditures of the other individuals providing parental effort. The parents of a brood have a great deal of common interest in the successful rearing of their offspring. But they also conflict in that one parent will often be tempted to force the other into a disproportionate effort. In the extreme case, one parent may desert the brood entirely. The greater the costs of parental effort, the greater the temptation, since a parent that expends little effort in the present attempt is likely to have more effort available for future attempts. As Maynard Smith (1977) pointed out, parental care can be viewed as an evolutionary game played between the two parents, each of which has two strategies, to give care or to abandon the brood. The game-theoretic approach requires that the pay-off to each player in the game can be designated for each of the combinations of possible strategies available to each of the players. In its simplest form the parents can be assumed to be equal in their expected pay-offs, and the relative sizes of pay-offs in the matrix determine the outcome of the parent's game (Fig. 2). Maynard Smith (1977) presented more explicit expressions for the pay-offs expected to the parents, and he concluded that the 'decision' of a parent to provide parental care is determined by the relative importance of the second parent's contribution to offspring survival and the availability of alternative mating opportunities.

Houston and Davies (1985), building on the earlier work of Chase (1980), have taken a game-theoretic approach to understanding patterns of parental effort in the dunnock (*Prunella modularis*), a bird with a variable mating system. They successfully predicted the relative efforts of males and females when breeding in a pair and when breeding in 'trios' composed of two males and one female. Other game-theoretic approaches (e.g. Maynard Smith 1977; Grafen and Sibly 1978; and Vehrencamp and Bradbury 1984) have followed up the initial work by Trivers (1972) on the dependence of mating systems upon patterns of parental effort, and recent game-theoretic work by Caraco and Brown (1986) opens up intriguing possibilities for species that breed 'communally'.

		parent 2	
		care	abandon
parent 1	care	a	b
	abandon	c	d

case	condition	ESS
I	$a > c > b > d$	both care
II	$c > a > b > d$	mixed stable
III	$a > c > d > b$	mixed unstable
IV	$c > a > d > b$	both abandon

Fig. 2. The simplest two-player game that could apply to parental effort. The matrix contains the pay-offs to parent 1 when playing against parent 2. If one assumes that the pay-offs for parent 2 are the same when it is playing against parent 1, then, given the nature of parental care, there are four most likely inequalities among pay-offs. Each of these have different predicted outcomes. In the 'mixed stable' ESS, both individuals could pursue a strategy composed of a mixture of abandoning some breeding attempts and caring for others, or there could be a polymorphism in the population, with the proportion of caring and abandoning individuals converging on the ESS. The ESS in the 'mixed unstable' case is a similar mixture of strategies; however, this mixture is not stable and, depending on initial conditions, the system will move toward pure 'abandon' or pure 'care' (see Maynard Smith 1982 for details).

Case IV includes the prisoner's dilemma (see text, section 5.2.2).

3. MEASURING PARENTAL EFFORT AND ITS FITNESS CONSEQUENCES

Given the broad variety of behaviours that can be construed as parental effort, it should come as no surprise that variation in all of them cannot be measured with a single unit. Thus, the parental effort of an incubating bird could be described in terms of kcal expended in warming the eggs, in terms of time expended on incubation (and thus not available for other activities), or in terms of increased risk of predation from sitting in a single spot for long periods. Similar possibilities for measurement with a variety of units exist for all types of parental effort.

The models we just discussed require that a good measure of effort should be related to offspring and parental survival, and the strength of their relation to both of these provide a natural criterion for choice among them. Many measures of parental effort used in the literature probably do poorly by this criterion. For instance, many studies on the costs of reproduction in birds (e.g. Walsberg 1983; Roby and Ricklefs 1986, Table 9) and mammals (see review in Gittleman and Thompson, in press) have used effort measures based on metabolic rates. While these measures may bear some relation to parental survival, the relationship will be weak if energy expenditure is independent of energy stores. Many rodents, for example, convert ingested food into milk. Consequently, energetic expenditures during lactation could be independent of parental survival if food is readily available. On the other hand, pinnipeds that use stored fat in lactogenesis (Fedak and Anderson 1982; Ortiz *et al.* 1984; Sadleir 1984) have the option of using their blubber for maintenance metabolism during periods of food shortage. Energy expenditure, by itself, is not likely to be a useful parental effort metric.

We believe the best method for determining the relationship between energy expenditure or any other potential measure of effort and parental or offspring survival is through path analysis (Li 1975; Duncan 1975). Path analysis has four virtues that we feel make it preferable to alternative techniques. First, if there are alternative measures of effort, such as parental energy expenditure and food delivered to offspring, path analysis provides an objective method for choice. Effort measures with higher coefficients linking them to components of fitness can be defended as better measures of effort (Fig. 3). Many parental effort measures are time-dependent, and these can be dealt with by treating effort at each of several times or ages as separate variables in the analysis (Fig. 3). Second, if there are variables besides parental effort that also affect parental or offspring survival, these can be included in the analysis and their relative importance weighed. Indeed, path analysis, in conjunction with best-subset regression (e.g. procedure RSQUARE, SAS Institute Inc 1985), provides an objective procedure for refining an initially complex web of potential causative factors to a reduced picture consisting of only those variables that are needed in the best-fitting model. Third, path analysis forces an explicit description of the causal and correlative links between measures of parental effort and other variables. And, fourth, because path coefficients are, in fact, partial regression coefficients, those associated with direct connections to components of fitness, i.e. parental and offspring survival, can be interpreted as selection gradients that measure the strength of directional selection on those characters (Lande and Arnold 1983; Arnold and Wade 1984).

Although path analysis is attractive, several pitfalls, many of which are shared with multiple regression techniques (e.g. Mitchell-Olds and Shaw 1987), must be avoided or overcome. Most troublesome of these is that path analysis assumes linearity in the response of the dependent variable to

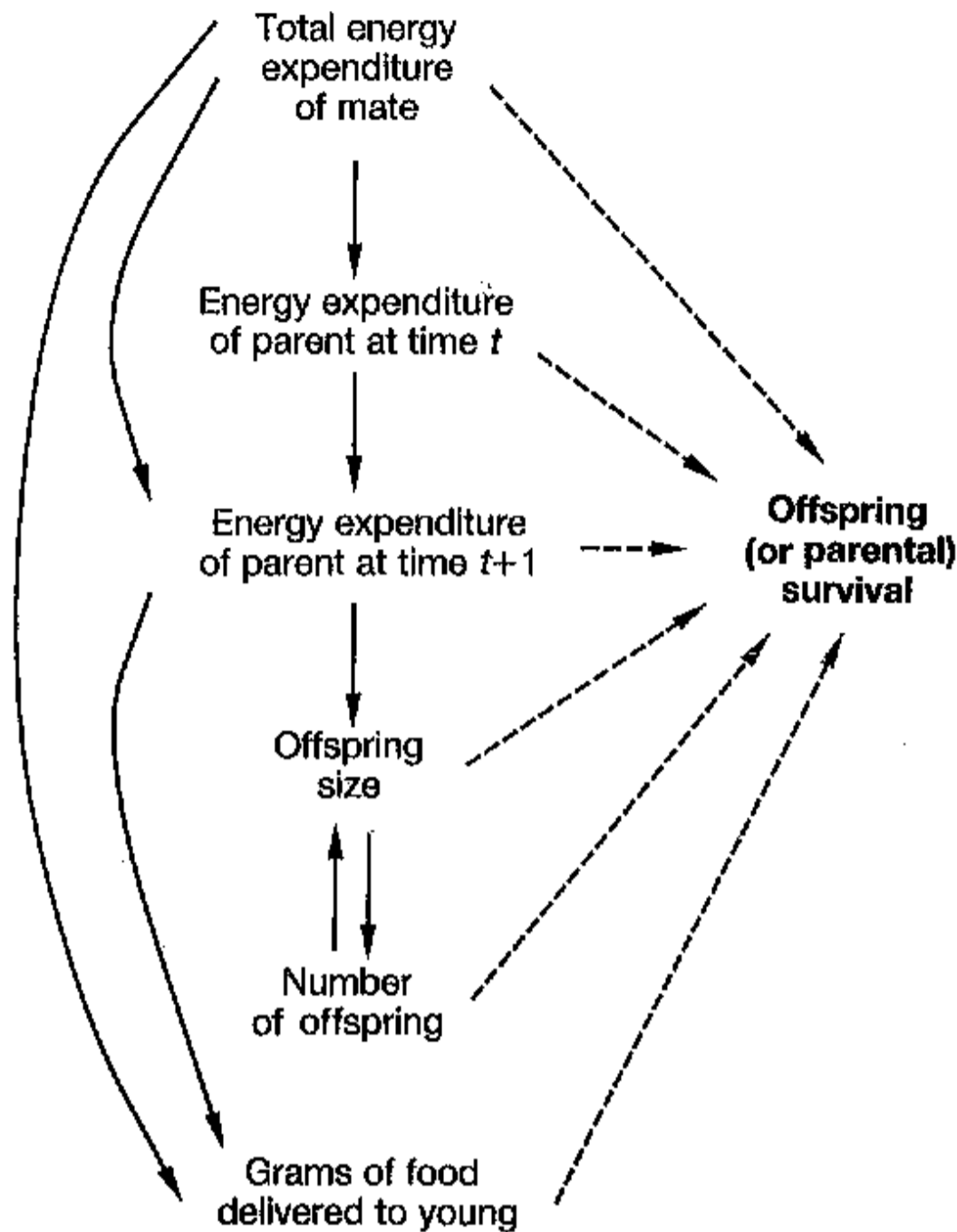


Fig. 3. A hypothetical path diagram relating different measures of parental effort to fitness components. Note that efforts at different times of the breeding season can be treated as separate entities in the analysis. Arrows connecting two measures indicate a causal relationship between them, with the 'cause' at the foot of the arrow and the 'effect' at its head. Also, the coefficients for those paths in dashed lines are selection gradients because they connect directly to a fitness component. See text for details and limitations of the approach.

independent variables. It is a good idea to check for linearity in these relations and do the necessary transformations before proceeding. Also, a path analysis should be viewed not as an inferential tool, but as a descriptive technique to increase the researcher's understanding of the potential causal relations among variables. Especially when path analysis is used to create a simplified picture of causal relations from a more complex precursor, testing of the significance of individual path coefficients is meaningless. To verify any purported causal relationships among variables one must experimentally alter one or two of those variables (such as total energy expenditure of mate—Fig. 3) while holding variation in all others as constant as possible. Such experimental manipulations are also the best way to measure the functional relations between effort and fitness components that many theoretical models require. Experimentally obtained data can then be fitted with non-linear regression techniques. (Because path analysis assumes linearity in causal effects, it is ill-equipped to measure these functional forms.)

An understanding of the quantitative dependence of costs and benefits upon variation in parental effort is crucial to both the optimization and game theoretic approaches: optimizers need to draw parental and offspring survival functions, and game-players need to fill in pay-off matrices. We thus turn now to a consideration of the empirical evidence for the effects of parental effort on offspring and parental survival and reproductive potential in birds and mammals, in particular, whether such costs and benefits exist and how they relate to each other quantitatively.

4. COSTS AND BENEFITS OF PARENTAL EFFORT

We have already pointed out in section 1 that purely phenotypic costs are worthy of investigation; however, even at the phenotypic level, there are problems in the detection of the costs of reproduction. A commonly observed pattern is that parents that produce the most young also have the best survival (e.g. Smith 1981), thus suggesting that parents are paying no cost for increased reproductive output. Such patterns may fail to evidence trade-offs, not because trade-offs between parental survival and offspring production do not exist, but because parental or environmental quality has an overwhelming effect on both. Individuals in such poor condition in nature as to reproduce poorly if at all are the same individuals who would be expected to have poor survival (see also van Noordwijk and de Jong 1986). Partridge and Harvey (1985) pointed out that the only conclusive way to search for trade-offs in the evolution of life histories is to conduct experiments that can break this pattern of covariation between individual condition, survival, and reproductive output. This can usually be done most effectively by conducting experimental manipulations (e.g. altering the number of offspring requiring care) of a set of individuals that are of equal condition or of experimental groups with the same distributions of condition among their members.

If theory is to be applied to the question of the determination of quantitative variation in parental effort, it is necessary that such variation affects offspring survival and the survival or reproductive potential of parents. In the following pages we will present such evidence for each of the principal parental care behaviours in the order in which they are generally expressed in the course of a breeding attempt. In reviewing this literature, we have been surprised to find how few quantitative data are available. We have also been impressed by the tremendous variety in kinds and extent of parental effort; for each behaviour we first provide a brief overview of this range of natural histories for both birds and mammals to highlight the potential for experimental studies that this variation presents.

4.1 Nest- and burrow-building

Nest-building is nearly ubiquitous in birds (see Collias and Collias 1984, especially their Appendix 1). The only species lacking any sort of nest are the brood-parasitic species and some penguins (*Aptenodytes*) that incubate their eggs upon their feet. The 'nest' in some groups (e.g. Charadriiformes) is often little more than a 'scrape' lined with a few stones, a bare branch (e.g. fairy tern, *Gygis*), or rock ledge (e.g. guillemots, *Uria*). In contrast, the most elaborate nests are built by some passerines (e.g. social weavers and icterids; Collias and Collias 1984), some storks and their relatives (e.g. hammerkop, *Scopus*), and the megapodes (Megapodiidae). As mentioned in Section 1, *Megapodius freycinet*, a member of the latter group, displays what must surely be the most diverse nest-building behaviour in any species of bird.

Birds use their nests while incubating and feeding offspring. Since the former function is carried out by the uterus in eutherians, many precocial mammals (e.g. some hystricomorph rodents, many ungulates; Eisenberg 1981) have eliminated the need for any nest or burrow whatsoever. However, burrow excavation is highly developed in monotremes, some marsupials, and many rodents. For example, the burrows of an individual *Nannospalax ehrenbergi*, an old world mole-rat, can reach up to 350 m in length (Corbet 1984), and a single Cape dune mole-rat (*Georhynchus capensis*) can excavate up to 500 kg of earth per month (Jarvis 1971). Many other groups build nests, either in sheltered surface areas or in trees and caves. No nest is larger than that of the beaver (*Castor*), with some lodges getting as large as 12 m in diameter and 2 m high and the associated dams ranging up to 660 m in length and 4 m in height (Warren 1927). Although beavers are monogamous, the larger of these structures are built by family groups, sometimes over several generations (Tevis 1950). All these burrows and structures are also used for non-reproductive functions, but variation in their extent must surely affect offspring and/or parental survival.

4.1.1 Effects on parents

Surprisingly little is known about how variation in nest construction affects parental survival or fecundity. Weeks (1978) studied the eastern phoebe (*Sayornis phoebe*), a species that builds its nest of mud. Those phoebes that built new nests or that built nests hanging from an overhang laid smaller clutches than those that re-used nests or built nests on a ledge. Other estimates of the costs of nest-building (e.g. Collias and Collias 1984; Withers 1977) have measured these costs in terms of metabolic expenditure, units which at present cannot be related to parental survival or fecundity. Relatively little is known about the costs of burrow or nest construction in mammals, though metabolic studies (e.g. Vleck 1979, 1981; Du Toit *et al.* 1985) of some rodents suggest that the costs may be very high. Such costs may have influenced the evolution of 'eusociality' in at least one species

(naked mole-rats, *Heterocephalus glaber*; Jarvis 1981; see also Peck and Feldman 1986).

4.1.2 *Effects on offspring*

There is a great deal of information on the effect of nest location on the survival of eggs and young birds (e.g. Burger and Shishler 1978; Page *et al.* 1985), but very little on the effect of nest quality *per se* on egg hatching and offspring survival. Collias and Collias (1984, p. 103) mention experiments in which removal or reduction of the nest lining in captive village weavers (*Ploceus cucullatus*) increased the percentage of time the female spent incubating, suggesting that reducing nest lining reduced the insulative properties of the nest. In mammals, we know of no study that directly relates offspring survival to variation in nest construction, but the studies by King (1963) on *Peromyscus* and Lynch (1987) on *Mus* that demonstrate a north—south cline in nest size indicate that such selection has probably at least occurred in the past.

4.2 Incubation, gestation, and brooding

Parent birds usually take responsibility for the incubation of their eggs, with the conspicuous exception of brood-parasitic species, which rely on incubation by their hosts. Incubation is essential for the normal development of all bird embryos with the exception of those laid by megapodes, in which the male's monitoring of the temperature of the incubation mound ensures the maintenance of appropriate temperatures in lieu of incubation (Frith 1985).

The nearest approach to the avian mode of reproduction among mammals is provided by the platypus (*Ornithorhynchus anatinus*), the only mammal that lays eggs in a nest. (Echidnas, in the Tachyglossidae, lay eggs in a marsupial-like pouch; Augee 1984.) Gestation is obviously a parental duty in which males cannot share, and, even in the platypus, the female incubates. This sexual stereotypy in care of the embryo contrasts with the situation in birds, in which males often take a large role in incubation, even doing all the sitting in some species (e.g. Kendeigh 1952).

The potential period over which any cost of embryo care must be incurred varies enormously between species. Gestation ranges from 8 days for the eastern quoll (*Dasyurus viverrinus*) to 660 days for elephants (*Loxodonta africana*; Eisenberg 1981). Note that, with the exception of the larger kangaroos, gestation length in marsupials is not substantially smaller than in comparably sized eutherians (Thompson 1987). However, marsupials do have smaller, more altricial young at birth (Russell 1982). Incubation periods are also quite variable, ranging from 11 days in the smallest passerines to about 80 days in some of the largest albatrosses (Tullett 1985).

4.2.1 *Effects on parents*

The costs of incubation in birds have usually been measured in metabolic terms, and there is considerable debate over the size of these costs (e.g. Walsberg 1983). In mammals, the energetic cost of gestation is usually considered much smaller than that of lactation (Millar 1977; Randolph *et al.* 1977; Mattingly and McClure 1982); however, this generalization has been called into question recently (Speakman and Racey 1987; Gittleman and Thompson, in press).

There are more direct indications of the cost of embryo care in effects on parental survival and reproductive capacity. The mortality cost of incubation can be high in at least one goose species. Female snow geese (*Chen caerulescens*) incubate their eggs continuously for approximately 23 days, during which time they limit their feeding to the small bits of vegetation that they can graze from the immediate vicinity of the nest while sitting. Females can lose over half their body weight during incubation, and those that begin incubation without adequate reserves are known to abandon their nest or die on the nest from starvation (Ankney and MacInnes 1978). In other precocial species (e.g. Hanson 1962; Anderson 1972; Korschgen 1977) considerable weight can be lost during incubation, but the costs of incubation are likely to be diminished considerably, since parents often share incubation duties and/or intersperse incubation duties with feeding.

Female mammals often have a variety of behavioural and physiological mechanisms that prevent any cost of reproduction from unduly influencing parental survival or fecundity (Galef 1983). For example, women athletes become amenorrhoeic when their body fat falls below about 20 per cent (Frisch 1985; Prentice and Whitehead 1987); this is presumably an adaptation to prevent pregnancy when body reserves are too low to support gestation. Such protective mechanisms will tend to obscure any costs of reproduction, and their presence suggests the existence of high costs of reproduction and strong past selection for mechanisms to avoid paying these costs.

Multiple gestations appear to cause the uterus to become less able to carry later litters successfully to term. Although litter size usually increases with the first and second births in many rodents, this is followed by a plateau period and an eventual decline (Biggers *et al.* 1962). Selection for increased embryo survival in mice in conjunction with embryo transplants has demonstrated that this is a female, not embryo, trait (Bradford 1979). Furthermore, litter size decreases more rapidly with parity in Mongolian gerbils that have had one uterine horn removed than in intact females (Norris and Adams 1982), again suggesting that early reproduction impairs future reproduction. Infant mortality in humans increases with increasing number of reproductive episodes and decreasing interbirth interval (e.g. Hibbs 1916; Shapiro *et al.* 1968; James 1970; Vavra and Querec 1973).

Although little evidence yet demonstrates that gestation or incubation diverts sufficient energy reserves away from storage or maintenance to lower future parental survival, these reproductive stages have been associated with increased risk of predation for both birds and mammals. Incubating birds are often literally 'sitting ducks' for nest predators (e.g. Southern *et al.* 1982; Sargeant *et al.* 1984). Pregnant swamp deer (*Cervus duvauceli*) are most prone to tiger (*Panthera tigris*) predation (Schaller 1967), whereas female wildebeest (*Connochaetes gnou*) suffer greatest mortality from hyaenas (*Crocuta crocuta*) during and shortly after pregnancy (Kruuk 1972).

4.2.2 Effects on offspring

Birth weight and newborn survival rates are inversely related to litter size in mammals (e.g. Machin and Page 1973; Cornu and Cognie 1985; König and Markl 1987), but it is difficult to study the means by which these trade-offs occur in the womb. By contrast, the effects of quantitative variation in incubation effort on offspring survival are relatively easy to study in birds. Both the mean incubation temperature as well as its variation directly influence egg hatching success (e.g. Lundy 1969; Romanoff and Romanoff 1972; Hunter *et al.* 1976). Monitoring egg temperature as a function of parental attendance (e.g. Drent 1970, 1973) should allow the measurement of the functional dependence of embryo survival on parental effort.

4.3 Feeding offspring

Among birds, post-hatching parental care is completely lacking only in the brood parasites and megapodes. In many precocial birds (*sensu* Winkler and Walters 1983), parental care is limited to tending the young (e.g. Safriel 1975; Lazarus and Inglis 1978; Ashkenazie and Safriel 1979; Maxson and Oring 1980; Pellis and Pellis 1982; Walters 1982, 1984), whereas in others the parents feed the young for a period ranging from a very small proportion (e.g. grebes, rails), through a quite large proportion (e.g. alcids), to essentially all (e.g. gulls) of the offspring's developmental period. In all altricial species but the brood parasites, feeding of young is the most conspicuous component of parental care. Parents of many passerines undertake in excess of 1000 feeding trips to their young per day (e.g. Royama 1966; Nur 1984a), and this behaviour would appear for many species to be the most energy-demanding phase of parental care.

Only in a few groups of birds (all pigeons and doves, a flamingo, and a penguin) is there a transfer of food resembling lactation (Jones 1985). Lactation duration is as variable as feeding duration is in birds. At one extreme, hooded seals (*Cystophora cristata*) are capable of weaning after 4 days of nursing, in which time they double in mass (Bowen *et al.* 1986). By contrast, vampire bats (*Desmodus rotundus*) require milk until they are more than 7 months of age, even though each infant weighs 16 per cent of its

mother's mass at birth (Schmidt and Manske 1973). Marsupials are distinctive in their habit of nursing two offspring of strikingly different age on two different mammary glands, shunting different quantities of milk of different composition to each (Short 1985). No eutherians appear to be so flexible, but they do vary enormously in the periodicity of lactation. Intervals between lactation episodes last an average of 7 days in northern fur seals (*Callorhinus ursinus*) in between 1–3 day nursing bouts (Gentry and Holt 1986). Similarly, 10-day old rabbits only nurse once each day for an average of 3 minutes and can ingest 25 per cent of their body weight at each feeding (Zarrow *et al.* 1965; Lincoln 1974). In contrast, young rats nurse 20 or more times per day, stay attached to the nipple a total of about 18 hours/day, and a 10-day old pup receives only about 0.2 per cent of its body weight in milk during one nursing bout (Lincoln *et al.* 1973; Lincoln 1983).

4.3.1 *Effects on parents*

A few studies have shown that feeding offspring has a survival cost to parents. Nur (1984*b*) manipulated broods of blue tits (*Parus caeruleus*) and found that parents with increased brood sizes lost more weight during the nesting season and had lower return rates to the same breeding population in the following season. Other authors have found decreases in weight during the chick-rearing period, though some (Freed 1981; Norberg 1981) have suggested that weight loss *per se* might be an adaptation to increase the efficiency of parental foraging flights to and from the hungry brood. This interpretation does not require, however, that weight reductions are made without any potential cost to parental survival; it merely requires that the gains from potential offspring production outweigh slightly increased parental costs. In mammals, similar evidence of costs exists. Female harp seals (*Phoca groenlandica*) that begin breeding in poor condition appear to deplete their energy reserves entirely by the end of lactation (Stewart 1986). Female mice that regularly reproduce die sooner than comparably aged virgin control mice (Muhlbock 1959), and Clutton-Brock *et al.* (1982) have documented an increase in the rate of mortality as a function of age for those red deer hinds that lactate versus those that do not (Fig. 4). Studies on mice have demonstrated that timing of implantation (e.g. McLaren and Ritchie 1963) and gestation outcome (Eisen and Saxton 1984; König and Markl 1987) are negatively affected by concurrent lactation and by the frequency and number of prior pregnancies. Lengthening of the gestation period during lactation is common in many rodents, bears, seals, roe deer, bats, armadillos, wallabies, kangaroos, and some mustelids (Short 1985) and appears to reduce the energetic demands on a female that is concurrently pregnant and lactating. In some species, embryonic diapause is under photoperiodic control (Follett 1985), and these raise the prospect of experimental manipulation of reproductive costs by altering the amount of lactation/gestation

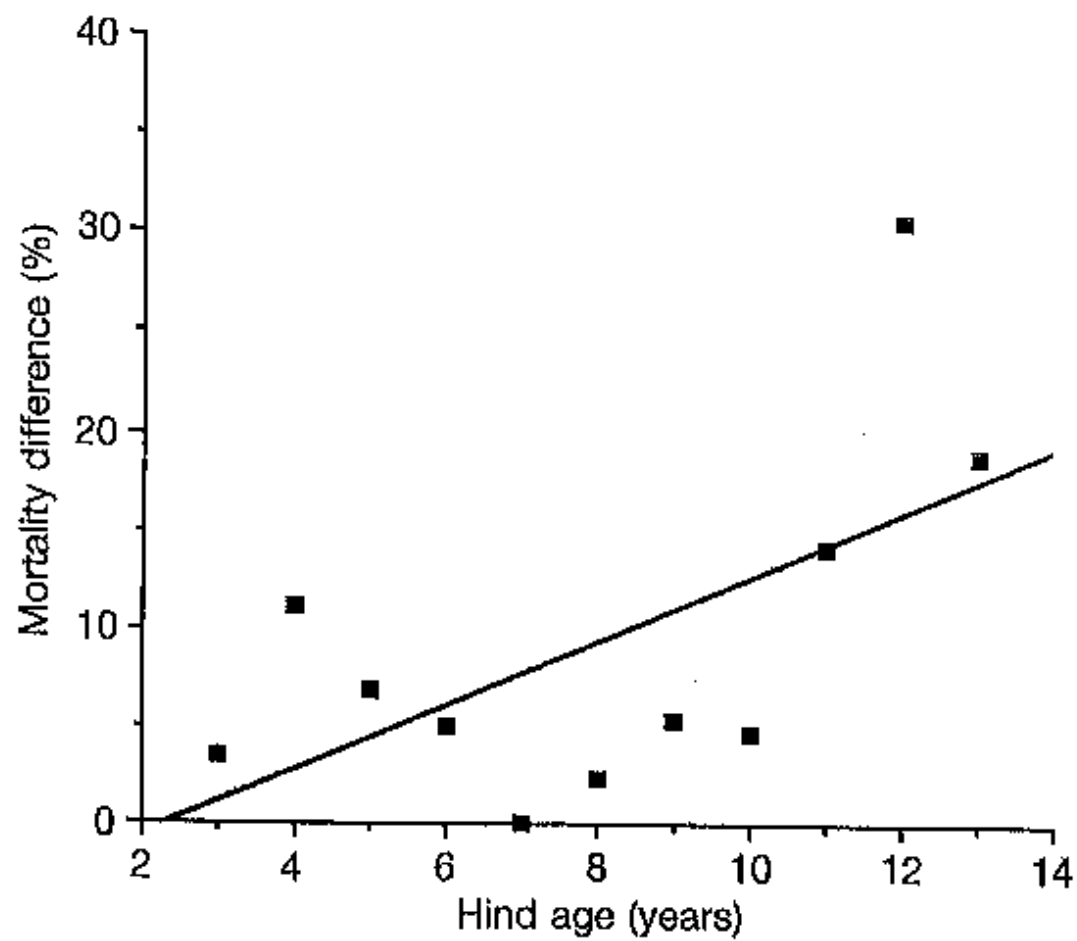


Fig. 4. The difference in mortality rate between red deer hinds that lactated in the previous season and those that did not for hinds of different ages. Lactating hinds have consistently higher mortality, and the difference tends to become exaggerated in older females. The solid line is a least-squares regression fit to the points ($R^2=0.40$; $p=0.03$). After Clutton-Brock *et al.* (1982, Fig. 4.20).

overlap through the experimental alteration of photoperiods in the laboratory.

Feeding offspring can also depress subsequent fecundity in both birds and mammals. Several authors (e.g. Røskaft 1985; Tinbergen 1987; Nur 1988) have demonstrated an effect of avian brood size (and presumably feeding effort) on subsequent reproductive output and timing of breeding, either in the same breeding season or in the following year. Similarly, red deer hinds that have nursed young in the previous year show significantly reduced fecundity compared to those that have not (Clutton-Brock *et al.* 1982). In mammals, undernourishment of the nursing parent decreases the quantity and quality of milk that a female can produce per unit time (e.g. Crnic and Chase 1978; Mattingly and McClure 1985). These observations, taken together with evidence for protective mechanisms such as brood-reduction, including in some cases cannibalism of young (e.g. Fuchs 1982), suggest that feeding offspring can be very costly.

If the heightened activity levels of birds feeding offspring lead to elevated visibility to predators or to decreased vigilance toward predators, then the risk of predation could be another important cost of variation in feeding effort (e.g. Skutch 1949). Orians (1973) observed that tropically nesting red-winged blackbirds (*Agelaius phoeniceus*) fed their young less frequently than did their temperate conspecifics; however, he attributed this more to depressed food availability at the tropical site rather than to an antipredator

adaptation, since, like their relatives to the north, females arrived at and left the nest conspicuously and often gave calls while doing so.

4.3.2 *Effects on offspring*

The effects of variation in parental feeding effort on offspring survival have not been measured explicitly in birds, but it seems reasonable to assume that there is a strong link between chick fledging success and parental feeding frequency and load size (e.g. Nur 1984*a*). In mammals, mice weaned from larger litters are usually smaller in size. These smaller mice exhibit compensatory growth after weaning but still have smaller litters subsequently than mice that were well nourished during development (Machin and Page 1973). Rats weaned at low weights also have reduced fecundity as adults, but they do not exhibit compensatory growth (Smart 1983). Insofar as reduced weaning weight affects an animal's ability to withstand environmental stress, these animals should presumably also have reduced survival. Evidence from birds (e.g. Perrins 1963; Perrins *et al.* 1973; Jarvis 1974; McGowan 1987) suggests that this is often a safe assumption.

In considering the effectiveness of parental feeding on offspring survival, it is important to distinguish between offspring response to the mean rate of provision versus its variance. For example, it appears as though the chicks of swifts and petrels (e.g. Lack 1956; Ricklefs *et al.* 1985) are particularly resistant to long periods without feedings. Pre- and post-hatch growth rates are probably parts of the same related syndrome of traits (but see Case 1978), and one obvious way for offspring to cope with variance in provisioning rate is to reduce overall metabolic rate and the rate of resource demand for growth. This would have the effect of reducing the impact of temporary periods of no parental care. But such a strategy also presumably reduces the ability of the offspring to capitalize with rapid growth on large amounts of food when they are supplied. The costs and benefits of these various growth strategies (cf. Case 1978; Ricklefs 1979, 1984; Sibly *et al.* 1985) must be better understood before the implications of variation in parental feeding effort can be understood completely.

4.4 **Defence of offspring**

When confronted by a potential predator to their young, most small birds and many social mammals respond with 'alarm calls' (e.g. Sherman 1977; Eisenberg and Kleiman 1977; Curio and Regelman 1985; Cheney and Wrangham 1986) but often little else. In larger species, defence against predators can be quite intense (see e.g. Kortlandt 1965; Byrne and Byrne 1988), with repeated dives or rushes at the predator, sometimes involving actual bodily contact. In some large mammals (e.g. buffalo, musk-ox, elephants), adults defend offspring by interposing themselves between the offspring and the predator (Tener 1965; Sikes 1971; Eisenberg and Lockhart

1972; Kruuk 1975). In many species of all sizes, however, defence against predators appears to be entirely left to subterfuge. The size-dependence of predator defence is nicely illustrated in waterfowl and shorebirds (Gochfeld 1984). In both groups, smaller species rely on escaping detection by predators through cryptic coloration and behaviour, sometimes supplemented with distraction displays, whereas larger species resort to active defence.

4.4.1 *Effects on parents*

This variability in defence behaviour within closely related groups at least suggests that there is variation in the costs and benefits of such behaviour. It seems reasonable to assume that parental defence, especially in its extreme forms of diving or rushing at predators, is a risky endeavour, and the limited information available (Myers 1978; Gochfeld 1984; Cheney and Wrangham 1986) indicates that this is indeed the case. Even less risky behaviours, such as mere alarm-calling, carry an elevated risk of predation for both mammals (e.g. Sherman 1977, 1980) and birds (short review in Curio and Regelman 1985). The observation that response intensity and quality of calls seem to vary in response to the risk represented by the predator (e.g. Patterson *et al.* 1980; East 1981a; Curio *et al.* 1983; Sherman 1985; Cheney and Wrangham 1986) suggests that risk to the defender is significant enough to have selected for adaptive adjustment of response. Sherman (1985) provides rare quantitative data on costs to callers. When attacked by raptors, Belding's ground squirrels (*Spermophilus beldingi*) that alarm-called were captured 2 per cent of the time, whereas those not calling were killed 28 per cent of the time. This apparent advantage of alarm-calling against aerial predators is countered by a disadvantage against terrestrial predators, which took 8 per cent of callers and only 4 per cent of non-callers.

In some bird species, there is evidence of a trade-off between time spent guarding young versus time spent in parental feeding, opening the way for a direct metabolic cost to the parent (e.g. Pellis and Pellis 1982; Walters 1982, 1984). Aggressive parental defence may also have a direct metabolic cost that is biologically significant, but we know of no data bearing on this possibility. In any event, it is difficult to imagine that the costs of the alarm calls that comprise the defence behaviour of many passerines and mammals are primarily metabolic.

4.4.2 *Effects on offspring*

The literature contains many reports of potential offspring predators that are successfully deterred or distracted by defence behaviour (e.g. Kruuk 1964; Wiklund 1982; Curio and Regelman 1985). Busse (1976) contributed some hard-to-find quantitative data on the efficacy of defence by male colobus monkeys (*Colobus badius*) against attacks by chimpanzees (*Pan troglodytes*): 36 per cent of unsuccessful attacks were accompanied by male defence, whereas only 6 per cent of their successful attacks were accompanied by male

defence. Some of the classic cases of avian offspring defence are of species that succumb to great predation at night, when active defence is not even attempted (e.g. Kruuk 1964).

5. PARENTAL CARE WITH CONFLICT

Evidence of the effects of variation in parental effort on the survival of parents and offspring helps support the application of optimization models to parental care. As mentioned in section 2, the same information on costs and benefits of parental effort can be used to fill in the pay-off matrix in a game-theoretic approach. This approach further assumes that 'players' in the parental care 'game' are indeed in conflict. We here review the evidence available to justify this assumption and try to highlight areas where further research appears especially needed.

5.1 Parent-offspring conflict

Perhaps the most fundamental source of conflict implicit in parental care is that between the genetic interests of the parent and its offspring. Trivers (1974) first explicitly modelled this conflict, pointing out that the genetic non-identity of parent and offspring in a sexual species leads to a different valuation of the costs of parental effort. As a consequence, offspring should be selected to demand more parental effort than the parents are prepared to expend. This initial insight has been developed through a variety of theoretical approaches and embellishments (e.g. Parker and McNair 1978, 1979; McNair and Parker 1979; Parker 1984; O'Connor 1978; Stamps *et al.* 1978; Bull 1985) and has proven robust to a variety of genetic and ecologic assumptions.

The parent-offspring conflict models (especially O'Connor 1978) make interesting predictions regarding the apportionment of food within a brood or litter. Individual offspring usually will be expected to demand more investment than the parent is willing to expend on any individual offspring, while the parent is expected to withhold food from the least needy and to preferentially feed those offspring that are most in need, since such a strategy would maximize offspring production for the parent. (If resources are extremely limiting, similar conflicts are to be expected over the timing and extent of brood/litter reduction.) Surprisingly, there is very little evidence that parents preferentially feed offspring in greater need of food. In many, if not most, bird species, food appears to be allocated according to the strength of the chicks' begging (e.g. Bengtsson and Rydén 1983; Muller and Smith 1978), and it appears as though the principal determinant of food receipt is the success of the chick in within-brood dominance interactions (e.g. Mock 1984). Thus, parent birds appear generally to be allowing parent-offspring

conflict to be resolved entirely by the offspring, apparently to the offspring's genetic advantage. The lone exception to this generalization is a recent study on captive budgerigars (*Melopsittacus undulatus*). In this species, Stamps *et al.* (1985) found that there was a strong negative correlation between the relative weight of a chick and its probability of being fed by its mother. By contrast, males feeding chicks displayed no such preferential feeding. This is an intriguing study, because it indicates that parental discernment is possible and that it may be subject to selective modification according to the ecological and social environment of the parent.

Evidence from the animal breeding literature (e.g. van Tienhoven 1968) indicates that the genotype of the offspring, not the parent, has the strongest influence on gestation duration. During lactation, it appears as though parent-offspring conflict is sometimes 'controlled' by the offspring and sometimes by the parent. Grey seal pups (*Halichoerus grypus*) apparently have milk available to them on demand (Fogden 1971; Lincoln 1983), while rabbits appear insensitive to the nutritional requirements of their young and instead regulate their milk availability by an internal clock that is independent of offspring demand (Findlay 1968; Findlay and Roth 1970; Lincoln 1983).

A problem with empirical studies searching for evidence of parent-offspring conflict is that conflict may not be expected during the phases of reproduction that are amenable to study. It may be that the only offspring that have substantial chances of postcare survival are those that are aggressive in intrabrood or intralitter dominance interactions. Thus, parent and offspring usually may not differ in their views of optimal allocation. Furthermore, parent-offspring conflict may become difficult to detect or even disappear when environmental variation is superimposed on the system (Bull 1985). Alternatively, parent-offspring conflict may still be expected, but it may be focused, for example, on conflict over the timing of termination of parental care, rather than on the apportionment of care. Several studies of birds (e.g. Davies 1976, 1978; East 1981*b*; Burger 1981) and mammals (e.g. Barash 1974; Berger 1979; Altmann 1980) have documented the increase in parental 'meanness' as the young approach independence, although some (e.g. Altmann 1980) still question that these conflicts are the result of genetic conflicts of interest.

Another interesting feature of the parent-offspring conflict models is that they can be modified according to the coefficient of relatedness between the adult providing care and the offspring. While most models have assumed that this relatedness is 0.5, the possibility exists for experimental or comparative work, especially in species with alloparents (see section 5.2), where this relatedness is different for different providers of care, leading to interesting predictions subject to experimental test. As the relatedness between care-provider and offspring decreases, conflict is expected to intensify, since the

optimal level of effort demanded by offspring will increase as its relatedness to the provider decreases.

5.2 Conflict between providers of care

Another potential area of conflict is between adults over how much parental effort to expend. In most birds and mammals, it is tempting to make a distinction between those adults whose gametes combine to form the offspring (i.e. parents *sensu strictu*) and other adults, related or not, that provide care (i.e. 'alloparents'). This distinction is difficult to make on the basis of parental care behaviour, since many 'monogamous' birds provide care to young that are the genetic offspring of others (e.g. Gowaty and Karlin 1984; Westneat 1987; Sherman and Morton 1988). Extra-pair copulations and/or egg-dumping have been discovered in virtually every 'monogamous' bird that has been investigated. While egg-dumping is not possible for most mammals, multiple mating by females can lead to multiple paternity within litters (e.g. Hanken and Sherman 1981). Unfortunately, no data appear to be available to determine how often males in groups such as the 'monogamous' canids, felids, and primates care for young that are not their offspring. Although it is clear that the 'parents' that are observed in the field are sometimes not parents in the strict sense, we will continue to use 'parents' whenever, on behavioural grounds, the probability of genetic parentage is high, reserving 'alloparents' for situations where this condition is not met.

5.2.1 *Who provides care?*

The game-theoretic work of Maynard Smith (1977), Grafen and Sibly (1978), and Vehrencamp and Bradbury (1984) has led to a tradition of viewing patterns of parental effort as constraints on mating systems. Under this view, males will yield to the temptation of desertion when they are 'emancipated' by the ability of females to raise offspring unassisted. Thus, male emancipation leads to polygyny (Trivers 1972; Emlen and Oring 1977), and the lack of such emancipation can lead to or enforce monogamy (e.g. Kleiman 1977; Wittenberger and Tilson 1980). Experimental tests of this hypothesis, through the experimental removal of male birds in monogamous pairs, have yielded mixed results (e.g. Hannon 1984; Martin *et al.* 1985; Martin and Cooke 1987; Wolf *et al.* 1988, esp. Table VI); however, the traditional interpretation remains strong.

As popular as this view has become, it should be pointed out that an alternative view is just as feasible, namely that a mating system could serve as a constraint on patterns of parental effort. May and Rubenstein (1985, Fig. 1.16) provide an example of this alternative view by showing that monogamous primates have larger neonates for their size than do their polygynous relatives. They interpret this difference by proposing that monogamous

females invest more in offspring because their mates will compensate for this disproportionate investment by carrying or provisioning the young or caring for the mother after parturition. Thus, parental effort is seen as a response to the mating system, not vice versa. Although Harvey and Clutton-Brock (1985, p. 574) have criticized May and Rubenstein's data, it seems premature to dismiss their interpretation as an impossibility. Neither of these views possesses priority, as parental effort and mating systems have almost certainly evolved together as joint responses to a combination of selective factors.

5.2.2 *How much care should be provided?*

The presence of conflict over who is to provide care raises the possibility that any joint effort by parents can be viewed either as co-operation (e.g. Chase 1980) or reciprocal altruism (Trivers 1971). In a biparental species, pay-offs to two parents raising a brood are sometimes likely to correspond to those of the prisoner's dilemma (i.e. Case IV, Fig. 2). In such situations, 'tit-for-tat' or other similar strategies can be evolutionarily stable solutions that yield co-operation if interactions between parental players are iterated an indefinite number of times (e.g. Axelrod and Hamilton 1981; Boyd 1988). Because most breeding seasons have a fairly predictable end-horizon, the assumption of indefinitely repeated interactions is likely not to be met, and theoretical development of alternative 'co-operative' solutions, if any, in this situation should be pursued. Surprisingly, we know of no attempts to test these ideas using parental effort, even though reciprocal altruism has been tenuously invoked to explain a variety of avian (Koenig 1988) and mammalian (Wilkinson 1988) examples of apparent altruism. One especially important empirical question needs to be addressed: what is the relative frequency in nature of each of the possible pay-off inequalities (Fig. 2)?

We have so far limited our discussion of conflict to the relatively simple situation of biparental care. Communally breeding species provide many extensions of the biparental theme, and these often complicated social systems offer many interesting theoretical questions amenable to the game-theoretic approach (e.g. Caraco and Brown 1986). They also provide exciting possibilities for experimental testing of models on conflict between providers of care.

6. CONCLUSION

Anyone who delves into the literature of parental care in birds and mammals soon appreciates that there is a tremendous amount of information available. Of this, a relatively small subset deals with quantitative variation in parental effort. Of this subset, an even smaller portion consists of quantitative observations of parental effort guided toward an understanding of the effects

of its variation on offspring and parental survival and reproduction. In this review, we have attempted to summarize such information as is available and to suggest theoretical and empirical tools available to explore these issues.

The tremendous variety of behaviours available for experimental manipulation present a compelling research opportunity. Experiments that measure the effects of quantitative variation in parental effort on parental survival and reproductive potential and the survival of offspring to reproductive age would allow one to apply any of the modelling approaches suggested in this review. Further, in providing measures of the selection gradients (i.e. path coefficients) acting on behavioural variation, such work would provide a valuable phenotype-based complement to the genotype-based approach used by many in studying the evolution of life histories.

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REFERENCES

- Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press, Cambridge, Massachusetts.
- Anderson, W. L. (1972). Dynamics of condition parameters and organ measurements in pheasants. *Bull. Ill. Nat. Hist. Surv.* **30**, 455–97.
- Andersson, M., Wiklund, C. G., and Rundgren, H. (1980). Parental defence of offspring: A model and an example. *Anim. Behav.* **28**, 536–42.
- Ankney, C. D. and MacInnes, C. D. (1978). Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* **95**, 459–71.
- Arnold, S. J. and Wade, M. J. (1984). On the measurement of natural and sexual selection: theory. *Evolution* **38**, 709–19.
- Ashkenazie, S. and Safriel, U. N. (1979). Time–energy budget of the semipalmated sandpiper (*Calidris pusilla*) at Barrow, Alaska. *Ecology* **60**, 783–99.
- Augee, M. L. (1984). Monotremes. In *The encyclopedia of mammals*, vol. 2 (ed. D. W. MacDonald), pp. 818–22. George Allen and Unwin, London.
- Axelrod, R. and Hamilton, W. D. (1981). The evolution of cooperation. *Science* **211**, 1390–6.

- Barash, D. P. (1974). Mother-infant relations in captive woodchucks (*Marmota monax*). *Anim. Behav.* **22**, 446–8.
- (1975). Evolutionary aspects of parental behavior of the alpine accentor. *Wilson Bull.* **87**, 367–73.
- Bengtsson, H. and Rydén, O. (1983). Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. *Behav. Ecol. Sociobiol.* **12**, 243–51.
- Berger, J. (1979). Weaning conflict in desert and mountain bighorn sheep *Ovis canadensis*, an ecological interpretation. *Z. Tierpsychol.* **50**, 188–200.
- Biggers, J. D., Finn, C. A., and McLaren, A. (1962). Long-term reproductive performance of female mice. II. Variation of litter size with parity. *J. Reprod. Fert.* **3**, 313–30.
- Bowen, W. D., Oftedal, O. T., and Boness, D. J. (1986). Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Can. J. Zool.* **63**, 2841–6.
- Boyd, R. (1988). Is the repeated Prisoner's Dilemma a good model of reciprocal altruism? *Ethol. Sociobiol.* **9**, 211–22.
- Bradford, G. E. (1979). Genetic variation in prenatal survival and litter size. *J. anim. Sci.* **49** (Suppl. II), 66–74.
- Bull, J. J. (1985). Models of parent-offspring conflict: effect of environmental variance. *Heredity* **55**, 1–8.
- Burger, J. (1981). On becoming independent in herring gulls—parent-young conflict. *Am. Nat.* **117**, 444–56.
- and Shishler, J. (1978). Nest site selection and competitive interactions of herring and laughing gulls in New Jersey. *Auk* **95**, 252–66.
- Busse, C. D. (1976). Chimpanzee predation as a possible selective factor in the evolution of red colobus monkey social organization. *Evolution* **31**, 907–11.
- Byrne, R. W. and Byrne, J. M. (1988). Leopard killers of Mahale. *Natural Hist.* **97**, 22–6.
- Caraco, T. and Brown, J. L. (1986). A game between communal breeders: when is food-sharing stable? *J. theor. Biol.* **118**, 379–94.
- Case, T. J. (1978). On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quart. Rev. Biol.* **53**, 243–82.
- Chase, I. D. (1980). Cooperative and noncooperative behavior in animals. *Am. Nat.* **115**, 827–57.
- Cheney, D. L. and Wrangham, R. W. (1986). Predation. In *Primate societies* (ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker), pp. 227–39. University of Chicago Press, Chicago.
- Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red deer; behavior and ecology of two sexes*. University of Chicago Press, Chicago.
- Collias, N. E. and Collias, E. C. (1984). *Nest building and bird behavior*. Princeton University Press, Princeton, USA.
- Corbet, G. B. (1984). Other old world rats and mice. In *The encyclopaedia of mammals, Vol. 2* (ed. D. MacDonald), pp. 666–71. George Allen and Unwin, London.
- Cornu, C. and Cognie, Y. (1985). The utilization of Romanov sheep in a system of integrated husbandry. In *Genetics of reproduction in sheep* (ed. R. B. Land and D. W. Robinson), pp. 383–90. Butterworths, London.

- Crnic, L. S. and Chase, H. P. (1978). Models of infantile undernutrition in rats: effects on milk. *J. Nutr.* **108**, 1755–60.
- Curio, E. and Regelman, K. (1985). The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Z. Tierpsychol.* **69**, 3–18.
- , Klump, G., and Regelman, K. (1983). An anti-predator response in the great tit (*Parus major*): is it tuned to predator risk? *Oecologia* **60**, 83–8.
- Davies, N. B. (1976). Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). *Behaviour* **59**, 280–95.
- (1978). Parental meanness and offspring independence: an experiment with hand-reared great tits *Parus major*. *Ibis* **120**, 509–14.
- Drent, R. H. (1970). Functional aspects of incubation in the herring gull. *Behav. Suppl.* **XVII**, 1–132.
- (1973). The natural history of incubation. In *Breeding biology of birds* (ed. D. S. Farner), pp. 262–310. National Academy of Sciences, Washington, DC.
- Duncan, O. D. (1975). *Introduction to structural equation models*. Academic Press, New York.
- Du Toit, J. T., Jarvis, J. U. M., and Louw, G. N. (1985). Nutrition and burrowing energetics of the cape mole-rat *Georhynchus capensis*. *Oecologia* **66**, 81–7.
- East, M. (1981a). Alarm calling and parental investment in the robin *Erithacus rubecula*. *Ibis* **123**, 223–30.
- (1981b). Aspects of courtship and parental care of the European robin *Erithacus rubecula*. *Ornis scand.* **12**, 230–9.
- Eisen, E. J. and Saxton, A. M. (1984). Effects of concurrent lactation and postpartum mating on reproductive performance in mice selected for large litter size. *J. anim. Sci.* **59**, 1224–38.
- Eisenberg, J. F. (1981). *The mammalian radiations*. University of Chicago Press, Chicago.
- and Kleiman, D. G. (1977). Communication in lagomorphs and rodents. In *How animals communicate* (ed. T. A. Sebeok), pp. 634–54. Indiana University Press, Bloomington, Indiana.
- and Lockhart, M. (1972). An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithson Contr. Zool.* **101**, 1–118.
- Emlen, S. T. and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–23.
- Fedak, M. A. and Anderson, S. S. (1982). The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *J. Zool., London* **198**, 473–9.
- Findlay, A. L. R. (1968). The effect of teat anaesthesia on the milk-ejection reflex in the rabbit. *J. Endocrinol.* **40**, 127–8.
- and Roth, L. L. (1970). Long-term dissociation of nursing behaviour and the condition of the mammary gland in the rabbit. *J. comp. Physiol. Psychol.* **72**, 341–4.
- Fogden, S. C. L. (1971). Mother–young behaviour of grey seal breeding beaches. *J. Zool., London* **164**, 61–92.
- Follett, B. K. (1985). The environment and reproduction. In *Reproduction in mammals, 2nd edn, book 4: reproductive fitness* (ed. C. R. Austin and R. V. Short), pp. 103–32. Cambridge University Press, Cambridge.
- Freed, L. A. (1981). Loss of mass in breeding wrens: stress or adaptation? *Ecology* **62**, 1179–86.

- Frisch, R. E. (1985). Maternal nutrition and lactational amenorrhoea: perceiving the metabolic costs. In *Maternal nutrition and lactational infertility* (ed. J. Dobbing), pp. 65–92. Raven Press, New York, USA.
- Frith, H. J. (1985). Megapode. In *A dictionary of birds* (ed. B. Campbell and E. Lack), pp. 344–5. T & AD Poyser, Calton.
- Fuchs, S. (1982). Optimality of parental investment: The influence of nursing on reproductive success of mother and female young house mice. *Behav. Ecol. Sociobiol.* **10**, 39–51.
- Galef, B. G., Jr (1983). Costs and benefits of mammalian reproduction. In *Symbiosis in parent-offspring interactions* (ed. L. A. Rosenblum and H. Moltz), pp. 249–78. Plenum Press, New York.
- Gentry, R. L. and Holt, J. R. (1986). Attendance behavior of Northern fur seals. In *Fur seals: maternal strategies on land and at sea* (ed. R. L. Gentry and G. L. Kooyman), pp. 41–60. Princeton University Press, Princeton, New Jersey.
- Gittleman, J. L. and Thompson, S. D. (in press). Energy allocation in mammalian reproduction. *Am. Zool.*
- Gochfeld, M. (1984). Antipredator behavior: aggressive and distraction displays of shorebirds. In *Behavior of marine animals, Vol. 5, Shorebirds* (ed. J. Burger and B. L. Olla), pp. 289–370. Plenum Press, New York.
- Gowaty, P. and Karlin, A. A. (1984). Multiple maternity and paternity in single broods of apparently monogamous eastern bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol.* **15**, 91–5.
- Grafen, A. and Sibly, R. (1978). A model of mate desertion. *Anim. Behav.* **26**, 645–52.
- Gross, M. R. and Sargent, R. C. (1985). The evolution of male and female parental care in fishes. *Am. Zool.* **25**, 807–22.
- Hanken, J. and Sherman, P. W. (1981). Multiple paternity in Belding's ground squirrel litters. *Science* **212**, 351–3.
- Hannon, S. J. (1984). Factors limiting polygyny in the willow ptarmigan. *Anim. Behav.* **32**, 153–61.
- Hanson, H. C. (1962). The dynamics of condition factors in Canada geese and their relation to seasonal stresses. *Arct. Inst. N. Am. Tech. Paper*, No. 12.
- Harvey, P. H. and Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution* **39**, 559–81.
- Hibbs, H. H., Jr (1916). *Infant mortality: its relation to social and industrial conditions*. Rumford Press, Concord, Connecticut.
- Houston, A. I. and Davies, N. B. (1985). The evolution of cooperation and life history in the dunnock, *Prunella modularis*. In *Behavioural ecology: the ecological consequences of adaptive behaviour* (ed. R. Sibly and R. Smith), pp. 471–87. Blackwell, Oxford.
- Hunter, R. A., Ross, H. A., and Ball, A. J. S. (1976). A laboratory simulation of predator-induced incubation interruption using ring-billed gull eggs. *Can. J. Zool.* **54**, 628–33.
- James, W. H. (1970). Neonatal death and birth order. *Ann. Hum. Genet. London* **33**, 385–94.
- Jarvis, J. U. M. (1971). Burrowing and burrow patterns of East African mole-rats *Tachyoryctes*, *Heliophobius*, and *Heterocephalus*. *J. Zool., London* **163**, 451–79.
- (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* **212**, 571–3.

- Jarvis, M. J. F. (1974). The ecological significance of clutch size in the South African gannet (*Sula capensis* (Lichtenstein)). *J. anim. Ecol.* **43**, 1–17.
- Jones, P. J. (1985). Crop milk. In *A dictionary of birds* (ed. B. Campbell and E. Lack), p. 120. T & AD Poyser, Calton.
- Kendeigh, S. C. (1952). Parental care and its evolution in birds. *Ill. biol. Monogr.* **22**, 1–358.
- King, J. A. (1963). Maternal behavior in *Peromyscus*. In *Maternal behavior in mammals* (ed. H. L. Rheingold), pp. 58–93. Wiley and Sons, New York.
- Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Rev. Biol.* **52**, 39–69.
- and Malcolm, J. R. (1981). The evolution of male parental investment in mammals. In *Parental care in mammals* (ed. D. J. Gubernick and P. H. Klopfer), pp. 747–87. Plenum Press, New York.
- Koenig, W. D. (1988). Reciprocal altruism in birds: a critical review. *Ethol. Sociobiol.* **9**, 73–84.
- König, B. and Markl, H. (1987). Maternal care in house mice. I. The weaning strategy as a means for parental manipulation of offspring quality. *Behav. Ecol. Sociobiol.* **20**, 1–9.
- Korschgen, C. E. (1977). Breeding stress of female eiders in Maine. *J. wildl. Manag.* **41**, 360–73.
- Kortlandt, A. (1965). How do chimpanzees use weapons when fighting leopards? *Yearbook Am. phil. Soc.* 327–32.
- Kruuk, H. (1964). Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus*). *Behav. Suppl.* **11**, 1–129.
- (1972). *The spotted hyena: a study of predation and social behavior*. University of Chicago Press, Chicago.
- (1975). *Hyaena*. Oxford University Press, London.
- Lack, D. (1956). *Swifts in a tower*. Methuen, London.
- Lande, R. and Arnold, S. J. (1983). Measuring selection on correlated characters. *Evolution* **37**, 1210–26.
- Lazarus, J. and Inglis, I. R. (1978). The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledging period. *Behaviour* **65**, 62–88.
- Li, C. C. (1975). *Path analysis: a primer*. Boxwood Press, Pacific Grove, California.
- Lincoln, D. W. (1974). Suckling, a time constant in the nursing behaviour of the rabbit. *Physiol. Behav.* **13**, 711–14.
- (1983). Physiological mechanisms governing the transfer of milk from mother to young. In *Symbiosis in parent-offspring interactions* (ed. L. A. Rosenblum and H. Moltz), pp. 77–112. Plenum Press, New York.
- Hill, A., and Wakerley, J. B. (1973). The milk ejection reflex of the rat: an intermittent function not abolished by surgical levels of anaesthesia. *J. Endocrinol.* **57**, 459–76.
- Low, B. S. (1978). Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.* **112**, 197–213.
- Lundy, H. (1969). A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hens egg. In *The fertility and hatchability of the hen's egg* (ed. T. C. Carter and B. M. Freeman), pp. 143–76. Oliver and Boyd, Edinburgh.

- Lynch, C. B. (1987). Genetic analysis of cold adaptation in laboratory and wild house mice. *Second Int. Conf. Quant. Genetics*, Abstracts, 70.
- Machin, D. and Page, S. (1973). Effects of reduction of litter size on subsequent growth and reproductive performance in mice. *Anim. Prod.* **16**, 1–6.
- Mangel, M. and Clark, C. W. (1986). Towards a unified foraging theory. *Ecology* **67**, 1127–138.
- and — (in press). *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, New Jersey.
- Martin, K. and Cooke, F. (1987). Bi-parental care in the willow ptarmigan: a luxury? *Anim. Behav.* **35**, 369–79.
- , Cooch, F. G., Rockwell, R. F., and Cooke, F. (1985). Reproductive performance in lesser snow geese: are two parents essential? *Behav. Ecol. Sociobiol.* **17**, 257–63.
- Mattingly, D. K. and McClure, P. A. (1982). Energetics of reproduction in large-littered cotton rats (*Sigmodon hispidus*). *Ecology* **63**, 183–95.
- and — (1985). Energy allocation during lactation in cotton rats (*Sigmodon hispidus*) on a restricted diet. *Ecology* **66**, 928–37.
- Maxson, S. J. and Oring, L. W. (1980). Breeding season time and energy budgets of the polyandrous spotted sandpiper. *Behaviour* **74**, 200–63.
- May, R. M. and Rubenstein, D. I. (1985). Reproductive strategies. In *Reproduction in mammals, 2nd edn, book 4: Reproductive fitness* (ed. C. R. Austin and R. V. Short), pp. 1–23. Cambridge University Press, Cambridge.
- Maynard Smith, J. (1977). Parental investment: A prospective analysis. *Anim. Behav.* **25**, 1–9.
- (1982). *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- McGowan, K. J. (1987). Social development in young Florida scrub jays (*Aphelocoma c. coerulescens*). PhD Dissertation, University of South Florida, Tampa, Florida.
- McLaren, A. and Ritchie, D. (1963). Nature of the systematic effect of litter size on gestation period in mice. *J. Reprod. Fert.* **6**, 139–41.
- McNair, M. R. and Parker, G. A. (1979). Models of parent–offspring conflict. III. Intra-brood conflict. *Anim. Behav.* **27**, 1202–9.
- McNamara, J. M. and Houston, A. I. (1986). The common currency for behavioral decisions. *Am. Nat.* **127**, 358–78.
- Millar, J. S. (1977). Adaptive features of mammalian reproduction. *Evolution* **31**, 370–86.
- Mitchell-Olds, T. and Shaw, R. G. (1987). Regression analysis of natural selection: statistical inferences and biological interpretation. *Evolution* **41**, 1149–61.
- Mock, D. W. (1984). Siblicidal aggression and resource monopolization in birds. *Science* **225**, 731–3.
- Mühlbock, O. (1959). Factors influencing the life-span of inbred mice. *Gerontologia* **3**, 177–83.
- Muller, R. E. and Smith, D. G. (1978). Parent–offspring interactions in zebra finches. *Auk* **95**, 485–95.
- Myers, J. P. (1978). One deleterious effect of mobbing in southern lapwing (*Vanellus chilensis*). *Auk* **95**, 419–20.

- Norberg, R. Å. (1981). Temporary weight decrease in breeding birds may result in more fledged young. *Am. Nat.* **118**, 838–50.
- Norris, M. L. and Adams, C. E. (1982). Lifetime reproductive performance of Mongolian gerbils (*Meriones unguiculatus*) with 1 or 2 ovaries. *Lab. Anim.* **16**, 146–50.
- Nur, N. (1984a). Feeding frequencies of nestling blue tits (*Parus caeruleus*): Costs, benefits and a model of optimal feeding frequency. *Oecologia, Berlin* **65**, 125–37.
- (1984b). The consequences of brood size for breeding blue tits. I. Adult survival, weight change and the cost of reproduction. *J. anim. Ecol.* **53**, 479–96.
- (1988). The consequences of brood size for breeding blue tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. *Evolution* **42**, 351–62.
- O'Connor, R. J. (1978). Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim. Behav.* **26**, 79–96.
- Orians, G. H. (1973). The red-winged blackbird in tropical marshes. *Condor* **75**, 28–42.
- Ortiz, C. L., LeBoeuf, B. J., and Costa, D. P. (1984). Milk intake of elephant seal pups: an index of parental investment. *Am. Nat.* **124**, 416–22.
- Page, G. W., Stenzel, L. E., and Ribic, C. A. (1985). Nest site selection and clutch predation in the snowy plover. *Auk* **102**, 347–53.
- Parker, G. A. (1984). Evolutionarily stable strategies. In *Behavioural Ecology, 2nd edn* (ed. J. R. Krebs and N. B. Davies), pp. 30–61. Blackwell Scientific, Oxford.
- and MacNair, M. R. (1978). Models of parent–offspring conflict. I. Monogamy. *Anim. Behav.* **26**, 97–110.
- and —— (1979). Models of parent–offspring conflict. Suppression: evolutionary retaliation of the parent. *Anim. Behav.* **27**, 1210–35.
- Partridge, L. and Harvey, P. H. (1985). Costs of reproduction. *Nature* **316**, 20.
- Patterson, T. L., Petrinovich, L., and James, D. K. (1980). Reproductive value and appropriateness of response to predators by white-crowned sparrows. *Behav. Ecol. Sociobiol.* **7**, 227–31.
- Peck, J. R. and Feldman, M. W. (1986). The evolution of helping behavior in large, randomly mixed populations. *Am. Nat.* **127**, 209–21.
- Pellis, S. M. and Pellis, V. C. (1982). Do post-hatching factors limit clutch size in the Cape Barren goose, *Cereopsis novaehollandiae* Latham? *Austral. wildl. Res.* **9**, 145–9.
- Perrins, C. M. (1963). Survival in the great tit, *Parus major*. *Proc. 13th Int. Ornithol. Congress*, 717–28. Amer. Ornith. Union, Baton Rouge, Louisiana.
- , Harris, M. P., and Britton, C. K. (1973). Survival of manx shearwaters *Puffinus puffinus*. *Ibis* **115**, 535–48.
- Prentice, A. M., and Whitehead, R. G. (1987). Energetics of human reproduction. *Symp. Zool. Soc., London* **57**, 275–304.
- Randolph, P. A., Randolph, J. C., Mattingly, K., and Foster, M. M. (1977). Energy costs of reproduction in the cotton rat, *Sigmodon hispidus*. *Ecology* **58**, 31–45.
- Reznick, D. (1985). Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–67.
- , Perry, E., and Travis, J. (1986). Measuring the costs of reproduction: a comment on papers by Bell. *Evolution* **40**, 1338–44.

- Ricklefs, R. E. (1979). Adaptation, constraint, and compromise in avian postnatal development. *Biol. Rev.* **54**, 269–90.
- (1984). The optimization of growth rate in altricial birds. *Ecology* **65**, 1602–16.
- , Day, C. H., Huntingdon, C. E., and Williams, J. B. (1985). Variability in feeding rate and meal size of Leach's storm petrel at Kent Island, New Brunswick, *J. Anim. Ecol.* **54**, 883–98.
- Roby, D. D. and Ricklefs, R. E. (1986). Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. *Physiol. Zool.* **59**, 661–78.
- Romanoff, A. L. and Romanoff, A. J. (1972). *Pathogenesis of the avian embryo*. Wiley-Interscience, New York.
- Rose, M. R. and Charlesworth, B. (1981). Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. *Genetics* **97**, 173–86.
- Røskoft, E. (1985). The effect of enlarged brood size on the future reproductive potential of the rook. *J. anim. Ecol.* **54**, 255–60.
- Royama, T. (1966). Factors governing feeding rate, food requirements, and brood size of nestling great tits, *Parus major*. *Ibis* **108**, 313–47.
- Russell, E. M. (1982). Patterns of parental care and parental investment in marsupials. *Biol. Rev.* **57**, 423–86.
- Sadleir, R. M. F. S. (1984). Ecological consequences of lactation. *Acta Zool. Fenn.* **171**, 187–90.
- Safriel, U. N. (1975). On the significance of clutch size in nidifugous birds. *Ecology* **56**, 703–8.
- Sargeant, A. B., Allen, S. H., and Eberhard, R. T. (1984). Red fox predation on breeding ducks in midcontinental North America. *Wildl. Mon.* **89**, 1–41.
- Sargent, R. C. and Gross, M. R. (1986). Williams' principle: An explanation of parental care in teleost fishes. In *The behavior of teleost fishes* (ed. T. J. Pitcher), pp. 275–93. Johns Hopkins University Press, Baltimore, Maryland.
- SAS Institute, Inc (1985). SAS user's guide: statistics. Version 5 Ed. SAS Inst., Cary, NC, USA.
- Schaffer, W. M. (1974). Optimal reproductive effort in fluctuating environments. *Am. Nat.* **108**, 783–90.
- Schaller, G. B. (1967). *The deer and the tiger*. University of Chicago Press, Chicago.
- Schmidt, U. and Manske, U. (1973). Die Jugendentwicklung der Vampirfledermause (*Desmodus rotundus*). *Z. Saugetierk.* **38**, 14–33.
- Shapiro, S., Schlesinger, E. R., and Nesbitt, R. E. L., Jr (1968). *Infant, perinatal, maternal, and childhood mortality in the United States*. Harvard University Press, Cambridge, Massachusetts.
- Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science* **197**, 1246–53.
- (1980). The limits of ground squirrel nepotism. In *Sociobiology: beyond nature/nurture?* (ed. G. W. Barlow and J. Silverberg), pp. 505–44. Westview Press, Boulder, Colorado.
- (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behav. Ecol. Sociobiol.* **17**, 313–23.
- and Morton, M. L. (1988). Extra-pair fertilizations in mountain white-crowned sparrows. *Behav. Ecol. Sociobiol.* (in press).
- Short, R. V. (1985). Species differences in reproductive mechanisms. In *Reproduction in mammals, 2nd edn, book 4: Reproductive fitness* (ed. C. R. Austin and R. V. Short), pp. 24–61. Cambridge University Press, Cambridge.

- Sibly, R. and Calow, P. (1983). An integrated approach to life cycle evolution using selective landscapes. *J. theor. Biol.* **102**, 527–47.
- , ———, and Nichols, N. (1985). Are patterns of growth adaptive? *J. theor. Biol.* **112**, 533–74.
- Sikes, S. K. (1971). *The natural history of the African elephant*. Elsevier, New York.
- Silver, R., Andrews, H., and Ball, G. W. (1985). Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *Am. Zool.* **25**, 823–40.
- Skutch, A. F. (1949). Do tropical birds raise as many young as they can nourish? *Ibis* **91**, 430–55.
- Smart, J. L. (1983). Undernutrition, maternal behaviour, and pup development. In *Parental behaviour of rodents* (ed. R. W. Elwood), pp. 205–34. Wiley and Sons, New York.
- Smith, J. N. M. (1981). Does high fecundity reduce survival in song sparrows? *Evolution* **35**, 1142–8.
- Southern, L. K., Patton, S. R., and Southern, W. E. (1982). Nocturnal predation on *Larus* gulls. *Colonial Waterbirds* **5**, 169–72.
- Speakman, J. R. and Racey, P. A. (1987). The energetics of pregnancy and lactation in the brown long-eared bat, *Plecotus auritus*. In *Recent advances in the study of bats* (ed. M. B. Fenton, P. A. Racey, and J. M. V. Rayner), pp. 367–93. Cambridge University Press, Cambridge.
- Stamps, J. A., Metcalf, R. A., and Krishnan, V. V. (1978). A genetic analysis of parent–offspring conflict. *Behav. Ecol. Sociobiol.* **3**, 369–92.
- , Clark, A., Arrowood, P., and Kus, B. (1985). Parent–offspring conflict in budgerigars. *Behaviour* **94**, 1–39.
- Stewart, R. E. A. (1986). Energetics of age-specific reproductive effort in female harp seals, *Phoca groenlandica*. *J. Zool., London* **A208**, 503–17.
- Tener, J. S. (1965). *Muskoxen in Canada: a biological and taxonomic review*. Department of Northern Affairs and Natural Resources, Ottawa.
- Tevis, L. (1950). Summer behavior of a family of beavers in New York State. *J. Mammal.* **31**, 40–65.
- Thompson, S. D. (1987). Body size, duration of parental care, and the intrinsic rate of natural increase in eutherian and metatherian mammals. *Oecologia* **71**, 201–9.
- Tinbergen, J. M. (1987). Costs of reproduction in the great tit: intraseasonal costs associated with brood size. *Ardea* **75**, 111–22.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quart. Rev. Biol.* **46**, 35–57.
- (1972). Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971* (ed. B. Campbell), pp. 136–79. Aldine, Chicago, IL, USA.
- (1974). Parent–offspring conflict. *Am. Zool.* **14**, 249–64.
- Tullett, S. G. (1985). Incubation. In *A dictionary of birds* (ed. B. Campbell and E. Lack), pp. 303–5. T & AD Poyser, Calton.
- van Noordwijk, A. J. and de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**, 137–42.
- van Tienhoven, A. (1968). *Reproductive physiology of vertebrates*. W. B. Saunders, Philadelphia, Pennsylvania.
- Vavra, H. M. and Querec, L. J. (1973). A study of infant mortality from linked records by age of mother, total birth-order, and other variables. *Vital Hlth. Stat. Ser. 20*, **14**, 1–51.

- Vehrencamp, S. L. and Bradbury, J. W. (1984). Mating systems and ecology. In *Behavioural ecology: An evolutionary approach, 2nd edn* (ed. J. R. Krebs and N. B. Davies), pp. 251–78. Blackwell, Oxford.
- Vleck, D. (1979). The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiol. Zool.* **52**, 122–36.
- (1981). Burrow structure and foraging costs in the fossorial rodent *Thomomys bottae*. *Oecologia* **49**, 391–6.
- von Haartman, L. (1954). Der Trauerfliegenschnäpper. III. Die Nahrungsbiologie. *Acta Zool. Fenn.* **83**, 1–96.
- Walsberg, G. E. (1983). Avian ecological energetics. In *Avian biology, Vol. VII* (ed. D. S. Farner and J. R. King), pp. 161–220. Academic Press, New York.
- Walters, J. R. (1982). Parental behavior in lapwings (Charadriidae) and its relationship with clutch sizes and mating systems. *Evolution* **36**, 1030–40.
- (1984). The evolution of parental behavior and clutch size in shorebirds. In *Behavior of marine animals, Vol. 5, Shorebirds* (ed. J. Burger and B. Olla), pp. 243–88. Plenum Press, New York.
- Warren, E. R. (1927). The beaver. *Am. Soc. Mammalogists Mon.* **2**, 1–72.
- Weeks, H. P., Jr (1978). Clutch size variation in the eastern phoebe in southern Indiana. *Auk* **95**, 656–66.
- Westneat, D. F. (1987). Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Anim. Behav.* **35**, 877–86.
- Wiklund, C. G. (1982). Fieldfare (*Turdus pilaris*) breeding success in relation to colony size, nest position and association with merlins (*Falco columbarius*). *Behav. Ecol. Sociobiol.* **11**, 165–72.
- Wilkinson, G. S. (1988). Reciprocal altruism in bats and other mammals. *Ethol. Sociobiol.* **9**, 85–100.
- Winkler, D. W. (1987). A general model for parental care. *Am. Nat.* **130**, 526–43.
- and Walters, J. R. (1983). The determination of clutch size in precocial birds. *Current Ornithol.* **1**, 33–68.
- Withers, P. C. (1977). Energetic aspects of reproduction by the cliff swallow. *Auk* **94**, 718–25.
- Wittenberger, J. F. and Tilson, R. L. (1980). The evolution of monogamy: hypotheses and evidence. *Ann. Rev. ecol. Syst.* **11**, 197–232.
- Wolf, L., Ketterson, E. D., and Nolan, V., Jr (1988). Paternal care in the dark-eyed junco: do males benefit? I. Paternal effects on growth and survival of the young. *Anim. Behav.* (in press).
- Zarrow, M. X., Denenberg, V. H., and Anderson, C. O. (1965). Rabbit: frequency of suckling in the pup. *Science* **150**, 1835–6.