Optimal allocation of parental investment

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Optimal investment decisions are evaluated for parents which allocate resources equally among offspring. Optimal investment predicts that:
1) Brood size should be positively correlated with total parental investment.
2) Brood size should decline with increases in maximum juvenile survival.
3) Brood size should increase as the minimum investment in offspring declines.
4) Brood size should increase with increases in the rate of change of juvenile survival with parental investment.
Total parental investment and juvenile survival should vary with environmental conditions. Optimum brood size should often be higher in good than in poor periods, but may be just the opposite in good and poor habitats. Optimal investment may frequently be achieved by differential allocation of resources among offspring. Sexual investment theory is a subset of optimal investment theory.
5) The degree of preferential partitioning of investment should depend upon the phenotypic variability of offspring and the length of parental care.
6) Investment-induced changes in phenotypic proportions (e.g., sex ratio) depend upon brood size.
Optimal investment differs from other life history models in its assumption that brood size is one of a series of mechanisms operating to optimize parental investment.
7) Reproductive costs should not generally increase with increased brood size.

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Introduction

One of the challenges of evolutionary ecology is to explain why biological species have such a great diversity of life histories. Studies have concentrated on life history events such as the timing, frequency and intensity of reproduction (Lack 1947, Cole 1954, Williams 1966a, Gadgil and Bossert 1970, Charnov and Schaffer 1973, Stearns 1976, 1977, Clutton-Brock 1984), the relative survival probabilities of offspring and parents (Murphy 1968, Schaffer 1974a, Charlesworth and Leon 1976, Michod 1979), the sex ratio of offspring (Fisher 1930, Trivers and Willard 1973, Maynard Smith 1978, Charnov 1982, Clutton-Brock et al. 1982, Gosling 1986), and more recently on size, phylogenetic and other constraints (Millar 1977, Stearns 1983, 1984, Hutchings and Morris 1985, Dunham and Miles 1985, Gittleman 1986). Theoretical explanations commonly assume tradeoffs between fecundity and subsequent offspring and par-

ental survival (Cody 1966, Charnov and Krebs 1974, Pianka and Parker 1975, Bell 1980), reproductive effort and survival (Williams 1966b, Schaffer 1974b, Schaffer and Rosenzweig 1977) or between density-dependent and density-independent selection (MacArthur and Wilson 1967, Pianka 1970, Gadgil and Solbrig 1972, Boyce 1984). Several recent tests which specifically evaluated life history tradeoffs have yielded both equivocal and conflicting results (Snell and King 1977, Law 1979, De Steven 1980, Smith 1981, Bell 1984a, b, Nur 1984, Reznick 1985, Morris 1986).

The optimal investment hypothesis (Morris 1985) gives a somewhat different perspective to life history evolution. According to this hypothesis, natural selection optimizes parental investment among offspring (Ricklefs 1968, Smith and Fretwell 1974, Brockelman 1975, Drent and Daan 1980, Högstedt 1980, Morris 1985). Brood size is the result of optimal allocation of investment (broadly defined as the commitment of re-
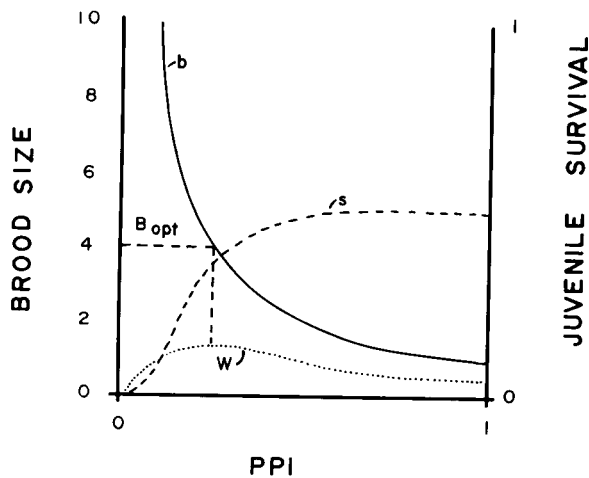
Fig. 1. The relationship of brood size and juvenile survival to proportional parental investment (PPI). The solid line (b) is the principle of proportional investment. The dashed curve (s) is one representation of how juvenile survival (survival to age of first reproduction) should increase with proportion of parental investment received. The dotted line (W) is the fitness curve as a product of brood size and juvenile survival. Optimum brood size (B_{opt}) corresponds to the maximum height of the fitness curve. As drawn, there is one optimum, but depending upon the actual shape of juvenile survival, multiple optima are possible.

sources and/or time and energy to reproduction) among offspring. Brood size is adjusted relative to that investment and parental survival rates are relatively insensitive to variation in the number of young produced. The theory implicitly assumes that parental 'decisions' on the amount of total reproductive investment are based primarily on cost-benefit analyses of parental survival and future reproduction as a function of that investment rather than being based on proximate investment indicators like brood size. In this paper, I develop the theoretical basis of optimal investment. I present a series of graphical models which generate several qualitative predictions appropriate to a variety of questions in evolutionary ecology.

Theory

To evaluate optimal investment theory we need to simultaneously consider the rewards of different degrees of parental investment in terms of brood size and offspring recruitment. I do this by plotting brood size and recruitment against the proportion of total investment allocated per offspring. If parents partition their reproductive investment equally among offspring, then in a brood of size n, each offspring can expect to receive 1/n of the parents' total investment. Proportional investment thus specifies a negative exponential relation between brood size and the proportion of the parents' total allocation of investment to reproduction (Fig. 1). Juvenile survival should generally increase with the proportion of the parents' total investment that each ju-

venile receives (Fig. 1). I assume a lower threshold below which the investment is so small that all juveniles die, and an upper asymptote corresponding to the maximum survival rate that can be attained by parental investment. The product of juvenile survival and brood size yields a fitness curve that allows us to assess which brood size maximizes the recruitment of young into the population. For organisms obeying the principle of proportional investment, brood size can be predicted by the magnitude of juvenile survival and how it varies with proportional investment. The actual survival curve will depend upon the total parental investment.

First, consider a population in which total investment per parent is constant. Proportional investment assumes that for any reproductive episode there is some optimal value of investment per offspring (IO) such that

$$TI = IO(b)$$

where TI is the total investment available for reproduction by a given parent and b is brood size (Morris 1985). If IO is more or less constant, brood size is proportional to TI. Brood size is correlated with total parental investment.

Consider the life history of a population where there is considerable temporal variation in the amount of resources available for reproduction. Compare a reproductive season of low resource availability (low total investment) and one of high resource levels (high total investment). In both cases we assume that offspring which receive 100% of the parents' reproductive investment have received investment in excess of that required for maximum survival. For any particular brood size, offspring born in the poor season (or year) receive progressively less investment than do those born in the good season because parents have fewer total resources
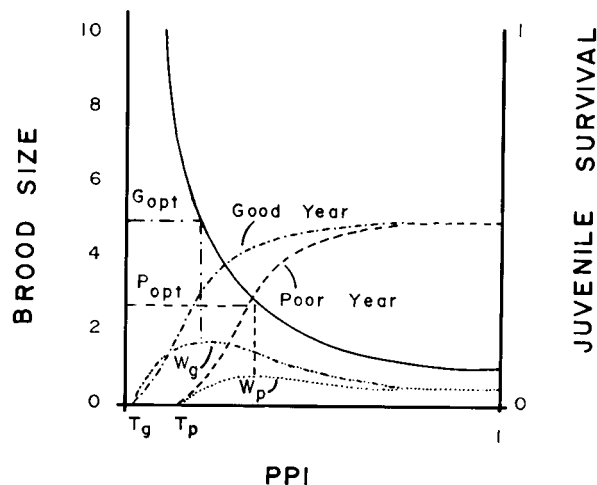

Fig. 2. Optimum brood size increases with reductions in the lower investment threshold. The peak of the fitness curve for the good year (W_g) which has a lower investment threshold (T_g) corresponds to a higher optimum brood size (G_{opt}) than does that for the poor year (P_{opt}) with a higher threshold (T_p).

Fig. 3 (left graph): BROOD SIZE (y-axis, 0 to 10), PP1 (x-axis, 0 to 1), JUVENILE SURVIVAL (right y-axis). Labels: Good Habitat, Poor Habitat, P_{opt}, G_{opt}, W_g, W_p.
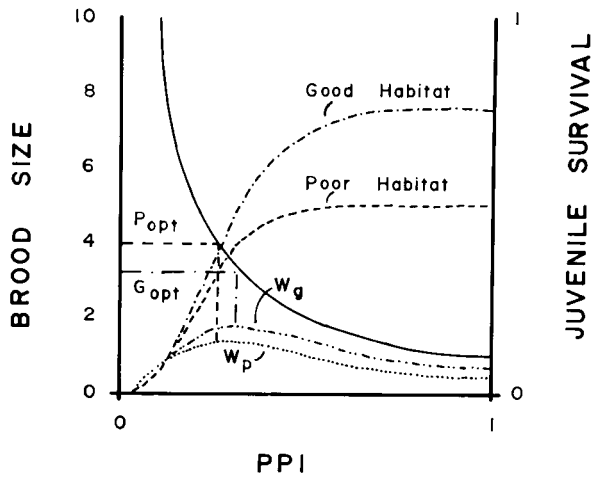
Fig. 3. Optimum brood size declines as maximum juvenile survival rates increase. The peak of the fitness curve for the good habitat (W_g) with higher asymptotic survival corresponds to a lower optimum brood size (G_{opt}) than does that for the poorer habitat (P_{opt}).

evaluate how natural selection might operate on juvenile survival? Consider parents for which there is some minimum threshold investment below which individual offspring do not receive an adequate share of resources to complete normal development or growth. All young below the threshold die. A modest increase in investment thresholds can result in major reductions in the optimum brood size (Fig. 4, upper). Now consider that there are other parents which have little to gain by further investment beyond the same threshold. Appropriate examples would include pelagic-spawning fishes, many invertebrates and plants where parents are incapable of providing post-reproductive parental care. For

available for reproduction. To achieve the same survival as juveniles in a good season they require a higher proportion of parental investment, and the optimum brood size is reduced (Fig. 2). As resources become more abundant, as in a good year, parents can invest more in reproduction without modifying their own survival. Each offspring, for a given brood size, receives increased parental investment, and a smaller proportion of the total investment is required to yield the same level of juvenile survival. Optimum brood size increases with increased total investment because investment thresholds are lowered.

Do we expect the same pattern with spatial variation in resources? Probably not. If populations in different habitats are near equilibrium with their respective carrying capacities, individuals in both habitats will have similar potential to extract resources and invest in offspring. No difference in brood size should be detected. Habitats differ in other ways in addition to resource levels. Good habitats may, for example, reward offspring with higher maximum survival per individual (a higher asymptote of survival as a function of proportional parental investment) than they would receive with the same investment in a poorer habitat. If population density is closely linked to resource abundance, resources available to individual parents will not differ between habitats, and the optimum litter size would be the same. But when juvenile survival varies between habitats, the optimum brood size may be lower in the better habitat (Fig. 3). In general, brood size declines with increases in maximum juvenile survival.

These two examples point out how important the shape and magnitude of juvenile survival can be in determining brood size. Can we use this information to

Fig. 4 (upper graph): SIZE (y-axis, 0 to 40), PP1 (x-axis, 0 to 1), SURVIVAL (right y-axis). Labels: A_{opt} (30), B_{opt} (10), W_A, W_B, T_A, T_B.

Fig. 4 (lower graph): BROOD (y-axis, 0 to 40), PPI (x-axis, 0 to 1), JUVENILE (right y-axis). Labels: A_{opt} (30), B_{opt}, W_A, W_B, A, B.
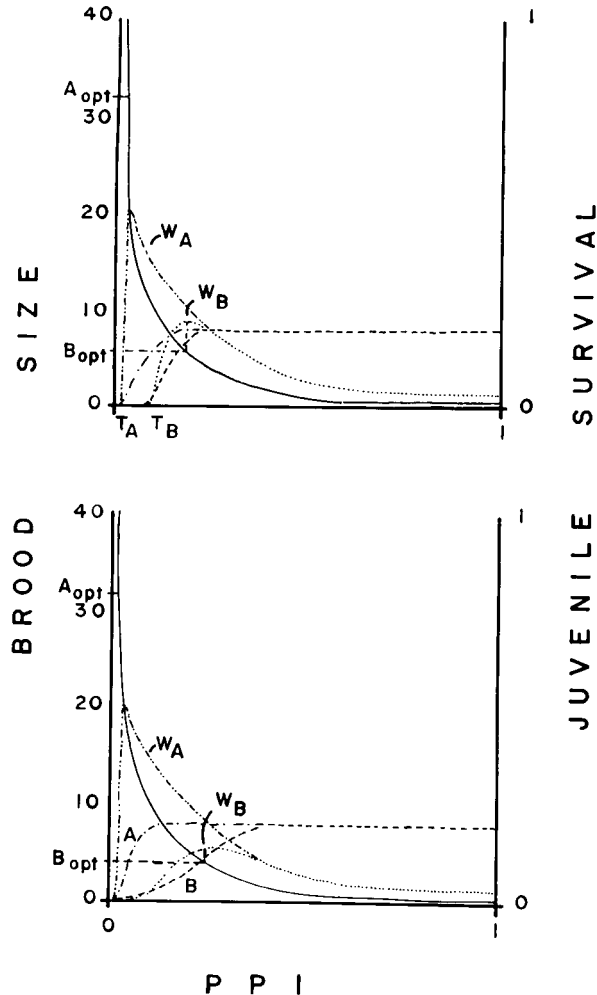
Fig. 4. The effects of variable investment thresholds and rates of juvenile survival on the optimum brood size in a fecund species. Upper - an increase in the investment threshold from T_A to T_B causes a five-fold reduction in the optimum brood size ($A_{opt} \gg B_{opt}$). Lower - investment thresholds are equal, but curve B has a more gradual increase in juvenile survival with investment and a greatly reduced optimum brood size. Lines as in previous figures except that the fitness curve is multiplied by 10 to ease interpretation.

334

these species the rate of juvenile survival may increase rapidly with small increases in investment (a steeper slope of survival as a function of proportional investment) and result in much larger brood sizes (Fig. 4, lower). Selection on the relationship of juvenile survival to parental investment may quickly modify brood size, especially if broods are already large.

I have drawn all survival curves as concave functions with a rapid increase in survival beyond the lower investment threshold which then tapers off with further increases in proportional investment. Other shapes are equally plausible. Multiplicative effects, for example, would result in convex survival curves. Nor is it necessary that survival curves reach an upper asymptote. Single offspring species (e.g., most alcids, many bats, whales) may frequently be characterized by survival curves which increase for all levels of parental investment. Differences in the shapes of survival curves will generate different quantitative predictions of brood size, but should not greatly influence my qualitative predictions.

Implications

Resources available for conversion into young (e.g., stored fat) vary continuously, whereas brood size varies discretely. Parents optimizing investment among offspring should often have some excess resources available to be channeled into reproduction beyond that demanded by the brood, but insufficient to produce an additional offspring. How should they partition the surplus? They have four choices. 1) Produce one more offspring; all offspring receive, on average, less of the investment. 2) Partition the surplus equally among offspring; average juvenile survival may increase. 3) Partition the surplus preferentially among offspring; some offpring may have greater demands or higher survival than others. 4) Save the investment for subsequent reproduction. The first choice is likely to be sub-optimal because average juvenile survival would be lowered. The last choice is likely to be sub-optimal as well because decisions on total parental investment should be independent of brood size. Optimal investment theory implicity assumes that parents have cues other than brood size (e.g., age, size, physiological conditioning, experience, seasonality) which determine the amount of reproductive investment. Having 'determined' how much investment is optimal for a given reproductive episode relative to the conflicting demands of parental growth, maintenance and survival, optimal investment is concerned only with how that total is partitioned in the current brood. Should the parent divide the investment equally or preferentially?

The partitioning decision will be molded by evolutionary costs and benefits. If the rewards to the parent of investing preferentially in certain phenotypes exceed the summed average reward by proportional allocation, then natural selection should favor preferential partit-

ioning. The partitioning will not be simple, and will probably depend on the degree of phenotypic variability. For organisms which produce large numbers of offspring with relatively little parental investment in any one, the parent may not have an opportunity to distinguish among them. Presumably such life histories have evolved because modest increases in parental investment have little effect on subsequent juvenile survival. For organisms with extended parental care and greater investment, there will be more time and opportunity for offspring to express their genetic differences. The parent has greater opportunity to assess variation in offspring 'quality' and to predict their relative chances of successful survival. The degree of preferential partitioning should depend upon the phenotypic variability of offspring and the length of parental care.

Alternative preferences could include providing weak or small offspring with extra resources to increase survival, or to do the same for a larger more robust or vigorous offspring. The decision will lie in the age- or stage-specific survival and reproductive rates of each. For some phenotypes we can make explicit preditions.

In many sexual species one sex is more expensive to produce than the other. When costs are unequal, a biased sex ratio in favor of the less expensive sex should result (Fisher 1930, Maynard Smith 1978). Similarly, when parental investment modifies offspring fitness, and where the variance in fitness of the sexes is asymmetrical, sex ratio may vary with resource levels and parental condition. When resources are scarce or parents are in poor condition, parents should produce relatively more of the less expensive sex; when resources are abundant, they may produce more of the expensive sex (Trivers and Willard 1973, Maynard Smith 1980, Clutton-Brock et al. 1982). The Trivers-Willard model is a subset of the more encompassing theory of optimal investment. Parental investment can be optimized by manipulating the sex ratio of offspring.

Sex ratio predictions may not be as straight-forward as suggested by Trivers and Willard (1973). Consider a hypothetical population in which the variation in reproductive investment potential varies from 10 to 15 units. Assume that the cost of producing a female is three units, that of a male is four units and that the parental rewards of the investment will be the same for each unit regardless of which sex receives it. How do the hypothetical parents optimize their reproductive investment potential? Parents with 10 units reproduce optimally with two female and one male offspring; those with 11, two males and one female; those with 12, all males or all females; those with 13, three females and one male; those with 14, two females and two males; and those with 15, five females or three males and one female. Resources will be simultaneously optimized proportional to the number and requirements of the young. Any other combination of sex in the offspring is sub-optimal for that parent because some resources available for reproduction will have been unused. The population sex

ratio would then be buffered against environmental and demographic variation in the amount of resources available for reproduction. Investment buffering may help explain controversial data on sex ratio adjustment (e.g., Myers 1978). Now consider another population with the same variation in resource availability but where females cost 11 units and males 13. Changes in the average investment available from 12 to 14 units would be expected to be accompanied by a change in the sex ratio. Sex ratio predictions with environmental quality may need to be restricted to parents which produce small broods.

What if the fitness potential of investment between the sexes is unequal? Consider, for example, that beyond the threshold of three and four units for females and males above, that an additional allocation of one unit has little effect on the survival of females, but results in an increase in the survival of males. Trivers and Willard (1973) predicted that this should lead to increased production of males by parents which could afford the increased investment. If parents can simultaneously manipulate both brood size and sex ratio to optimize their investment, then the rewards of increased investment can be equalized among parents with differing investment potential. Again, the prediction of changes in sex ratio would seem to be restricted to small brood sizes where optimization options are limited. If a parent in good condition gains by producing five-unit males, then so too does one in poor condition, as long as it can afford the investment (see also McGinley 1984). Optimal reproduction in our hypothetical species might now be: 10 units, two five-unit males; 11 units, one five-unit male and two females; 12 units, one five-unit male, one four-unit male and one female; 13 units, two five-unit males and one female; 14 units, two five-unit males and one four-unit male; 15 units, three five-unit males. Presumably such a biased sex ratio would increase the temporal variance in reproductive success of female offspring which would similarly increase their value relative to that of males. The generality of the Trivers and Willard hypothesis seems to depend upon brood size and how rewards relate to asymmetrical investment.

In my simple examples I have assumed that costs and rewards are discrete variables. In reality, neither costs nor investment are discrete, and subtle variation in preferential investment among phenotypes may often be difficult to detect. It would, nevertheless, be rewarding to compare individual investment decisions among species. Variation in investment among other phenotypes could be modified similarly to that for sexual phenotypes.

Offspring have a strong influence on their parents' investment decisions. Conflicts of interest frequently develop between individual offspring and parents which attempt to proportionately allocate investment (Trivers 1974). This can lead to intense sibling rivalries where asymmetry in competitive ability among sibs can be reinforced (more investment to those of high competitive ability) or reduced (invest in those of low competitive ability) by preferential investment.

Discussion

Optimal investment assumes that brood size is proportional to the overall reproductive investment of the parent(s). It implicitly assumes that natural selection operates primarily on investment rather than on brood size, brood size being one of the mechanisms which optimizes that investment. For parents which optimize their investment in this way there will be no reproductive tradeoff with brood size (see also Charnov 1986) and no apparent cost of reproduction as a function of brood size. Reproduction should seldom occur without risk, however, and we would expect some basic level of reproductive cost when compared to individuals which have not reproduced or which have made a sub-optimal investment. We should also expect costs associated with increased reproductive investment relative to the parents' ability to provide that investment. A first estimate of that cost could be the relation of parental survival to reproductive effort. Empirical tests will be difficult because an experienced or reproductively efficient parent may be able to provide a higher reproductive effort with little or no additional physiological, survival or reproductive cost. To study costs with optimal investment, there seems to be no alternative to detailed studies which evaluate age- or stage-specific strategies of individual parents under different environmental or experimental conditions. Methods which might be especially useful are manipulation of resource levels or other reproductive cues used by parents.

Spatial and temporal variability in resources are analogous to what we might expect to find in terms of variation among parents or among species. Parents which invest more resources directly into offspring should produce a larger brood size than those with fewer resources (Fig. 2). The parent which can manipulate the maximum survival of its young may gain by reduced brood size (Fig. 3). These predictions are complicated by parents whose behavior responds to resource availability. A parent which is forced to forage more frequently or intensely during periods of resource shortage may be less able to incubate, shelter or guard young. Juvenile survival would decline across all levels of investment, and brood size would be reduced. Nevertheless, brood size can still be viewed as a consequence of the allocation of parental investment.

It is implicit in optimal investment theory that during any given reproduction, investment in offspring should generally be less variable than the total parental investment (Morris 1985). Consistent with this assumption, Brockelman (1975) summarized several examples demonstrating that brood size varies with environmental conditions while egg or newborn size is relatively invariant. Similarly, an impressive body of evidence shows that birth and weaning weights of mammals have sub-

336

stantially less residual variation after correction for differences due to parental size than do other traits which estimate total investment (Millar 1977, 1981, Stearns 1983, Bekoff et al. 1984, Harvey and Clutton-Brock 1985, Gittleman 1986). Early life history traits appear constrained in mammals by common and narrow requirements of lactation and extended maternal care, and it may not be appropriate to use broad phylogenetic comparisons of life history traits in other taxa to evaluate variation in investment.

Many species invest preferentially in some offspring at the apparent expense of others, and their life history appears to be contrary to the theory of optimal investment. Several predatory bird species begin incubating eggs as they are laid, but may raise only some of the resulting young to fledging (Perrins and Birkhead 1983). What would happen to these same parents if they proportionately allocated investment among offspring? In good years all offspring would receive resources beyond the lower investment threshold, and reproductive success would be maximized. In bad years, none would receive the threshold investment and all would perish. But that's not the point; optimal investment predicts that these parents should manipulate brood size relative to resource availability. Why do they produce sub-optimal brood sizes? Organisms living in highly variable environments may not be able to accurately forecast their investment potential. Such species can hedge their bets against environmental uncertainty by a relatively small investment in overproduction of young in poor years (Lack 1954). Alternatively, over-production may compensate for total brood failure (Clark and Wilson 1981) or act as insurance against variable viability in older sibs (Cash and Evans 1986). Yet these same parents ultimately 'decide' which offspring receive investment, and brood size is adjusted accordingly.

Brood size attrition seems to be especially common in plants (Willson and Burley 1983) which may be less able than animals to buffer environmental variability by behavioral adjustments to resource availability. We should not expect organisms to be perfect in their ability to predict their investment potential, or in their ability to optimally partition that which is available. The theory predicts instead that, as soon as organisms are able to accurately forecast that investment, they should optimize it among offspring by using whatever behavioral or physiological mechanisms are available to manipulate brood size or otherwise modify their investment.

The observation that clutch-sizes of many birds are larger in good than in bad habitats (Perrins and Birkhead 1983), also seems to conflict with predictions of the theory. I have assumed in my predictions about habitat variation in brood size, that population density is proportional to resource availability. This need not be the case, especially if breeding density depends upon survival over the non-breeding season (e.g., Fretwell 1972). In such seasonally breeding species, habitat variation may effectively be acting like temporal variation

in resources; larger brood sizes occur where per caput resource levels are highest. I also implicitly assume that population density equilibrates among habitats such that resource availability per individual is more or less equal (the ideal free distribution of Fretwell and Lucas 1970). Territorial species can be expected to violate free distribution assumptions, with the result that resource levels, as well as resources available for reproduction, are greater in the better habitat (Fretwell and Lucas 1970).

Differences in juvenile survival as a function of parental investment may often lead to a dichotomy of parents which produce many small offspring versus those which produce fewer offspring, but invest more in each one (Fig. 4). Proportional investment can thus generate polar life histories similar to those expected under extreme r and K selection (MacArthur and Wilson 1967, Boyce 1984), and creates another complexity in distinguishing among causes of life history variation. An alternative view would argue that optimal investment is the mechanism by which density-dependent and density-independent selection mold polar life histories. Increased intraspecific density reduces resources available for reproduction, increases the minimum investment threshold, and thereby causes a reduction in brood size. The converse would occur under density-independent selection.

Optimal allocation assumes different phenotypic expressions of parental investment with changes in the availability of resources for reproduction. As pointed out by a referee, this suggests an analysis of the degree of environmental control over allocation decisions. Each genotype has a reaction norm associated with it which specifies the phenotypic expression of that genotype along environmental gradients (e.g., Bradshaw 1965, Gupta and Lewontin 1982, Via and Lande 1985). Knowing how reaction norms evolve will provide much needed insight into the evolution and significance of plastic life histories (Dobson and Murie 1987). Such an analysis for a complex of quantitative traits dealing with resource allocation represents a formidable challenge and would seem to require isolating appropriate genotypes. Investment decisions related to the size and number of offspring may not be tightly linked to those determining the timing of reproduction, the sex of offspring, or behavioral control of preferential post-reproductive parental care.

The next logical step in optimal investment theory is to determine the precise conditions favoring proportional versus preferential investment. Cost-benefit analyses like those of Charnov (1986) hold special promise. Analogous models predict how parents should allocate reproductive resources over their lifetime (e.g., Schaffer 1974b). Empirical and comparative studies should concentrate on how parents actually allocate resources among offspring. For which kinds of species do parents proportionately allocate reproductive investment among offspring? What are the relative rewards of

proportional and preferential allocation to parent and offspring? Are these rewards linked to other life history traits and to environmental variation? Do parents producing large broods tend to allocate investment more evenly than parents with smaller broods? Does the pattern of investment change during the period of parental care as offspring demonstrate their relative abilities at growth and survival? Do asexual species allocate investment more evenly than do sexual species? Most importantly of all, how does juvenile survival vary in response to reproductive allocation?

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