The cost of reproduction: do experimental manipulations measure the edge of the options set?

C.M. Lessells

NIOO, Boterhoeksetstraat 22, PO Box 40, 6666ZG Heteren, Netherlands

ABSTRACT. *The cost of reproduction: do experimental manipulations measure the edge of the options set?.-* The cost of reproduction has often been measured using experimental manipulations, particularly when the goal has been to quantify the exact shape of the relationship in order to predict optimal reproductive strategies which can be tested against reality. However, the correct measurement of the cost of reproduction relies on parents modifying their effort optimally in response to the manipulation assuming that the extra young are their own. While many experiments show that parents do indeed change their effort in a way consistent with the predictions of such an optimality model, other optimality models predicting changes in parental effort are not excluded and in some cases the parental response to brood manipulation seems not to be optimal. This suggests that greater care should be taken in interpreting the results of manipulation experiments, particularly when the exact shape of the trade-off is important.

KEY WORDS. Cost of reproduction, Parental care, Parental effort, Parental investment, Experimental manipulation, Family size

Introduction

Interest in the empirical measurement of the cost of reproduction has centred on two main questions: first, whether there is a cost of reproduction (Alerstam & Högstedt, 1984; Bell & Koufopanou, 1986; Nur, 1988), and second, the extent to which it accounts for the observed reproductive strategies of organisms. The first question requires only that a negative realtionship is demonstrated between current and future reproduction, but the second requires accurate quantification of the form of the relationship because this determines the predicted

optimal reproductive strategy to be tested against reality (fig. 1; Gadgil & Bossert, 1970; Bell, 1980). How one makes such empirical measurements has itself been the subject of considerable and ongoing debate (Reznick, 1985; Partridge & Sibly, 1991; Reznick 1992a, 1992b; Partridge, 1992; Bailey, 1992), but the calculation of genetic correlations and the use of experimental manipulations seem to offer the only potential methods. Of these, it is experimental manipulations that have been used in the majority of attempts to quantify the cost of reproduction (Partridge, 1989; Dijkstra et al., 1990; Lessells, 1991; Moreno, en prensa). This paper addresses the question of whether such experimental
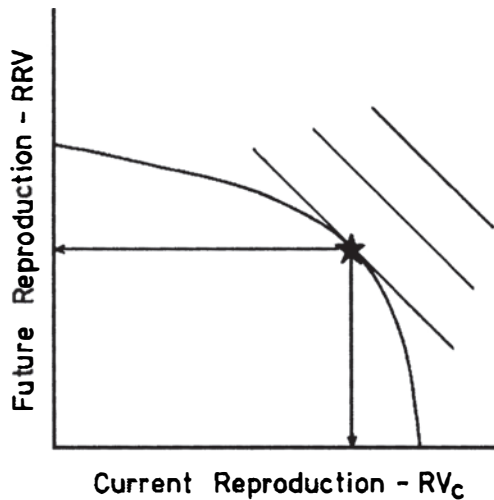
FIGURE 1. The cost of reproduction is the trade-off between current and future reproduction (Williams, 1966). The area under the curve represents possible combinations of current and future reproduction (the 'options set' *sensu* Sibly & Calow, 1986). The cost of reproduction could be represented by plotting any component of future reproduction (e.g. adult survival) against any component of current reproduction while other components are held constant. However, because natural selection is expected to maximize reproductive value (RV)(Williams, 1966; Charlesworth, 1980; Yodzis, 1981), plotting residual reproductive value (RRV) against the reproductive value of the current family (RVc) enables the optimal combination of RRV and RVc (indicated by a star) to be found where the highest line of slope -1 intersects the trade-off curve (Williams, 1966; Pianka & Parker, 1975; Bell, 1980). In constant sized populations, maximizing lifetime reproductive success (LRS) is equivalent to maximizing RV (Charlesworth, 1980; Lande 1982), and the optimal reproductive strategy can be found in the same way by plotting residual reproductive success against current reproductive success.

[El costo de reproducción es el compromiso entre la reproducción actual y futura. El área bajo la curva representa las posibles combinaciones entre la reproducción actual y futura.]

manipulations do indeed correctly determine the shape of this trade-off, or whether more care needs to be exercised in interpreting their results.

Experimental manipulation is needed, rather than measurement of the observed relationship ('phenotypic correlation') between current and future reproductive output because individuals may vary, for instance, in their size, condition or territory quality. Well-endowed individuals may then do well reproductively both now and in the future, leading to an apparently negative cost of reproduction (Perrins & Moss, 1975; Högstedt, 1981; van Noordwijk & de Jong, 1986; Nur, 1988). Experimental manipulation solves this problem because it allocates individuals to different experimental groups randomly, so that on average members of each of the groups are equally well-endowed. Differences between the groups in, for example, future reproduction can then be interpreted as the result of experimentally induced differences, such as current reproduction.

Although experimental manipulation solves the problem of variation in individual circumstances, there is another problem that it does not circumvent. Figure 1 illustrates the cost of reproduction as the trade-off between current and future reproduction. The area under the curve represents possible combinations of values that can be achieved by an individual -the 'options set' (Sibly & Calow, 1986)- and the trade-off bounds this area. The idea of an experimental manipulation is to move individuals along the edge of the options set by increasing or decreasing their current reproduction, record their consequent future reproduction and hence determine the shape of the trade-off. However, experiments do not directly manipulate current reproductive output, they manipulate current family size in the hope that parents will increase their reproductive effort. In other words the change in current and future reproductive output that one observes has not been forced on the organism but is the result of a choice by the parents about how much, if at all, they change their effort. The important point about this

is that a change in effort that is not optimal for the change in family size will move the observed combination of current and future reproduction into the options set and away from the trade-off curve: experimental manipulations will only measure the cost of reproduction correctly when parents change their effort by an optimal amount with respect to the experimental change in family size.

How should parents modify their parental effort in response to experimental changes in family size?

The first step in assessing whether parents do respond optimally in response to experimental manipulations is to predict what the optimal response should be. This requires knowledge of how the efforts of the parents translate into benefits in terms of increased current reproductive success and costs in terms of decreased future reproductive success. Such relationships are rarely known in sufficient detail to predict, for instance, exactly how many worms a parent blackbird should bring or how loudly it should give alarm calls, but general assumptions about the shapes of relationship enable qualitative predictions about responses to brood size to be made. Optimal parental investment will also depend on whether a second parent is investing in the family (Chase, 1980; Houston & Davies, 1985; Winkler, 1987) and will differ between parents and offspring (Trivers, 1974; Charnov, 1982; Lazarus & Inglis, 1986; Godfray, 1991; Godfray & Parker, 1991 & 1992). These complications generated by conflict between the members of a pair or parents and offspring are ignored in this paper which considers the optimal investment from the point of view of a single parent.

In the arguments below, a distinction is made between parental care, parental effort and parental investment. 'Parental care' (PC) is measured in units of what the offspring receive. Thus the biomass of prey delivered to a nest is a measure of parental care. 'Parental effort' (PE) is also a behavioural measure, but this time from the point of view of the parent and how hard it is working. Thus parental effort might be measured in time or energy expended. 'Parental investment' (PI) is not only defined as anything done by the parent for the offspring that increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring (Trivers, 1972), but is also measured in units of decrease in future reproductive output (residual reproductive value)(see Trivers, 1974; fig.3). Under these definitions, the contribution of each offspring to the reproductive value of the current brood (RV_0) is likely to show diminishing returns from increasing parental care, at least at higher levels of care. The relationship will therefore be montonically increasing with a decreasing slope or sigmoidal (fig. 2a; Smith & Fretwell, 1974; Nur, 1984; Lazarus & Inglis, 1986; Winkler, 1987). Because the relationships between parental effort and parental care, and parental investment and parental effort are likely to be accelerating functions (fig. 2b and fig. 2c; Nur, 1984; Lazarus & Inglis, 1986; Winkler & Wallin, 1987), the relationships between RV_0 and both parental effort and parental investment are likely to be of the same form as the relationship between RV_0 and parental care. Moreover, because care, effort and investment are monotonically related, qualitative predictions made in one unit will hold true in the other units.

The way in which optimal investment varies with brood size also depends on the way in which the benefits of parental care are divided between the family members. Lazarus & Inglis (1978, 1986) distinguish between 'shared' investment, in which the benefit of parental care (for instance food brought to a brood) is received by only one offspring and 'unshared' investment, in which all the offspring may gain simultaneously from the same parental care (for instance parental vigilance for predators). Unshared investment may in turn protect
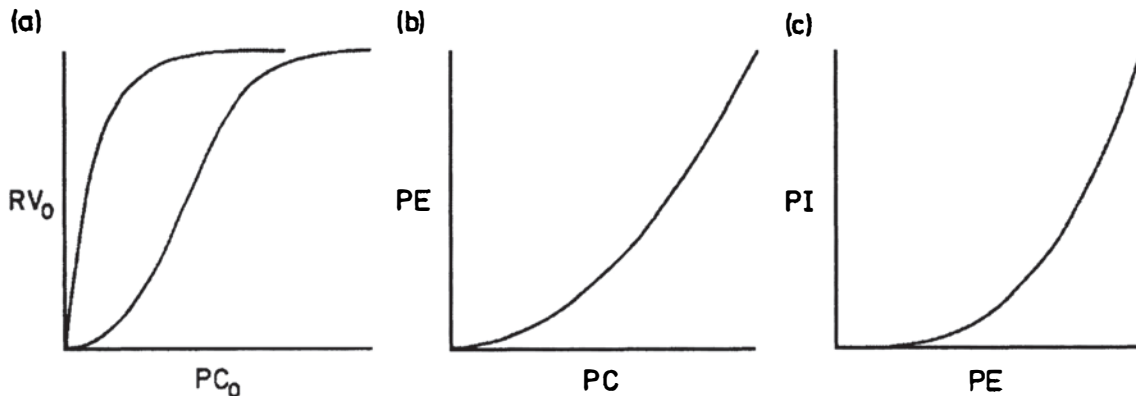
FIGURE 2. The probable shapes of relationships between (a) reproductive value of each of the current family (RVo) and the parental care that it receives (PCo), (b) parental effort (PE) and total parental care in the family (PC), and (c) parental investment (PI) and parental effort (PE).

[Formas probables de relaciones entre (a) valor reproductivo de cada miembro de la familia actual (RVo) y el cuidado parental que recibe (PCo), (b) esfuerzo parental (PE) y cuidado parental total en la familia (PC), e (c) inversión parental (PI) y esfuerzo parental (PE).]

against 'brood loss' (Lazarus & Inglis, 1978) where the total benefit of a given amount of parental care increases in direct proportion to the family size (e.g. when a predator would take the whole family if it found it), or against 'fixed loss' where the total benefit is independent of brood size (e.g. when a predator always takes a single offspring). In reality, any kind of parental care will rarely fall neatly into one of these categories, but this paper considers each of the three categories separately. Moreover, if all forms of investment were unshared, the optimal family size would be infinite. However, while this implies that some element of parental investment must always be shared, in manipulation experiments the manipulation may have taken place after that stage in the life cycle and the remaining investment approximate to being unshared. The predictions made below therefore include the unshared case.

A number of authors (Nur, 1984; Lazarus & Inglis, 1986; Winkler, 1987; Kacelnik & Cuthill, 1990) have made various analyses predicting optimal investment in relation to family size when parental care is divided equally between offspring.

One method is to plot the reproductive value of the current family (RV_c) against parental investment (PI)(fig. 3a). This curve is the benefit in RV units in relation to PI. In addition, because of the way in which PI is defined, a line of slope 1 through the origin is the cost in RV units in relation to PI. Optimal PI occurs where benefit minus cost is maximized, which is where the highest line of slope 1 intersects the RV_c curve.

This simple graphical method also gives the net benefit of any level of PI as the intercept on the y axis of a line of slope 1 through the corresponding point on the RV_c curve (except in the case of fixed loss unshared investment, when the net benefit is this intercept minus the intercept of the RV_c curve). This allows three special cases to be examined: first, if the intercept of the tangent of slope 1 to the RV_c curve is negative, making no PI at all would give a higher net benefit, and the family should be abandoned (fig. 3b). Second, if the RV_c curve never reaches a slope of 1, all intercepts of lines of slope 1 through points on the RV_c curve will be negative and the brood should be abandoned (fig. 3c). Third,
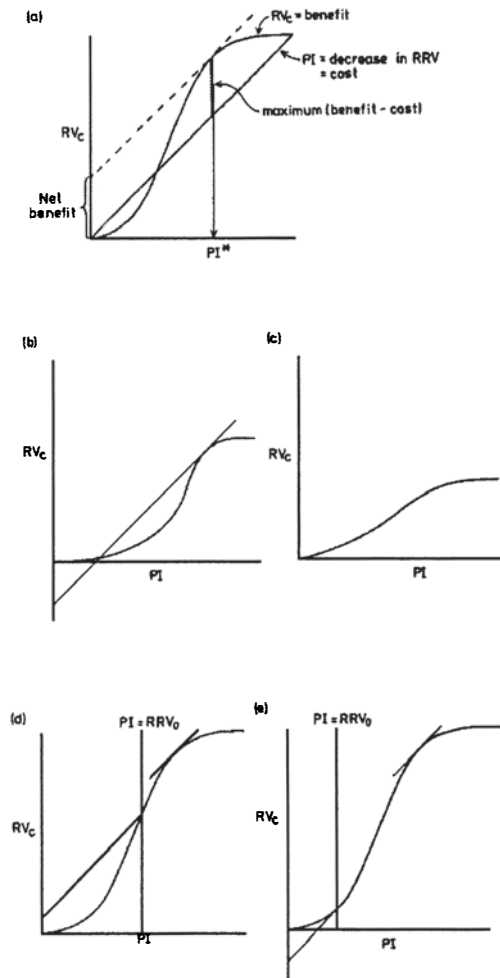
there is a maximum possible value of PI equal to the residual reproductive value when no PI is made (RRV0). If the theoretically optimal PI is above this level, the optimal behaviour depends on the intercept of the line of slope 1 through the intersection of the RVc curve with the line PI=RRV0. If this is greater than zero, the optimal level of PI is RRV0, in other words catastrophic investment leading to a residual reproductive value of zero (fig. 3d). If the intercept is below zero, the family should be abandoned (fig. 3e).

The graphical model and the results of the previous analyses can now be used to review the predicted changes in PI with brood size (fig. 4; table I), in particular how overall investment and care per chick should change in response to experimental manipulation, and whether manipulation should ever lead to abandonment of the family. The models predict that total PI in the brood should increase in the shared or unshared-brood loss cases, and remain constant in the unshared-fixed loss case. At the same time, the parental care received per chick (and hence their individual RV) should decrease in the shared case, increase in the unshared-brood loss case, and remain constant in the unshared-fixed loss case. The predictions over when broods should be abandoned also differ between the cases. Experimentally enlarged or reduced families may be deserted in the shared case, only experimentally reduced families in the unshared-brood loss case, and neither in the unshared-fixed loss case.

FIGURE 3. A graphical method of finding the optimal parental investment in the current family. (a) If the reproductive value of the current family (RVc) is plotted against parental investment in the family (PI), optimal PI (PI*) is found where the highest line of slope 1 (dashed line) intersects the curve. This is because optimal PI maximizes $RV = RVc + RRV$. By definition, PI is the reduction in RRV below the RRV if no current investment were made (RRV0); i.e. $RV = RVc + RRV0 - PI$. Optimal PI is found where dRV/dPI is zero; i.e. where $dRVc/dPI = 1$. (b) If the tangent to the curve of slope 1 (dashed line) has a negative intercept with the y axis, net benefit (RVc - PI) is higher when PI is zero and the family should be abandoned. (c) If the RVc curve never reaches a slope of 1, net benefit is again maximized when PI is zero and the family should be abandoned. (d) If the theoretically optimal PI is above RRV0 and the intercept of the line of slope 1 through the intersection of the RVc curve and the line PI=RRV0 is positive, the optimal PI is RRV0. (e) If the intercept is negative the optimal PI is zero, and the family should be abandoned.

[Un método gráfico para obtener la inversión parental óptima en la familia actual.]

TABLE I. Qualitative predictions made by models of optimal parental investment of responses to experimental manipulation of family size when parents treat extra young as their own.
[Predicciones cualitativas realizadas por modelos de inversión parental óptima de respuestas a manipulación experimental del tamaño de la familia cuando los padres tratan al jóven extra como suyo.]

Type of Investment	Response to enlarged family[1]:		Abandon enlarged family?	Abandon enlarged family?	Authority
	PI	PCo			
Unshared-brood loss	+	+	Never	Sometimes	Tait, 1980; Taborsky, 1985; Lazarus & Inglis, 1986 figure 4
Unshared-fixed loss	0	0	Never	Never	Lazarus & Inglis, 1986 figure 4
Shared	+	-	Sometimes	Sometimes	Nur, 1984; Lazarus & Inglis, 1986; Mock & Parker, 1986; Winkler, 1987; Kacelnik & Cuthill, 1990 figure 4

1: Predicted response to an enlarged family, unless abandonment is favoured. PI = parental investment in the entire family. PCo = parental care per offspring. + = increases. 0 = no change. - = decreases.

How do parents modify their parental effort in response to experimental changes in family size?

Manipulation experiments investigating changes in parental effort in relation to family size have been conducted mainly in fish, where parental effort in terms of clutch or brood defence has been measured, and birds, where energy expenditure during incubation, nest defence and brood provisioning rate have been investigated (Table II). The majority of these studies show that parental effort increased with manipulated family size. The proportion of species showing an increase in PE with family size does not differ markedly between studies of clutch or brood defence in fish (80%; n=5), clutch or brood defence in birds (70%; n=5), incubation in birds (100%; n=4), and brood provisioning in birds (86%; n=18). A few of the studies showed no increase in parental effort with family size (Robertson & Biermann, 1979; Winkler, 1985, 1991; Gard & Bird, 1990; Fitzgerald & Caza, 1993) or an asymptote in parental effort at higher family sizes (Leffelaar & Robertson, 1986; Smith et al., 1988; Török & Toth 1990; Beissinger, 1990; Wright & Cuthill, 1990a). In no case was there a decrease in parental effort with increasing family size.

The studies of brood provisioning in birds also allow the relationship between parental care per offspring (PCo) and brood size to be investigated. In general PCo decreased (Hussell, 1972; Henderson,
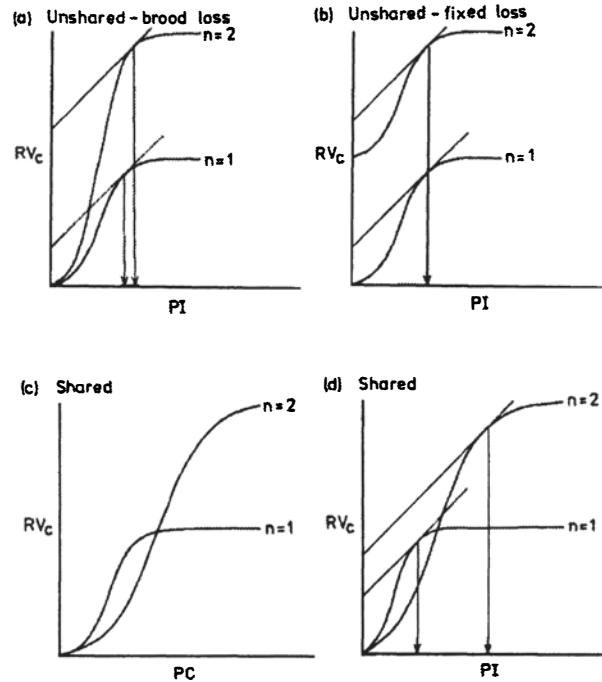
FIGURE 4. Optimal parental investment in relation to experimentally manipulated family size. (a) Unshared-brood loss: RVc for any value of PI is the product of family size (n) and RVo at that PI. As a result, the slope of the RVc curve is n times the slope of the RVo curve ($dRVc/dPI = n.dRVo/dPI$). Because the curve is convex up (d^2RVc/dPI^2 is negative), the value of PI for which the RVc curve has a slope of 1 will increase with n; in other words, optimal PI increases with family size. Moreover as the intercept of the line of slope 1 increases with increasing n, even when PI is constrained by RRV0, experimentally enlarged families should never be abandoned, but experimentally reduced families may be abandoned. (b) Unshared-fixed loss: RVc for any value of PI is RVo for that value of PI plus (n - 1) times the asymptotic value of RVo. Thus the RVc curve always has a slope of 1 at the same value of PI, and optimal PI does not vary with family size. Moreover, because net benefit of PI (the intercept of the tangent to the curve of slope 1 minus the intercept of the RVc curve) does not vary with family size, families should not be abandoned in response to experimental enlargement or reduction. (c) Shared: when RVc is plotted against total parental care in the family (PC), curves for different family sizes are of exactly the same shape, but differ in scale. This is because each offspring in a family of size n will contribute the same RV as an offspring in a family of 1 if the larger family receives n times as much PC. At this level of PC, RVc of the larger family will also be n times larger. (d) These RVc versus PC curves can be transformed into RVc versus PI curves by rescaling the x axis. Each part of the x axis must be rescaled by a factor equal to the slope of the PI versus PC curve. This reduces the slope of the RVc curve by the same factor. If the PI versus PC curve is accelerating (fig. 2), points on the RVc curve representing the same PC per offspring will have lower slope with increasing family size, but the RVc curve will reach any given slope at a higher value of PI with increasing family size. Hence optimal PI increases, but optimal PC per offspring decreases, with increasing family size. Whether the intercept of the line of slope 1 increases or decreases with family size depends on the shapes of the RVc versus PC, and PI versus PC curves. Thus an experimental reduction in family size may lead to a negative net benefit and abandonment. Enlargement of family size will always eventually lead to one of the three conditions for abandonment (fig. 3b, 3c and 3e).

[Inversión parental óptima en relación al tamaño de la familia manipulado experimentalmente.]

1975; Robertson & Biermann, 1979; Cronmiller & Thompson, 1980; Nur, 1984; Leffelaar & Robertson, 1986; Beissinger, 1990; Carey, 1990; Dijkstra et al., 1990; Török & Toth, 1990; White et al., 1991; Martins & Wright, 1993a) or remained constant (Tarburton, 1987), and never increased in enlarged broods.

The models of optimal PI also predict that experimentally manipulated broods may be abandoned. While abandonment rarely follows experimental enlargement of families (Andersson & Eriksson, 1982), and may be interpreted in other ways (see below), abandonment of experimentally reduced families is not uncommon (Ward, 1965; Rothstein, 1982; Mrowka, 1987; Armstrong & Robertson, 1988; Beissinger, 1990; Winkler, 1991). Families are also sometimes deserted after natural partial losses (Tait, 1980; Mock & Parker, 1986).

Other explanations for modifications in parental effort in response to experimental changes in family size

The above review shows that parents do indeed modify their parental effort in a way predicted by models of optimal parental investment, and hence suggest that the relationship between current and future reproduction measured by such experiments is the true cost of reproduction. However, a fit with qualitative predictions does not carry great weight, and this section considers other explanations for the observed responses. Any of these would alter the optimal pattern of PI away from that predicted above, and hence move the measured values of current and future reproduction away from the edge of the options set.

In making experimental manipulations to measure the cost of reproduction, the aim is to discover how successful those parents would have been if they had produced the extra young themselves. The predictions of optimal PI made

above are therefore also based on them behaving as though they had produced the extra young themselves. Thus the predictions made above assume that the parents are aware of the increase in family size but still treat all the young as their own.

One alternative is that parents are aware of the increase in family size but treat the extra young as the result of intra-specific brood parasitism (IBP). This is especially true for females, who are likely to have better information than males about the original family size. The model described above can be used to predict optimal PI if extra young are treated as the result of IBP (fig. 5). If added young are the result of IBP, the value of RV_c is reduced to a fraction n_{own}/n_{exp} of its value if all the young were the parent's own (where n_{own} is the family size produced by the parent and n_{exp} is the experimentally manipulated family size), and the slope of the RV_c versus PI curve will be reduced by the same amount. In the unshared-brood loss case, this makes the RV_c versus PI curve coincide exactly with that for the unmanipulated family. Thus parents should not change their PI in response to experimental changes in family size (rather than increasing it), and manipulated families should never be abandoned. In the unshared-fixed loss case, the slope of the RV_c curve will be reduced, and hence the optimal PI will be reduced (rather than remaining constant) when families are enlarged. The net benefit of PI decreases (although RV_c at PI* increases) and the slope of the RV_c curve is reduced so abandonment may be favoured (fig. 3b and 3c); this is because the parasitic young dilute the probability that a predator will take the parent's own young to an extent that it is not worth the cost for a parent to try and protect its family. In the shared case, the slope of the RV_c will also be reduced. The optimal PI in response to family enlargement will be increased, but not as much as if the extra young were the parent's own. Net benefit is reduced at the new optimal PI value and the slope of the RV_c curve is reduced, so abandonment becomes more likely. Thus the qualitative predictions about PI are

TABLE II. Changes in parental effort in response to experimental manipulation of family size.
[Cambios en el esfuerzo parental en respuesta a la manipulación experimental del tamaño de la familia.]

Species	PE[1]	Authority
Defence of eggs/fry		
blue gourami *Trichogaster trichopterus*	+	Kramer, 1973
a cichlid *Aequidens coeruleopunctatus*	+	Carlisle, 1985
bluegill sunfish *Lepomis macrochirus*	+	Coleman et al., 1985
smallmouth bass *Micropterus dolomieui*	+	Ridgway, 1989
threespine stickleback *Gasterosteus aculeatus*	0	Fitzgerald & Caza, 1993
Incubation energy expenditure		
starling *Sturnus vulgaris*	+	Biebach, 1984
blue tit *Parus caeruleus*	+	Haftorn & Reinertsen, 1985
pied flycatcher *Ficedula hypoleuca*	+	Moreno & Carlson, 1989
collared flycatcher *Ficedula albicollis*	+	Moreno et al., 1991
Nest defence		
redwinged blackbird *Agelaius phoeniceus*	+/0[2]	Robertson & Biermann, 1979
American goldfinch *Carduelis tristis*	+	Knight & Temple, 1986
great tit *Parus major*	+	Windt & Curio, 1986
tree swallow *Tachicyneta bicolor*	0	Winkler, 1991
Canada goose *Branta canadensis*	+	Wiacek in Sjöberg, 1994
Brood provisioning rate		
pied flycatcher *Ficedula hypoleuca*	+	von Haartman, 1954
snow bunting *Plectrophenax nivalis*	+	Hussell, 1972
glaucous-winged gull *Larus glaucescens*	+	Henderson, 1975
redwinged blackbird *Agelaius phoeniceus*	+	Robertson & Biermann, 1979
	+	Cronmiller & Thompson, 1980
brewer's blackbird *Euphagus cyanocephalus*	+	Patterson et al., 1980
blue tit *Parus caeruleus*	+	Nur, 1984
California gull *Larus californicus*	0	Winkler, 1985
tree swallow *Tachicyneta bicolor*	+/0[3]	Leffelaar & Robertson, 1986
house sparrow *Passer domesticus*	+	Hegner & Wingfield, 1987
white-rumped swiftlet *Aerodramus spodiopygius*	0/+[4]	Tarburton, 1987
great tit *Parus major*	+/0[3]	Smith et al., 1988
snail kite *Rostrhamus sociabilis*	+[5]	Beissinger, 1990
field sparrow *Spizella pusilla*	+	Carey, 1990
kestrel *Falco tinnunculus*	+	Dijkstra et al., 1990
American kestrel *Falco spaverius*	0	Gard & Bird, 1990
collared flycatcher *Ficedula albicollis*	+[6]	Török & Toth, 1990
starling *Sturnus vulgaris*	+[7]	Wright & Cuthill, 1990a, 1990b
	+	White et al., 1991
eastern phoebe *Sayornis phoebe*	+	Conrad & Robertson, 1992
swift *Apus apus*	+	Martins & Wright, 1993a

1: Sign of the correlation between the amount of PE and manipulated brood size. 2: + for egg defence, 0 for chick defence. 3: + for decreased broods, 0 for increased broods. 4: 0 between broods of 1 and 2, + between broods of 2 and 3. 5: reached plateau at high brood sizes. 6: reached plateau in experimentally increased broods. 7: reached plateau at high brood sizes in mates of experimentally handicapped birds

TABLE III. Qualitative predictions made by models of optimal parental investment of responses to experimental enlargement of family size when the enlargement is due to intra-specific brood parasitism.
[Predicciones cualitativas realizadas por modelos de inversión parental óptima, de respuestas al aumento experimental del tamaño de la familia, cuando dicho aumento se debe a parasitismo de incubación intraespecífico.]

Type of investment	Response to enlarged family[1]:		
	PI	PCo	Abandon family?
Unshared-brood loss	0	0	Never
Unshared-fixed loss	-	-	Sometimes
Shared	+		Sometimes

1: Predicted response to an enlarged family, unless abandonment is favoured. PI = parental investment in the entire family. PCo = parental care per offspring. + = increases. 0 = no change. - = decreases.

changed if the parent interprets additional young as the result of IBP rather than its own. However, the range of responses predicted overall for both shared and unshared cases does not change greatly (compare tables I and III). The only new prediction is that PI should decrease in the unshared-fixed loss case. Thus our ability to distinguish whether a parent is behaving as though added young are its own or the result of IBP depends either on knowledge of the type of PI involved, or on unshared-fixed loss investment. In reality, any kind of PC is likely to have shared and unshared elements, so that this discrimination is unlikely to be possible.

While family enlargements cannot naturally occur unless some of the young are not the parent's own, this is not the case for reductions in family size. However, the disappearance of some eggs or young may affect RVc not only directly by changing family size but because the future prospects of the family have changed: families that have suffered

partial predation may be at greater risk of predation in the future either because individual predators return later to finish off the family, or because a partial loss indicates that the family is more vulnerable to predation, for instance because of the part of the habitat that it is in, than an average family. In such circumstances it may pay a parent to reduce investment in the current family over and above the reduction expected on the basis of the change in family size. Similarly, goldeneye *Bucephala clangula* females may desert when seven eggs are added to their clutch simultaneously because such a high level of nest parasitism would normally indicate that the nest had a high chance of failure through interference by other females (Andersson & Eriksson, 1982). In both of these cases it is assumed that parents are aware of the change in family size, but respond to it by making new estimates of environmental risks which then affect their optimal strategy.

Lastly, parents may be unaware of a change in family size but still respond to the manipulation by changing their estimate of environmental suitability. For instance, a parent bird feeding its chicks may perceive an experimental manipulation as an increase in how hard it has to work to satiate its chicks. Such an increase in exertion might normally imply a deterioration in the environment, and the parents should then respond according to the effects that environmental deterioration usually has on the relationships between the reproductive value of a chick and the care it receives, and between the RRV of a parent and its effort. Depending on these relationships, the change in optimal PI can vary not only in magnitude, but also in direction (Carlisle, 1982). If environmental deterioration affects the parents' or offsprings' prospects independently of parental effort (for instance by affecting overwinter survival), then the optimal change in PI depends on the relative effects on parents and young (Horn, 1978). In any case the optimal response by the parents can easily encompass the observed responses to experimental manipulation.

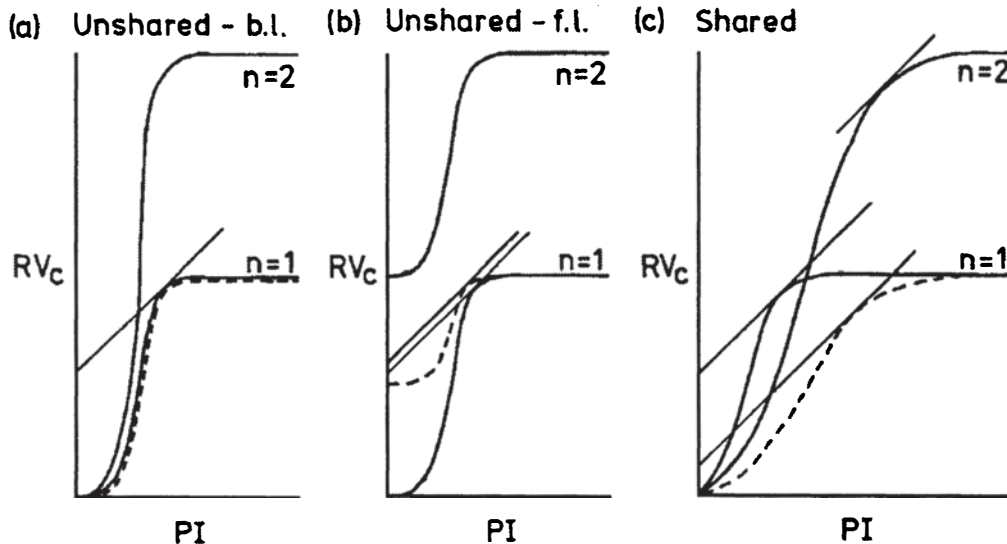## (a) Unshared – b.l. (b) Unshared – f.l. (c) Shared

FIGURE 5. Optimal parental investment in relation to experimentally manipulated family size when added young are treated as the result of intra-specific brood parasitism. (a) Unshared-brood loss: experimental manipulation of the family increases the total RV of the family by a factor nexp/nown (where nexp is the family size after manipulation, and nown is the family size before manipulation), but only a proportion nown/nexp are the parent's own chicks. Thus the RV of the current family to the parent (dashed line) remains unchanged, and hence optimal PI is unchanged. (b) Unshared-fixed loss: experimental manipulation increases the total RV of the family by an amount (nexp - nown) times the asymptotic value of Ro, but only a proportion nown/nexp are the parent's own chicks. As a result, the slope of the RVc curve is lowered throughout, optimal PI is decreased, and enlarged families may be abandoned because the net benefit of PI becomes negative (see fig. 3b and c). (c) Shared: experimental manipulation changes the total RV of the family as shown in fig.3 c and d, but only a proportion nown/nexp are the parent's own offspring. As a result, the optimal PI is higher than for the original unparasitized family, but lower than for a family of the same overall size size but containing no parasitic young. The amount of parental care received by each offspring is likewise less than in a family of the same overall size containing no parasitic young, and even lower than in a family of the original unparasitized size.

[Inversión parental óptima, en relación al tamaño de la familia manipulado experimentalmente, cuando los jóvenes añadidos son tratados como resultado del parasitismo de incubación intraespecífico.]

Do parents modify their parental effort in response to experimental manipulations in a way that correctly delineates the cost of reproduction?

The above section shows that, while the observed responses to experimental manipulation are consistent with parents noticing the extra young but treating them as their own, there are other ways in which the parents might be responding which would also predict similar responses to experimental manipulation. Unfortunately, there are no studies which distinguish unequivocally between the possibilities. However, goldeneye females desert their broods earlier when the brood is smaller at the time of desertion or has suffered higher mortality. When each of these two correlated variables is

controlled for using partial correlation, only the relationship with previous mortality remains. One interpretation of these results is that females are changing their estimate of the future survival prospects of the brood, rather than reacting solely to the effect of brood size *per se* on the RV of the brood (H. Pöysä & J.Virtanen , pers. comm.).

In addition, we can ask whether there are other aspects of the response to manipulated brood size which appear not to be optimal. The models of parental effort presented above assumed that parents invest equally in all the young, but this may not always be the best strategy (O'Connor, 1978). It might, for instance, pay parents to ignore some of the extra young, even if they believe them to be their own. That parents would have done better by rejecting some of the enlarged family seems to be the case in about 20% of bird species in which manipulation experiments have been carried out (review by Dijkstra et al., 1990); in these species parents with experimentally enlarged families fledged fewer young than controls and therefore would have done better by ejecting at least some of the extra young (or using some less drastic method of brood reduction; e.g. Martins & Wright, 1993b), even if the extra young were the result of IBP and the parents could not recognize their own offspring. The measurements of current and residual reproductive value for parents of these families must lie at some point in from the edge of the options set.

Conclusions and prospects

Experimental measurements of the cost of reproduction rely on the asumption that parents modify their parental effort optimally and as if the extra young were there own. In many cases parents do modify their effort in a way that is consistent with the qualitative predictions of models making these assumptions. However, optimality models making other assumptions produce predictions which are similar, and in some cases parents would have done better by a strategy of brood reduction than by attempting to raise the extra young. Thus we should be wary of accepting uncritically that the current and residual reproductive values revealed by experiments lie at the edge of the options set on the trade-off curve.

Given these difficulties of interpretation, what other approaches are possible? One option is to look in more detail at the rules by which parents decide on their level of PE. Natural selection should equip parents with rules that enable them to modify their effort in appropriate ways in response to events normally met. In some ways it would be surprising if, for instance, parent birds did modify PE in a way that was optimal if extra young were there own. Determining which cues parents are sensitive to might give some insight into the way in which rules about investment are shaped. Recent studies have investigated how parent birds provision broods in relation to the begging behaviour of chicks (e.g. Bengtsson & Ryden, 1983; Redondo & Castro, 1992). Similar studies could be used to investigate whether parents are sensitive to brood size *per se*, or respond only indirectly through changed levels of hunger and begging by the chicks.

The second option is to measure the relationships between RV_0 and PC, and between PC, PE and PI, rather than attempting to measure the relationship between current and residual reproductive value without the intervening variables. Such an approach has been taken by Daan et al. (1990) in their study of kestrels *Falco tinnunculus*. They measured the relationships between PC in terms of prey caught and PE in terms of flight time, and residual RV and PE. In essence they were then able to use these to calculate the position of the trade-off curve rather than measuring it directly. The predictions they made of optimal clutch size and laying date on the basis of these calculations were remarkably close to the observed values. They did

not, however, measure all three of the relationships in figure 2: they assumed that chicks required a fixed amount of food to fledge successfully. In principle there is no reason why this relationship should not also be measured and incorporated into the model.

To a large extent the two approaches suggested above are extensions rather than alternatives to direct measurements of the relationship between current and residual reproductive value. Despite the problems, the direct measurements have yielded considerable insights into both the components of fitness in which the costs of reproduction are paid and the ecological and physiological causes of costs of reproduction. The purpose of this paper is therefore not to dissuade experimenters from carrying out such experiments, but to suggest that greater care should be taken in interpreting the measured current and residual reproductive values as delineating the trade-off that is the cost of reproduction.

Summary

The cost of reproduction (fig. 1) has often been measured using experimental manipulations, particularly when the goal has been to quantify the exact shape of the relationship in order to predict optimal reproductive strategies which can be tested against reality. However, the correct measurement of the cost of reproduction relies on parents modifying their effort in an optimal fashion in response to the manipulation assuming that they treat the extra young as their own. By making certain assumptions concerning the relationships between the reproductive value of an offspring (RV_o), parental care (PC), parental effort (PE) and parental investment (PI) (fig. 2), it is possible to predict how parents should modify their parental investment in response to experimental manipulations (figs. 3 & 4; table I). While many experiments show that parents do indeed change their effort in a way consistent with the predictions of this optimality model (table II), other optimality models (e.g. fig. 5; table III) predicting changes in parental effort are not excluded and in some cases the parental response seems not to be optimal. This suggests that greater care should be taken in interpreting the results of manipulation experiments, particularly when the exact shape of the trade-off is important.

Resumen

El costo de la reproducción: ¿miden las manipulaciones experimentales la realidad de las opciones establecidas?

El costo de la reproducción (fig. 1) ha sido a menudo medido usando manipulaciones experimentales, particularmente cuando el fin era cuantificar la forma exacta de la relación, con objeto de predecir las estrategias reproductivas óptimas, que pueden ser testadas con la realidad. Sin embargo, la medida correcta del costo de la reproducción se basa en que los padres modifiquen su esfuerzo, de forma óptima, en respuesta a la manipulación, asumiendo que tratan al joven extra como si fuera suyo. Haciendo ciertas suposiciones sobre la relación entre el valor reproductivo de una prole (RV_o), el cuidado parental (PC), el esfuerzo parental (PE) y la inversión parental (PI) (fig.2), es posible predecir cómo los padres deberían modificar su inversión parental en respuesta a las manipulaciones experimentales (fig.3 y tabla I). Aunque muchos experimentos muestran que los padres en realidad cambian su esfuerzo de acuerdo con las predicciones de este modelo (tabla II), no se excluyen otros (por ejemplo fig. 5; tabla III) y en algunos casos la respuesta de los padres parece no ser óptima. Esto sugiere que los experimentos de manipulación deben interpretarse con mas cuidado, especialmente cuando la forma exacta del compromiso es importante.

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