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Physiological mechanisms underlaying reproductive trade-offs

J. Moreno

Museo Nacional de Ciencias Naturales-CSIC, J. Gutierrez Abascal 2, 28006 Madrid, Spain

ABSTRACT. *Physiological mechanisms underlaying reproductive trade-offs*.- The existence of trade-offs between fecundity and survival is central to theories of life-history evolution. Comparisons of life history traits of individuals in different unmanipulated situations show that mere correlations cannot detect reproductive costs. Experimental studies show that phenotypic plasticity in fecundity is adaptive, as individuals in some populations optimize reproductive investment in relation with enviromental conditions. In some experiments, the survival costs are not paid by parents but by offspring, when parental effort does not increase sufficiently in response to offspring demand. The level of parental effort may be constrained below offspring requirements by physiologycally determined survival costs. Some experiments include only certain, presumably more costly breeding phases. However, evaluation of the complete reproductive cycle is necessary as costs of exertion during consecutive phases may accumulate. In breeders where costs are paid after reproducing, there is growing evidence that energetic work level is constrained below a short-term sustainable maximum, and that increased energy expendidure may decrease survival prospects. One proximate mechanism may be effected by observed delays and contractions in postreproductive events like moult and migration in birds. The effects of hormones on reproductive investment on one hand and on antiparasite resistance on the other may also be involved. Nutritional resources used in reproduction may be taken from those necessary for immune system maintenance. Deterioration of performance late in life (senescence) may be linked to increased levels of parental effort early in life, and thus express the existence of reproductive costs. We must presently focus on studies in energetics, endocrinology, immunology, parasitology, etc., which may explain how phisiology mediates the genetic correlations determining life history evolution.

KEY WORDS. Life history evolution, Fecundity, Survival, Reproductive costs, Parental effort, Phenotypic plasticity, Energy expenditure, Hormones, Antiparasite resistence, Immune system, Senescence, Physiology

Introduction

To any layman, the question if reproduction should be costly in a general sense seems trivial. The obvious answer is, of course, that it should be. Nothing in life is for free. However, in life-history evolution the question is more complex (Stearns, 1991). Given that animals cannot allocate unlimited resources to reproducing and surviving at the same time, how operate the trade-offs between these and related determinants of fitness and are they effecting the observed patterns of age-specific fecundities and intrinsic mortalities?

I will only consider here one of the possible ways in which present reproductive investment may affect subsequent survival and reproduction, namely physiologically. The so-called ecological costs, like increased risks of predation (Shine, 1980; Magnhagen, 1991), will not be discussed here. The clear avian bias in my exposition is only partly due to my background. Most field experiments dealing in detail with reproductive costs have been performed on birds for practical reasons. I will try to discuss other animal taxons whenever possible.

Initially, most students of animal life histories went to the field and compared the fecundities and subsequent survival patterns of individuals in their study populations. The phenotypic correlations thus obtained seldom reflected any trade-offs. Typically, the correlations found were not negative but positive (Petersen, 1992) or not significant (Michener & Locklear, 1991; Waser & Jones, 1991). Sometimes negative correlations or negative effects of reproduction are only apparent in certain years (Laurie & Brown, 1990; Festa-Bianchet & King, 1991). Theoretically one should not expect trade-offs to be found when comparing individuals with different resource levels (vanNoordwijk & deJong, 1986; Lessells, 1991). Some authors control for variables like adult size and habitat as expressions of resource levels (Morris, 1992). However, there are other possible factors affecting resource availability like territory quality (Högstedt, 1980), individual experience (Ainley et al., 1983) and condition due to maternal effects (Schluter & Gustafsson, 1993), which are more difficult to control.

The interpretation of life-history theory which predicted when comparing two stable populations that, if one had higher fecundity it should also present lower adult survival, has been found to be too simple (Sutherland et al., 1986). Other life-history traits than adult survival (age at maturity, juvenile survival, etc.) may be involved in trade-offs against fecundity (Karr et al., 1990; Blondel et al., 1992). Although some studies have reported survival costs (Dufresne et al., 1990), costs in reduced growth (Ryser, 1989) or future fecundity costs (Orell & Koivula, 1990), the consensus is slowly being reached that only experimental manipulations can reveal trade-offs by displacing individuals from their resource allocation phenotype (Lessells, 1991).

The experimental approach

An increasing number of field or laboratory experiments in which parental reproductive effort is manipulated have been performed in the last decades. One should bear in mind before considering the evidence for or against the existence of costs, that present trends in editorial work by scientific journals tends to bias the number of reports in favor of positive or confirmative studies. If experiments do not detect costs, the articles tend to be depreciated, leading to the question of how many studies not showing any costs (sometimes called inconclusive by editors) are tucked away in drawers.

Recent reviews of field experiments done by enlarging and reducing brood size in birds (Lindén & Møller, 1989; Dijkstra et al., 1990; Lessells, 1991) have shown that frequently parents do not suffer survival or future fecundity costs. Normally it is the chicks that suffer in enlarged broods (Hegner & Wingfield, 1987; Wiggins, 1990; Török & Toth, 1990; Källander & Smith, 1990). Graves (1991) has raised the point that sample sizes in these experiments are often insufficient to detect survival costs. In a recent study on birds claiming not to have found survival costs in adults, sample sizes in the enlarged and reduced groups were less than ten individuals (Wheelwright et al., 1991). In the only published field manipulation on mammals, sample sizes in the enlarged and control groups were 4 and 6 (Hare & Murie, 1992). Analyzing the frequency of occurrence of significant trade-offs and of negative trade-offs, we can see that negative trade-offs are significantly more common than positive ones, and that differences in the frequencies of trade-offs affecting parents and offspring reported earlier are not apparent when only considering the sign of the correlations (table I).

Another question raised by the absence of survival costs is if parents have responded sufficiently to the experimental manipulation. It is clear from some studies that parents are not responding to the manipulation by adjusting effort to nestling demand (Korpimäki, 1988). This is observed as a decelerating function of feeding frequency with brood size with a plateau for enlarged broods (Smith et al., 1988; Källander & Smith, 1990; Török & Toth, 1990). Linear increases in feeding frequency with brood size are rarer (Nur, 1984). Plateaus in parental effort may be explained by the dependence of offspring survival on parental survival before juvenile independence (Tuomi, 1990). Parental care may have evolved to avoid survival costs for parents during reproduction. Another related explanation is that postreproductive survival may drop precipituously and not linearly after a certain threshold in parental effort (Drent & Daan, 1980). In any case, survival costs for adults may be rarely observed because parental response is constrained by the risks involved in surpassing thresholds in work or exertion. These constraints are thus limiting fecundity without becoming apparent in experiments. Their consequence is that offspring fare less well in enlarged broods. It is only when parents respond linearly to offspring demand that survival costs can be expected. To negate the existence of reproductive costs when offspring suffer the consequences of parental reluctance to increase their work level (e.g. Pettifor et al., 1988) seems inappropriate, as the sacrifice in current reproduction to favour increased future prospects is evidence for a reallocation of resources between reproduction and survival (Lessells, 1991; Hochachka, 1992; Boggs & Ross, 1993). It is necessary to point out that some direct measure of parental effort should be used

TABLE I. The effect of sample size on the significance of trade-offs and the percentages of trade-offs which were significant resp. negative in experimental studies of reproductive costs in birds published up to 1990 (from Møller and Lindén, unpublished).

[El efecto del tamaño de muestra sobre la significación de los trueques, y el porcentaje de trueques que fueron significativos o negativos resp. en estudios experimentales de costes reproductivos en aves publicados antes de 1990.]

Sample size in significant trade-offs	nonsignificant trade-offs
99 + 81 (19)	48 + 39 (79)

Mann-Whitney U-test: z=2.27 P=0.023

	Significant trade-offs		Negative trade-offs
Total	38 %	(94)	78 %
Adult survival	6 %	(16)	75 %
Adult fecundity	50 %	(62)	76 %
Parents	28 %	(67)	85 %
Offspring	63 %	(27)	79 %

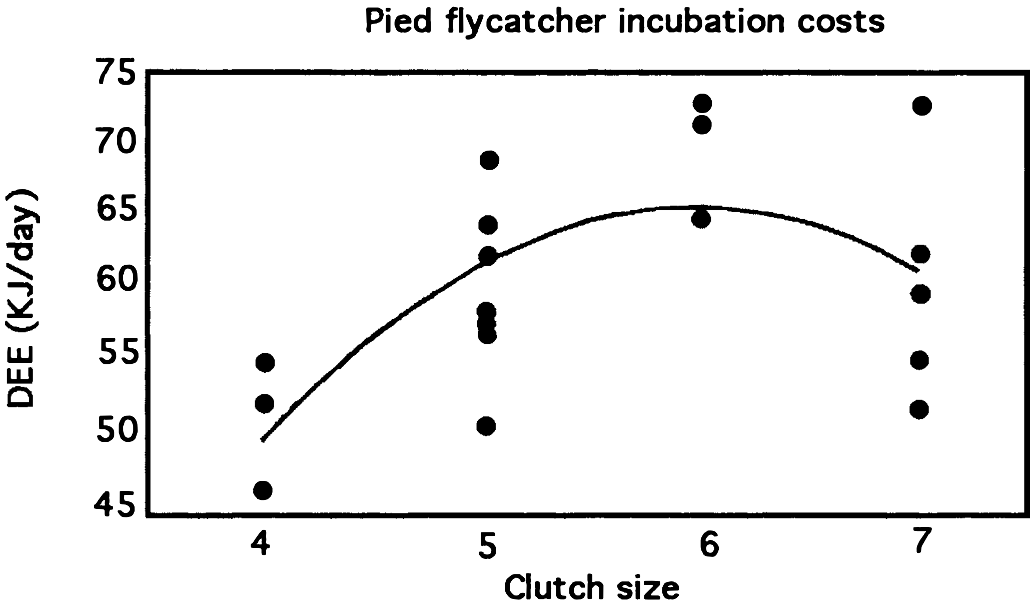

FIGURE 1. Daily energy expendidure (DEE) of female Pied Flycatchers during incubation as a function of clutch size, as measured with doubly-labelled water: $y=-79.11+48.54x-4.06x^2$, $r=0.65$, $p=0.002$; significance of coefficients: constant $t=1.63$, $p=0.12$, x $t=2.74$, $p=0.015$, x^2 $t=2.59$, $p=0.021$. From Moreno & Sanz 1994.

[Gasto energ6tico diario (DEE) de hembras de papamoscas cerrojillo durante la incubaci6n en funci6n del tamaño de puesta, medido con agua doblemente marcada.]

in these analyses, and not brood size raised, as depending on territory quality each young raised can imply different costs to the parents (Ens et al., 1992).

Another problem with brood size manipulations in birds is that they do not really simulate the costs incurred by parents laying a certain number of eggs. Females may suffer costs by the reduction of reserves involved in laying more eggs. It is of course difficult to induce females to lay more eggs than originally intended, but indeterminate layers may respond to removal at the beginning of the laying period appropriately (Haywood, 1993). This possibility should be tried. Incubation appears not to be as cheap as normally envisaged (Williams, 1991). Clutch size has been shown to significantly affect female mass loss (Moreno & Carlson, 1989), hatching success (Moreno et al., 1991) and parental energy expenditure during incubation (fig. 1, Moreno & Sanz in press). If female condition at the end of incubation affects her capacity to brood and feed nestlings (Lifjeld & Slagsvold, 1986), incubation costs could affect the optimal clutch size. The possibility that the effects of parental effort during subsequent breeding phases may accumulate should be taken into account when performing field manipulations.

An increasing number of avian studies show individual optimization of clutch size (Högstedt, 1980; Gustafsson & Sutherland, 1988; Pettifor et al., 1988; Daan et al., 1990; Tinbergen & Daan, 1990; Robinson & Rotenberry, 1991; Pettifor, 1993a; b). Apparently, individuals are able to adjust clutch size to their capacity to care properly for offspring, which may depend on territory quality or individual proficiency in finding food. The ability to optimize clutch size may become apparent only for older birds (Gustafsson, 1990). Also in mammals, some evidence for condition-dependent life history traits has been found (Kenagy et al., 1990; Dobson, 1992; Morris, 1992). In squamate reptiles, future fecundity costs appear unimportant compared with direct physiological or ecological survival costs (Shine & Schwarzkopf, 1992). The conclusion from avian field experiments is at present that clutch size is mostly adjusted to maximize the number of young recruited to the population without affecting parental survival markedly (Hochachka, 1992).

Energetics and survival

Although adult survival may not be impaired by experimental manipulations, the plateau in parental response and the evidence of starving or slowly growing nestlings suggests that a threshold in parental work capacity has been reached which would affect parental survival prospects in a nonlinear fashion (Drent & Daan, 1980). A "prudent parent" would not surpass such a threshold, which Drent & Daan suggested would lay around 4 times the basal metabolic level. Bryant (1991) has later reviewed the evidence for such a general threshold in birds, and found that individuals of many species where DEE during nestling rearing has been measured with doubly-labelled water, normally exceed the 4xBMR energetic level. This fact does not disclaim the existence of a threshold which may vary between species. Apparently, species normally using high-cost activities, are expending more energy with respect to body mass on a continuous basis (Peterson et al., 1990; Bryant & Tatner, 1992).

Although a general threshold may not be found, there is increasing evidence that parent birds are prudent. Several studies show that parent birds have spare time while feeding nestlings (Masman et al., 1989; Weathers & Sullivan, 1989; Mock, 1991), and are able to raise their DEE above the normal level for long periods (Masman et al., 1989). If parents can raise more nestlings by working harder, why don't they? It is also suggestive of a threshold, that DEE is normally not dependent on brood size (Masman et al., 1989; Moreno, 1989; Tatner, 1990; Mock, 1991) or litter size in mammals (Kenagy et al., 1990). Apparently, parents adjust brood or litter size to their condition or feeding capacity, so that all are working at a similar level of expenditure. Why do not low quality parents raise their effort, for which there seems to be scope, and thereby raise as many young as high quality parents? The answer must lie in some cost, either ecological or physiological, which parents do not want to incur. In some studies, parents do not raise their metabolism when feeding enlarged broods (figs. 2-3, Moreno & Cowie, unpubl.). This is another indication that we shouldn't expect physiological survival costs of manipulations for parents, if we are not able to show a response in metabolic terms.

Sustained intense work has been shown to affect negatively survival probabilities in worker bees (Wolf & Schmidt-Hempel, 1989), kingfishers (Reyer, 1984) and house martins (Bryant, 1991). In kingfishers there is also a negative effect of DEE on mass loss, which could be involved in the reduced survival probabilities (Reyer & Westerterp, 1985). Other studies have also shown mass losses in parents feeding more intensively (Nur, 1984; Smith et al., 1988). However, mass loss in birds feeding nestlings remains a contentious issue, as it can be evidence for reduced time for self-feeding (Moreno, 1989b) or an adaptation to reduce flight costs (Norberg, 1981; Freed, 1981). The positive relationship between experimental brood size and feeding rate and the negative between brood size and female survival in blue tits detected by Nur (1984; 1988) has not been corroborated in another study of

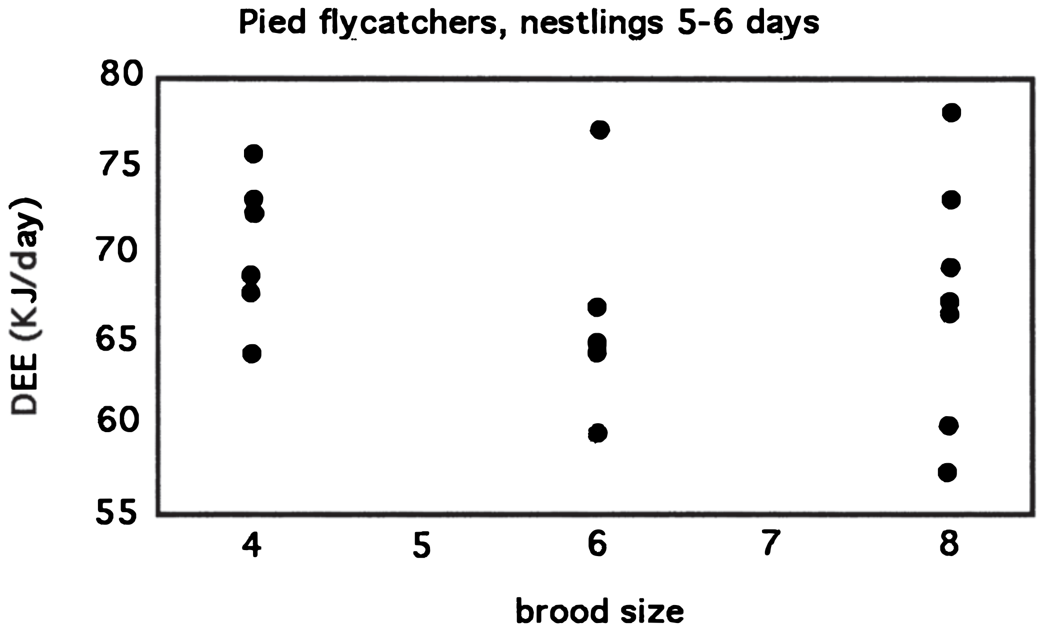

FIGURE 2. Daily energy expendidure (DEE) of male and female Pied Flycatchers (no difference between sexes) feeding nestlings of 5-6 days as a function of brood size, as measured with doubly-labelled water. Broods of 4 were reduced, broods of 8 were enlarged. All broods contained originally 6 nestlings. From Moreno, Cowie & Sanz, in prep.

[Gasto energético diario (DEE) de machos y hembras de papamoscas cerrojillo (no hay diferencia entre sexos) cebando pollos de 5-6 días en función del tamaño de nidada, medido con agua doblemente marcada. Las nidadas de 4 eran reducidas, las nidadas de 8 aumentadas. Todas las nidadas contenían originalmente 6 pollos.]

the same population (Pettifor, 1993b). Reid (1987) observed increased foraging time, reduced body mass and reduced survival in adult glaucous-winged gulls feeding enlarged broods. This study included parents caring for broods more than twice the maximum observed in nature. In a comparison of middle-aged and old collared flycatcher females feeding young, it was shown that DEE was significantly correlated with feeding rate, that old females delivered food significantly more often (thus had higher DEE), that they lost significantly more mass (probably due to their higher DEE) and that they, in contrast to younger females, suffered increased survival costs with the number of young fledged (Pärt et al., 1992). Only the direct link between survival and DEE is missing, but this study reflects the fact that old individuals may incur survival costs which younger individuals are not willing to. The most convincing evidence to date for a survival cost of heavy work is the study on the European kestrel by Daan and co-workers. They have been able to show that parents respond to manipulations by working harder (Dijkstra et al., 1990, unpubl.), and that hard-working parents of enlarged broods survive less well (Dijkstra et al., 1990, unpubl.). The link between energetic exertion and parental survival is still tenuous and requires confirmation in further studies and other animal taxons. But even if it was confirmed in the future, we would still have to explain how this connection works. Why are

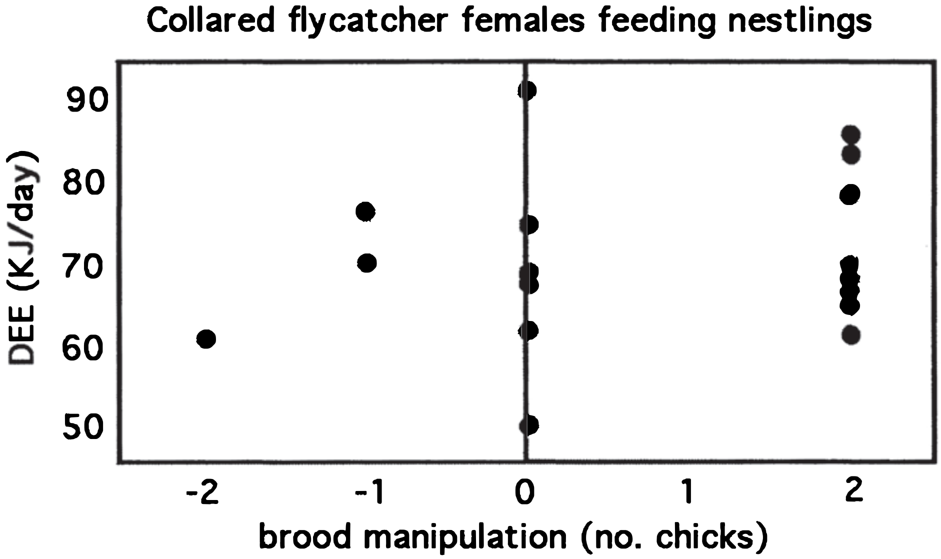

FIGURE 3. Daily energy expendidure (DEE) of female Collared Flycatchers feeding 9-10 days old nestlings, as measured with doubly-labelled water, in relation with the number of chicks raised with respect to original clutch size. No relationships was found. See Pärt, et al., 1992, for details.

[Gasto energético diario (DEE) de hembras de papamoscas collarino cebando pollos de 9-10 días, medido con agua doblemente marcada, en relación con la diferencia entre tamaños de nidada experimental y el tamaño de puesta original. No existe relación.]

animals more prone to die when working harder?

Condition and postreproductive activities

There is increasing evidence for birds that impaired condition provokes changes in the timing and duration of important postreproductive life stages. Thus, greater reproductive effort as indicated by a larger brood (see above), leads to delayed annual molt (Bensch et al., 1985; Lessells, 1986; Earnst, 1992). Molt and breeding compete for resources as indicated by negative consequences of molt-breeding overlap on reproductive success (Morton & Morton, 1990) and by interference of prolonged molting processes with breeding (Weimerskirch, 1991). Also, induced feather growth proceeds more slowly when caring for enlarged broods (White et al., 1991). Finishing the annual molt in time appears to be important, as delayed molting is compressed in time (Meijer, 1991), with possible energetic repercussions. Delayed molt may affect premigratory fattening and timing of migration in migrants and the occupation of winter territories and food storing in temperate residents. Possible delays and compressions in these important cyclic events may

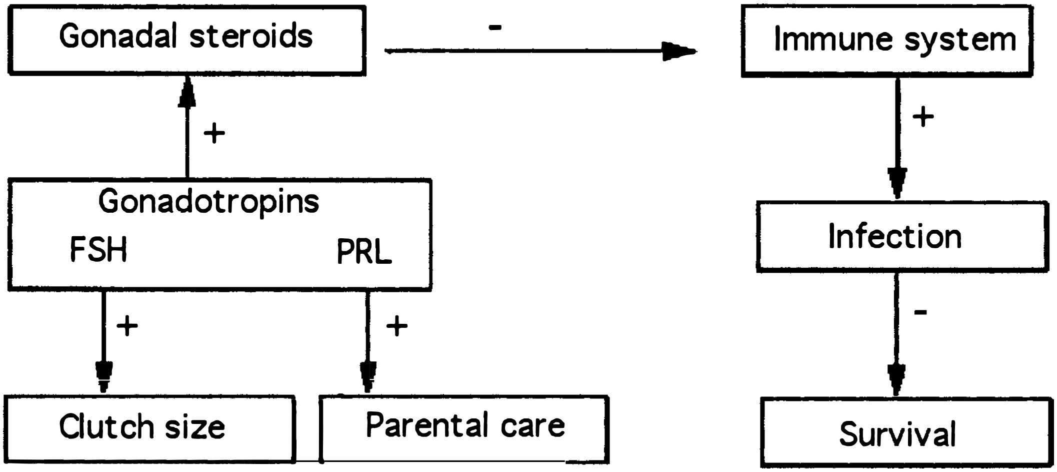

FIGURE 4. Schematic representation of the interactions between reproductive hormone levels, reproductive effort, inmunological response and survival. From Grossman 1985.

[Representaci6n esquem4tica de las interacciones entre niveles de hormonas reproductivas, esfuerzo reproductivo, respuestra inmunol6gica y supervivencia.]

affect postreproductive survival probabilities. The effects of parental exertion on molt is only one example of reproductive costs paid after reproduction itself. Other cases may be envisaged, like the costs of prolonged parental care for lactating female mammals (Clutton-Brock et al., 1982). However, much more work has to be devoted to clarifying these issues.

Resistance against parasites and diseases

It has been known for some time that the immune system is regulated by gonadal steroids (fig. 4, Grossman, 1985). Thus, depression of the cell-mediated immune response by estrogen leads to increased mortality, while castration increases resistance to infection. Testosterone has immunosuppresssive effects, and may affect survival through increased parasite or disease prevalence (Folstad & Karter, 1992). T-implants can have negative effects on male condition and survival (Marler & Moore, 1988; Nolan et al., 1992). Some avian studies have shown increased levels of haematozoan infection during the breeding season (Applegate & Beaudoin, 1970; Beaudoin et al.; 1971; Bennett & Cameron, 1974; Kirkpatrick & Suthers, 1988; Weatherhead & Bennett, 1991). Parasitic nematodes may increase their egg production in response to hormonal changes related to host pregnancy in some mammals (Festa-Bianchet, 1989). These effects could be due to immunosuppression by reproductive hormones. However, there is as yet no convincing evidence showing that increased levels of hormones mediating a greater parental effort like FSH (Sinervo

TABLE II. Evidence for declines in reproductive performance due to age (senescence) in field studies of birds and mammals.

[Evidencia de declives en la eficacia reproductiva debidos a la edad (senectud) en estudios de campo de aves y mamíferos.]

	Age of decline	Expression of decline
Birds		
Blue Tit [1]	4 years	later laying, lower success, smaller broods, lower postfledging survival
Great Tit [1]	5 years	later laying, lower success, smaller broods, lower postfledging survival
Coll. flycatcher [2]	4 years	later laying, smaller clutches, lower breeding success
Snow goose [3]	7 years	Egg hatchability, brood survival
Glauc.-w. gull [4]	17 years	smaller clutches, smaller eggs
Wand. Albatross [5]	>20 years	smaller eggs, reduced breeding success, lower survival
Mammals		
Red deer [6]	12 years	Fecundity , birth weight and calf survival decrease, mortality rises
Bison [7]	17 years	Fecundity

Data from: 1 Dhondt, 1989; 2 Gustafsson & Pärt, 1990; 3 Rockwell et al., 1993; 4 Reid, 1988; 5 Weimerskirch, 1992; 6 Clutton-Brock, 1984; 7 Green, 1990.

& Licht, 1991) or prolactin (Pedersen, 1989, Ketterson et al., 1990), have deletereous effects on survival. This link is necessary to prove that reproductive hormones mediate reproductive costs.

An alternative interpretation is that reproductive effort directly weakens the immune system (Festa-Bianchet, 1989). There is preliminary evidence that specific immune responses which require rapid lymphocite proliferation are reduced as nutritional resources are re-allocated to support a high level of energy expenditure by parent birds (V. Apanius, pers. comm.). These exciting results would show that reproduction in itself may be costly due to higher risks of infection. Exploring the relationship between immune function, nutritional resources and reproductive effort appears at present the most promising area for theoretical and empirical life history research.

Somatic maintenance and senescence

Senescence is the decline in organismic performance with age, leading to decrements in survival probabilities due to intrinsic causes and in reproductive success. Senescence in reproductive parameters appears widespread in birds (Dhondt, 1989; Gustafsson & Pärt, 1990; Hamer & Furness, 1991; Weimerskirch, 1992; Rockwell et al., 1993) and mammals (Clutton-Brock, 1984; Green, 1990) (table II), although in some studies, apparent cases of senescence in reproductive performance may be due to alternative life history strategies in the same population (Pugesek & Diem, 1990). The main theory to explain senescence (Williams, 1957), postulates that genes selected for fecundity early in life may have pleiotropic adverse effects on late survival and reproduction. As reproduction becomes increasingly less important with age for fitness, these antagonistic pleiotropic effects may be selected for, thus leading to senescence. The mechanisms linking increased fecundity early in life with reduced performance later on, may be the same as those mediating age-specific reproductive costs (Partridge, 1987). The first experimental evidence for a link between increased reproductive effort at young ages and a subsequent reduction in reproductive performance has been presented by Gustafsson & Pärt (1990) on the Collared Flycatcher. The physiological basis underlying decreased performance is still a matter of speculation. Reduced protein turnover at the cellular level has been proposed, along with immune system decay and complex interactions in the neuroendocrine system, as a causal determinant of ageing (Holehan & Merry, 1986). The theory of the disposable soma (Kirkwood & Rose, 1991) explains ageing phenomena as the result of tuning the investment in somatic maintenance at a level that is enough to survive the natural expectation of life in the wild, but not higher. Studies of the physiological and biochemical basis of ageing may help us understand the operation of the physiological costs of reproduction.

Conclusions

Future studies of reproductive costs should

1) broaden the taxonomic range of species included,

2) adopt an experimental approach,

3) explore the form of the trade-off functions,

4) increase sample sizes if possible in order to augment the power of tests, otherwise report signs of trade-offs without claiming to have disproved the existence of costs,

5) include in field manipulations as many stages of the reproductive cycle as possible,

6) try to explain through comparative analyses the difference between species in their response to manipulations,

5) link changes in time/energy use with survival (interaction with physiologists),

6) explore the effects of changing reproductive hormone levels on the immune system and thus on infection probability (interaction with physiologists),

7) explore the relationship between nutritional resources, immune function and reproductive effort, and

8) relate physiological reproductive exertion to impaired somatic maintenance and repair (interaction with molecular biologists).

Resumen

Mecanismos fisiológicos que determinan costes reproductivos.

La existencia de trueques entre fecundidad y superviviencia es clave en las teorías sobre evolución de ciclos vitales. Las comparaciones de parámetros vitales de individuos en situaciones no manipuladas diferentes, muestran que meras correlaciones no permiten detectar costes reproductivos. Estudios experimentales muestran que la plasticidad fenotípica en cuanto a fecundidad es adaptativa, ya que individuos de algunas poblaciones optimizan la invesión reproductiva en función de las condiciones ambientales. En algunos experimentos, los costes de supervivencia no son pagados por los adultos sino por los descendientes, cuando el esfuerzo parental no aumenta suficientemente en respuesta a la demanda de la progenie. El nivel de esfuerzo parental puede estar constreñido por debajo de los requerimientos de la progenie por costes de supervivencia determinados fisiológicamente. Algunos experimentos incluyen solo algunas fases reproductivas, las presumiblemente mas costosas. Sin embargo, la evaluación de todo el ciclo reproductivo es necesaria, ya que los costes debidos al esfuerzo durante fases consecutivas puede acumularse. En reproductores para los que los costes se pagan después de la reproducción, existe cada vez mas evidencia de que el nivel de gasto energético está constreñido por debajo de un máximo sostenible a corto plazo, y que un mayor gasto energético puede reducir las posibilidades de supervivencia. Un posible mecanismo subyacente puede deberse a los observados retrasos y contracciones en eventos postreproductivos como la muda y la migración de aves. Los efectos de las hormonas sobre la inversión reproductiva por un lado y sobre la resistencia al parasitismo por otro también podrían estar involucrados. Los recursos nutritivos utilizados en la reproducción pueden ser restados de los necesarios para el mantenimiento del sistema inmunológico. El deterioro de la productividad con la edad (senectud) puede estar relacionado con mayores niveles de esfuerzo parental en la juventud, y por tanto expresar la existencia de costes reproductivos. Debemos centrar el esfuerzo en este campo en estudios sobre energética, endocrinología, inmunología, parasitología, etc., que puedan explicar como la fisiología determina las correlaciones genéticas que subyacen a la evolución de ciclos vitales.

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