Good genes, old age and life-history trade-offs

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Summary

The possibility of using old age of a mate as an indicator of genetic quality is currently controversial. Early verbal models as well as a recent simulation study noted that female choice for old mates is beneficial because longevity indicates viability in the current environment. In contrast, a quantitative genetic model of the relationship between age and breeding value of fitness casts strong doubts on the mechanism. The present analysis shows, however, that these doubts are mainly the result of assuming that all variation among individuals arises from differences in allocation between components of fitness. This neglects the possibility of variability in condition as a whole. Instead, when allowing for persistent variability in condition and assuming optimal reaction norms in allocation, it is shown that correlations between survival and genetic quality or fitness can easily be established at all ages. On the other hand, the results also suggest that the validity of verbal arguments is limited, and counterexamples can be generated where low-quality individuals should invest more in survival. Therefore, resolution of the old age indicator problem requires specification of the constraints acting on life-history characteristics.

Keywords: age indicator mechanism; good genes; life-history trade-offs; mate choice; sexual selection

Introduction

It has been suggested that a male with a long lifespan has proven his viability, and females should consequently prefer such males as mates (Trivers, 1972; Halliday, 1978, 1983; Manning, 1985). This hypothesis is a specific example of the more general 'good genes' model, or indicator mechanism, for choosy behaviour in females (e.g. Andersson, 1994). Here, the indicator used for male quality assessment is age, hence the name 'age indicator mechanism' used in this paper.

Indicator mechanisms with condition-dependent sexual traits have been shown to be both logically consistent (Andersson, 1986; Grafen, 1990; Iwasa *et al.*, 1991) and supported by empirical studies (Johnstone, 1995), although the mechanism of maintaining sufficient levels of heritable variation is still a controversial issue (e.g. Pomiankowski and Møller, 1995; Rowe and Houle, 1996). When age has been used as the indicator of quality, however, modelling has been lacking for a long time, the mechanism being expressed in the form of verbal arguments only (Trivers, 1972; Halliday, 1978, 1983; Manning, 1985).

Much experimental and observational data have been collected documenting either female choice for older mates (Burley, 1981; Grant and Grant, 1987; van Rhijn and Groothuis, 1987; Conner, 1989; Komers and Dhindsa, 1989; Korpimäki, 1989; Poole, 1989; Côté and Hunte, 1993; Enstrom, 1993; Hasselquist *et al.*, 1996; Sundberg and Dixon, 1996) or a failure to find any such effect (Berven, 1981; Alatalo *et al.*, 1986; Halliday and Verrell, 1988; Hill, 1990; Koenig, 1991; Petrie, 1993; Olsson and Madsen, 1995). Likewise, studies seeking heritable fitness advantages in choosing old mates have provided conflicting results (Watt *et al.*, 1986; Howard *et al.*, 1994).

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Against this extensive empirical background, it is surprising that the very first formalization of the old age indicator mechanism (Hansen and Price, 1995) leads to a complete rejection of the hypothesis except in some very special cases. On the other hand, another analysis based on simulated gene frequencies suggested that mate choice in favour of old age should be beneficial in a wide variety of environments (Kokko and Lindström, 1996).

In this paper, I argue that these different results depend on two aspects of life-history theory, both models taking one into account and neglecting the other. It is well known that the observed correlations between all components of fitness may be positive despite an inherent negative trade-off (Falconer and Mackay, 1996). This is because individuals may differ not only in allocation, but also in acquisition of condition (van Noordwijk and de Jong, 1986; Houle, 1991; Rowe and Houle, 1996). Hansen and Price (1995), using a quantitative genetic model, implicitly assumed that all differences between individuals are due to differences in allocation. Thus, high survival at old age is correlated with low survival or fecundity at an early age via an intrinsic trade-off constraint. The result is a decrease in breeding value for fitness with age, except in cases with sharply increasing fecundity with age. On the other hand, in the study of Kokko and Lindström (1996), males differed in condition only, and their model allowed no differences in allocation. As a result, high-quality males will have increased survival at all ages, and the long-lived males will be a high-quality subset of their cohort.

Clearly, a solution to this problem requires taking life-history theory into account (Partridge and Endler, 1987), with consideration of both allocation and acquisition of condition. This paper combines these into an age-structured optimization model, in which condition is to be allocated to different life-history traits, and males vary in their condition. Condition is assumed to be of interest to the female, inasmuch as it is associated with genetic quality, leading to higher fitness. Within the scope of this paper, this means making the assumption that heritable genetic variation for condition persists in the population, but the argument applies equally to cases where females benefit directly from the good condition of their mate.

The optimal allocation is calculated for males differing in condition. It is then checked whether males with good condition allocate more to survival at all ages than a male of poorer condition. If this is the case, a female choosing an old mate will be choosing in favour of good condition. It turns out that, even in cases where there is no fecundity increase with age, such solutions are far more easily found than Hansen and Price (1995) suggest. On the other hand, it is also shown that the verbal reasoning behind the early models (e.g. Manning, 1985) does not always hold: Examples can be found where investment in longevity is beneficial for males of low quality only.

Resource allocation and life-history trade-offs

To show that the verbal description of the age indicator mechanism is possible within the framework of quantitative genetics, there is no need to alter the equations given by Hansen and Price (1995). It only has to be shown that both early and old age survival can increase simultaneously with fecundity, genetic quality and fitness, given that both the condition, C (cf. Rowe and Houle, 1996), and allocation, A, can differ between individuals. I consider an optimality model of condition-dependent resource allocation to male fecundity and survival. Condition-dependence of allocation is expected in life-history problems (Roff, 1992), as well as in sexual advertisement (Nur and Hasson, 1984; Price *et al.*, 1993; Johnstone, 1995). On the other hand, the maintenance of substantial levels of genetic variation in fitness-related traits has recently gained new support (Price and Schluter, 1991; Pomiankowski and Møller, 1995; Houle *et al.*, 1996; Rowe and Houle, 1996). I therefore assume that, at equilibrium, individuals will differ in condition, but that their allocation

of condition to life-history traits – that is, the reaction norm of condition-dependent reproductive effort – is optimal.

I use A_{Fx} to denote the allocation of condition C_x to fecundity F_x at age x (e.g. sexual advertisement), and A_{Px} to denote the corresponding allocation to survival P_x. Fecundity and survival at age x are increasing functions of allocation to the corresponding trait:

$$\frac{dF_x}{dA_{Fx}} \geq 0 \qquad \frac{dP_x}{dA_{Px}} \geq 0 \tag{1}$$

To analyse the worst-case situation for the age indicator model, I assume that there are strict trade-offs between fitness components, so that allocation in one component always decreases the availability of resources to another. In other words, sexual advertisement has viability costs in this model. The constraint of individual condition then limits the total allocation:

$$A_{Fx} + A_{Px} \leq C_x \tag{2a}$$

With fixed C_x, this is the 'age-specific constraint' model. Alternatively, to allow for trade-offs that act for the complete lifetime of an individual, the individual can increase the total usage of resources within 1 year, but with the cost of reducing resources available in other years. Thus, the constraint $C = \sum C_x$ is interpreted as a single lifetime quality parameter:

$$\sum_{x=1}^{\infty} A_{Fx} + \sum_{x=1}^{\infty} A_{Px} \leq C \tag{2b}$$

With this 'lifetime constraint' formulation of resources, an individual can increase advertisement effort in 1 year, but with the cost of decreasing survival or reproductive success in all other years (see Gustafsson *et al.*, 1995).

From the relationships in Equation (1), together with positive relationships between fitness and F_x and fitness and P_x, it follows that the optimal solution will satisfy the equality in Equations (2a,b). This is the dominance criterion: Any strategy that leaves resources unused is dominated by another, and is therefore a suboptimal choice. Also, fitness will be a non-decreasing function of condition, C_x: A male can always obtain at least the fitness of a male with lower condition by choosing the same allocation. The optimal choices for A_{Fx} and A_{Px} depend on the functions $F_x(A_{Fx})$ and $P_x(A_{Px})$ at each age x, as well as on the values of C_x. Equation (2) suggests that better overall condition, C_x, is likely to lead to increased survival, since more resources are available to be allocated to A_{Px} when C_x is high. However, investing the surplus in fecundity, A_{Fx}, instead of A_{Px}, may increase fitness more.

I consider the simplest possible age-dependent model, where condition C_x depends on individual quality only. For analytical tractability, I also assume a stationary population, so that the basic reproductive number

$$R_0 = \sum_{i=1}^{\infty} F_i \prod_{j=1}^{i} P_i \tag{3}$$

can be used as a measure of individual fitness. The task of an individual of condition C_x is now to maximize R_0 by choosing the allocations A_{Fx} and A_{Px} optimally, with the constraint of Equation (2a) or (2b).

For the form of Equation (2a), the solution is obtained recursively by dynamic programming. Consider the term $P_k F_k$ of the expression

$$R_0 = P_1 F_1 + P_1 P_2 F_2 + \cdots + P_1 \cdots P_k F_k \tag{4}$$

The optimal allocation at age k will be independent of previous allocations, so that the principle of optimality of Bellman and Dreyfus (1962) is satisfied. Non-dominated allocation strategies (i.e. no resources are wasted) lead to a negative trade-off between P_k and F_k through the equality in Equation (2a), and the optimum can be graphically determined (Fig. 1A).

Differences in total quality can be seen to allow the possibility of a simultaneous increase in both P_k and F_k when the quality of the male increases. Trade-offs at an earlier age behave similarly (Fig. 1B). The expected number of offspring produced at age k is $R_k = P_k F_k$. Denoting its maximum value by R_k^*, the function to be maximized at age $k-1$ is $R_{k-1} = P_{k-1}(F_{k-1} + R_k^*)$. The value of R_k^* never decreases with male condition since high-quality males can allocate at least as much resources as lower-quality males. As a result, they have at age $k-1$ an advantage of obtaining a greater increase in R_{k-1} as well.

For the 'lifetime constraint' form of Equation (2b), the solution is obtained numerically by considering combinations of C_x values that satisfy $\sum C_x = C$, and solving the above procedure for each allocation trial.

The number of functions satisfying Equation (1) is infinite, and a large variety of forms can be considered biologically feasible. In cases where females benefit from choosing an old mate, the slope of $F_x(A_{Fx})$ probably steepens with both x and A_{Fx}, but the exact form depends on the details of female choice rules. The female, on the other hand, bases her preference on maximizing the quality of her mate. Instead of determining the general outcome of such games between the sexes, my aim is to show that, with given and fixed functions for $F_x(A_{Fx})$ and $P_x(A_{Px})$, the strength (and sign) of the correlation between male quality and survival depends on the form of the trade-off between $F_x(A_{Fx})$ and $P_x(A_{Px})$.

Results

Once male qualities are allowed to vary, early and old age survival and fecundity can all simultaneously increase with the quality of the male (Figs 1 and 2). With choices of $F_x(A_{Fx})$ and $P_x(A_{Px})$ with decreasing marginal gains, survival increases with condition C at all ages – not only when allocating resources gives the highest response at old age (Fig. 2A), but also when the gains are equal at all ages (Fig. 1), or if young age gives the greatest response (Fig. 2B). The 'lifetime constraint' model (Equation 2b) gives different predictions because of the added freedom of allocating all conditions to a single year if necessary, such that differences among years are increased (Fig. 2). The possibility of semelparity (Fig. 2B) is the most extreme case: Here, the correlation between old age survival and male quality disappears (but does not become negative), because survival after maturation becomes suboptimal for males of any quality. In iteroparous solutions, none of the fitness components – early or late life fecundity and survival – show negative correlations among individuals of different quality, despite the trade-offs that are intrinsically present within an individual (Equation 2b).

Will quality differences always override the intrinsic trade-offs? There are three possible exceptions. First, if trade-offs act over the lifetime of the individual and not only within 1 year, early age fitness benefits may override the late life benefits (Hansen and Price, 1995). However, as the above example shows, both P_x and F_x can be increasing functions of C at all ages even with this assumption (Fig. 2). Due to a decreasing marginal gain in P_x and F_x, it is not beneficial to spend resources endlessly in young age reproduction and survival.

Secondly, if differences in male quality are negligible but allocation varies markedly among individuals (i.e. allocation is not optimal), the intrinsic trade-offs are not covered by differences in total quality (Fig. 3). In the context of sexual displays, this interpretation requires that individuals vary in their reaction norms of condition-dependence, but have no quality differences *per se*.
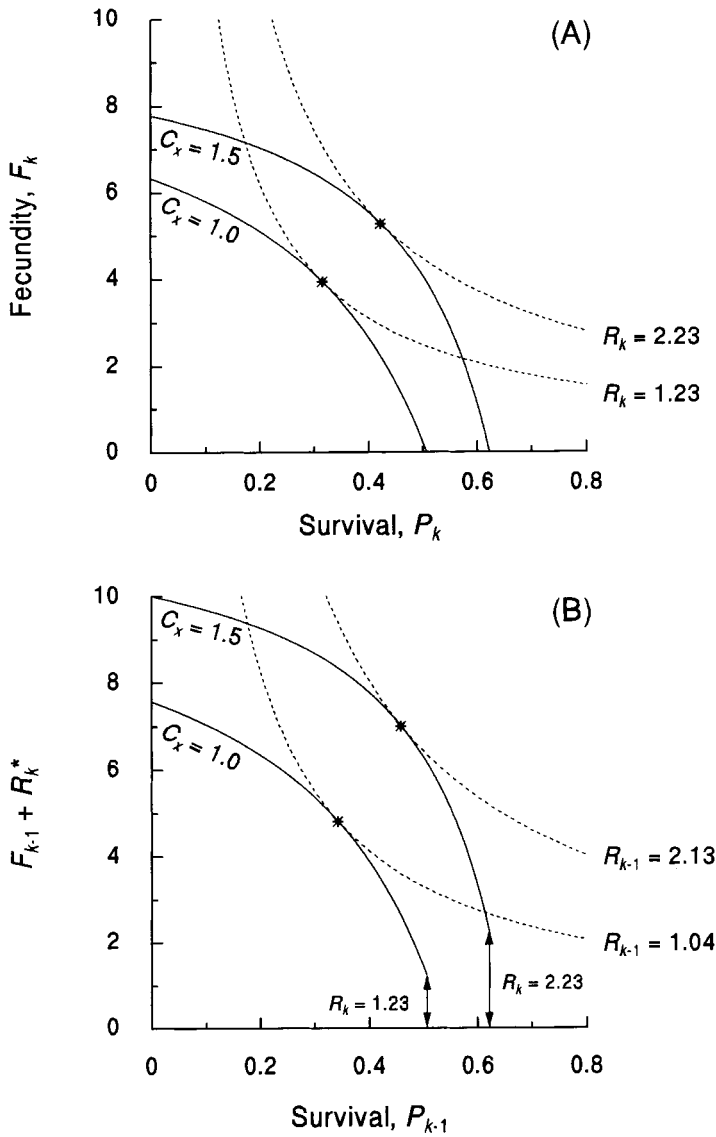
Figure 1. (A) Forms of trade-off (solid lines) between survival P_k and fecundity F_k in the last age class, resulting from allocation functions $P_k(A_{Pk}) = 0.8(1 - \exp(-A_{Pk}))$ and $F_k(A_{Fk}) = 10(1 - \exp(-A_{Fk}))$, given for values $C_x = 1.0$ and $C_x = 1.5$. The optimum allocation that maximizes $R_k = P_k F_k$ is marked for high- and low-quality males. High-quality ($C_x = 1.5$) males have higher values for both F_k and P_k, and hence for their product R_k^*. (B) Trade-off functions for age $k - 1$ in the above case, exemplified with $P_{k-1}(A_{Pk-1})$ and $F_{k-1}(A_{Fk-1})$ that are equal to $P_k(A_{Pk})$ and $F_k(A_{Fk})$. The difference in high- and low-quality males remains, and it is recursively transferred to each age class $x = k, k - 1, \cdots, 1$.

(A) *Gains increasing with age*

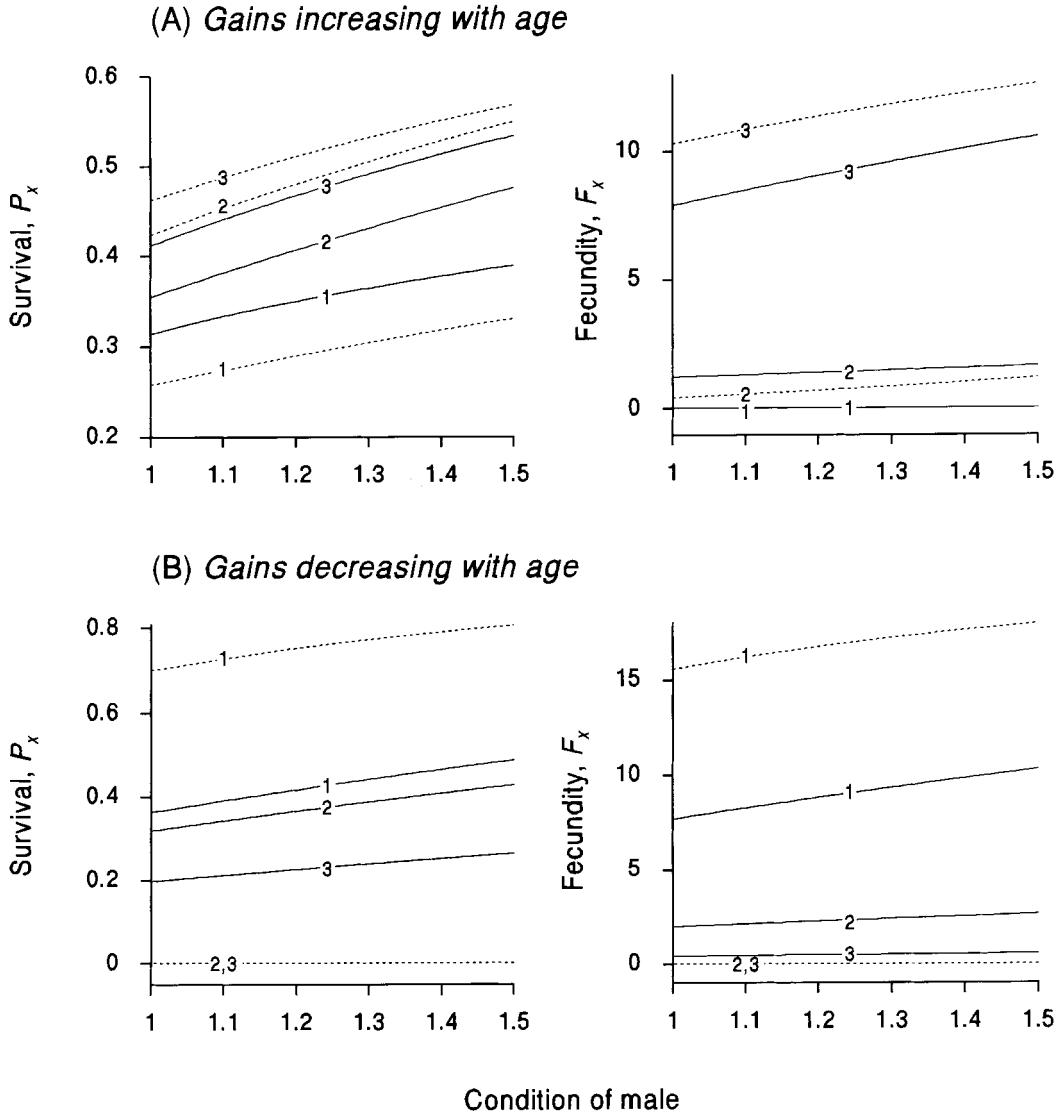

(B) *Gains decreasing with age*

Condition of male

Figure 2. Examples of optimal allocation and the resulting dependence of survival and fecundity on individual condition. Solid lines refer to the 'age-specific constraint' model (Eq. 2a), with condition referring to C_x, and dotted lines to the 'lifetime constraint' model (Eq. 2b), with condition referring to the annual average, $C/3$. Age is given on the curves. Functions used to build the examples are $F_x = \alpha_x(1 - \exp(-A_{Fx}))$ and $P_x = \beta_x(1 - \exp(-A_{Px}))$, with: (A) Gains increasing with age, x: $\alpha_1 = 1$, $\alpha_2 = 5$, $\alpha_3 = 20$, $\beta_1 = 0.5$, $\beta_2 = 0.8$ and $\beta_3 = 0.9$. (B) Gains decreasing with age, x: $\alpha_1 = 20$, $\alpha_2 = 5$, $\alpha_3 = 1$, $\beta_1 = 0.9$, $\beta_2 = 0.8$, and $\beta_3 = 0.5$. In the lifetime constraint model, the optimum solution is semelparity at age 1, with zero fecundity and survival at later ages.

Thirdly, with specific forms of the trade-off between survival and fecundity, the optimal strategy may shift with the condition of the male in more diverse ways than in the above examples. With an increasing marginal gain in fecundity, it may become optimal for males of the highest quality to

decrease survival in favour of very intense advertisement (Figs 4A, 5). Very high fecundity associated with the highest resource allocations might result, for example, from females choosing the most intense sexual displays of many males. Note, however, that an increasing marginal gain is not sufficient in itself to produce this effect (Fig. 4B).

The prediction of dominance remains, whether or not longevity correlates with fecundity: high-quality males produce more offspring in their lifetime. If their success is a result of female choice for intense advertisement only, with no respect to age, this means that the choice itself remains advantageous for the female, even if trade-offs may allow the existence of short-term 'cheaters' (Kokko, 1997). Whether females can also use age as such as a criterion for quality, depends on the form of trade-offs in a perhaps too delicate way to be measured in nature (Fig. 4). However, both diminishing returns (Fig. 1) and increasing returns (Fig. 4B) provide solutions, where old age itself – either alone or hand in hand with sexual advertisement – functions well as a choice criterion.

Discussion

Is it possible to infer genetic quality from old age? According to both a widespread verbal model (e.g. Manning, 1985) and a simulation study with males varying in condition because of recurrent mutation (Kokko and Lindström, 1996), one is tempted to conclude 'yes'. However, using the quantitative genetics model of Hansen and Price (1995), the answer is a fairly strict 'no'. One of the major points of Hansen and Price's model is that the correlation between old age survival and fitness is weak, and it may even be strongly negative due to trade-offs between old age survival and the more important fitness components expressed in early age.

However, as shown in this paper, such a conclusion may be premature. A life-history model incorporating strict trade-offs among all fitness components demonstrates that the different components of fitness – early fecundity, late fecundity, early survival and late survival – may all
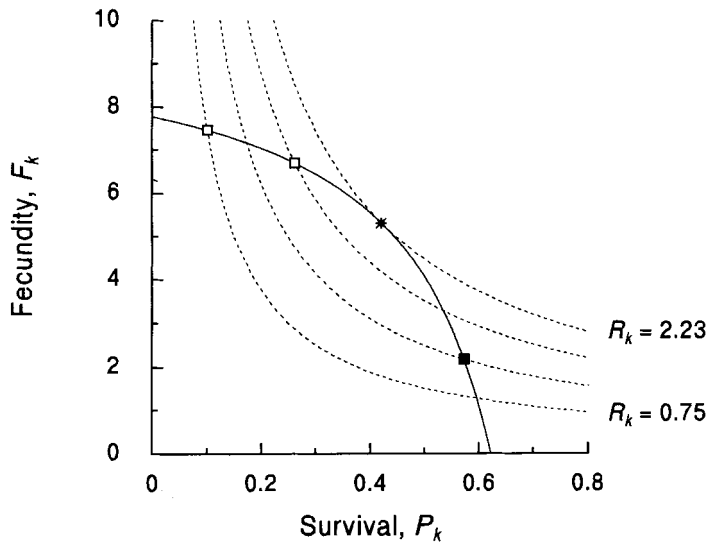

Figure 3. The case of Fig. 1A with no quality differences, but assuming that allocation is not optimal and varies among individuals. A high-survival male (solid square) will have low fecundity. As a result, he may obtain a larger or smaller value of R_k than a low-survival male (two open squares).
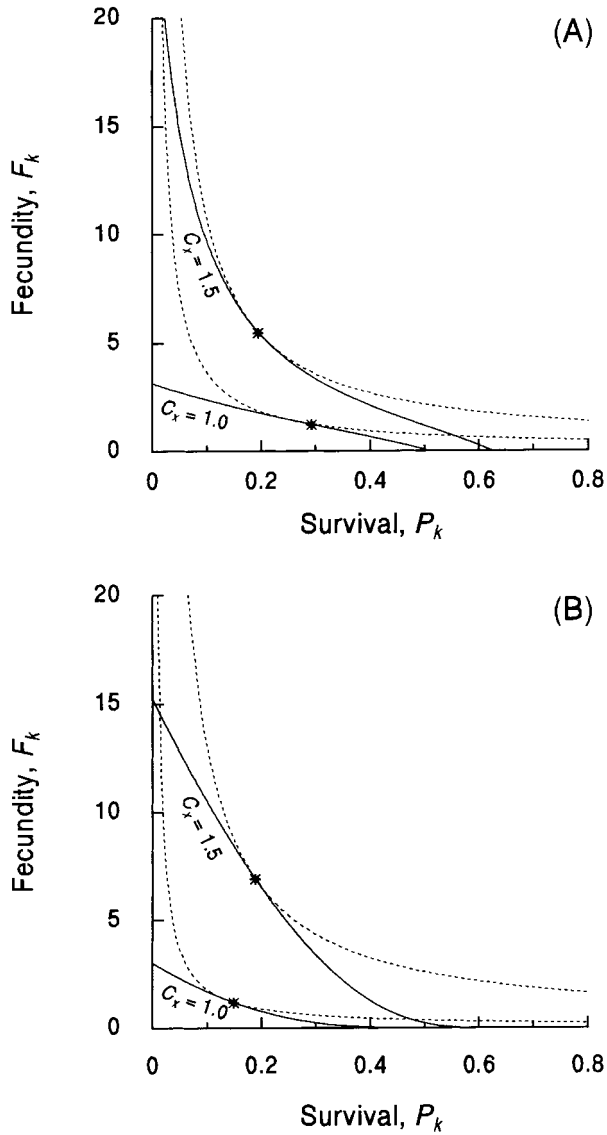
Figure 4. (A) Case with optimal allocation with P_k equal to the case of Fig. 2A, but with increasing marginal gain in fecundity, $F_k = 2 \cdot \tan(A_{Fk})$. High-quality males ($C_x = 1.5$) survive less well from age $k - 1$ to age k than low-quality males ($C_x = 1.0$), but their age class sires more offspring (higher R_k^*) because of disproportionately high fecundity of surviving males. (B) Another case with strongly increasing marginal gain in fecundity, $F_k = 3 \cdot A_{Fx}^4$, also results in a concave trade-off function between F_k and P_k, but this variant still shows increasing survival with quality.

simultaneously be correlated with each other as well as with the fitness R_0 and the condition C of the male. Trade-offs act as constraints within individuals, not among individuals that may well differ in their condition (van Noordwijk and de Jong, 1986; Rowe and Houle, 1996). Given that variability in condition exists, high survival at old age does not necessarily correlate with low values
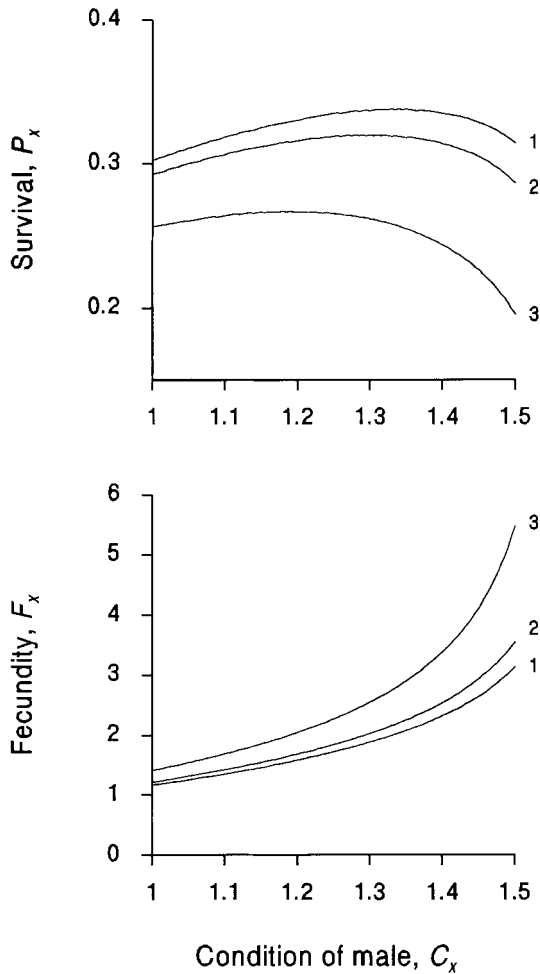
Figure 5. The optimal survival and fecundity curves for the example in Fig. 4A, showing a non-linear relationship between quality and longevity of the male.

of other fitness components among individuals, despite the existence of an inherent trade-off between fitness components (Charlesworth, 1990). This pattern is commonly found in field studies of reproductive success (Clutton-Brock, 1988; Clinton and Le Boeuf, 1993), and careful experimentation is required to reveal the intrinsic trade-off (e.g. Cordts and Partridge, 1996).

On the other hand, the results also provide counterexamples for the age indicator mechanism. In some cases, semelparity with maturation age 1 is favoured in males of any quality (Fig. 2B), and there is no need to assess the quality of older males since they never exist. Also, more severe counterexamples can be constructed, where males of lower quality invest more in survival than high-quality males. Although it is unclear whether such extreme life histories occur in nature, such examples show the pitfalls that may be overlooked when using verbally expressed ideas without careful verification.

The results emphasize the importance of specifying whether one is interested in the trade-offs themselves – the inherent constraints causing negative correlations between life-history traits, assuming that individual condition does not vary or is controlled for (Partridge and Sibly, 1991) – or in the observed correlations caused by these trade-offs plus the differences in condition between individuals. The former is of interest to life-history theory, including the evolution of senescence (Medawar, 1946; Williams, 1957; Rose, 1985, 1991), and its demonstration requires controlling for variability in condition (van Noordwijk and de Jong, 1986; Alatalo *et al.*, 1990; Schluter *et al.*, 1991). The latter, however, is of interest when inferring condition on the basis of the observed life-history traits of an individual (e.g. for a female performing mate choice). These differences in condition become important for mate choice if heritable genetic variation of condition can be maintained in the population (Kokko and Lindström, 1996; Rowe and Houle, 1996), or, in the case that phenotypic variability is of environmental origin only, if the female obtains direct benefit from a male in a good condition (Price *et al.*, 1993). As shown in this paper, the outcome depends on both allocation (which in turn depends on the form of inherent life-history trade-offs) *and* on the condition distribution of potential mates.

To summarize, the simple model described in this paper demonstrates that strong correlations between genetic quality and old age survival are by no means impossible; indeed, on the contrary, they are probably widespread. In cases where correlations are found (e.g. Watt *et al.*, 1986), it remains to be shown whether they can counteract other arguments presented by Hansen and Price (1995) against the benefit of old age – that is, the effects of evolutionary disequilibrium and germ-line mutations. However, given that strong correlations between longevity and condition can be easily established once male condition is allowed to vary, old age advertising for good genes surely remains a plausible hypothesis for female choice.

Acknowledgements

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