

A MODEL OF MATE DESERTION

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Abstract. Using a very simple model, in which the reproductive strategy of an individual is considered to be completely specified by the time he cares for each brood, we find the evolutionarily stable strategies, and characterize them in terms of the parental abilities of males and females. We predict *inter alia* that: (1) If at any stage the sexes are complementary, either by specialization or by the need for constant attendance with the young, so that two parents are much better than either parent alone, then only at extreme sex ratios will either parent desert. (2) If the sex ratio is unity, then the first parent deserts when both parents are twice as good as the deserted parent alone. (3) Except at extreme sex ratios, if one sex is very much worse than the other at caring for the young, then that sex will desert first. (4) Where the male deserts first, the more heavily the sex ratio is biased towards males, the less the relative advantage of both parents over the female alone is, at the time of desertion. We conclude with some general points about modelling mate desertion and parental investment.

Introduction

The problem of mate desertion is that of when an animal should leave its young, and try to find another mate. At any particular time, if he stays, he is improving the chances of his present young, but may be deserted by his mate; if he deserts, he will begin his next brood earlier and will increase the number of future offspring he produces, but his mate may decide not to care for the young alone.

Trivers (1972) suggested that the parent which has invested less at any given time should be tempted more to desert, having less to lose; this 'concorde' fallacy is discussed by Dawkins & Carlisle (1976). Trivers (1972) defined 'parental investment' as 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring'. In the present model we distinguish between the cost to the parent and the benefit to the offspring; the parent has a fixed amount of resource and allocates it so as to produce the greatest possible number of breeding offspring. An earlier version of the model was essentially similar to the continuous breeding case of Maynard Smith (1977), although it was developed independently.

Mate desertion has been dealt with using game theory (Dawkins 1976; Maynard Smith 1977), assigning pay-offs to strategies such as 'guard' or 'desert' (Maynard Smith) or 'faithful' or 'philanderer', 'coy' or 'fast' (Dawkins). These models, and the present model, take into account the strategy which the opposite sex is playing when finding the optimal strategy

for an individual; the present model also takes into account the strategy which the other individuals of the same sex are playing.

The Model

Assumptions

The model deals with a continuous, uniform breeding season, and with a stable population in which the sexes have an invariant breeding lifespan (cf. Maynard Smith 1977). This invariance of breeding lifespans allows us to regard the breeding sex ratio in the population as fixed (Fisher 1958). We assume that the benefit (defined as number of offspring that survive to breed) from a given brood depends only on how long each parent stays with it before deserting.

Our aim is to find that pair of strategies, for males and females, such that any deviant is penalized, i.e. any individual adopting a different strategy from that employed by others of its sex produces fewer breeding offspring. Such strategies are evolutionarily stable in the sense of Maynard Smith (1977). Note that the strategy of each individual then maximizes the benefit it achieves per unit time.

The Single-Parent Case

As an illustration of the method to be employed, we discuss first the single-parent case. A parent whose mate deserts immediately after copulation must decide when to leave the young.

Figure 1 is a graph showing the expected benefit from a brood as a function of the time the parent stays with it. If this parent can find a new mate and begin a new brood immediately,

then it should leave at time a , thereby maximizing benefit per unit time (and lifetime benefit since lifespan is fixed). If there is necessarily a gap c between deserting one brood and starting the next, then the parent should stay until time b , again to maximize benefit per unit time. The quantity the parent is maximizing is $g(t)/(t+c)$. This method of optimizing has been used by others, e.g. Smith & Fretwell (1974), Brockelman (1975) and Parker & Stuart (1976).

The Two-Parent Case

The male strategy is specified by t_1 , the female strategy by t_2 , where t_1 is the time between a male becoming committed to a female and deserting the brood, and t_2 is the time between a female becoming committed to a male and deserting the brood. Let c_1 be the time between a male deserting the brood and becoming committed to a new female, and let c_2 be the analogous time for a female. t_1+c_1 is therefore a complete cycle, and all of a male's reproductive life is spent in t_1 or in c_1 . Figure 2 shows this and illustrates the 'sex-ratio constraint'. If there are twice as many females as males, then the males' cycle can be only half as long as the females'; otherwise, when the males desert the females, there are not enough females for them all to obtain mates. Let r represent the breeding sex ratio, that is, the number of breeding males divided by the number of breeding females. When breeding lifespans are equal, the argument of Fig. 2 shows that $r = (t_1+c_1)/(t_2+c_2)$. We shall assume that r is a constant.

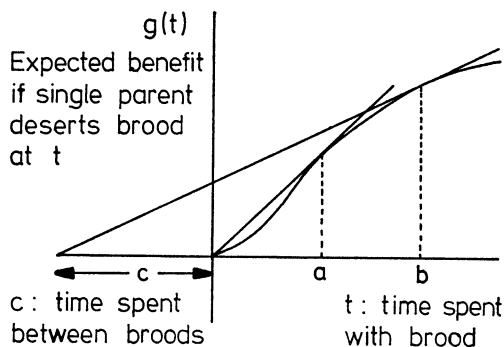


Fig. 1. A hypothetical graph of the benefit a single parent can expect to obtain from a brood by spending time t with it. Such a parent should maximize $g(t)/(t+c)$. If no time has to be spent between broods, it should leave at a , but if after deserting it must always wait for c before breeding again, then it should stay until b . Such a strategy produces the highest rate of reproduction possible under the restrictions of the model.

Since the expected benefit from a brood is determined by t_1 and t_2 , let $f(t_1, t_2)$ be the benefit from a brood where the male stays for t_1 , and the female for t_2 . The function of $f(t_1, t_2)$ defines a surface in a three dimensional space, just as the function $g(t)$ defined a line in a two dimensional space.

Note that there cannot be an advantage to playing 'hard-to-get', because in a population with single females and single males which could be breeding but are not, an individual who left its previous brood and played 'easy-to-get' would leave more offspring than others of the same sex. For this reason, we assume that at any one time there may be either surplus males or surplus females, but not both. Not all single individuals need be 'surplus', however; a female may need time between males to recuperate, and a male may have some task to perform between females (such as building a nest in some birds). These times we will refer to as minimum c -values. At equilibrium, either

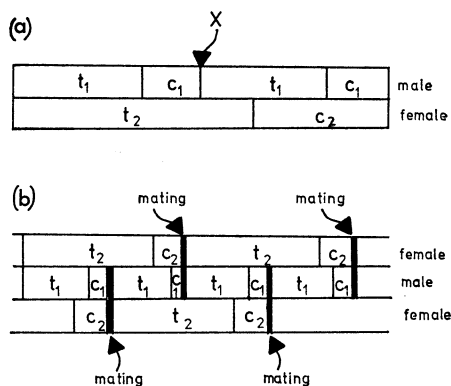


Fig. 2. Illustration of sex ratio constraint. (a) These values of t_1 , c_1 , t_2 and c_2 are only possible if there are twice as many females as males. Otherwise at 'X' there would be no females for the males to mate with. Here, the complete male cycle ($= t_1 + c_1$) is half of the complete female cycle ($= t_2 + c_2$); and the number of males must be half the number of females. In general

$$\frac{\text{Number of males}}{\text{Number of females}} = \frac{t_1 + c_1}{t_2 + c_2}$$

We assume this to be constant. (b) Here the males mate with the upper females, then leave, court and mate with the lower females, and then leave in time to court and mate with the upper females again as they finish caring for the young. The synchrony of breeding is only a convenience for exposition. The argument applies equally to unsynchronized mating provided that each individual keeps to its cycle.

c_1 or c_2 is minimal, while the other is greater than or equal to its minimal value.

In summary, the males can manipulate t_1 , the females t_2 ; and each individual is trying to maximize its benefit per unit time. This benefit will depend on the strategies adopted by other individuals of both sexes. The evolutionarily stable strategies are such that the males play that t_1 which maximizes $f(t_1, t_2)/(t_1 + c_1)$, taking the t_2 the females play as given, the females play that t_2 which maximizes $f(t_1, t_2)/(t_1, c_2)$, taking the t_1 the males play as given, and either c_1 or c_2 is minimal.

Now, taking each pair of values t_1, t_2 in turn we ask: if this is the population strategy, and no individual can better it by changing how long it stays, given that its mate will play the population strategy, what must c_1 and c_2 be? Figure 3(a) illustrates how the c -values are found. Associated with each pair t_1, t_2 is a pair c_1, c_2 which follows from assuming the point to be a stable population strategy. Since

$$r = \frac{t_1 + c_1}{t_2 + c_2}$$

this allows us to calculate what the sex ratio must be if t_1, t_2 is the population strategy. So we can draw lines of constant sex ratio on a graph of t_1 against t_2 ; Fig. 4 shows an (imaginary) example of such a graph.

Since the partial derivatives of $f(t_1, t_2)$ at the population strategy represent the rate at which each male and each female is reproducing, and since all males together reproduce at the same rate as all females together, we can also write

$$\frac{\partial}{\partial t_2} f(t_1, t_2) = \frac{\partial}{\partial t_1} f(t_1, t_2)$$

This equation can be read: at the equilibrium point (\hat{t}_1, \hat{t}_2) , the slope of the f -hill parallel to the t_2 axis equals 'r' times the slope parallel to the t_1 axis.

If we know the function $f(t_1, t_2)$ for a population, and we know the sex ratio, then by constructing lines of constant sex ratio (or r -contours) we can find the r -contour for the population's sex ratio. On this line lie all allowable pairs of t_1, t_2 values. Not all of these pairs are possible however. Only those pairs for which one c -value is minimal and the other is

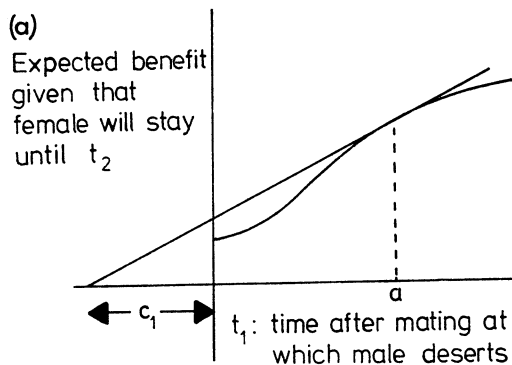


Fig. 3(a)

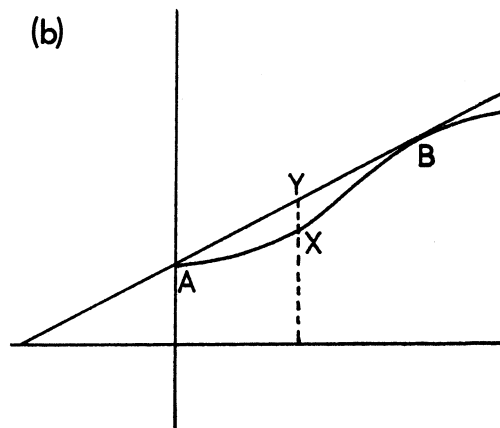


Fig. 3(b)

Fig. 3. (a) Calculation of c_1 . Knowing that the female will leave at some particular t_2 , and knowing that the males leave at time a , and knowing that no male can do better than leave at time a , we wish to find out what value c_1 must take for this to be true. We do this by taking the tangent at a and extending it to the time axis. Similar operations give us the value of c_2 . Thus if the point (t_1, t_2) is a stable population strategy, c_1 and c_2 are determined. Then $r = (t_1 + c_1)/(t_2 + c_2)$. Performing this operation for all possible strategies allows us to draw r -contours as in Fig. 4. (b) Axes as in (a). Points on the f -curve between A and B such as X do not lie on any horizon and so can never be stable pure strategies (see text). However, if an individual plays alternately A and B it can have a stable mixed strategy, Y on average, which does lie on a horizon.

not less than minimal are possible equilibrium points.

Discussion

We consider only pure strategies in the model presented here. That is, we do not consider the possibility of an individual sometimes playing

one value of t , sometimes another. For most of the $f(t_1, t_2)$ surface the only stable strategies are pure strategies, but for certain parts of the surface the analysis presented so far does not hold. We assumed that for each point on the surface we could find a c_1 , and a c_2 such that the point would appear on the horizon when viewed from c_1 (or c_2) behind the t_2 (or t_1) axis. Figure 3(b) illustrates this and shows some points which cannot be on a horizon. In this region males could play a mixed strategy (e.g. Y) that does result, on average, in a point on the horizon provided that its components (here A and B) also lie on it. As yet we do not have the ESS conditions for mixed strategies.

A second problem, pointed out to us by Professor Peter Taylor, is that the ridge on the f -hill above the $t_1 = t_2$ line may be a knife-edge. At any point thereon the partial derivatives are undefined and it may be an ESS for a range of sex ratios.

A Special Case of the Model

We now wish to make the additional assumption that the rate of increase of expected benefit from a brood at any one time depends only on the expected benefit from the brood at that time

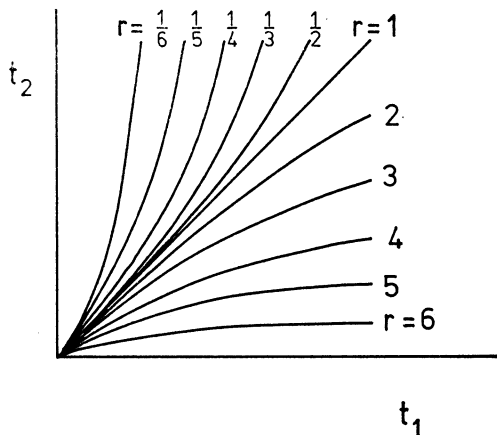


Fig. 4. The t_1, t_2 plane with (imaginary) r -contours. r is the sex ratio at breeding and equals (number of males)/(number of females). The shape of the r -contours depends on the form of the function $f(t_1, t_2)$; those shown are for illustration only and are not necessarily plausible. One r -contour can be thought of as joining points on the surface of $f(t_1, t_2)$ which have their partial derivatives $\partial f/\partial t_1$ and $\partial f/\partial t_2$ in the ratio $1:r$ (see text). As a population has a fixed sex ratio (in this model), the appropriate r -contour for the population represents the set of possible stable strategies to which the sex ratio constraint restricts the population.

(in other words, the current state of development of the brood) and on whether the male, or the female, or neither has already been deserted. This means that if today there are two females singlehandedly looking after broods which have reached the same stage of development, then the females are equally capable of caring for the young; even if one was deserted immediately after copulation and has taken 2 weeks to reach the present stage while the other was deserted yesterday and with the help of a mate has taken only 1 week to reach the present stage.

Figure 5 shows the rate of increase of benefit of a brood under three different conditions: first if both parents are still with it, second if the female only remains, and third if the male only remains. The rate of increase of benefit is plotted against the benefit already attained

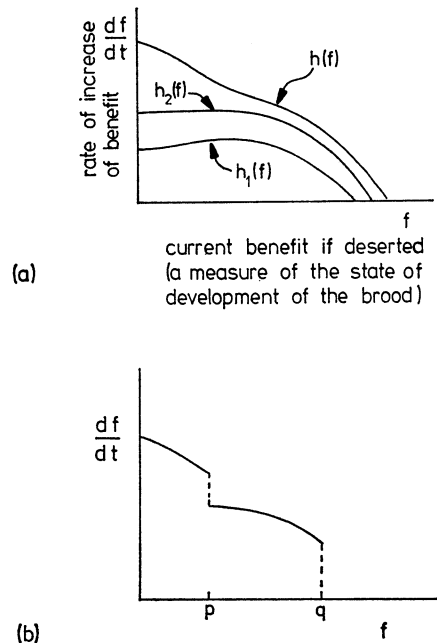


Fig. 5. The h -curves. (a) At any particular stage of development f (current benefit if deserted) both parents together could improve the benefit of the brood at rate $h(f)$. The female alone could improve the benefit at the rate $h_2(f)$, and the male alone at the rate $h_1(f)$. Thus the h -curves represent how good the parents are at caring for the young at each stage of development of the brood. (b) The curve of rate of increase of benefit for a brood in which the male deserted when the benefit was p , and the female when it was q . Until p , both parents cared, and so the $h(f)$ curve is used until p ; between p and q the female-only $h_2(f)$ curve is followed; and thereafter there is no increase in benefit.

(which is what each parent would receive if the brood received no parental care thereafter).

In order to proceed we need to know what benefit is obtained by a pair in which the male deserts at time t_1 and the female at time t_2 . In addition it is necessary to know how these depend on the rates of increase of benefit that can be obtained by different combinations of parents at different times. Figures 6 and 7 show how these quantities are obtained for the situation depicted in Fig. 5. Figure 6 indicates how the graph in Fig. 5 can be used to obtain

curves of benefit against time, while Fig. 7 shows how the graph for a particular brood deserted by the male at t_1 and the female at t_2 can be derived from Fig. 5. Figure 8 shows (imaginary) curves of benefit against time given that either both parents care, only the male

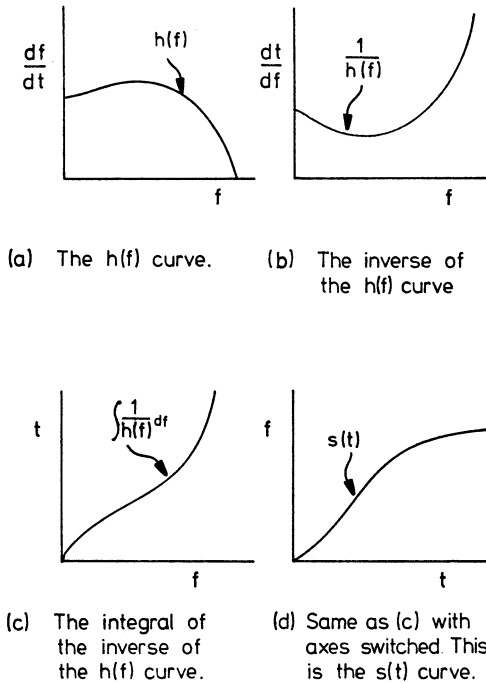


Fig. 6. (a) Shows how much benefit is gained by staying on for another unit of time. (b) Shows how much time must be spent to gain a unit of benefit. (c) Shows how much time altogether must have been spent to reach a given benefit, since (b) tells us how long it takes for each small step on the way to the benefit level. (d) Is just (c) turned on its side, and shows us the function $s(t)$. Thus we obtain

$s(t)$ as the benefit if abandoned of the brood after being cared for by both parents until time t .
 $s_1(t)$ as the benefit if cared for by only the male until time t
 $s_2(t)$ as the benefit if cared for by only the female until time t

Note that $s^{-1}(y) = \int^y \frac{1}{h(f)} df$ is the time both parents must care for the brood to reach benefit y .)

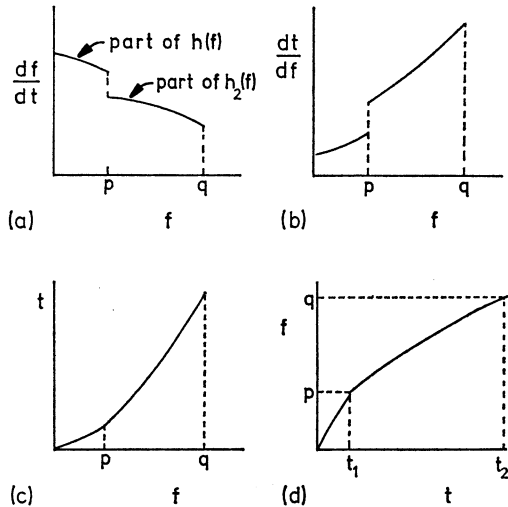


Fig. 7. Following the method of Fig. 6, we derive the benefit of a brood as a function of time (d) from the h -curves (a). (a) The rate of increase of benefit of a brood deserted by the male at p and the female at q . See Fig. 5(b). (b) Time needed to achieve unit increase in benefit at each stage of development of the brood. (c) Total time needed to reach a given level of benefit. (d) Graph (c) with axis switched and the relation between p, q and t_1, t_2 shown.

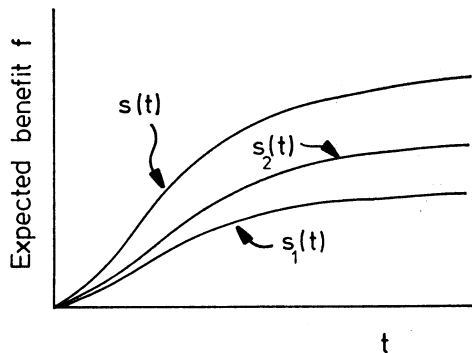


Fig. 8. The s -curves are derived from the h -curves as in Fig. 6. $s(t)$ is the benefit if both parents care and then abandon at time t ; $s_1(t)$ and $s_2(t)$ show the benefit if the male only or the female only, respectively, care and then abandon at time t .

cares, or only the female cares; these curves are called $s(t)$, $s_1(t)$ and $s_2(t)$ respectively.

We are now in a position to find some properties of the r -contours that follow from the special assumption made above.

When $t_1 < t_2$, $s(t_1)$ is the benefit when the male deserts. $s_2^{-1}[s(t_1)]$ is the length of time it would have taken the female to produce that benefit in the brood by herself. Here s_2^{-1} indicates the inverse function to s_2 , i.e. if $b = s_2(a)$ then $a = s_2^{-1}(b)$. Thus $s_2^{-1}(y)$ indicates the time it would take a female alone to produce benefit y . By the additional assumption for this special case, $s_2^{-1}[s(t_1)] + t_2 - t_1$ is the length of time the female would have to stay to produce the eventual benefit by herself; and therefore $s_2\{s_2^{-1}[s(t_1)] + t_2 - t_1\}$ is that eventual benefit. So for $t_1 < t_2$

$$f(t_1, t_2) = s_2\{s_2^{-1}[s(t_1)] + t_2 - t_1\}$$

For convenience, let $x = s_2^{-1}[s(t_1)] + t_2 - t_1$. Now $f(t_1, t_2) = s_2(x)$.

So

$$\begin{aligned} \frac{\partial}{\partial t_1} f(t_1, t_2) &= \frac{\partial}{\partial t_1} s_2(x) \\ &= \frac{\partial}{\partial x} s_2(x) \cdot \frac{\partial x}{\partial t_1} \end{aligned}$$

and

$$\begin{aligned} \frac{\partial}{\partial t_2} f(t_1, t_2) &= \frac{\partial}{\partial t_2} s_2(x) \\ &= \frac{\partial}{\partial x} s_2(x) \cdot \frac{\partial x}{\partial t_2} \end{aligned}$$

But note that $\partial x / \partial t_2 = 1$.

Therefore

$$\begin{aligned} \frac{\partial / \partial t_1 f(t_1, t_2)}{\partial / \partial t_2 f(t_1, t_2)} &= \frac{\partial x}{\partial t_1} \\ &= -1 + \frac{d}{dt_1} s_2^{-1}[s(t_1)] \end{aligned}$$

It has been noted already that

$$\frac{\partial}{\partial t_2} f(t_1, t_2) = r \frac{\partial}{\partial t_1} f(t_1, t_2)$$

It follows that

$$\frac{1}{r} = -1 + \frac{d}{dt_1} s_2^{-1}[s(t_1)] \quad \text{for } t_1 < t_2$$

But the right-hand side of this expression is independent of t_2 , and so for $t_1 < t_2$, r is independent of t_2 . This means that the r -contours must be as drawn in Fig. 9, beginning on the $t_1 = t_2$ line, and extending parallel to the nearer axis. Similarly

$$r = -1 + \frac{d}{dt_2} s_1^{-1}[s(t_2)] \quad \text{for } t_2 < t_1$$

This has the consequence that, provided only one of the r -contours corresponds to the population's sex ratio, we know when the first parent will desert, and which parent it will be.

We now proceed to find a relation between the sex ratio and the relative abilities of the parents to care for the young when the first parent deserts. From the construction of the s -curves in Fig. 6, it is clear that

$$s^{-1}(y) = \int_0^y \frac{1}{h(f)} df$$

and

$$s_2^{-1}(y) = \int_0^y \frac{1}{h_2(f)} df$$

Applying the Mean Limit Theorem

$$\frac{d}{dy} s^{-1}(y) = \frac{1}{h(y)}$$

and

$$\frac{d}{dy} s_2^{-1}(y) = \frac{1}{h_2(y)}$$

Therefore

$$\frac{d}{dt_1} s_2^{-1}s(t_1) = \frac{1}{h_2[s(t_1)]} \cdot \frac{ds(t_1)}{dt_1}$$

Writing $s(t_1) = g$, and noting that $t_1 = s^{-1}(g)$, we have

$$\begin{aligned} \frac{d}{dt_1} s_2^{-1}s(t_1) &= \frac{1}{h_2(g)} \cdot \frac{dg}{dt_1} \\ &= \frac{1}{h_2(g)} \cdot \frac{dg}{ds^{-1}(g)} = \frac{h(g)}{h_2(g)} \end{aligned}$$

But we have already seen that for $t_1 < t_2$

$$\frac{1}{r} = -1 + \frac{d}{dt_1} s_2^{-1}[s(t_1)]$$

and so

$$r = \frac{1}{[h(g)/h_2(g)] - 1}$$

and similarly for $t_2 < t_1$,

$$r = \frac{h(g)}{h_1(g)} - 1$$

with g being the expected benefit when the first parent deserts.

This formula guides our attention to the importance of relative parental ability in determining which parent will desert, and when. Intuitively it is obvious that if, for example, the coloration of the male makes his presence

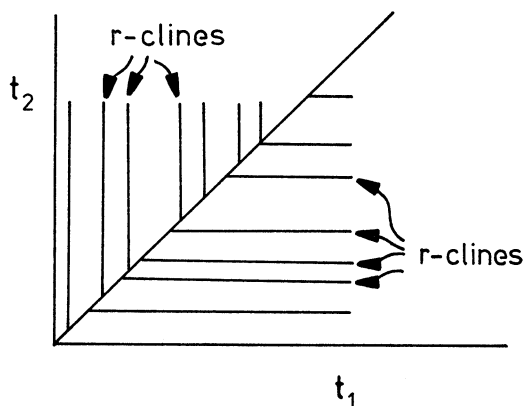


Fig. 9. The shape of r -contours in the special case of the model. Each r -contour extends from the central line ($t_1 = t_2$) and runs parallel to the nearer axis. This means that if we know to which r -contour a population is confined, then we know when the first parent leaves, and which parent it is. The actual value of a given r -contour is given by the formula:

$$\frac{1}{r} = -1 + \frac{d}{dt_1} s_2^{-1}s(t_1) \text{ if } t_1 < t_2$$

$$r = -1 + \frac{d}{dt_2} s_1^{-1}s(t_2) \text{ if } t_2 < t_1$$

If both parents are equally good at caring for the young, then the values of r associated with r -contours which meet on the diagonal in the figure are reciprocals of each other.

detrimental to the survival of the brood he should not stay, whereas he might very well stay if a disproportionate advantage were to accrue from his assistance. Of course, the ratio between male and female parental abilities may change with time as the environment and the needs of the young develop. In this case we can use the formula as a guide to when each parent should be tempted to desert. For example, if at any stage the sexes are complementary, either by specialization or by the need for constant attendance at the nest, so that two parents are much better than either parent alone, then only at extreme sex ratios will either parent desert. If the sex ratio is unity, then the first parent deserts when both parents are twice as good at caring for the young as the deserted parent alone, and if one sex is very poor at looking after the young compared to the other, then that sex will desert first. It is also the case that where the male deserts first, the more heavily the sex ratio is biased towards males, the less the relative advantage of both parents over the female alone is, at the time of desertion. Some of these predictions are illustrated in Fig. 10.

Discussion

These predictions are derived from a very simple model, in which the strategy of each individual is described only by the period of time that he cares for each brood. A more realistic model might use many variables to specify a strategy, and such strategies should be evaluated not only in terms of the numbers of sons and daughters that are expected to reach the age of first breeding, but also in terms of the hazards with which a parent is faced on their behalf. A daily tally of risks run and benefits gained eventually determines fitness (cf. Sibly & McFarland 1976).

We have assumed that the environment is deterministic and constant, that is, we have not allowed seasonal variation or environmental stochasticity. We have also considered breeding sex-ratio and parents' abilities to care for their offspring as 'givens', not subject to change. In deriving the special case predictions we assume that the rate of increase of benefit from a brood depends only on who is caring for it and what benefit has already been achieved.

With these qualifications we predict who will desert and when for any given h -curves (which specify how rate of increase of benefit from a brood depends on who is caring for it and what the expected benefit is at that time: Fig. 10)

