

Evolution of unstable and stable biparental care

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Evolutionarily stable strategy models suggest that biparental care will be stable when parents partially compensate for changes in care by the other parent. Previous work has emphasized the relationship between parental expenditure and the current component of fitness (e.g., offspring survival and fecundity) in causing partial compensation. This study shows that partial compensation depends critically on the effect of current parental expenditure on a parent's future fitness (e.g., survival to and fecundity in subsequent breeding seasons). Partial compensation is favored and biparental care is stable when future fitness is a concave-down function of expenditure (i.e., each increment of expenditure is more costly than the previous). However, when future fitness is a convex-down function of expenditure (i.e., each increment of expenditure is less costly) biparental care is unstable. *Key words*: evolutionarily stable strategy, fitness, fecundity, parental care, parental expenditure. [*Behav Ecol* 7:490–493 (1996)]

In most birds and many other animals, both parents provide parental care (Clutton-Brock, 1991). Evolutionarily stable strategy (ESS) models in which parental investment comprises two discrete strategies, care or desert, suggest that biparental care is stable when the gain in offspring survival from a second parent's care exceeds the reproductive gains obtainable via desertion for both male and female parents (Maynard-Smith, 1982). ESS models investigating continuously variable parental investment strategies indicate that biparental care will be stable when one parent reacts to reduced care from the other parent (for example, amount of food given to young) by increasing its own expenditure, and vice versa, provided that the reaction does not fully compensate for the change by the other parent (Chase, 1980; Houston and Davies, 1985).

More formally, stable biparental care occurs when the optimal expenditure reaction curves of the two parents intersect, with the product of the gradients at the point of intersection being ≤ 1 (Motro, 1994). Empirical support for model predictions comes from Wright and Cuthill (1989), who showed that starling parents with nestlings show partial compensation to reduced foraging by their partners, and from Houston and Davies (1985) and Hatchwell and Davies (1990), who showed that foraging rates of alpha and beta male dunnocks approximately follow predictions of a three-parent model.

Underlying the stability of biparental care (Houston and Davies, 1985; Motro, 1994) and, more generally, optimal parental effort (Winkler, 1987; Winkler and Wilkinson, 1988), is the relationship between parental expenditure and fitness. In organisms that breed more than once but have nonoverlapping broods, the fitness consequences of a given level of parental expenditure used to rear the current brood can be divided into future (e.g., effect on parental survival and fecundity) and current (e.g., effect on offspring survival and fecundity) components.

Clutton-Brock and Godfray (1991: 247) emphasized the importance of the current component on the stability of biparental care by stating that "Houston and Davies (1985) showed that where offspring fitness increases as an asymptotic function of parental expenditure once parental expenditure

exceeds some threshold level, each parent should respond to increases in care by its partner by reducing its own expenditure." However, the offspring fitness function described above (Figure 1A) is likely to occur in most cases of parental care because neither offspring survival nor fecundity can increase without limit. In addition, if the offspring fitness function is sigmoid, optimal parental expenditure is likely to be above the point of inflection, where the two shapes are equivalent (Figure 1A). Optimal parental expenditure before the point of inflection is unlikely because in this range each increment of expenditure produces increasing gains in offspring fitness (Winkler, 1987).

The ubiquity of the asymptotic offspring fitness function makes it unlikely to be the sole cause of stable biparental care, which is not universal in species with parental care. Motro (1994) has shown that biparental care can be either unstable or stable, depending on the complementarity of parental care, when parental expenditure has a linear cost in terms of parental future fitness. When the two parents' care has a strongly superadditive effect on offspring survival, biparental care is stable. When care is weakly superadditive, purely additive, or less than additive, biparental care is either unstable or stable, with the two parents working at very different rates. In this study, I show that when the care of the two parents is additive, the stability or instability of biparental care depends critically on the relationship between the future component of parental fitness and parental expenditure. In particular, the concave-down future fitness function examined by Houston and Davies (1985) cannot lead to unstable biparental care, whereas a convex-down function can. Data suggest that the parental fitness function in birds may be concave down, thereby making biparental care stable, although the general shape of this function has not been determined for any bird or mammal species (Winkler and Wilkinson, 1988). A possible case of a convex-down function in foundress associations of queen ants is discussed.

ANALYSIS

Results of Houston and Davies

When the parental expenditure reaction curves cross once, optimal expenditure in a biparental species leads to four basic outcomes (Chase, 1980; Clutton-Brock, 1991; Houston and Davies, 1985) (Figure 2): (1) stable biparental care, (2) fe-

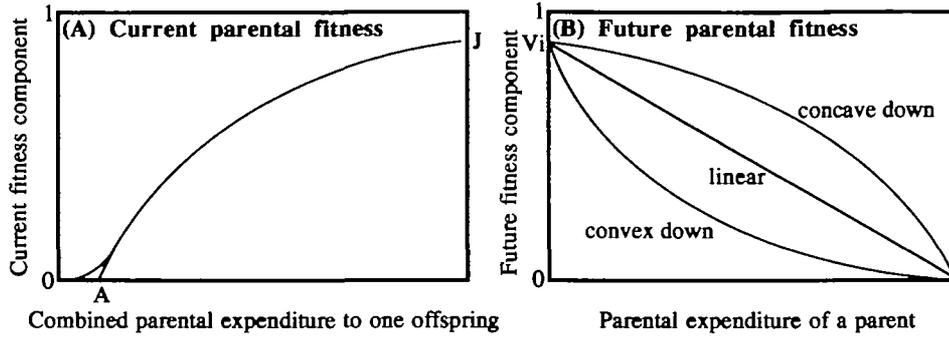


Figure 1
Theoretical curves for (A) effect of parental expenditure received by one offspring from all parents on that offspring's contribution to the current component of parental fitness; (B) effect of parental expenditure by a specified parent on that parent's future component of fitness (e.g., survival and future fecundity). In panel A, sigmoid and nonsigmoid functions are shown.

male-only care, (3) male-only care, (4) unstable biparental care, leading to care by only one parent depending on initial conditions. Only the first three can be obtained from the explicit model examined by Houston and Davies. The fourth depends on the reaction curves having gradients of < -1 (Figure 2D), but the optimal reaction curves of Houston and Davies always have gradients of > -1 . This is seen by examining their Equations 4 and 5:

$$E_m^* = (L_m - kE_f) / (Nc + k)$$

$$E_f^* = (L_f - kE_m) / (Nc + k).$$

In these equations (parameters are defined in Appendix A), the optimal effort of a focal male or female parent, E_m^* or E_f^* , is a linear function of the effort of the other parent with intercept $L_i / (Nc + k)$ and gradient $-k / (Nc + k)$, where $L_i = \ln(P_i/k/V_i c) + c + kA$. The gradient lies between 0 and -1 , because the terms k , c , and N are positive. The values of k and c are positive because only positive numbers can generate the fitness curves shown (Houston and Davies, 1985).

Convex-down future fitness function

The model of Houston and Davies (1985) can be modified to examine the effect of changing the future fitness function from concave-down to convex-down (Figure 1). Equations that can generate these shapes are:

Convex down $V_i e^{-aNE_i}$

Concave down $V_i [1 - e^{-c(1-NE_i)}]$.

The second equation is from Houston and Davies (1985). Following Houston and Davies (1985), the fitness of a parent, i , λ_i , is defined as the fitness from offspring reared during the current breeding season plus future fitness:

$$\lambda_i = P_i N J [1 - e^{-k(E_i + E_o - A)}] + V_i e^{-aNE_i}.$$

Houston and Davies defined these two components of parental fitness as number of surviving offspring and parental survival, but they can be thought of more generally as current and future. The optimum level of expenditure by parent i , E_i^* , in response to expenditure by the other parent, E_o is de-

termined by differentiating λ_i with respect to E_i , finding the maximum, and then solving for E_i^* :

$$d\lambda_i / dE_i = kP_i N J e^{-k(E_i + E_o - A)} - aN V_i e^{-aNE_i} \tag{1}$$

$$0 = kP_i N J e^{-k(E_i^* + E_o - A)} - aN V_i e^{-aNE_i^*}$$

$$\ln(aV_i) - aNE_i^* = \ln(kP_i J) - k(E_i^* + E_o - A)$$

$$E_i^* (k - aN) = \ln(kP_i J / aV_i) + kA - kE_o = M_i - kE_o$$

$$E_i^* = M_i / (k - aN) - kE_o / (k - aN), \tag{2}$$

where $M_i = \ln(kP_i J / aV_i) + kA$. (M_i is positive for biologically meaningful values of its component parameters for the fitness functions used.) Equation 2 shows that the gradient of the optimal reaction of the focal parent to the expenditure of the other parent is $-k / (k - aN)$. For $k > aN$, the gradient is < -1 and the intercept is positive to give the fourth pair of reaction curves shown in Chase (1980), Houston and Davies (1985), and elsewhere (Clutton-Brock, 1991; Clutton-Brock and Godfray, 1991). For the first derivative of parental fitness to be a maximum when equal to zero (that is, an optimum), the second derivative of parental fitness must be negative. The condition for this is also $k > aN$ (see Appendix B).

DISCUSSION

Concave-down future fitness function: possible causes and evidence

Given the likelihood that the offspring fitness function in birds is asymptotic (Figure 1A), this study suggests that the stability of biparental care in birds may be caused by a concave future parental fitness function with respect to current parental expenditure.

A concave-down future fitness function means that each increment of parental care is more costly to the parent than the previous increment (Winkler and Wallin, 1987; cf. Schaffer, 1974). When the main component of parental care is food, each additional increment of food given to young would cause an increased predation risk if parents increase their provisioning rate by foraging farther from the nest, in more dangerous situations, or with decreased vigilance (Askenmo, 1979; Da-

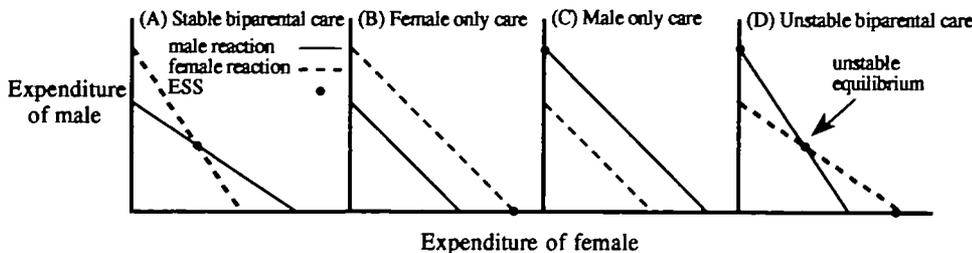


Figure 2
Optimal parental expenditure as a function of the other parent's expenditure. ESS, evolutionarily stable strategy.

vies, 1992; Lima, 1987; Winkler and Wilkinson, 1988). Additional food increments may also be increasingly costly if parents increasingly lose physical condition (Askenmo, 1979; Drent and Daan, 1980). This is plausible in birds, given the high energetic demands and seeming upper limit of foraging (Bryant, 1988; Drent and Daan, 1980).

In more direct support of the idea that future fitness in birds is a concave-down function of parental expenditure, and in particular that parents lose condition when working hard, Askenmo (1979) showed that the proportion of male pied flycatchers with slightly enlarged broods (nine young) returning to breed next year was drastically reduced (18% return rate) in comparison to males with unmanipulated broods (seven to nine young; 38% return). Numerous studies show that the future fitness of parents reduces with increasing brood size, either by reducing survival or future fecundity [for review, see Nur (1989), Partridge (1989); see Pettifor et al. (1988) for an exception]. A major problem in using variation in brood size to determine the shape of the future fitness function is that parental expenditure, not brood size, is the relevant predictor variable and need not be directly proportional to brood size (Drent and Daan, 1980; Nur, 1984).

Experimental determination of the relationship between current parental expenditure and the future component of parental fitness is not a trivial empirical problem (Winkler and Wilkinson, 1988). Not only is it laborious to measure parental care (i.e., foraging trips, guarding) and problematic to translate this into a common currency of expenditure, but variation in expenditure may affect future parental fitness in several ways, necessitating the collection of large amounts of data on parental survival and future fecundity. One factor ameliorating the difficulty, however, is that it is sufficient to know the general shape of the relationship (Winkler, 1987), in this case whether it is concave or convex down, rather than the exact shape.

Determining the effect of parental expenditure on future fitness is complicated by the need to vary expenditure but minimize random variation in costs due to factors such as territory quality and predation. Male dunnocks in polyandrous trios are a possible experimental system allowing a paired design within territories, year, and sex (with appropriate control in case male status affects survival independent of expenditure). In dunnocks, a male's access to the female during her fertile period, which can be varied experimentally, influences his feeding of nestlings (Burke et al., 1989; Davies, 1992). Davies (1992) reports no difference in annual mortality between alpha and beta males, which is unsurprising given that alphas and betas have similar natural paternity (53% versus 44%; Burke et al., 1989) and hence may have similar expenditures (Hatchwell and Davies, 1990).

Convex-down future fitness functions: possible cause and example

What conditions could cause a convex-down future fitness function? Such a shape could also result from food gathering if additional increments of food are less costly to collect; for example, when foraging experience reduces foraging cost. Although this is unlikely in birds exploiting a well-known territory containing many feeding sites, it could occur when each food site is very large, sufficient to supply a whole breeding season, but hard to find or learn how to exploit.

An intriguing possible example of a convex-down future fitness function leading to unstable biparental (or multiparental) care occurs in the ant (*Acromyrmex versicolor*). In *A. versicolor*, nests are founded by queens after mating flights, with most nests founded by multiple queens (Rissing et al., 1986). In most ants with queen-founded nests, foraging by queens

does not occur and queen body reserves are used to rear the first workers (Hölldobler and Wilson, 1991). However, in *A. versicolor*, foraging by queens for leaves is necessary to initiate the fungus garden. Because nests are founded under a tree (Rissing et al., 1986), a single food patch sufficient for nest founding is nearby. Because an inexperienced forager-queen would need to find this source of leaves, whereas an experienced forager need only return to the known source, it is likely that additional increments of food are decreasingly costly to collect. In keeping with the expectation of unstable biparental care in such a situation, only one queen normally acts as a forager in multiqueen associations (Rissing et al., 1989). Queen size and ovary development do not differ between foragers and nonforagers, and there is no overt physical conflict among queens (Rissing et al., 1989).

APPENDIX A

Definitions of parameters

- E_i Parental expenditure of parent i
- P_i Probability that i is a parent of the brood
- N Number of offspring in brood
- J Maximum value of current component of fitness (e.g., offspring survival)
- k Constant affecting relationship between current component of fitness and expenditure of all parents
- A Amount of parental expenditure needed to make current component of fitness > 0
- V_i Maximum value of future component of fitness (e.g., parental survival)
- c Constant affecting future component of fitness (concave down model)
- a Constant affecting future component of fitness (convex down model)

APPENDIX B

Derivatives of parental fitness

The second derivative of parental fitness, f'' , is negative when the first derivative, f' , is zero:

$$f' = kP_i N J e^{-k(E_i + E_o - A)} - aN V_i e^{-aNE_i}$$

$$f'' = -k^2 P_i N J e^{-k(E_i + E_o - A)} + a^2 N^2 V_i e^{-aNE_i}$$

Substitute $E_i = (M_i - kE_o)/(k - aN)$, at $f' = 0$ (Equation 2):

$$f'' = a^2 N^2 V_i e^{-aN(M_i - kE_o)/(k - aN)} - k^2 P_i N J e^{-k((M_i - kE_o)/(k - aN) + E_o - A)}$$

$$f'' = \ln(a^2 N^2 V_i) - \ln(k^2 P_i N J)$$

$$+ (k - aN)(M_i - kE_o)/(k - aN) + k(E_o - A)$$

$$f'' = \ln(a^2 N^2 V_i)$$

$$- \ln(k^2 P_i N J) + M_i + kA$$

Substitute $M_i = \ln(kP_i J/V_i a) + kA$ to give:

$$f'' = \ln(a^2 N^2 V_i) - \ln(k^2 P_i N J) + \ln(kP_i J/V_i a)$$

$$f'' = \ln(a) + 2 \ln(N) + \ln(aV_i) - \ln(k) - \ln(N)$$

$$- \ln(kP_i J) + \ln(kP_i J) - \ln(V_i a)$$

$$f'' = \ln(a) + \ln(N) - \ln(k) = \ln(aN) - \ln(k)$$

Thus, f'' is negative when $k > aN$.

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