

## Parental investment decision rules and the Concorde fallacy

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**Summary.** Investment theory states that animals should base their parental investment decisions on expected benefits, and not on whether or not past investment will be wasted. Otherwise, they would commit the Concorde fallacy. If reproduction has a cost, however, then past investment and expected benefits are necessarily confounded. Assuming a cost of reproduction, animals will be selected to maximize their remaining lifetime reproductive success, subject to a tradeoff between present and future reproduction (Williams' principle). We extend Williams' principle and develop an experimental design that would allow past investment and expected benefits to be varied independently. This design illustrates the importance of the value of the brood *relative* to the value of future reproduction.

### Introduction

An important goal of behavioral ecologists is to understand how animals make decisions on parental investment. Williams (1966), in one of the first parental investment models, proposed that at any point in time a parent is selected to maximize its remaining lifetime reproductive success, subject to a tradeoff between present and future reproduction (Williams' principle). Williams' principle assumes that reproduction has a cost. In other words, past investment of time and energy devalue a parent's own future reproduction. Moreover, Williams realized that there are two components to a parent's remaining lifetime reproductive success: (1) the survival and future reproduction of the brood at stake, and (2) the parent's own expected future reproduction in subsequent brood cycles. Thus, in-

vestment into the brood will tend to increase the value of the brood's future while simultaneously decreasing the value of the parent's own future. Parental investment decisions therefore should weigh the value of the brood *relative* to the value of the parent's own future reproduction.

Trivers (1972) predicted that brood desertion in animals with biparental care would be more likely in the sex with the lower cumulative parental investment. Trivers' emphasis on not wasting past investment led others (Dawkins and Carlisle 1976; Boucher 1977; Maynard Smith 1977) to point out that a central principle of investment theory (e.g. Williams 1966) is that pending investment should depend on expected benefits, and not on whether or not past investment will be wasted. Violation of this principle has become known as committing the Concorde fallacy (Dawkins 1976).

There is some evidence that animals do assess their expected future reproduction. For example, Keenleyside (1983) found that mate desertion by males in the biparental cichlid, *Herotilapia multispinosa*, increases with the proportion of females in the population, i.e. with the males' expected future reproduction. However, other studies of parental investment decisions have suggested: (i) some animals in fact commit the Concorde fallacy, behaving so as not to waste their past investment (Weatherhead 1979, 1982, Dawkins and Brockmann 1980); or, (ii) some animals can only assess their future benefits through their past investment (e.g. Weatherhead 1979), a limitation that sometimes will cause them to behave suboptimally with respect to maximizing their lifetime reproductive success.

Weatherhead (1979) found for savannah sparrows (*Passerculus sandwichensis*) that past investment (time since clutch initiation) was a better indicator of nest defense than the time remaining in

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the season to renest if the initial nest failed. This result led him to suggest that savannah sparrows commit the Concorde fallacy. Unfortunately, past investment (time) and expected future benefits may have been confounded. Although the *relative* value of the offspring increases as the parent's expected future reproduction decreases, offspring fledged early in the season may have higher value than offspring fledged late in the season, because of their longer development period before migration and overwintering (e.g. Perrins 1979). Thus, it is difficult to predict whether parent birds that initiate their clutches earlier should show higher or lower nest defense, for the same stage of offspring development.

Dawkins and Brockmann (1980) with digger wasps (*Sphex ichneumoneus*), and Weatherhead (1982) with redwinged blackbirds (*Agelaius phoeniceus*), both studied systems in which past investment varied among individuals while gains to the offspring at stake were roughly equal. Both studies found a positive correlation between past investment and current investment and suggested that these animals may commit the Concorde fallacy. Both studies assumed no tradeoff between past investment and future reproduction (see Fagerstrom 1982). For example, there is evidence in hymenoptera that an individual's total flight time during its life span is fixed (Neukirch 1982), and there is evidence in birds that parents who fledge their offspring late in the season are unlikely to have time to initiate another clutch (Weatherhead 1979).

To test the Concorde fallacy, one must vary past investment and expected benefits independently, and consider both the brood at stake and the parent's expected future reproduction as expected benefits. To clarify how past investment and current investment are related under natural selection, we develop an extension of Williams' model.

### Model

We assume a static situation in which offspring age (and thus time) is constant, but in which past parental investment (time and energy) and brood size are free to vary (e.g. through brood predation). Assuming that all the parents are on equal terms, we ask, "How does perturbing brood size or past investment affect optimal brood defense?" Let

$$R = b s(D) + f(I) S(D); \quad (1)$$

where  $R$  is the parent's remaining lifetime reproductive success;  $b$  is brood size;  $s$  is the probability of an offspring surviving a predator's attack, which

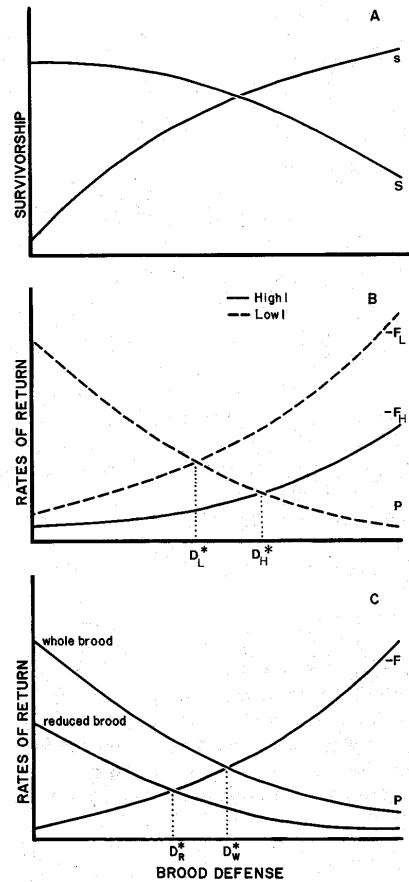


Fig. 1A-C. A graphical analysis of Williams' (1966) tradeoff model. A Offspring survivorship ( $s$ ) and adult survivorship ( $S$ ) versus brood defense ( $D$ ). B The optimal brood defense ( $D^*$ ) will occur where the rates of return on brood defense for present reproduction ( $P$ ) and for future reproduction ( $F$ ) are equal but opposite in sign:  $P = -F$ . When brood size ( $b$ ) is held constant while past investment ( $I$ ) varies,  $D^*$  increases with increasing  $I$ . C When  $I$  is held constant while  $b$  varies,  $D^*$  decreases with brood size reduction.

is assumed to increase with diminishing returns with brood defense,  $D$  (parental risk, Fig. 1A);  $f$  is the expected future reproduction of the parent if it survives, which is assumed to be a decreasing function of past investment into offspring,  $I$ ; and  $S$  is the probability that the parent survives a predator's attack and thus reproduces again in the future, which is assumed to increase with diminishing returns as brood defense (risk) decreases (Fig. 1A). The optimal brood defense ( $D^*$ ), which

maximizes  $R$ , occurs where

$$dR/dD = b ds/dD + f(I) dS/dD = 0. \quad (2)$$

The term,  $b ds/dD$ , is the rate of return on brood defense for present reproduction ( $P$ ), and the term,  $f(I) dS/dD$ , is the rate of return on brood defense for future reproduction ( $F$ ).  $D^*$  occurs where  $P = -F$ . Our assumptions about the shapes of the functions  $s(D)$  and  $S(D)$  (Fig. 1A) assure that

$$d^2R/d^2D < 0$$

and that  $D^*$  maximizes  $R$ . It follows that if individuals vary in past investment and have equal brood sizes, then  $D^*$  is an increasing function of past investment,  $I$  (Fig. 1B). Furthermore, if individuals vary in brood size and have equal past investments, then  $D^*$  is an increasing function of brood size,  $b$  (Fig. 1C). In addition, increasing both  $b$  and  $I$  will have a larger effect on  $D^*$  than increasing only one of these parameters. Note that halving  $b$  is effectively equivalent to doubling  $f(I)$ .

### Discussion

The following kind of experiment would test the model. Divide parents (e.g. nesting birds) with equally aged clutches into three treatments. Parents in treatment 1 lose half their eggs shortly after laying them; parents in treatment 2 lose half their eggs during the late incubation phase; and parents in treatment 3 suffer no brood predation. Let brood defense be scored shortly after the manipulation in treatment 2, before the eggs hatch. When comparing treatments 1 and 2, brood size is constant but the parents in treatment 2 have the larger past investment,  $I$ , and thus the lower expected future reproductive success,  $f(I)$ . (There is good evidence in birds that incubation costs increase with clutch size (Biebach 1981)). According to our model, the parents in treatment 2 would have more at stake and should show the higher brood defense (Fig. 1B). When comparing treatments 2 and 3, however, the two groups would have the same past investment but different brood sizes. The parents in treatment 3 therefore would have more at stake than those in treatment 2, and should show higher brood defense (Fig. 1C).

Such an experiment would test four hypothetical parental investment decision rules. (1) If a parent's brood defense is independent of both brood size and past investment, then brood defense should be equal among treatments:  $3 = 2 = 1$ . (2) If a parent bases its brood defense on past invest-

ment alone, and is unable to assess expected benefits in any other way, then brood defense should show the following ranked order among treatments:  $3 = 2 > 1$ . (3) If a parent bases its brood defense on offspring number alone (or the brood's value), and is unable to use other cues to estimate its expected future reproduction, then brood defense should be ranked among treatments:  $3 > 2 = 1$ . (4) If a parent increases its brood defense with increasing past investment and with increasing brood size, as predicted by our model, then brood defense should be ranked among treatments:  $3 > 2 > 1$ . This result would falsify the first three hypotheses and would support Williams' (1966) principle that at any point in time an animal invests in its brood so as to maximize its remaining lifetime reproductive success, subject to a tradeoff between present and future reproduction. Failure to consider Williams' principle may mislead one to believe that animals commit the Concorde fallacy.

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