

AVIAN NEST DEFENCE: THEORETICAL MODELS AND EVIDENCE

by

TOMAS REDONDO¹⁾

(Cátedra de Biología y Etología, Facultad de Veterinaria, UNEX, 10071 Cáceres, Spain)

(With 4 Figures)
(Acc. 20-V-1989)

Introduction

Many bird species display conspicuous anti-predator behaviour while caring for their eggs or young. Predation is the main cause of nest failure (RICKLEFS, 1969; CLARK & WILSON, 1981) and since eggs and altricial nestlings are unable to actively defend themselves, selection should have acted on parents to diminish predation pressures. Most observations of parental defence in birds have reported an increase in both frequency and strength of the response during the breeding cycle. This phenomenon has been explained in four ways:

a) The probability of a nest to be preyed upon increases with nestling age as a consequence of two factors: nests containing older nestlings are more conspicuous (because chicks utter louder calls and are fed at a higher rate) and more profitable to predators due to their higher body weight. Parents should counteract the increasing risk of nest predation by enhancing their defensive tactics (GREIG-SMITH, 1980).

b) Increased nest defence reflects cumulative past investment in offspring: parents value (and, hence, defend) more their offspring the more they have been cared for (TRIVERS, 1972). Such an explanation should however be a fallacious one because natural selection cannot work on past investment (which is, in fact, already wasted) but on future reproductive potential of the offspring (DAWKINS & CARLISLE, 1976; BOUCHER, 1977).

¹⁾ I thank R. CAMPAN, A. KACELNIK and J. LAUGA for helpful comments on earlier drafts of this manuscript; S. EDEN for kindly offering me his unpublished material; J. CARRANZA for some illuminating arguments and M. A. MULERO for help with mathematics. The Department of Mathematics, UNEX, provided financial and material support.

c) Should parents not commit this so-called "Concorde fallacy" (but see CARLISLE, 1985), adults will increase nest defence as their offspring become more valuable in terms of future reproductive value. As the breeding cycle advances, offspring have higher chances of reaching their own reproductive age and so become more valuable to parents (ANDERSSON *et al.*, 1980).

d) The increasing pattern of nest defence is an artifact resulting from methodological procedures employed by field workers. Most studies of nest defence involve revisitation of the same nest at varying intervals. Pairs defending nests against investigators may become positively reinforced by their "success" in moving away the intruder with no damage for themselves and their broods and they will be more willing to defend the next time the intruder (frequently the same individual) appears (KNIGHT & TEMPLE, 1986a).

Hypotheses a-c) and d) offer a functional and a causal explanation, respectively, of the same phenomena and may indeed be not mutually exclusive. KNIGHT & TEMPLE (1986a, b, c) have shown that an increase in nest defence (*i.e.* an increase in frequency and/or intensity of the defensive response) during the breeding cycle is less apparent, or absent, in naive *vs* experienced birds, thus offering support for the revisitation hypothesis. However, some results on naive birds have reported on an increasing pattern of nest defence as nestlings get older (SHALTER, 1979; PATTERSON *et al.*, 1980; RÖELL & BOSSEMA, 1982; REGELMANN & CURIO, 1983; STEPHENS, 1984; CURIO, 1987; see also KILPI, 1987) so none of the two hypotheses can be rejected. When both age of the brood and number of visits to nests are considered separately for the same individuals, a combination of both results in a higher proportion of variance explained, suggesting that they are superimposed factors (BREITWISCH, 1988).

Much of the interest underlying an explanation of nest-defence patterns based on life-history traits lies in the fact that theoretical models of allocation of reproductive effort can be tested in the field by comparing predictions about parental investment decision rules with observed investment in nest defence under a variety of conditions. Since defence of offspring enhances their survival at a cost to the parents' future reproductive expectancies, it is likely to be a good indicator of the parental willingness to invest in offspring (TRIVERS, 1972; BIERMANN & ROBERTSON, 1981). In this paper I will discuss previous models of avian nest defence with the aim of elaborating a single synthetic model. I will also review available data on nest defence when looking for evidence supporting the model's predictions. Defending birds have proved to be sen-

sitive to many subtleties of the methodology employed by observers (KNIGHT & TEMPLE, 1986b). Being aware that we are far from understanding how results may have become affected by methodological procedures, I will assume such effects to be mainly of a quantitative order, *i.e.* defence measurements may be over- or subestimated as a consequence of methodology.

Previous models of nest defence.

Theoretical models aimed to explain the observed patterns of nest defence are cost-benefit models. They balance the tradeoff between two variables on which parental fitness is assumed to depend.

BARASH (1975) suggested that increasing brood age diminished within-season renesting potential of parents while increased offspring survival chances with a sharp levelling-off just before chicks are about to leave the nest. Such an explanation does not take into account how survival probability of offspring should become affected by parental defence nor is valid for single-brooded species whose renesting potential is negligible throughout the breeding cycle (REID & MONTGOMERIE, 1985).

ANDERSSON *et al.* (1980) developed a model in which parental fitness was assumed to be a function of the parents' survival probability from time t in the current breeding cycle to the next breeding season plus the equivalent survival probability of the current batch of offspring. Survival probabilities of parents and offspring decrease and increase, respectively, with the level of parental defence. Optimal levels of defence, which are those that maximize parental fitness, are then showed to increase with brood age just because the difference in survival probabilities of parents and their offspring becomes smaller as the young get closer to the next breeding season.

In such a model, all parents are assumed to be equal with regard to their future reproductive expectancies: residual reproductive value (PIANKA & PARKER, 1975) is kept as a constant for all birds in a population. This assumption is unrealistic and a model intended to predict optimal levels of parental care should weigh the expected benefits derived from investment in a current brood relative to lifetime expected fitness (CARLISLE, 1982). Both CARLISLE (1982) and SARGENT & GROSS (1985) develop models in which parental fitness is a function of the level of parental care weighted between two additive, current and future, components but they make no predictions about the level of care which should be optimal at different times of the current breeding attempt.

WALLIN (1987) has proposed a modified version of this model in which there is a variable (parental condition and experience) that could account for some variations in residual reproductive value.

CURIO *et al.* (1984) proposed a model of brood defence based on great tit (*Parus major*) demography parameters. This model takes into account within-season survival parameters of parents and offspring together with parental residual reproductive value. It assumes that the intensity of brood defence is directly proportional to the value of the brood at stake (represented by the survival probability of the batch of offspring to the end of the breeding cycle) and inversely to the potential loss of fitness due to death suffered from defence (the sum of the endangered residual reproductive value plus the proportion of the current brood that will die if the parent dies during brood defence). This model integrates a higher number of factors which are likely to affect parental fitness and leads to a wider set of predictions than those previously commented. I feel, however, that it entails two minor flaws. I) Since it is based on specific demographic data, some of its predictions may be difficult to extend beyond tits' life history. A more general treatment could have led to similar predictions for species with no life-table data available. II) Intensity of defence should be proved to be a function of parameters such as brood size or residual reproductive value by *a posteriori* derivating optimal level of defence from a parental fitness function. While such a procedure might lead to identical results, it only makes assumptions about parameters influencing parental fitness and not about the relationships between such factors.

Finally, PATTERSON *et al.* (1980) claimed that models of nest defence only take into account factors related to reproductive value of parents and their offspring, while neglecting how defensive responses may be affected by what they term "stimulus value" of the predator: frequency and intensity of predator-prey interactions over evolutionary time, the effectiveness of the predator in preying upon offspring at different developmental stages, the effectiveness of the defence response in deterring the predator and the risks the parents incur in responding. They also suggested some other factors that should be included in a model of nest defence: age-dependent reproductive tactics of the parents, environmental influence on reproductive success and age-dependent variations in the offspring survival probabilities while still dependent on parental care.

CURIO *et al.* (1984) included in their model some of these factors (residual reproductive value and offspring differential mortality conditioned to parental death) but their model lacks considerations about

predator characteristics, age-related changes in the offspring survival chances and environmental influence beyond the effect that different habitats exert on residual reproductive value of parents (CURIO *et al.*, 1984, 1985).

WINKLER (1987) has recently developed a general model of parental care which takes into account relative allocation of parental effort to current and future broods. In this model, optimal amount of investment is considered to be a function of life-history parameters on which it is likely to depend. Such a procedure yields equations from which it can be directly inferred how variations in a parameter affect optimal effort levels.

Now I will suggest a model of nest defence that aims to integrate previous models. It starts from a two-component parental fitness function (CARLISLE, 1982; SARGENT & GROSS, 1985) expressed as expected reproductive value at key moments of a bird's lifetime reproductive schedule (ANDERSSON *et al.*, 1980; CURIO *et al.*, 1984). Fitness function is then maximized with respect to the intensity of defence and predictions set up by observing how changes in life-history parameters affect the value of the optima (SARGENT & GROSS, 1985; WINKLER, 1987). I have included two new factors on which offspring survival probabilities are likely to depend: stimulus value of the predator (*sensu* PATTERSON *et al.*, 1980) and self-protective behaviour of well-developed chicks. Some of the predictions emanating from this model, and some of the arguments employed in discussing them, were independently developed in a recent review of nest defence in birds (MONTGOMERIE & WEATHERHEAD, 1988). This review includes a simple, graphic model which generates many useful predictions but which is constrained by the shape that cost-benefit functions are assumed to have. Specially those predictions concerning optimal responses in defence level to variations in stimulus value of the predator, time in the breeding cycle and brood size are virtually identical to those generated by the following analysis.

The model

I will make two assumptions concerning the consequences of defending a brood upon survival probabilities of parents and their offspring.

First, I will assume that parental defence increases the offspring survival probability. Although such an assumption has been criticised (NUR, 1981), anti-predator behaviour has been shown to reduce nest predation (GÖRANSSON *et al.*, 1975; ANDERSSON & WIKLUND, 1978; BUITRON, 1983).

Furthermore, some studies have found an inverse relationship between the intensity of nest defence and the probability of a nest to be preyed upon (ANDERSSON *et al.*, 1980; GREIG-SMITH, 1980; BLANCHER & ROBERTSON, 1982; KNIGHT & TEMPLE, 1986c; BYRKJEDAL, 1987) while others have failed in doing so (MCLEAN *et al.*, 1986) or have found a weak relationship (MILLER, 1985; BREITWISCH, 1988; KNIGHT & TEMPLE, 1988). At a given age, the probability of a chick reaching independence from parents is assumed to be a positive, asymptotic function of the level of parental defence. Being offspring survival defined in this way, older chicks have a higher probability of reaching independence than younger ones over any level of parental defence. Second, I will assume that mortality risk for a parent increases as a function of the level of defence. Accordingly, the probability of a parent reaching the time at which offspring become independent is a decreasing function of defence level. Predator harassment entails a direct risk for parents that may be killed or injured by the predator (CURIO, 1978; CURIO & REGELMANN, 1986a; WALLIN, 1987). In addition, nest defence is an energy-demanding activity that may lower the yet impaired body condition of breeding adults. Nest-defence activity may also attract new predators to the nest (MCLEAN *et al.*, 1986) or brood parasites (ROBERTSON & NORMAN, 1977) which will in turn demand more defence. Over any level of defence, parents tending older offspring have a higher probability of surviving at the end of the period of parental care.

I will now examine how parental fitness depends on factors which may become affected by the intensity of nest defence.

Let the fitness function for a parent to be:

$$F = F_c + F_f$$

where F_c is the expected increment in fitness obtained from the current brood and F_f that obtained from future broods.

F_c is the fitness that parents can obtain if offspring survive to the next breeding season. It can be set equal to brood size B devalued by the coefficient of relationship between parents and their offspring and multiplied by the probability of offspring surviving to the onset of the next breeding season:

$$F_c = r B p \quad (1)$$

where p is the combined probability of offspring surviving from time t in the current breeding cycle to the time T at which they become independent from parents and the probability of surviving from time T

to the onset of the next breeding season. Let both probabilities to be, respectively, $O(t)$ and $S(T)$. We can write:

$$p = O(t) S(T)$$

and, substituting in (1),

$$F_c = r B O(t) S(T) \quad (2)$$

$S(T)$ includes all causes of juvenile losses and is expectedly greater for birds in a good body condition at time T .

The probability of offspring reaching independence for a given age t is also a function of their chances of surviving a predator attack. There are three variables which may positively affect the offspring's probability of surviving:

a) Level of parental defence, L .

b) The nestlings' ability to escape from or deter the predator. The rate at which nestlings are able to perform a successful escaping response is a function of their sensory-motor development which is, in turn, a function of t , $E(t)$. $E(t)$ is likely to remain near zero for most of the nestling period but increase steeply shortly before fledging.

c) The potential risk posed by the predator, P . For a given level of defence, offspring reach higher probability of survival the more effective is the predator in taking the brood. For instance, if parents incubating eggs engage in defence against a predator specialized on fledglings, no immediate benefit to the offspring is achieved (the model ignores long-term benefits derived from moving on predators which may be dangerous in the future). Also, nestlings in safe nests will benefit less than those occupying more exposed nest sites, *etc.*

Both L , $E(t)$ and P have a positive effect on offspring survival probabilities, so partial derivatives of the offspring survival function with respect to each of them are positive.

Now we can extend eq.(2) to:

$$F_c = r B S(T) O(t, L, E(t), P).$$

At any given combination of $L, P, E(t)$ values, offspring survival is higher at higher values of t .

The term F_f is equivalent to the residual reproductive value that parents can expect at the end of the current breeding cycle multiplied by the probability of parents surviving from time t to T , $P(t)$:

$$F_f = r v P(t).$$

Parental survival function also depends upon the effort put into nest defence, L . Different kinds of predators pose different risks to defending

parents. Both risk to the parent, R , and defence level L make parents' survival probability to decrease. For simplicity, I will assume R not to be a function of L , that is, R does not affect the shape of the curve relating parental survival to L , but only its absolute value. So,

$$F_f = rv P(L, R, t).$$

Again, for any combination of R and L values, parental survival is greater at higher values of t .

Total fitness function can be put as:

$$F = r B S(T) O(t, L, E(t), P) + rv P(L, R, t). \quad (3)$$

Holding all variables other than L constant, at the maximum of F , its partial derivative with respect to L will be zero:

$$\partial F / \partial L = r B S(T) \partial O / \partial L + rv \partial P / \partial L. \quad (4)$$

Following WINKLER (1987), optimal defence level L^* , that is, the value of L at this maximum, can be considered as a function of a given parameter (for example, brood size B), $L^*(B)$ being implicitly defined by the condition $\partial F(B, L^*(B)) / \partial L = 0$. We are now interested in how small changes in B affect L^* , that is, the sign of dL^*/dB . By differentiating $\partial F / \partial L$ with respect to B , we obtain:

$$\begin{aligned} \frac{d}{dB} \frac{\partial F}{\partial L} &= \frac{dB}{dB} \frac{\partial}{\partial B} \frac{\partial F}{\partial L} + \frac{dL^*}{dB} \frac{\partial}{\partial L} \frac{\partial F}{\partial L} = 0 \\ &= \frac{\partial}{\partial B} \frac{\partial F}{\partial L} + \frac{dL^*}{dB} \frac{\partial^2 F}{\partial L^2} = 0. \end{aligned}$$

Therefore,

$$\frac{dL^*}{dB} = - \frac{\frac{\partial}{\partial B} \frac{\partial F}{\partial L}}{\frac{\partial^2 F}{\partial L^2}} \quad (5)$$

Since F is at a maximum, $\partial^2 F / \partial L^2$ is negative. We should now look at the sign of the numerator to determine whether $L^*(B)$ is an increasing or decreasing function. By developing the numerator of eq. (5):

$$\begin{aligned} - \frac{\partial}{\partial B} \frac{\partial F}{\partial L} &= - \frac{\partial}{\partial B} \left[r B S(T) \frac{\partial O}{\partial L} + rv \frac{\partial P}{\partial L} \right] \\ &= - r S(T) \partial(O) / \partial L + 0. \end{aligned}$$

Both r and $S(T)$ are positive and $\partial O / \partial L$ was assumed to be positive, thus

the numerator is negative. Consequently, dL^*/dB is positive, and optimal levels of defence should increase with brood size.

An identical development results in L^* to be an increasing function of r and $S(T)$. When differentiating with respect to rv , the opposite is true, parents expending higher amounts of effort in nest defence with lower residual reproductive value (because $\partial P/\partial L$ is assumed to be negative). These and other (see below) predictions of the model are summarized in Table 1.

TABLE 1. Predictions of the model: Expected response of optimal defence levels, L^* , to variations on the parameters on which parental fitness is assumed to depend

Parameter	Symbol in text	Effect on L^*
Parent-offspring relatedness	r	positive
Brood size	B	positive
Offspring post-fledging survival	$S(T)$	positive
Residual reproductive value of parents	rv	negative
Brood number		positive †
Time in the breeding season		positive †
Past investment		positive †
Differential mortality by sex		see text †
Age of parents		positive †
Potential risk posed by the predator to offspring	P	positive
Potential risk posed by the predator to parents	R	negative
Offspring age	t	positive
Offspring age-dependent ability to escape from the predator	$E(t)$	positive

† rv -correlated traits, not directly included in the model but frequently used for testing predictions about the effect of rv on L^* .

The effect of predator type.

Different kinds of predators were represented in the model by variables P and R .

When solving for dL^*/dP :

$$\begin{aligned} \frac{d}{dP} \frac{\partial F}{\partial L} &= \frac{\partial}{\partial P} \frac{\partial F}{\partial L} + \frac{dL^*}{dP} \frac{\partial^2 F}{\partial L^2} = 0 \\ &= \frac{\partial}{\partial P} \left[r B S(T) \frac{\partial O}{\partial L} + rv \frac{\partial P}{\partial L} \right] + \frac{dL^*}{dP} \frac{\partial^2 F}{\partial L^2} = 0 \end{aligned}$$

$$= r B S(T) \frac{\partial}{\partial P} \frac{\partial O}{\partial L} + \frac{dL^*}{dP} \frac{\partial^2 F}{\partial L^2} = 0$$

Therefore,

$$\frac{dL^*}{dP} = \frac{-r B S(T) \frac{\partial}{\partial P} \frac{\partial O}{\partial L}}{\partial^2 F / \partial L^2}.$$

Now, dL^* has the same sign as the mixed derivative in the numerator. As it was defined before, higher values of P increases $\partial O / \partial L$ over all values of L , that is, a "unit" of effort yields higher increments in offspring survival probabilities when P is higher. A graphical approach leading to this conclusion by assuming a sigmoidal pattern for the $O(L)$ function can be found in Fig. 1a-c. The same holds for any other asymptotic function provided that $O(L) = 0$ at $L = 0$ (Appendix 1). Consequently, L^* is an increasing function of P .

Conversely, when solving for dL^*/dR , it results in L^* being a decreasing function of R . The necessary condition by which the mixed derivative in the numerator were negative holds for any decreasing function $P(L)$ provided that $P(L) = 1$ at $L = 0$ and $P(L)$ to show lower values the higher is R over all values of L (Fig. 1d-f).

The effect of offspring age.

When differentiating $\partial F / \partial L$ with respect to t , we obtain

$$\begin{aligned} \frac{d}{dt} \frac{\partial F}{\partial L} &= \frac{\partial}{\partial t} \frac{\partial F}{\partial L} + \frac{dL^*}{dt} \frac{\partial^2 F}{\partial L^2} = 0 \\ &= \frac{\partial}{\partial t} \left[r B S(T) \frac{\partial O}{\partial L} + r v \frac{\partial P}{\partial L} \right] + \frac{dL^*}{dt} \frac{\partial^2 F}{\partial L^2} = 0 \\ r B S(T) \frac{\partial}{\partial t} \frac{\partial O}{\partial L} + r v \frac{\partial}{\partial t} \frac{\partial P}{\partial L} + \frac{dL^*}{dt} \frac{\partial^2 F}{\partial L^2} &= 0 \end{aligned}$$

Therefore,

$$\frac{dL^*}{dt} = \frac{-r B S(T) \frac{\partial}{\partial t} \frac{\partial O}{\partial L} - r v \frac{\partial}{\partial t} \frac{\partial P}{\partial L}}{\partial^2 F / \partial L^2} \quad (6)$$

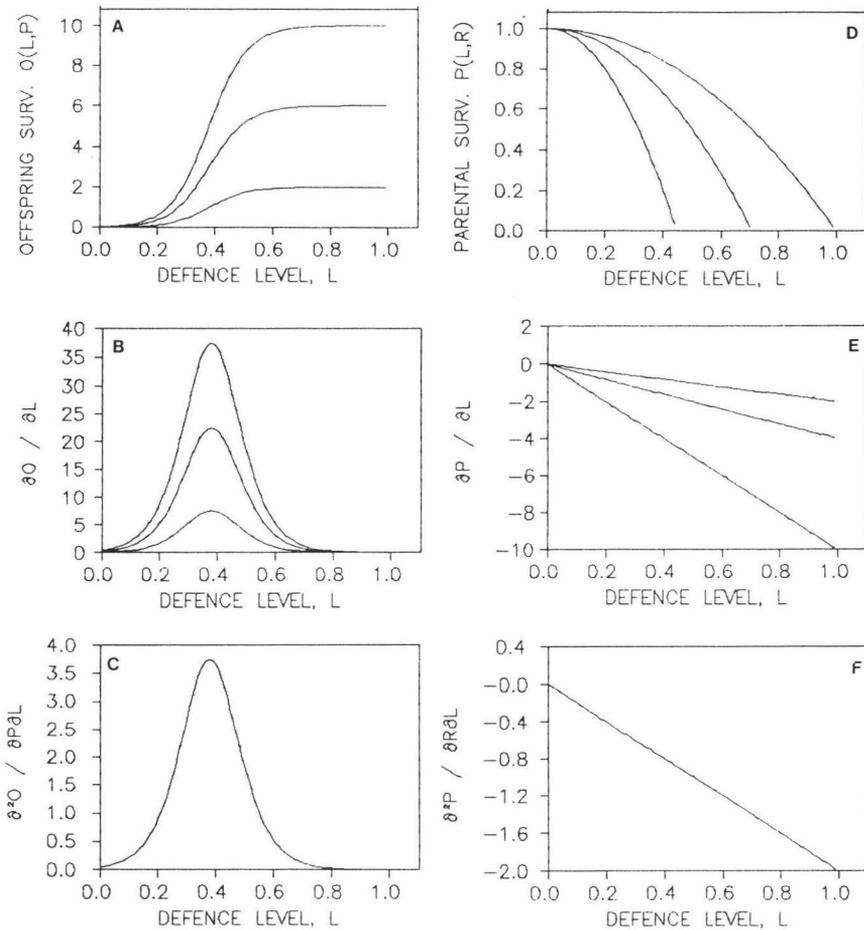


Fig. 1. A, Expected offspring survival at fledging as a function, $O()$, of defence level, L , and potential risk to offspring posed by the predator, P . The function plotted is $O(L,P) = (1+P)/(1+300e^{-15}L)$. The function is taken from WINKLER (1987, fig. 1). B, Partial derivatives of $O()$ with respect to L at given P values. C, Mixed derivative of $O()$ with respect to L and P . D, Parental survival as a function, $P()$, of defence level, L , and risk to parents posed by the predator, R . The function plotted is $P(L,R) = 1-RL^2$. E, Partial derivatives of $P()$ with respect to L at given R values. F, Mixed derivative of $P()$ with respect to L and R .

Again, the denominator is negative, so the sign of dL^*/dt depends on the signs and magnitudes of the two mixed derivatives in the numerator. The probability of parental survival should increase over all values of L as time within the current breeding cycle approaches T . Parents at high t

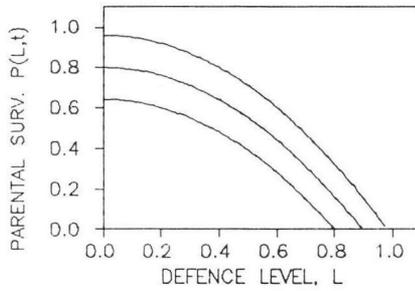


Fig. 2. Expected parental survival at fledging time as a function, $P()$, of defence level, L , and offspring age, t . The function plotted is $P(L,t) = 0.6 + 0.04t - L^2$. The function is taken from WINKLER (1987, fig. 6). Its partial derivative with respect to L is $-2L$, and the mixed derivative with respect to L and t is zero.

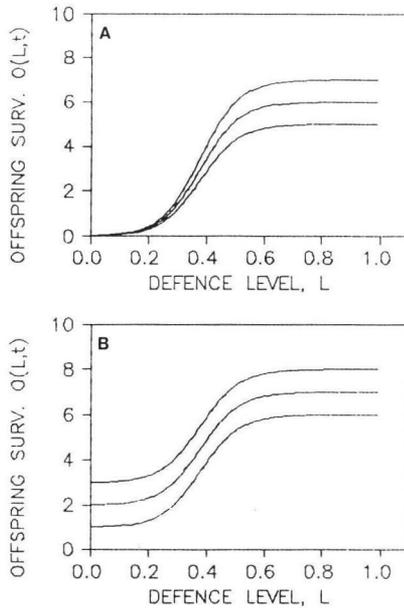


Fig. 3. A, Expected offspring survival at fledging as a function, $O()$, of defence level, L , and offspring age, t , by assuming $O()$ to be zero in the absence of parental defence ($L = 0$) at any t value. The function plotted is $t/(1 + 300e^{-15} L)$. For a graphic interpretation of the mixed derivative with respect to L and t see Fig. 1 and Appendix 1. B, Offspring survival, $O(L,t)$, by assuming $O()$ values to be proportional to t in the absence of parental defence. The function plotted is $O(L,t) = 5/(1 + 300e^{-15} L) + t$. The partial derivative of this function with respect to L is $22500e^{-15} L/(1 + 300e^{-15} L)^2$ and consequently the mixed derivative with respect to L and t is zero.

values can risk more than those at low ones in order to achieve the same survival probability. This is a consequence of parents tending older offspring being nearer to the time at which they must survive. Thus, increments in defence level at $P() = 0$ are proportional to increments in $P()$ at $L = 0$ (Fig. 2). Return rates dP/dL can be assumed to be the same for any t value and, consequently, the mixed derivative $\partial^2 P / \partial t \partial L$ is zero.

Conversely, $\partial^2 O / \partial t \partial L$ is positive or zero, depending on how defence affects offspring survival probabilities. When offspring survival becomes near zero at very low L values, then a "unit" of effort put in older offspring results in higher increments of offspring survival probabilities just because they are nearer to T . This is probably the situation that a parent must confront when predators are about the very site of the nest, *i.e.* when the chances for a brood to be preyed upon are very high (no matter how old nestlings are) if parents are unable to deter the predator. In such a case, the mixed derivative is positive and L^* will increase with increasing offspring age (Fig. 3a).

A different situation could arise, at least on theoretical grounds, when offspring have some chances of surviving with no parental defence. In the extreme case shown in Fig. 3b, in which nestling survival in the absence of parental defence is proportional to age, no variations in $\partial O / \partial L$ should appear, thus $\partial^2 O / \partial t \partial L$ is zero. Optimal defence level should remain the same over all t values.

Most real situations are likely to be intermediate between these two extremes. What is relevant for our analysis is that the lower are the chances of offspring surviving an attack with no parental defence, the steeper will be the increase in optimal defence levels with offspring age. For example, field observations involving predators or models at the nest site are predicted to show steeper patterns of nest defence with time in the breeding cycle than those involving potentially dangerous predators but which are away from the nest (*i.e.* wandering mammals or raptors flying over a breeding territory).

As a corollary, parents will increase their effort in response to any change in offspring development causing nestlings' survival probability to increase faster. The daily rate of increase in nestlings' probability of survival is higher when chicks have just crossed through a "bottleneck" period after which some causes of mortality become reduced. For example, altricial nestlings improve their survival chances once they have acquired the ability for thermoregulation. Also, the sigmoidal growth pattern of most species makes nestlings to be specially sensitive to food shortages during the intermediate phase of exponential growth. Most

developmental changes making nestlings better able to cope with environmental adversities occur around the middle of the nest period (O'CONNOR, 1984). Consequently, we should expect steeper patterns of nest defence with time at the end of the nest period, that is, the curve $L^*(t)$ should be positively accelerated.

Offspring self-defensive behaviour.

Older nestlings may develop self-defensive tactics against a predator which is about to take them (*i.e.* jumping out of the nest or defecating over predators). In many passerines, escaping responses appear after nestlings cross some age threshold shortly before leaving the nest. Such a response suddenly increases nestlings' probability of survival and should be taken into account when analyzing the effect of offspring age upon optimal defence levels.

Equation (6) can be extended to:

$$\frac{dL^*}{dt} = \frac{-r B S(T) \frac{\partial}{\partial t} \frac{\partial}{\partial L} O(t, E(t))}{\partial^2 F / \partial L^2}.$$

By the chain rule,

$$\begin{aligned} \frac{dL^*}{dt} &= \frac{-r B S(T) \left[\frac{\partial t}{\partial t} \frac{\partial}{\partial t} \frac{\partial t}{\partial t} \frac{\partial}{\partial t} \frac{\partial E}{\partial t} \frac{\partial}{\partial E} \frac{\partial O}{\partial L} \right]}{\partial^2 F / \partial L^2} \\ &= \frac{-r B S(T) \frac{\partial}{\partial t} \frac{\partial O}{\partial L} + \frac{\partial E}{\partial t} \frac{\partial}{\partial E} \frac{\partial O}{\partial L}}{\partial^2 F / \partial L^2}. \end{aligned} \quad (7)$$

The ability of nestlings to escape from the nest must remain constant at some value near zero below some age threshold. Consequently, $\partial E / \partial t$ is zero and equations (6) and (7) are the same. However, once $\partial E / \partial t$ becomes positive, the slope of $L^*(t)$ increases. This is so because nestlings having higher $E(t)$ values enjoy higher survival probabilities over all L values and $O(L)$ becomes highly reduced at $L=0$ (Fig. 4). Consequently, the two mixed derivatives in the numerator are positive and parents will increase their defence level in response to self-protective behaviour of chicks. Parents should no more increase their effort in response to increasing offspring age once chicks develop full escaping abilities, *i.e.* when an increase in defence level at low L values does not

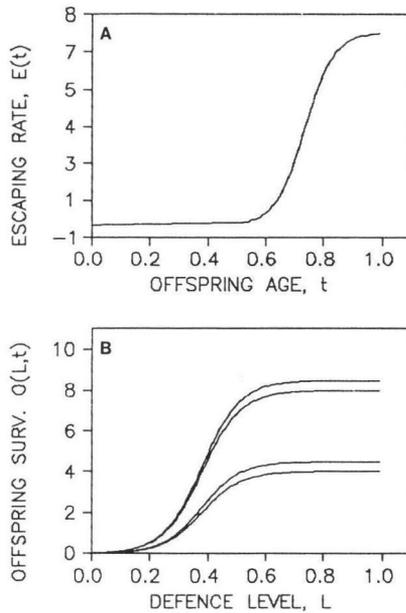


Fig. 4. A, The rate at which nestlings can perform a successful antipredator escaping response, $E(t)$, as a function of age, t . It is assumed for $E(t)$ to remain near zero for most of the nestling period and sharply level-off just before fledging. B, Expected offspring survival as a function, $O()$, of defence level, L , and offspring ability to escape from a predator, $E(t)$. The function plotted is $(t + E(t))/(1 + 300e^{-15L})$. The appearance of self-defensive behaviour has the effect of a rapid increase in offspring's survival probabilities over time, thus the situation is a particular case of that shown in Fig. 3A.

increase offspring's probability of survival as dramatically as when chicks have just left the nest, because chicks are more and more able to escape predators by themselves and have a less chance of being captured once the brood is dispersed (MONTGOMERIE & WEATHERHEAD, 1988). Consequently, defence levels are likely to peak around fledging time.

Measures of nest defence

Studies on nest defence differ in the variables estimating parental investment. This fact requires some consideration before going on to examine available data for testing the model's predictions.

The four variables most commonly measured in studies of nest defence are:

- a) Distance to the dummy or predator (WEATHERHEAD, 1979, 1982;

REGELMANN & CURIO, 1983; CURIO *et al.*, 1984, 1985; KNIGHT & TEMPLE, 1986a, b, 1988; McLEAN *et al.*, 1986; BREITWISCH, 1988).

b) Direct aggression towards the dummy or predator. It includes hovers, dives and strikes (RÖELL & BOSSEMA, 1982; STEPHENS, 1984; KNIGHT & TEMPLE, 1986b, 1988; LEA & VOWLES, 1985; McLEAN *et al.*, 1986; BREITWISCH, 1988).

c) Latency in displaying a response (REGELMANN & CURIO, 1983; CURIO *et al.*, 1984, 1985; KILPI, 1987).

d) Calling rate. Calls recorded are commonly referred to as mobbing or alarm calls and, when differentiated, they are usually pooled as a unitary category (WEATHERHEAD, 1979, 1982; PATTERSON *et al.*, 1980; RÖELL & BOSSEMA, 1982; REGELMANN & CURIO, 1983; CURIO *et al.*, 1984, 1985; GOTTFRIED *et al.*, 1985; KNIGHT & TEMPLE, 1986a, b, c; McLEAN *et al.*, 1986; BREITWISCH, 1988). Three studies, however, report on two functionally different types of call. Stonechats *Saxicola torquata*, robins *Erithacus rubecula* and american goldfinches *Carduelis tristis* display warning and distraction calls when defending their nests. In both robins and stonechats warning calls probably warn mates and offspring, making nestlings to become silent (GREIG-SMITH, 1980; EAST, 1981) while in american goldfinches, it is the distraction call that makes chicks to be quiet (KNIGHT & TEMPLE, 1986c). Red-winged blackbirds used seven types of calls in response to predator models (KNIGHT & TEMPLE, 1988). One of them, a female-specific scream, also caused nestlings to stop begging while elicited strong defensive responses in other adults.

Some birds lure the predator away from the nest by means of distraction displays rather than defending it directly (BARASH, 1975; McFARLAND, 1984; MILLER, 1985; REID & MONTGOMERIE, 1985; BYRK-JEDAL, 1987). It is possible that some of the instances of nest defence recorded as variations in calling rate and/or distance to the predator should be more properly included in this last category.

I will consider all these variables as measures of parental willingness to defend the nest. In doing so, I need to assume that they are linked to a common factor. The fact that such measurements correlate in most studies justifies the assumption (WEATHERHEAD, 1979, 1982; RÖELL & BOSSEMA, 1982; REGELMANN & CURIO, 1983; GOTTFRIED *et al.*, 1985; KNIGHT & TEMPLE, 1986b; BREITWISCH, 1988 but see McLEAN *et al.*, 1986 and KNIGHT & TEMPLE, 1988 for a lack of correlation between calling rate and direct aggression, and REGELMANN & CURIO, 1983 for latency to approach). Accordingly, I will also include those studies that considered a subjective scoring of nest defence as a composite index which

combines (but not weighs) such variables (GOTTFRIED, 1979; ROBERTSON & BIERMANN, 1979; ANDERSSON *et al.*, 1980; BIERMANN & ROBERTSON, 1981; BLANCHER & ROBERTSON, 1982; BUITRON, 1983; ELLIOT, 1985; GOTTFRIED *et al.*, 1985; McLEAN *et al.*, 1986; WALLIN, 1987).

Both distraction displays and direct nest defence benefit the offspring: otherwise they should have been selected against as a wasteful effort since long ago. In addition, both activities entail a risk for the parent (CURIO, 1978; BUITRON, 1983; CURIO & REGELMANN, 1986a), thus fulfilling the two basic model's assumptions. I will now examine if predictions can be supported by data accumulated over the last two decades.

Predictions of the model

1. Individual variation in life-history parameters should lead to high within-population variability in optimal defence levels.

Interindividual variability in nest defence is expectedly higher if levels of defence depend on individual life histories rather than on factors with less interindividual variability like age-dependent predation risk or number of visits. This is so because life-history theory accounts for additional sources of variation, some of which take discrete values (*i.e.* parental age for seasonal breeders or saved investment in past clutches which were preyed upon), thus resulting in a multimodal distribution of defence values. When dealing with interindividual variability, virtually all studies report on it as being very high (RÖELL & BOSSEMA, 1982; BLANCHER & ROBERTSON, 1982; REGELMANN & CURIO, 1983; BUITRON, 1983; REID & MONTGOMERIE, 1985; KNIGHT & TEMPLE, 1986a, c; McLEAN *et al.*, 1986). WALLIN (1987) provides evidence of individual adjustments in defence level of female tawny owls *Strix aluco*.

2. Defence intensity should decrease with increasing risk for the parent.

Risk (*i.e.* chance of the nest to be preyed upon or of the parent to be killed or injured) is difficult to be directly measured and most authors estimate it in an indirect way, by means of an intermediate variable (weaponry, distance and degree of exposure).

When confronted with dangerous predators, parents often resort to less risky defensive behaviours (CURIO, 1975) or tend to stay farther away from them (KRUUK, 1964). Sandpipers *Charadrius montanus* strike ungulates (which may endanger the nest but not the adults) while displaying distraction behaviour against humans (GRAUL, 1975). Blue

herons *Florida caerulea* defend their nests against small predators and other herons but not against large mammals (WERSCHKUL, 1979). European robins give seep alarm calls when defending their nests against corvids, which may be dangerous to both parents and the nest, while they give distraction calls if confronted with squirrels, that only prey on eggs and nestlings (EAST, 1981). In lapwings tested with different predator models, the closeness of attack was inversely related to the risk posed by each predator (ELLIOT, 1985). Colonial rooks, showing communal nest defence, are more aggressive than solitary nesting pairs (RÖELL & BOSSEMA, 1982) and pheasants, which incur little risks in defending broods against *Circus* harriers, attack them directly instead of seeking for cover (CARROLL, 1985). In tawny owls, females in a good body condition (estimated by a ratio weight/wing length) defended their nests more intensively (WALLIN, 1987). If parents have been selected for evaluating the risk posed by different predators, as in fact they do (CURIO *et al.*, 1983) so as to optimize their parental investment decision rules, it is expected for them to have developed mechanisms for prospective adjustment of the response against recognizable predators as a function of past experience. Such a mechanism could explain why birds in revisited nests show higher defence levels than naive ones. With increasing boldness, parents may progressively monitor the risk posed by investigators in a way that the value of R decreases between successive visits at the nest.

3. Defence should reach a higher level when the nest is at a higher predation risk.

This prediction holds for all factors causing offspring survival probability to increase at a constant level of parental defence. Gulls use their most effective deterrents against predators in close proximity to the offspring or posing particularly great danger to them (KRUUK, 1964). MONTGOMERIE & WEATHERHEAD (1988) discuss some possible costs derived from increasing defence level as the predator gets closer to the nest (*i.e.* SHIELDS, 1984), since parents would reveal nest location in this way.

Different kinds of predators should elicit responses according to the nesting stage on which they preferentially prey. This prediction is borne out by most studies (VERBEEK, 1973; GOTTFRIED, 1979; PATTERSON *et al.*, 1980; EAST, 1981; BUITRON, 1983; GOTTFRIED *et al.*, 1985). One study (KNIGHT & TEMPLE, 1986c) fails however in corroborating it.

Nest site also affects levels of defence. Cormorants nesting in more

exposed sites defended more than those enjoying better-protected nests (SIEGEL-CAUSEY & HUNT, 1981). Magpies with unroofed nests suffer from higher crow predation than those with roofed nests and attack more strongly a caged crow placed close to their nests (RÖELL & BOSSEMA, 1982). Nests poorly concealed in vegetation are also more defended than well-concealed ones (MCLEAN *et al.*, 1986). Also, species nesting at lower heights above ground defend their nests more strongly against snakes than species nesting higher (GOTTFRIED, 1979). In seabirds, those pairs nesting in shores frequented by people are more prone to human predation and defend their nests more intensively than pairs nesting off-shore (JACKSON *et al.*, 1982) or in less-disturbed areas (BURGER & GOCHFELD, 1983). It seems reasonable to expect that those species adapted to breed in vulnerable nest-sites have also been selected to employ more effective defensive tactics in response to heavier predation pressures. This could explain the correlation between defence intensity and nest conspicuousness found by RICKLEFS (1977) among neotropical passerines.

If predators are more likely to prey upon a nest the older the nestlings it contains, increasing nest defence with age may reflect predation risk rather than increasing reproductive value of nestlings. No evidence exists about the ability of predators to estimate nest contents without gaining access to them. In addition, higher loudness of old nestlings' begging calls may be accompanied by changes in structure that make them less locatable and susceptible to higher environmental degradation (REDONDO & ARIAS DE REYNA, 1988). The only study aimed at relating defence levels to nestling age and expected risk of predation resulted in age being the best predictor of defence intensity (GREIG-SMITH, 1980).

Finally, while GOTTFRIED (1979) found that species suffering from higher predation rates showed the highest defence levels, MILLER (1984) felt that frequency of distraction displays in sandpipers was badly tuned to local predation pressures.

4. Level of defence should increase with brood size.

Evidence regarding the effect of clutch (eggs) and brood (nestlings) size upon defence intensity comes from two sources. First, when dealing with unmanipulated brood size, contradictory results are found. When studying nest-defence behaviour of four North-american passerine species, GOTTFRIED (1979) found that it was positively correlated with clutch size in three of them when defending against a snake but not against a jay. In his words, "snakes may be perceived as more likely than jays to inflict

serious injury or death to the parent'. Such an explanation remains to be tested, however. In great tits, brood size in first broods do not correlate with intensity of defence while in second broods it does (REGELMANN & CURIO, 1983; CURIO *et al.*, 1984; CURIO, 1987). In stonechats, parents increase their rates of warning calls, but not those of distraction calls with larger brood sizes (GREIG-SMITH, 1980). In this species, warning calls are probably not directed to predators but silence nestlings. Larger (and noisier) broods may require higher rates of warning calls to become silent, so this effect might reflect risk for the nest instead of brood value. Among tawny owls, WALLIN (1987) found a positive correlation between brood size and defence level. This finding should be taken cautiously, however, since both brood size and brood survival negatively correlated with laying date. Finally, BREITWISCH (1988) found no correlation between defence levels and both clutch and brood size for mockingbirds.

Life-history theory predicts that a bird should value a large brood more than a smaller one because the first one contributes with a higher proportion of genes to its lifetime reproductive output. When reasoning in this way, we need to assume that animals can estimate in some way what their average clutch size should be, hence value a current brood with reference to it. There is evidence that clutch-size is to some degree inherited (NOORDWIJK *et al.*, 1980). Moreover, it seems likely that short-term modifications of clutch size induced by environmental conditions (like food availability or laying date) are also heritable (PERRINS & BIRKHEAD, 1983). What this means is that a female should value its brood maximally because it represents a fixed proportion of its total reproductive output when number of breeding attempts is kept constant throughout lifetime. The contribution of a clutch to a male's reproductive output equals that of his mate under perennial-monogamous mating systems. Assessment of relative brood value for a serial-monogamous male involves evaluating potential clutch size of any female in the population.

When variations in clutch size are the result of unpredictable environmental conditions no prospective assessment of a brood reproductive value can be made because its size may be equally above or below the lifetime average depending on factors which cannot be predicted by the bird. Birds, however, should be able to assess the relative value of a brood under several conditions. Adjustment of defence levels to brood size may be conspicuous in second and third broods because size of previous ones might be taken as a reference. Great tits, that adjust brood defence to brood size in second but not in first broods

(CURIO, 1987) could be behaving in this way. Birds should also be selected to respond to deviations from expected size in their current brood, as manipulation experiments have indeed revealed (see below). We should therefore, for most cases, not expect birds to gear their brood defence with brood size relative to the population average but to deviations from individually expected values. MONTGOMERIE & WEATHERHEAD (1988) comment on the adaptive explanations offered for an intriguing discovery made by RICKLEFS (1977): a positive correlation between clutch size and defence intensity among *different* species.

Experiments with artificially manipulated brood size have found a relationship in the direction predicted by the model between intensity of defence and clutch size (ROBERTSON & BIERMANN, 1979; KNIGHT & TEMPLE, 1986a; WINDT & CURIO, 1986; CURIO, 1987). Some have also found a positive correlation of defence levels with manipulated brood size (GREIG-SMITH, 1980; KNIGHT & TEMPLE, 1986c) while others have not (ROBERTSON & BIERMANN, 1979; CURIO, 1987).

The fact that hatching of eggs prevents parents from adjusting their defence intensity to brood size has been explained by invoking constraints in time and energy budgets of parents feeding nestlings. In *Agelaius phoeniceus*, feeding rates increase with brood size and the tendency for parents to increase nest defence with brood size may conflict with the higher food demands of larger broods (ROBERTSON & BIERMANN, 1979). The high intra-brood mortality of nestlings due to starvation in this marsh-nesting species (RICKLEFS, 1969) may stress this explanation. Great tit parents caring for the largest broods show, in fact, lower defence levels and less marked increase of defence with brood age than those caring for smaller broods (REGELMANN & CURIO, 1983). Parents feeding small young also failed to adjust their defence levels to brood size so the possibility of an energetic constraint can be ruled out (REGELMANN & CURIO, 1983). However, experiments involving parental feeding rates after brood reduction show that parents are not able to estimate brood size directly but respond to brood-size correlated factors such as satiation (CURIO, 1987). For species in which brood reduction due to starvation occurs, brood size may be correlated with reproductive success only if nestlings receive adequate amounts of food. This is so not only because brood reduction may occur before fledging but also because young fledging in a poor body condition have, as a rule, lower probabilities of winter survival (PERRINS, 1965; EDEN, 1985; GROVES, 1984; TINBERGEN, 1987). Accordingly, large broods may be as valuable as smaller ones except under exceptionally good conditions of food availability.

One more factor comes to complicate the effect of brood size. Larger broods are more vulnerable to predation than small ones (PERRINS, 1965). This is probably due to the combined effects of larger broods being noisier, fed at higher rates and having longer fledging schedules than smaller ones (PERRINS & BIRKHEAD, 1983). Food supply may ultimately determine differential growth rates and sibling competition, leading some populations or species to adjust their defence level to brood size. Note, however, that such a correlation might reflect differences in nest vulnerability rather than in brood value.

5. Variations in defence levels should reflect variations in residual reproductive value of parents.

I will examine separately several situations reflecting differences in parental residual reproductive value. The following variables have been often employed for testing hypotheses about the effect of residual reproductive value upon defence level. In our model, the parameter rv should be considered as an inclusive estimation of reproductive value accounting for the whole set of variables.

5a. *Brood number.*

Second and subsequent broods should be more defended than first ones because increasing brood number diminishes the chances of starting a new brood in the current breeding season. This is expectedly relevant for reproductive decisions of many bird species in which over-winter mortality is high. No study has found evidence of this kind, however (GREIG-SMITH, 1980; REGELMANN & CURIO, 1983; CURIO *et al.*, 1985). Such a finding does not falsify this model's prediction because first and second broods differ in many ways other than their reneating expectancies (CURIO *et al.*, 1985). In tits and magpies, second-brood chicks are of a lower quality because of their reduced post-fledging survival (PERRINS, 1970; EDEN, 1985). Brood number is expected to affect defence levels because it alters residual reproductive value. However, this relationship may be just the opposite assumed when testing the effect of brood number upon defence. A long-term study in the great tit showed that birds laying second clutches lived, in fact, longer than those laying first broods only (BOER-HAZEWINKEL, 1987).

5b. *Time in the breeding season.*

Following the above reasoning, birds breeding late in the season should have a lower residual reproductive value than birds nesting earlier

because prospects for initiating a replacement or subsequent nesting cycle decrease with time. Given the confounding effects that brood number exerts over the estimated residual reproductive value, time in the season should reflect defence adjustments more accurately when only first broods are taken into account. REGELMANN & CURIO (1983) and CURIO *et al.* (1984) report on a seasonal increase in brood defence for the great tit, though not very marked, and WEATHERHEAD (1979) reports on an even less apparent effect for a tundra population of Savannah sparrows *Passerculus sandwichensis* for which re-nesting potential is virtually zero beyond the earliest days in the season. Female red-winged blackbirds incubating eggs defended them less as time in the breeding season advanced while the opposite trend was found for females tending nestlings (BIERMANN & ROBERTSON, 1981). In this study, clear differences were apparent only late in the season, just when predation was more intense. This suggests that an increase in nest defence during the breeding season may reflect predation risk for the nest rather than decreasing reproductive value of the parents (BIERMANN & ROBERTSON, 1981; CURIO *et al.*, 1984). Another set of factors may obscure the relationship between time in a season and expected defence intensity. If parents raising their 1st brood perceive the environment as becoming unsuitable for a following nesting attempt, they might then value their current brood higher as the season progresses, hence defence becomes independent of residual reproductive value (CURIO *et al.*, 1984). Seasonal breeders should concentrate their nesting times around peaks of food abundance and late broods may have lowered survival probabilities because of a decrease in food supply (CARLISLE, 1982) or have a smaller size (PERRINS, 1970; REESE & KADLEC, 1985). In tawny owls, both defence intensity, brood size and brood survival decreased during the breeding season (WALLIN, 1987). In many species, first-year breeders lay later in the season than experienced pairs (PERRINS, 1965; ERPINO, 1968; RÖSKAFT *et al.*, 1983). Since novice pairs achieve lower nesting success than older ones (PERRINS, 1965; RÖSKAFT *et al.*, 1983) they should not value their broods as much as those of more experienced birds.

5c. *Past investment.*

Birds differing in their past reproductive effort should also differ in their future reproductive expectancies because increased effort results in higher mortality risks (ASKENMO, 1979; COLEMAN *et al.*, 1985; PUGESEK, 1987; but see REZNICK, 1985): parents run higher risks in defending off-

spring or invest time and energy in them which could be otherwise employed for self-maintaining (CARLISLE, 1982). According to this, some animals might rely on past investment as an indicator of expected residual reproductive value and so commit the Concorde fallacy, while others might not (CARLISLE, 1985). Two studies (ROBERTSON & BIERMANN, 1979; WINDT & CURIO, 1986) have tested whether parents base their decisions upon past *vs* future investment by manipulating the clutch size of females with a similar amount of past investment. They found that birds actually adjusted their defence effort to variations in clutch size, a result which is also predicted from clutch-size considerations. On the contrary, WEATHERHEAD (1979) found that Savannah sparrows seem to commit the Concorde fallacy: females invested more than males, suffered from heavier weight losses and displayed strongest defence responses during the nesting period. Aiming to test the effect of past investment upon investment decisions in red-winged blackbirds, WEATHERHEAD (1982) manipulated experimentally the incubation period of females and recorded their nest defence behaviour once eggs hatched. Defence increased with nestling age in the expected way for clutches with normal and long incubation times but not for clutches with short (up to six days) times. Also, defence was clearly higher for clutches with long *vs* normal times but the difference was much less apparent for short *vs* normal ones (WEATHERHEAD, 1982, Fig. 1). Weatherhead invoked an explanation for such results based on hormonal regulation of incubation behaviour. I feel he was correct when doing so. Prolactin levels rise during incubation to reach a peak at the time eggs hatch and such increment is thought to be responsible for the increase in nest-defence behaviour (LEA & VOWLES, 1985). Birds in a breeding condition are much prone to mob predators than non-breeding ones (SHALTER, 1979; SHIELDS, 1984; CULLY & LIGON, 1986). Also, parents rearing older nestlings are more likely to defend chicks of a different age than those rearing younger chicks (CONOVER *et al.*, 1980). For the red-winged blackbird, HOLCOMB (1979) reports on small amounts of prolactin early in the incubation period that gradually increase. In WEATHERHEAD's (1982) experiment, unexpected results concerning females with a short incubation period may reflect a deficitary concentration in prolactin.

5d. *Sexual differences.*

In most bird species, males live longer than females, thus enjoying a higher average reproductive value at a given age. However, differential mortality of females cause the adult sex ratio to be male-biased, hence

prospects for finding and changing mates are higher for females than for males. While this effect might compensate for the lower reproductive performance of shorter-lived females, evidence suggests that older males (which run increased risks of mate loss) pair more often than younger ones (PERRINS & McCLEERY, 1985), so average residual reproductive value of males is probably higher than that of females of the same age. Females should then value a current brood more than their mates and defend it more intensively. Confidence of parenthood, which is greater for females, also predicts a higher effort by females (MONTGOMERIE & WEATHERHEAD, 1988). Contrary to this prediction, most studies reveal that males defend their broods more than females do (see CURIO, 1980 and REGELMANN & CURIO, 1986 for a review; also BREITWISCH, 1988). Among raptors, higher investment by males in nest defence also seems to be the rule (JAMIESON & SEYMOUR, 1983; ANDERSSON & WIKLUND, 1987 and refs therein; *cf.* WALLIN, 1987). Interestingly, polyandrous female jacanas, showing less relative parental investment than males and other associated sex-reversed features, contribute at least equally than do males to offspring defence (STEPHENS, 1984).

Although not included in the model, the effect of mate parental effort upon optimal effort levels of the focal parent may lead to predictions different from that derived from the inclusion of residual reproductive value as the only source for explaining sexual differences in optimal allocation of effort. The analysis made by WINKLER (1987) is appropriate for this purpose. The most commonly predicted response in Winkler's model should be an increase in effort by the focal parent when the mate decreases its effort and *vice versa*. REGELMANN & CURIO (1986) have suggested a hypothesis for explaining why should be males the sex more likely to increase in effort for a species with a higher average male reproductive value. By incurring higher risks in defence, male great tits may counteract two major negative consequences of female-biased mortality: decreased viability of the current brood due to uni-parental (male) care and lower prospects for successfully re-mating resulting from mate loss. This is the same argument employed by MONTGOMERIE & WEATHERHEAD (1988), which states that a "unit" of effort put in defence by females is more costly to them than is to males because females have already invested heavier in another forms of parental care (laying and incubating).

Among polygynous red-winged blackbirds, the intensity of male nest defence was positively correlated with harem size. Males chose to defend the nests of primary females instead of those of secondary females, sug-

gesting that nest defence may function as a form of mate investment (KNIGHT & TEMPLE, 1988).

5e. *Age of parents.*

Although parents' age can affect negatively residual reproductive value in long-lived species with high prospects for an individual to reach senescence, most birds suffer from high mortality rates due to predation. Predation pressures may remain fairly constant during an individual's reproductive life span which is usually well below the age at which animals should begin to show signs of senescence. For this reason, age of parents can be barely employed as a *rv*-correlated trait, at least for passerines. The only evidence of age affecting defence levels comes from gulls, older pairs defending their offspring more than younger ones (PUGESSEK, 1983), and geese (RATCLIFFE, 1974 in MONTGOMERIE & WEATHERHEAD, 1988). On the contrary, not WALLIN (1987) nor BREITWISCH (1988) did detect differences in absolute defence levels relative to age of parents in tawny owls and mockingbirds, respectively.

6. Defence should increase with brood quality.

Broods in which offspring are surviving or growing better than might be expected should be more defended than less successful ones (CARLISLE, 1982). Quality of young was included in the model as the probability of surviving during winter. Weight at fledging is correlated with overwinter survival (EDEN, 1985; refs in CURIO & REGELMANN, 1986) and this has led some workers to test this prediction by comparing levels of defence of pairs tending nestlings with different weights in unmanipulated broods. None of these studies have found a relationship in the direction predicted by the model (BLANCHER & ROBERTSON, 1982; CURIO & REGELMANN, 1986a; CURIO, 1987). CURIO & REGELMANN (1986b) suggest that parents with larger broods may be higher quality parents and be the better defenders. I feel, however, that assessment of brood quality may be under constraints similar to those proposed when dealing with brood size. According to this view, parents should respond to changes in the quality of their current brood, because it deviates from the value that parents can expect based on references such as actual food supply, brood size and the amount of parental care given. I predict that parents will respond adequately to changes in growth rates or body condition (*i.e.* diseases, *etc.*) induced experimentally within a brood.

7. Increasing nest defence with offspring age.

Evidence for an increase in nest defence with brood age comes from most studies on unmanipulated broods (ERPINO, 1968; CURIO, 1975, 1987; GRAUL, 1975; SHALTER, 1979; WEATHERHEAD, 1979, 1982; ANDERSSON *et al.*, 1980; GREIG-SMITH, 1980; PATTERSON *et al.*, 1980; BLANCHER & ROBERTSON, 1982; RÖELL & BOSSEMA, 1982; JAMIESON & SEYMOUR, 1983; REGELMANN & CURIO, 1983; CURIO *et al.*, 1984; STEPHENS, 1984; ELLIOT, 1985; REID & MONTGOMERIE, 1985; WALLIN, 1987; BREITWISCH, 1988; more references in MONTGOMERIE & WEATHERHEAD, 1988). When nestlings of different ages are interchanged between nests, parents adjust their defence level to the new experimental situation according with the model's prediction (KNIGHT & TEMPLE, 1986c). This suggests that parents can assess offspring age by using information other than time from hatching.

Some studies have failed in finding such a relationship. GOTTFRIED (1979) found no difference in defence levels between eggs and young in two out of four species of passerine studied. He explained this result as these two species, the most aggressive ones, displaying maximum defence levels with independence of the nesting stage. Nests employed by KNIGHT & TEMPLE (1986a) as controls (naive) for testing the revisitation hypothesis also failed to increase defence levels with offspring age. BIERMANN & ROBERTSON (1981) detected differences between eggs and nestlings in nest defence levels only for pairs breeding late in the season. BUITRON (1983) reported on magpies not increasing defence levels with offspring age against natural predators wandering over the breeding territory, a finding which might reflect a weak tendency for birds to increase defence effort consistent with the model's prediction. Two more studies (MCLEAN *et al.*, 1986; KNIGHT & TEMPLE, 1986c) also found no difference between defence devoted to eggs or young. These two studies, however, only considered nestlings belonging to the first half of the nestling period. In the next section, I will make clear that the rate at which parental defence is expected to increase with brood age should be greater for old nestlings than for younger ones. Pooling all data for the nestling period may subestimate defence intensity if younger broods are over-represented. CURIO *et al.* (1985) found defence levels in great tit second broods not to increase with offspring age but small sample size and age of young, which was significantly lower in second broods, might account for this finding. Considering the high variability which is commonly found in nest-defence studies, lack of significant differences may not

indicate actual equality between mean values of egg and nestling periods. In this sense, only the study of KNIGHT & TEMPLE (1986a) seems to run counter the prediction.

Most studies involving temporal patterns of brood defence do not extend over the entire period of parental care. Consequently, we lack information about the predicted drop in defence intensity which should occur once offspring become independent from parents (but see GREIG-SMITH, 1980). KILPI (1987) reports a decrease in parental defence in gulls at the time juveniles begin to form their own flocks.

8. The temporal pattern of nest defence should reflect changes in offspring survival probabilities.

Differences in daily mortality rates between eggs and nestlings are usually due to a higher probability of nests containing chicks to be preyed upon (RICKLEFS, 1969). As we have seen, nestlings are more defended than eggs and such differences become clearer when predation is most intense (BIERMANN & ROBERTSON, 1981), thus reflecting differences in predation risk. For nestlings, daily mortality rates are usually higher for young nestlings than for old ones (TATNER, 1982; ALERSTAM & HÖGSTEDT, 1983; TIAINEN, 1983). This is partly a consequence of the increased ability of older nestlings to cope with environmental adversities, thus we expect daily rates of increase in nest defence to be higher late than early in the nestling stage, *i.e.* the shape of the curve reflecting defence level against nestling age should be positively accelerated. This is true for most studies showing information at this respect (BARASH, 1975; CURIO, 1975; WEATHERHEAD, 1979; GREIG-SMITH, 1980; EAST, 1981; BREITWISCH, 1988). A convex curve and a fairly lineal one can be found in the studies of ANDERSSON *et al.* (1980) and BLANCHER & ROBERTSON (1982) respectively, but they reflect changes in a composite index of aggression rather than actual values of defence measures.

When nestlings are near to fledging, disturbances may cause the brood to jump out the nest, leaving it prematurely. The occurrence of escaping behaviour increases the nestlings' survival probability (PATTERSON & PETRINOVICH, quoted by CLARK & WILSON, 1981) and enhances the effectiveness of parental defence behaviour. For precocial nestlings, a similar breakpoint occurs short after hatching. We then expect altricial species to show a peak in defence intensity at the time of fledging and precocial ones to display it at hatching (ARMSTRONG, 1956 in BARASH, 1975; MONTGOMERIE & WEATHERHEAD, 1988). In some altricial species

(ERPINO, 1968; GREIG-SMITH, 1980; MCFARLAND, 1984) and precocial ones (GRAUL, 1975; FUCHS, 1977; JENNI & BETTS, 1978; MILLER, 1984; STEPHENS, 1984; BYRJEDAL, 1987; KILPI, 1987; BRUNTON, 1988) this is just what occurs. The fact that patterns of defence mirror changes occurring in the curves of the offspring survival probabilities provides non trivial support for an explanation of defence patterns based on reproductive value of the offspring.

General discussion

From this analysis, it can be concluded that life-history theory can account for most of the variability observed in the patterns of avian nest defence. However, we have found some predictions to receive strong support while others can barely be borne out by available data. For none of the variables involved, however, careful experiments for testing their effect upon defence intensity have yet been made while controlling for the effect of the remaining ones (MONTGOMERIE & WEATHERHEAD, 1988).

Nestling age seems to be the best predictor of defence level for most species. Predator characteristics (risk to the parents and to the nest) are also related to intensity of defence in a straightforward direction. Some predictions, like those concerning the effect of quality and quantity of young, may originate from a fallacious reasoning because it is expected for birds to tune their reproductive effort to a population average rather than to the expected individual lifetime reproductive value. When more properly tested, by means of experimental manipulation, brood size affects defence levels as predicted. We lack similar experiments for testing the effect of brood quality so the question of the extent to which birds gear their effort to offspring quality remains open.

Given the preponderant role that residual reproductive value should play in a life-history model of parental investment strategies, it seems paradoxical that factors presumably related to future reproductive expectancies lead to a highly confusing relationship with defence levels. Factors like brood number or time in the breeding season, may not directly affect residual reproductive value or this effect being compensated for by others which reduce reproductive value of the current brood, hence leading to unexpected results. This fact should be kept in mind when testing hypothesis about patterns of investment by assuming simple relationships between residual reproductive value and timing in the breeding season. Finally, predictions based on sex of the parent and past investment seem to be verified.

If birds are to assess the relative reproductive value of a current breeding attempt in order to maximize their lifetime fitness, they should base their decisions on the most reliable parameters influencing residual reproductive value. Offspring age, number and quality or past investment can be more properly assessed than seasonal effects, which are sensitive to unpredictable environmental fluctuations. A model aimed at predicting patterns of parental investment should ultimately weigh the effect of different parameters on which birds are expected to base their decisions.

Summary

Functional explanations for variations in levels of avian nest defence have been often based upon assumptions concerning optimal allocation of reproductive effort. Such a theoretical framework has led to the formulation of mathematical models aimed at predicting patterns of nest defence in the field. Here, a model is proposed that, starting from a general theoretical standpoint about optimal parental care, integrates previous models and generates new predictions concerning variables not previously included, namely predatory risk for both parents and offspring and age-dependent defensive tactics of nestlings. Optimal levels of parental defence are then expected to increase with (1) parent-offspring relatedness, (2) brood size, (3) offspring quality, (4) potential risk for the offspring, (5) offspring age, and (6) enhancement of offspring's self-defensive tactics while (7) parental residual reproductive value and (8) potential risk for parents are expected to exert a negative effect upon optimal levels of defence. Empirical data are reviewed for testing the model's predictions. Available data provide strong support for predictions concerning parameters 4, 5, 6, and 8. Failed tests concerning parameters 2 and 3 are shown to be flawed in the sense that we should expect defence levels to reflect intra-, instead of inter-individual variations in size and quality of the brood. A more detailed analysis is made concerning variations in residual reproductive value-correlated traits, such as brood number or time in the breeding season. It is argued that, when dealing with such traits, severe violations of basic assumptions (*i.e. coeteris paribus* statements or absence of an actual correlation between such traits and residual reproductive value) can occur, leading to unexpected results. It is concluded that life-history theory can account for most of the variability observed in nest defence patterns.

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Resumen

Las variaciones observadas en la intensidad de defensa de las crías por las aves han sido a menudo explicadas, desde el punto de vista funcional, por hipótesis basadas en la distribución óptima del esfuerzo reproductor. En este marco teórico han sido formulados modelos matemáticos que pretenden predecir los patrones de defensa parental en la naturaleza. En este artículo se propone un modelo que, partiendo de supuestos generales acerca de la optimización del cuidado parental, integra los modelos anteriores y genera nuevas predicciones relativas a variables no consideradas previamente, como el riesgo de depredación para padres e hijos y la adquisición de tácticas defensivas por parte de las crías en el curso del desarrollo. Se predice que el nivel óptimo de defensa parental aumentará con: (1) el grado de parentesco entre padres e hijos, (2) el tamaño de la camada, (3) la calidad de las crías, (4) el riesgo potencial para el nido, (5) la edad de las crías y (6) la mejora en la capacidad de auto-defensa de las crías, mientras que (7) el valor reproductivo residual de los padres y (8) el riesgo potencial en que incurren, se espera que ejerzan un efecto negativo sobre el nivel óptimo de defensa. Una revisión de los datos empíricos disponibles muestra que las predicciones relativas a las variables 4, 5, 6 y 8 se encuentran suficientemente apoyadas. Se pone de manifiesto que los intentos fallidos de verificar las predicciones relativas a las variables 2 y 3 son erróneos ya que esperan que los niveles de defensa reflejen variaciones inter-, en lugar de intra-individuales, en el tamaño y calidad de la camada. Se estudian en mayor detalle las variables ligadas al valor reproductivo residual, tales como el número de puesta o su localización temporal dentro de la estación reproductora. Es posible encontrar, en relación con tales variables, importantes violaciones de algunos supuestos teóricos básicos (p.ej. condiciones de tipo *coeteris paribus* o ausencia de una correlación real entre la variable y el valor reproductivo residual) que pueden dar lugar a la aparición de resultados inesperados. Se concluye que la teoría de los historiales de vida puede explicar la mayor parte de la variabilidad que se observa en los patrones de defensa de las crías.

Appendix 1. Conditions for survival functions $O()$ and $P()$ to have, respectively, positive and negative mixed derivatives with respect to defence level and predatory risk.

Let $O(L,P)$ be the expected offspring survival at fledging time as a function of defence level, L , and predation risk for the offspring, P . Over any L value, $O(L,P_1) < O(L,P_2)$ given $P_1 < P_2$ and $P_1, P_2 > 0$.

For $\partial^2 O / \partial L \partial P$ to be positive, the condition $\partial O / \partial L|_{P_1} < \partial O / \partial L|_{P_2}$ must hold. For simplicity, let $f'(L) = \partial O / \partial L|_{P_1}$ and $g'(L) = \partial O / \partial L|_{P_2}$. So,

$$f'(L) < g'(L),$$

that is

$$f'(L) - g'(L) < 0; \quad g'(L) - f'(L) > 0.$$

Consequently,

$$(g(L) - f(L))' > 0 \text{ or } d(O(L,P_2) - O(L,P_1))/dL > 0.$$

It is a sufficient condition for the mixed derivative to be positive that the difference between survival functions at given P values to increase with increasing L values.

Recall that $O() = 0$ at $L = 0$. Assuming that changes in P do not alter the shape of the curves but their asymptotic value, any function monotonically “spreading” from the origin will hold the condition.

An identical analysis can be applied to parental survival $P()$ as a function of defence level, L , and predation risk for parents, R . In this case, over any L value, $P(L,R_1) > P(L,R_2)$ given $R_1 < R_2$ and $1 > R_1, R_2 > 0$.

For $\partial^2 P / \partial L \partial R$ to be negative, the condition $\partial P / \partial L|_{R_1} > \partial P / \partial L|_{R_2}$ must hold. In this case, the sufficient condition is that $d(P(L,R_1) - P(L,R_2))/dL$ to be positive. Again, any function monotonically “spreading” from $(0,1)$ will hold it.

