



RISKS AND REWARDS OF NEST DEFENCE BY PARENT BIRDS

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ABSTRACT

Nest and offspring defence by birds can be treated as an optimization problem wherein fitness benefits are determined by the survival of the current brood and fitness costs depend upon the probability that the parent will survive to breed again. At the optimal intensity of defence, net fitness benefits are maximized. Unlike many other aspects of animal behavior, the reproductive consequences of nest defence can often be measured directly.

Within this optimality framework, we review the current adaptive hypotheses to explain both interspecific and intraspecific variation in nest defence behavior, and we present some new ideas of our own. Most research to date has focused on seasonal patterns of nest defence to test the prediction that the intensity of nest defence should increase through the nesting cycle either because renesting potential declines or because the probability of offspring survival increases rapidly relative to that of the parents. Studies testing the renesting potential hypothesis have both supported and rejected it, but few studies to date have been controlled well enough to allow us to distinguish between the two hypotheses.

The intensity of nest defence is also predicted to increase with parental experience and confidence of parenthood; offspring number, quality and vulnerability; and nest accessibility and conspicuousness. The response of parents is also expected to vary with the relative armament and mobility of parent and predator and the relative roles of the parents in caring for their offspring. Although there is some evidence supporting many of these predictions, most have not been explicitly tested while holding other factors constant. The tendency for researchers to ignore variables that might influence the intensity of nest defence makes the conclusions of most studies that find support for any single adaptive hypothesis relatively unconvincing. Like Optimal Foraging Theory, however, a comprehensive functional theory of nest defence based on life-history theory can help us to elucidate many of the patterns observed in this important aspect of the parental care behavior of a wide variety of animals.

INTRODUCTION

FOR THE PAST quarter century ornithologists have devoted considerable research effort to determining the fitness consequences of clutch size, body size, and mate choice in birds, presumably because these factors have an obvious influence on reproductive performance. For many birds, however, the single

most important variable affecting fitness is nest predation (Ricklefs, 1969). Nest predators commonly destroy the entire contents of a nest and may eliminate a substantial proportion of all nests that a female constructs. Ricklefs (1969), for example, calculated that, for six common North American passerine birds, 55 per cent of all eggs and 66 per cent of all nestlings were taken by predators. Under such intense selection pressure, we should expect a variety of adaptations, like crypticity and nest

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defence behavior, designed to reduce the vulnerability of nests to predators. Of these adaptations, nest defence behavior has received the most experimental and theoretical attention, but neither theory nor field studies on the adaptive significance of avian nest defence have been comprehensively reviewed.

In the mid-1950s, Armstrong (1954, 1956), Simmons (1952, 1955) and Skutch (1955) all summarized large numbers of observations of nest defence in birds and attempted to classify these behaviors according to the parental drive involved. At that time nest defence behavior was of particular interest because it was believed to be relatively stereotyped in a way that could tell us something about the origins of such behavior and therefore about phylogenetic relationships among species. Gochfeld's (1984) extensive review of antipredator behavior in shorebirds continued in this tradition of cataloging and analysing nest defence activities.

In recent years, behavioral ecologists have begun posing questions about the fitness consequences of defending a nest or brood against predation, thereby shifting the focus from descriptive, interspecific comparisons of behavior to experimental studies on the benefit of this behavior to the performing individuals. Williams (1966) clearly laid the foundation for this new emphasis by modelling the fitness costs and benefits of parental decisions in the framework of life-history theory, an approach that was later expanded into a general theory of parental investment by Trivers (1972). Kruuk (1964), Ricklefs (1969, 1973) and others interpreted some of the patterns that they observed as being molded by individual selection, but Barash (1975) was the first to explicitly use nest defence behavior to test a prediction from parental investment theory. Since then more than 40 studies of nest defence in birds have either tested parental investment theory experimentally or have used the theory to interpret their observations. Despite all of this interest there is some debate about whether parental investment theory has really been properly tested (Nur, 1983) or even supported (Knight and Temple, 1986a) by these studies and relatively little effort has been directed toward testing alternative hypotheses (but see Reid and Montgomerie, 1985; Knight and Temple, 1986a) or examining the variety of fac-

tors that might account for such variation (but see Curio, Regelmann, and Zimmerman, 1984).

In this paper we review both the theoretical and empirical literature on the adaptive significance of nest defence by birds. While the models and predictions that we discuss should be widely applicable to any animal involved in parental care, almost all of the work done so far on nest defence has focused on birds. Despite this, some recent work on nest defence in fish (e.g., Coleman, Gross, and Sargent, 1985) demonstrates that they might be better experimental animals than birds for critically testing some of the basic assumptions of the theory.

We also restrict our discussion to the defence of nests against heterospecific predators. While predation by conspecifics has received considerable attention recently in the context of sexually selected infanticide (e.g., Power and Doner, 1980), this kind of predation is unlikely to be as risky to parents as defence against heterospecific predators and may therefore involve different kinds of defensive behaviors. The analysis of nest defence behavior against heterospecifics is now at a stage where a survey of both theory and evidence is needed to help focus future work on the important questions (e.g., Knight and Temple, 1986a,b).

HISTORICAL BACKGROUND

Naturalists since Aristotle (see Cresswell, 1878) have written about the conspicuous and often unusual nest defence behavior of birds. Surprisingly though, it was not until the 20th Century that nest defence was considered interesting enough to be worthy of serious study. Even Darwin (1872) described the phenomenon only briefly, and attributed it to fright or anger in parent birds. For Darwin, this was an uncharacteristic reliance on proximate explanations.

The first serious review of nest defence in birds was written as a series of articles in the British journal *Oologists' Record* by the Reverend F. C. R. Jourdain (1936, 1937a,b). In these papers he gathered together all of the cases of "injury-feigning" known to him and attempted to provide an ultimate explanation for their occurrence. Previously, several naturalists had suggested that the bizarre behavior of paren-

tal birds in the presence of a predator was a consequence of a "partial paralysis caused by the sudden shock of discovery" (Jourdain, 1936). It was believed that this paralysis was due to a conflict of emotions (or instincts), one which told the bird to flee for its life and the other which said "stay and look after your offspring" (e.g., Dewar, 1928). Jourdain correctly rejected this interpretation for many cases of nest defence because the actions of the parent(s) seemed deliberate and in direct response to the behavior of the predator. He noticed, for example, that the female Reed Bunting (*Emberiza schoeniclus*) clearly acts as if to draw the predator away from the nest and stops her display for a few seconds if the predator does not respond (Jourdain, 1936).

Apparently unknown to Jourdain when he began writing (see p. 34 in Jourdain, 1936), American ornithologists were simultaneously arguing about nest defence. In 1934, Herbert Friedmann published a hypothesis virtually identical to that of Dewar (1928) in which he suggested that injury-feigning "is a compromise between fear and reproductive emotions . . . [The] result is a crippled departure." H. S. Swarth wrote a letter to the editor of the American journal *The Auk* objecting to Friedmann's interpretation on the grounds that nest defence behavior was far from universal in birds, occurring largely in doves and waders. He could not accept that a fear-care conflict would occur in only two taxa of birds. While Swarth's (1935) argument is not as compelling as Jourdain's, his letter provoked a flood of correspondence to the journal about the widespread occurrence of injury-feigning, particularly in passerine birds (e.g., Grimes, 1936).

Jourdain's papers and Swarth's letter both fostered considerable observation and speculation about nest defence. In the late 1940s, for example, the journal *British Birds* published no less than 33 notes on the subject. Most people agreed that the behavior was probably adaptive—even Aristotle (Cresswell, 1886) had suggested that the distraction behavior of females helped their young to survive. The question, in modern parlance, was whether the nest defence behavior of parents was molded by natural selection or was simply a fright response or a conflict of drives that happened to have survival value. Although this question has not been explicitly addressed in the intervening

half century, most scientists would now agree that such complex behavior is unlikely to have arisen entirely as an accidental consequence of a conflict of drives. Probably because of Jourdain's efforts, however, most subsequent studies of nesting behavior in birds included a serious description and discussion of nest defence.

By the late 1940s there were enough published descriptions of nest defence that a serious review of the behavior was possible. Armstrong (1949), and, shortly thereafter, Skutch (1955) and Simmons (1952, 1955), were particularly concerned with the origins of these nest defence displays. Studies of shorebirds had suggested that many of these behaviors were highly stereotyped and Armstrong was interested in examining their relation to other kinds of threat and epigamic displays. This approach was entirely consistent with mainstream ethology of the day wherein behavior was studied primarily either for insights into taxonomic relations among species or for patterns that could be elucidated in the evolutionary history of ritualization (Armstrong, 1954, 1956; Simmons, 1952, 1955).

Ethologists have also studied nest defence behavior to help answer more general questions about the proximate control of animal activities. For example, some exhaustive studies by Curio and his coworkers have focused on asking whether and how parents could recognize different predators (Curio, 1975) and whether antipredator behavior could be socially transmitted rather than learned through direct experience (Curio, Ernst, and Vieth, 1978). Similarly, studies of nest defence have provided some useful insight into the nature of innate behaviors, fixed action patterns, and conflicts of drives (see Gochfeld, 1984, for discussion).

Only recently has the adaptive nature of nest defence been explicitly addressed in experimental studies. There can be no doubt that the burgeoning of interest in nest defence during the past decade is the direct result of having some useful theory to test (Trivers, 1972; Ricklefs, 1973: 245; Barash, 1975; Andersson, Wiklund, and Rundgren, 1980). In the remainder of this paper we review the various adaptive hypotheses about nest defence behavior, we present some new hypotheses of our own, and we evaluate the available data and

tests relevant to each hypothesis from studies of birds.

WHAT IS NEST DEFENSE?

In this paper we only consider as nest defence behavior that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent. We restrict ourselves to nest defence that meets these conditions because it lends itself to a cost-benefit analysis of parental behavior wherein there is a tradeoff between the loss of nest contents and the probability of the parent's own survival. Thus, parental behavior that results in changes in physical features of the nest that might render it cryptic (e.g., such as how or where it is constructed) will not be considered here because these actions involve no danger to the parent. Thus the nest-covering by some shorebird species (MacLean, 1974) does not lend itself to such a cost-benefit analysis because parents performing this behavior probably suffer no increased survival costs.

Our cost-benefit approach to nest defence behavior is based on two findings from field studies. First, Greig-Smith (1980), Andersson, Wiklund, and Rundgren (1980), and Blancher and Robertson (1982) provide evidence for a positive relation between the intensity of parental defence and nest success, although MacLean, Smith, and Stewart (1986) could find no effect. While such an assumption will seem to be obviously correct to an adaptationist, it is possible that nest defence behavior has other functions. In some cases, interactions with predators may be a way of advertising male quality (Curio, 1980) even if it has little or no effect on the predator. Second, Curio and Regelmann (1985) have assembled a large number of references showing that birds risk injury or death when mobbing or displaying to a predator. Although none of these references provide clear evidence of parent birds being killed or injured while defending their nest, birds attempting to attack or scold predators are obviously at some risk (Curio and Regelmann, 1985). The dearth of information on parental risk during nest defence is not surprising both because the act of predation itself is so rarely observed, despite hours of detailed field study (e.g., Pettingill, 1976) and because selection will favor successful predation

avoidance. Buitron (1983), in a study of nest defence in Black-billed Magpies (*Pica pica*), recorded four instances of predation on parents, but she did not actually observe any of these acts and was therefore unable to determine if the predation occurred during nest defence. Brunton (1986), on the other hand, recorded a Killdeer (*Charadrius vociferus*) being killed by a fox while performing distraction and threat displays near its nest.

Alarm calls, direct attacks on the predator, and various distraction and defensive displays are clearly nest defence behaviors that may enhance a parent's reproductive success while entailing some survival cost. For example, two parents calling and flitting around a predator could have a confusing effect which distracts the predator's attention away from the nest. The effect of such distraction displays may be enhanced if alarm-calling attracts other breeding birds in the vicinity to mob the predator (Curio, Ernst, and Vieth, 1978).

Alarm calls and distraction displays are also used to draw potential predators away from the vicinity of the nest rather than simply distracting their attention (Jourdain, 1936; Simmons, 1955; Gochfeld, 1984). Greig-Smith (1980) illustrated the route by which he was eventually led away from the nests of Stonechats (*Saxicola torquata*) when he followed the movements of alarm-calling parents and East (1981) found that European Robins (*Erithacus rubecula*) most often moved away from the nest while alarm calling. Behaviors such as injury-feigning, pseudo-sleeping, and false incubation appear to be this form of predator distraction. Although injury-feigning was originally thought to occur only in ground-nesting birds, it has been described in a wide variety of tree-nesting species (e.g., Grimes, 1936; Jourdain, 1936, 1937a,b). False incubation and pseudo-sleeping seem to be confined almost entirely to the shorebirds (Gochfeld, 1984).

FACTORS INFLUENCING RISK-TAKING

A General Model

Like many aspects of animal behavior, nest defence can be treated as an optimization problem. The intensity of nest defence performed by a parent entails some risk (e.g., injury, death) and results in some benefits (survival of the offspring). Thus fitness cost/benefit

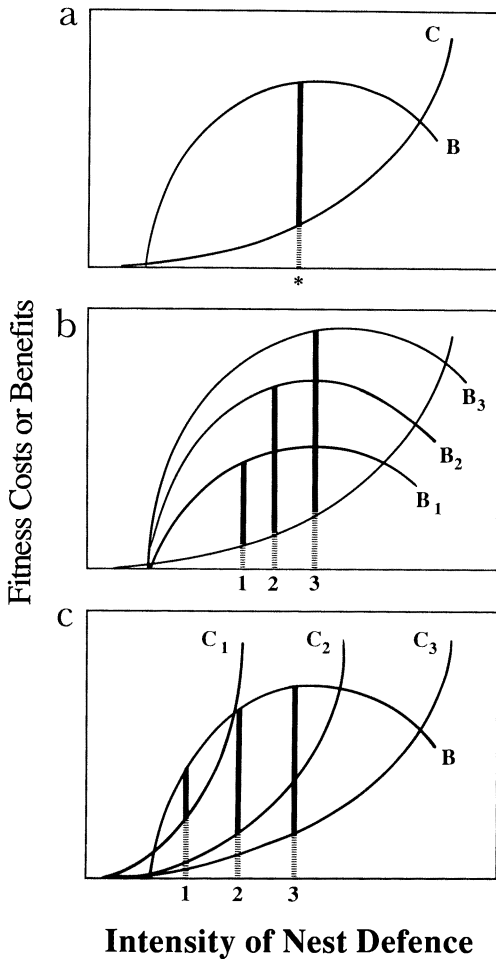


FIG. 1. GRAPHICAL MODELS OF NEST DEFENCE
 Fitness benefits, B, are determined by survival of the current brood; costs, C, are the loss of future reproductive success due to injury or death of the parent as a result of nest defence. In each case the optimal intensity of nest defence (*) is defined by the maximum difference between fitness costs and benefits as in graph (a). The optimal intensity of nest defence increases with increasing benefits, as in graph (b), and with decreasing costs, as in graph (c).

models can be used to predict the optimum level of nest defence in a given situation (see Andersson, Wiklund, and Rundgren, 1980; Curio, Regelman, and Zimmerman, 1984; Sargent and Gross, 1985), the optimum being the intensity of nest defence that maximizes fitness.

We illustrate the general relationship be-

tween fitness costs and benefits and the intensity of nest defence in Fig. 1 (a-c). We use this basic model throughout this review because it is general enough to apply to most aspects of nest defence behavior. We define the fitness costs and benefits of nest defence with reference to reproductive value (V_x), as a convenient measure of an individual's value to itself at any time in its life (Fisher, 1930). Reproductive value at age x is determined by both the fecundity of present and future broods (b) and the probability that the parent will survive to each future breeding period (l). Thus

$$V_x = b_x + \sum (l_t/l_x)b_t$$

where b_x is current reproduction at age x and $\sum (l_t/l_x)b_t$ is the residual reproductive value (i.e., accrued from all future broods). Here we define benefits as the fitness accrued from the present brood (b_x) and fitness costs as any loss in residual reproductive value that result from nest defence. A parent can increase its fitness benefits by defending the present brood and thereby helping its offspring to survive and reproduce. Fitness costs, however, also increase if such nest defence also decreases the probability that the parent will survive (l_t/l_x) to age t . Natural selection will favor nest defence behavior that maximizes the difference between these benefits and costs (see also Patterson, Petrionovich, and James, 1980; Sargent and Gross, 1985; Lazurus and Inglis, 1986, for related examples). For a given set of conditions, we can then determine the optimal intensity of nest defence and we can make predictions of how defence intensity should vary with those conditions.

For both costs and benefits, we assume curvilinear relationships (Fig. 1a). Thus, we expect the costs to the parent to increase exponentially as it increases the intensity of its nest defence behavior (i.e., gets closer to the predator, increases alarm calls or distraction displays). The parent should be at relatively little risk until the predator is within striking distance but risk will increase rapidly as the parent gets closer to the predator or makes itself otherwise more vulnerable (e.g., see references in Curio and Regelman, 1985).

Note that we equate risk and cost here. Most analyses of nest defence behavior fail to distinguish between risk and the intensity of nest defence. We assume that the risks (or costs)

of nest defence are positively related to the intensity of defensive behavior (e.g., alarm call frequency, closeness of approach, attack frequency) and we recognize that a given intensity of defence can have different costs for different individuals both within and between species and for the same individual at different times. Thus a female who is weakened by egg production or is smaller than her mate might incur more costs than a male for a given intensity of defence.

On the benefit side, we expect that a very low intensity of nest defence will have little effect on a predator but the probability of offspring survival rises quickly to a maximum as nest defence increases. This assumption is supported by the positive correlation between nest success and the intensity of nest defence that has been reported in several studies (e.g., Greig-Smith, 1980; Byrkjedal, 1987). Although the precise shapes of the cost and benefit curves will also vary for different combinations of parent and predator species, the general qualitative relation between the costs and benefits of nest defence, as illustrated in Fig. 1, should hold in most situations (see Sargent and Gross, 1985; Lazarus and Inglis, 1986, for more detailed argument).

Although we have relatively few empirical data to support the assumptions of this model, such simple graphical models have proven to be valuable in the development of ideas in ecology and behavior (e.g., MacArthur and Wilson, 1967; Krebs and Davies, 1984). As demonstrated below, this simple model helps us to generate useful predictions that provide the focus for further empirical study. Such data are needed before more sophisticated models can be derived.

To simplify the following presentation, we refer repeatedly to two simple variations on this graphical model in which either the benefits (Fig. 1b) or the costs (Fig. 1c) of a given level of nest defence vary. In each case our goal is to describe and evaluate simple predictions concerning factors affecting nest defence behavior. We find that these simple graphical models help to clarify the expectations from theory.

Parental Characteristics

Renesting Potential

Barash (1975) proposed that a bird's renesting potential should have an important effect

on its willingness to take risks in defence of its nest. This is a life history problem in which selection should favor behaviors that maximize lifetime reproductive success whenever there is a tradeoff between current and future reproductive effort as outlined above (see also Hamilton, 1964; Pianka and Parker, 1975). Thus, a bird with high renesting potential should risk less than a bird with low renesting potential (Curio, Regelmann, and Zimmerman, 1984) because costs for the latter are higher (Fig. 1c). Remember that costs are defined by the probability of parental survival to the next breeding episode.

Renesting potential is a function of two things: (1) the period until another breeding attempt is possible, and (2) the survival probability of the parent during that period. This causes renesting potential to vary asymmetrically through the annual cycle of most bird species. If it is assumed that the breeding season is longer than the time required to complete a single nesting attempt, and that the female is capable of replacing a lost clutch, then renesting potential will be at its maximum at the beginning of the season because a lost nest can usually be replaced in a matter of days. Even for short-lived species, the probability of an individual surviving for several days should be close to unity. Eventually, renesting potential within a season rapidly diminishes so that the probability of raising offspring from a replacement nest decreases to zero and the period until the next possible nesting attempt suddenly changes from several days to many months (i.e., the next breeding season). Survival probability between breeding seasons is often relatively low—for small passerine species it may be less than 50 per cent (Ricklefs, 1974).

Renesting potential is expected to affect nest defence behavior in two ways. First, through a breeding season parents should increase their nest defence as renesting potential declines, reaching a maximum response when the opportunity to renest in that breeding season is zero (Barash, 1975; Weatherhead, 1979a). This is true because the value of a brood is directly proportional to the cost of replacing it (Dawkins and Carlisle, 1976; Boucher, 1977). Second, through its lifetime, a parent's nest defence behavior should change with its own life expectancy if survival probability varies with age (Williams, 1966; Goodman, 1974).

We discuss the evidence for these two effects separately.

Within breeding seasons. Several studies have reported results consistent with the prediction that a parent should increase the intensity of nest defence during a breeding season as a consequence of decreasing renesting potential. The most convincing support comes from studies of Great Tits (*Parus major*) where the number of days remaining in the breeding season explained a small but significant amount of variation in defence response as predicted (Regelmann and Curio, 1983; Curio, Regelmann, and Zimmerman, 1984).

Using a natural experiment, Barash (1980) examined nest defence in two subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys gambelli* and *Z. l. pugetensis*) with different renesting potentials — *pugetensis* was capable of raising at least two broods in a breeding season while *gambelli* could breed only once. Barash (1980) predicted and found that the double-brooded subspecies (*pugetensis*) defended their nests less vigorously. Barash made this prediction because he assumed that the one nest of *gambelli* was worth relatively more than the first nest of *pugetensis*. While this interpretation could be correct there are two serious shortcomings to the study. First, it is not clear whether the *pugetensis* nests were studied early or late in the breeding season. If they were late nests, then the defending parents would have had relatively low renesting potential during that season and they should have defended their nests as vigorously as did *gambelli* parents if renesting potential alone was determining the intensity of nest defence. Second, we do not know whether parents in these two populations had the same probability of surviving to the next year. Unless such probabilities were similar, renesting potential may not be the only explanation for differences in nest defence behavior (see also Curio, Regelmann, and Zimmerman, 1984).

Based on the observations above, Barash (1980) also made the general prediction that nest defence should be more vigorous in single-brooded than multi-brooded species. Even if all else was equal (life expectancy, types of predators encountered, and so forth), this prediction should only hold when comparing defence by single-brooded species with that of multi-brooded species defending nests early in the season. Since even closely related species

often use very different nest defence behavior (see Gochfeld, 1984; Byrkjedal, 1987) such an interspecific comparison will be difficult in practice because of the problem of assessing the intensity of nest defence on a common scale. We therefore caution researchers against a simple interspecific test of Barash's prediction if all of these problems are not taken into account.

A number of other studies have reported a seasonal increase in nest defence (e.g., Simons, 1955; Barash, 1975; Greig-Smith, 1980; Biermann and Robertson, 1981; East, 1981), but none of these attempted to examine the influence of renesting potential while controlling other factors that might also have been responsible for the pattern (e.g., changing probabilities of parent and offspring survival—see below). In each of these studies the seasonal increase in nest defence was vaguely attributed to be in support of parental investment theory but alternative hypotheses have rarely been considered.

In contrast, at least three studies find no support for the predicted pattern. In a tundra population of Savannah Sparrows (*Passerculus sandwichensis*), with a relatively brief breeding season, renesting potential explained almost none of the variation in nest defence behavior (Weatherhead, 1979a). A recent study of Song Sparrows (*Melospiza melodia*) with a longer breeding season yielded similar results (Weatherhead, unpub.). Similarly, in stonechats there was no detectable difference in nest defence behavior between first, second and third broods during a season even though renesting potential was presumably declining (Greig-Smith, 1980). This latter result is in direct opposition to the predictions of Barash (1980) for multi-brooded species. On balance, then, unequivocal evidence for the influence of renesting potential on risk-taking is relatively slim. More studies are needed that can assess the importance of renesting potential while controlling other factors, like the changing probability of parent and offspring survival during any breeding episode (see below).

Within lifetimes. Birds can be grouped into two broad classes with regard to life history patterns (Ricklefs, 1974). For some relatively long-lived species, survival probability declines rapidly in old age. For small, short-lived species, mortality is apparently not age-dependent after the first year of life. Thus, although some

eventual senescence is expected in all birds, few individuals in small species live to an age when the probability of survival until the next year begins to decline. When survivorship is age-dependent (e.g., with senescence), an increase in parental effort (e.g., nest defence) is expected as residual reproductive value declines (Pianka and Parker, 1975). No change in parental effort is expected, however, when there is no year-to-year change in residual reproductive value — i.e., before senescence in long-lived large species, or throughout the lives of most short-lived smaller birds.

For species with senescence (i.e., age-dependent mortality rates), the limited evidence available so far supports the prediction of increasing nest defence (i.e., higher reproductive effort) as parental survivorship decreases (i.e., as costs decrease — Fig. 1c). In California Gulls (*Larus californicus*) both the intensity of nest defence and the rate of adult mortality increased with parental age (Pugesek, 1983). Similarly, Snow Goose (*Anser caerulescens*) females more than 5 years old defended their nests more aggressively than birds 2 to 5 years old (Ratcliffe, 1974) and there is some evidence of a decline in survivorship after the age of 6 years (M. Richards, pers. commun.). These results, though consistent with predictions, point to a serious difficulty in unambiguously testing this hypothesis in species with age-dependent mortality. If older birds expend higher reproductive effort both in nest defence and in all other aspects of offspring rearing, we should expect the increased expenditure to exact a cost that ultimately manifests itself by a higher mortality rate. But is higher reproductive effort the proximate cause or the ultimate consequence of higher mortality among older birds? It may prove difficult to separate these two factors experimentally, especially with birds, because they are relatively long-lived and it is often difficult to perform life history experiments on such organisms (see Bell, 1980, for discussion). In addition, experienced birds may be able to defend more vigorously than relatively naive birds without higher cost because of their familiarity with a predator. Thus age-related differences in defence behavior could be, at least in part, attributable to differences in experience (see below).

The other life history pattern—a constant

mortality rate through life—is thought to be common in passerine birds (Ricklefs, 1974). Unfortunately, however, this generalization is based on limited evidence—few survivorship data are available for older birds in any population because of high mortality rates and because of the relative rarity of long-term studies (Deevey, 1947; Ricklefs, 1974; O'Connor, 1984). Even so, among the younger age classes for which survivorship is known to be age-independent, we should find no increase in the intensity of nest defence with age.

To date, two studies have supported this prediction. Curio (1975) found no significant difference in the nest defence response of yearling and older Pied Flycatchers (*Ficedula hypoleuca*). Similarly, Weatherhead (unpub.), found no age-related variation in nest defence behavior in Song Sparrows, a species in which survivorship is known to be independent of age after the first year of life (Halliburton and Mewaldt, 1976).

Parental Experience

Both the costs and benefits of nest defence should change with the experience of parents. First, as parents gain experience in raising offspring, the probability that chicks will survive and breed should increase independently of the amount of risk taken in nest defence (i.e., as a consequence of increased effectiveness of parenting in other respects — Fig. 1b). Because offspring are relatively more valuable to them, experienced parents should invest more in their defence.

Second, experience in dealing with nest predators should result in both changes in individuals through their lifetime and differences between populations. Within individuals the costs for a given level of nest defence (Fig. 1c) should decrease with experience as parents learn about the capabilities of nest predators. As these costs decrease with experience, a higher intensity of nest defence is favored (Fig. 1c). Thus, changes in both costs and benefits of nest defence with parental experience result in an increase in nest defence behavior. To date, the effect of such experience has rarely been assessed irrespective of variation in parental age. Thus, although we know that in some species older birds engage in more vigorous nest defence, it is unclear whether such a change in behavior reflects increased ex-

perience or decreasing probability of parental survival, as outlined above.

Studies involving repeated presentations of model or human predators at the same nest allow us to test the influence of experience without the confounding effects of parental age, and they appear to support the predictions. Red-winged Blackbird (*Agelaius phoeniceus*) and American Robin (*Turdus migratorius*) parents, for example, increased the intensity of nest defence with more exposures to both humans and model raccoons whereas parents tested only once gave the same response regardless of the stage of the nesting cycle (Knight and Temple, 1986a). Knight and Temple (1986a) argued that the increasing response of parents faced with repeated presentations was due to behavioral habituation. We suggest, however, that such a response may result from a change in the perceived costs of nest defence behavior—with experience parents learn that they can engage in more intensive defence without increasing the actual risk. A naive parent should be relatively cautious of nest predators until it can assess the nature of the threat. Even though the actual risk involved does not change, a parent's perception of the costs should change as it learns more about the predator's abilities. Thus it seems reasonable that parental experience can contribute to the increased response of parents tested through the nesting cycle, but also that offspring age may have some influence on nest defence independent of that experience (see below).

Experience could also have the opposite effect on parental response as a result of changes in perceived benefits. If experience indicates that an apparent predator poses no threat to the nest then defence is no longer warranted. For example, repeated experience with a model predator sometimes results in indifference in as few as five exposures (e.g., Hinde, 1954; Curio, 1975). In such cases, it seems clear that parents no longer respond as if model predators were a threat to their nest. Because experience can affect nest defence in opposite ways, both consistent with our model, it is important that the frequency of exposure to model predators be varied and assessed as an independent variable in future work (see MacLean, Smith, and Stewart, 1986).

At the population level, differences in the

density of a particular nest predator can also affect parental experience and consequently their nest defence behavior. Urban American Crows (*Corvus platyrhynchos*), for example, responded less vigorously to a human intruder in the vicinity of their nest tree than did rural crows, but their response to an actual nest visit was much more intense (Knight, Grout, and Temple, 1987). The authors of this study suggest that urban crows may have perceived little threat from humans (i.e., no benefit to be derived from nest defence) until the nest tree was climbed. On the other hand, because of being continuously persecuted by humans, rural crows appear to perceive humans as more dangerous. As a result they attacked humans at a greater distance from the nest but were more cautious than urban crows when their nest tree was climbed. This example illustrates again how experience can influence both the costs (risk to the parent) and benefits (predator deterrence) of nest defence behavior.

Sex of Parent

Sexual differences in nest defence behavior are expected whenever there is a differential in such things as (1) confidence of parenthood, (2) renesting potential, (3) perception of risk, (4) life history characteristics, and (5) the ability to raise offspring unaided. To assess the influence of each of these factors on nest defence, we will assume that all other sexual characteristics are equal. Also, since a sexual differential in two or more of these characters can lead to opposite predictions, it is essential that their influence be evaluated separately.

The confidence of parenthood for male birds is almost always less than that for females (Trivers, 1972). Thus females should take more risk in nest defence because the expected fitness benefits are higher than those of males for the same costs (Fig. 1b; see also Weatherhead, 1982). Such a sexual differential is expected particularly in species nesting in dense aggregations (Beecher and Beecher, 1979; Gladstone, 1979) or asynchronously (Montgomerie, in press) where there is some opportunity for cuckoldry. For example, female Savannah and Song Sparrows consistently defend their nests more vigorously than their mates (Weatherhead, 1979a, unpub.). Even though the very short breeding season of subarctic Savannah Sparrows (Weatherhead,

1979b) might be expected to limit the opportunities for extra-pair copulations, the behavior of males in this population suggests the risk of cuckoldry is substantial (Weatherhead and Robertson, 1980).

In populations with a biased sex ratio, males and females may sometimes differ in their potential for reneating. In a population of monogamous birds with a male-biased sex ratio, a female has the higher probability of finding a mate and reneating if the present mate is lost (e.g., by desertion or predation). In such cases, females should defend nests relatively less than males because the lifetime costs accrued by a female from a given act of nest defence are, on average, higher than those of a male (Fig. 1c). In practice, this will be a difficult prediction to test because of confounding variables (such as experience, confidence of paternity, and the perception of risk). Such a difference in the residual reproductive value of males and females, however, may help to account for the fact that male Great Tits mob nest predators more vigorously than do females (Curio, 1980; Regelmann and Curio, 1983).

The intensity of nest defence performed by each parent may also be different because of differences in risk for a given level of defence (i.e., different costs — Fig. 1c). For example, nest defence may be more risky for females than males if females are weakened by the rigors of nest-building and egg-production. In 4 days, female Baird's Sandpipers (*Calidris bairdii*) lay 4 eggs with a total mass that is 117 per cent of their body mass. Such a drain on female energy reserves may be responsible for the fact that they take fewer risks than males during nest defence, particularly in the period immediately following egg-laying (Reid and Montgomerie, 1985). This argument gains support from the fact that the intensity of nest defence by female Tawny Owls (*Strix aluco*) varies with their condition as measured by their weight controlled for body size (Wallin, 1987).

Similarly, in sexually dichromatic species the brighter sex may be more vulnerable to predators (see Baker and Parker, 1979, for discussion). Thus, minimal nest defence (such as alarm calls given from cover) by the bright sex may be as risky as a vigorous response (such as a broken-wing act at close range) from the duller sex (Fig. 1c). This prediction is testable

in species with delayed plumage maturation where subadult males in dull plumage often attempt to breed (Rohwer, Fretwell, and Niles, 1980). Although subadult males have less experience than adults, they may sometimes engage in more vigorous nest defence if their dull plumage puts them at less risk.

There are often substantial differences in body size between males and females that could affect their respective vulnerability to the same predator. When predators are relatively small, the larger parent might be expected to respond more vigorously if its size puts it at less risk than its mate. Conversely, the relatively smaller parent may be at less risk if it is more maneuverable and it should therefore respond more vigorously (i.e., the costs are lower — Fig. 1c). Such differential maneuverability may account for two examples of differences in the nest defence response of male and female raptors. Male Snowy Owls (*Nyctea scandiaca*) are more aggressive and attack human intruders more than females, the latter relying more on distraction displays (Wiklund and Stigh, 1983). Andersson and Wiklund (1987) found similar results in the Rough-legged Buzzard (*Buteo lagopus*). In both studies the authors attributed these differences to the greater maneuverability of males owing to their smaller size, a fact that results in a given level of nest defence being less risky for them than for females. In fact, both studies suggested that the need for males to be effective nest defenders may be an important selection pressure that contributes to reversed sexual dimorphism in raptors.

Differences in life history characteristics, such as mortality rate, could also account for sexual differences in nest defence by virtue of altering the costs of such behavior (Fig. 1c). Thus if one sex suffers a higher overwinter mortality, for whatever reason, its loss in residual reproductive value (i.e., the risk involved in nest defence) will be lower and more intense defence can be expected. We know of no studies where such an effect has been looked for.

Similarly, a difference in costs will also favor a sexual difference in the intensity of nest defence when parents do not have the same ability to raise a brood on their own. Thus a parent taking risks would suffer increased costs if its mate is unable to raise the brood on its own and less intense nest defence would be favored (Fig. 1c). This is similar to the explana-

tion proposed by Regelman and Curio (1983) to explain the differences in nest defence behavior of male and female Great Tit parents — females can raise a brood unaided but males cannot until after the nestlings no longer require brooding. As a result females have more to lose than males from a given level of nest defence (i.e., they have increased costs — Fig. 1c) and this may account for the fact that they engage in less vigorous nest defence than males during incubation and brooding periods. Note, however, that female Great Tits are also in poorer body condition than males right after egg-laying (Curio, 1980), so their perception of risk may also be altered, as argued above.

Past Parental Effort

Adjusting the intensity of nest defence with respect to past parental effort is consistent with our model only if such effort is a reliable index of expected benefits (Maynard Smith, 1977; Weatherhead, 1982). Parents that base their defensive decisions on past effort irrespective of future benefits are making a decidedly non-optimal response (Dawkins and Carlisle, 1976; Boucher, 1977), often called the Concorde Fallacy. Because nest defence is a readily quantifiable parental decision that is assumed to indicate the value of the brood to the parent, a few studies of birds have tried to use this behavior to test the Concorde Fallacy either by examining the influence of past effort (e.g., incubation period — Weatherhead, 1979a, 1982; Curio, 1983) or expected benefits (e.g., clutch size — Robertson and Biermann, 1979). Unfortunately, because of the difficulty of testing the Concorde Fallacy the results of these studies are equivocal. This difficulty arises because it is often impossible to alter past effort without also changing the parent's perception of future benefits (Weatherhead, 1982). Although Sargent and Gross (1985) outline the necessary protocol to provide a convincing test of alternative rules governing parental decisions including testing the Concorde Fallacy, these have not yet been applied to a study of birds.

Parental Interactions

In species with uniparental care, a given level of risk will often be less tolerable than in species with biparental care since injury or death of the parent that cares for the young has much greater ramifications for the survival

probabilities of the young. Thus the reproductive benefits for a given level of nest defence are sometimes lower for a single parent than for two parents and a lower level of nest defence is expected (Fig. 1c). Even in a species with biparental care, however, such a difference in benefits will only occur if one parent is able to raise some offspring with reduced or no help (Lyon and Montgomerie, 1985).

The effectiveness of defence by one parent compared to that by two parents will also influence how members of a pair respond to a predator. If two parents are at least twice as effective as one parent at deterring predators then both birds should cooperate fully. When two parents are less than twice as effective as one, however, a conflict of interest arises and it is useful to ask how vigorously each should defend (see Regelman and Curio, 1983, 1986). Existing asymmetries between parents (age, plumage brightness, size) may force one parent to take greater risks than it otherwise would were the two parents perfectly cooperative. Alternatively, the arrival of its mate might allow a parent to decrease the intensity of nest defence without putting its offspring at greater risk (Regelman and Curio, 1986). Moreover, in species where mortality is age-dependent (i.e., where senescence occurs), a young bird mated to an older bird might be able to take advantage of its mate's willingness to take greater risks defending the nest.

Curio, Regelman, and Zimmerman (1984) discovered a third type of mate interaction affecting nest defence. Male Great Tits defended first broods more vigorously than their mates but defended second broods with equal intensity. The authors suggested that a male defending a first brood may engage in more vigorous nest defence as a signal of male quality in order to ensure that the female remain for a second brood. Males who do this should achieve an advantage whenever females are in short supply as long as the increase in costs is more than offset by the advantages of raising a second brood. Once the female has committed to nesting a second time there is no advantage to the male to be derived from taking greater risks.

Offspring Characteristics

Offspring Age

Ricklefs (1973: 245) and Barash (1975) argued that offspring become more valuable as

they age (from newly laid eggs through to fledging) because of the increasing parental investment necessary to replace them if they are lost. This differs from the previously discussed question of how risk-taking should vary through a breeding season in that the changing probability that the offspring will survive (as they approach independence) is thought to be the driving variable rather than changing re-nesting potential of the parents. An offspring's probability of survival to some future time changes from a very low value when the eggs are first laid to a relatively high value when the chicks leave the nest. Andersson, Wiklund, and Rundgren (1980) have pointed out that during that same period a parent's probability of survival changes relatively little, possibly even declining slightly owing to the cost of reproductive efforts. Thus, any offspring becomes relatively more valuable to the parent during the nesting cycle. Because of this increase in the benefits of nest defence (Fig. 1b), the offspring warrant increased risk-taking by the parents, at least until nest departure. Once the young leave the nest their value to parents continues to increase but the benefits from a single act of defence decline (Fig. 1b) because (1) fledglings become more capable of escaping danger and (2) predators are unlikely to be able to destroy an entire brood once it has dispersed from the nest. Thus the intensity of defence by parents should decline after the brood departs from the nest, as the brood becomes increasingly dispersed, and as the ability of offspring to escape from predators improves.

Parents should therefore take relatively low risks early in incubation, but the intensity of defence should increase gradually through to hatching as the probability that eggs will hatch increases. For parents with altricial young, we then expect a rapid rise in nest defence, from hatching of the young until their departure from the nest (Fig. 2), as the probability increases that the offspring will survive to reproduce (Andersson, Wiklund, and Rundgren, 1980). In species with precocial young, nest defence should reach a peak at hatching because that is when chicks leave the nest (Fig. 2). Barash (1975) suggested that this difference in the pattern of nest defence was a fundamental difference between precocial and altricial birds attributable to newly hatched precocial

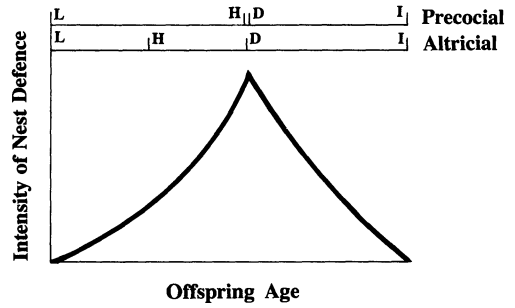


FIG. 2. VARIATION IN THE OPTIMAL INTENSITY OF NEST DEFENCE WITH OFFSPRING AGE FOR PRECOCCIAL AND ALTRICIAL BIRDS

L indicates egg-laying; H, hatching; D, nest departure; and I, the age at independence from parents.

young being more likely than altricial young to survive without parental care if the parent died defending them. It can now be seen, however, that both types of birds have the same pattern if compared on the basis of offspring location (in or out of nest) rather than offspring age. The expected pattern of nest defence with respect to nest departure of the young has been described for both precocial, nidifugous (Swarth, 1935; Simmons, 1955; Stephen, 1963; Gramza, 1967; Lemmetyinen, 1971, 1972) and altricial, nidicolous birds (Greig-Smith, 1980). To date, however, only one study (Greig-Smith, 1980) has quantified brood defence in altricial birds after nest departure.

The pattern of nest defence within a breeding episode has been well documented and has consistently shown qualitative agreement with the predicted pattern in both passerines (Patterson, Petrino-vich, and James, 1980) and non-passerines (Armstrong, 1956; Gramza, 1967; Pugsek, 1983); in birds nesting on the ground (Barash, 1975; Gottfried, 1979; Greig-Smith, 1980), on shrubs and trees (Erpino, 1968; Weatherhead, 1982; Roell and Bossema, 1982; Buitron, 1983), and in holes (Curio, 1975; Regelman and Curio, 1983); in both solitary (East, 1981) and colonial species (Andersson, Wiklund, and Rundgren, 1980; Shields, 1984); and in both arctic (Weatherhead, 1979a; Reid and Montgomerie, 1985) and temperate regions (most studies cited above), though not yet in the tropics. Although the pattern is clear, interpretations have often been confused by the

failure to separate the effects of offspring age from renesting potential. In many species both renesting potential and relative parent and offspring survival probabilities change through the nesting cycle and should have the same qualitative effects on nest defence behavior. Ideally, the influence of nestling age and renesting potential should be separated either statistically or experimentally. For example, in both Savannah (Weatherhead, 1979a) and Song Sparrows (Weatherhead, unpub.) nestling age explained substantially more of the variance in nest defence behavior than did renesting potential. Similarly, Regelmann and Curio (1983) found that the age of the nestlings explained much more of the variance in nest defence behavior by Great Tits than did renesting potential. Collectively these results suggest that whereas both factors affect nest defence as predicted, nestling age has a much greater effect than does renesting potential.

Experimentally the problem can be tackled by looking at defence in species with no renesting potential or by studying nest defence late in the season when renesting potential is negligible. In Arctic-nesting Baird's Sandpipers, where the breeding season is too short to allow more than one nesting attempt, there was a significant correlation between nestling age and nest defence intensity (Reid and Montgomerie, 1985), thereby demonstrating that nestling age per se can influence nest defence behavior as predicted by Andersson, Wiklund, and Rundgren (1980).

Knight and Temple (1986a) have recently suggested that a strong seasonal response by parental American Robins and Red-winged Blackbirds may be due to habituation to the predator model rather than being a response to changes in either renesting potential or the relative probabilities of parent and offspring survival as expected from theory. They demonstrated that no general increase in nest defence occurred when individual nests were visited only once during the nesting cycle. Unfortunately, visits during the finding of some nests, and the presentation of both a human and a predator model (in randomized order) during many tests, invalidates their claim that those nests were visited only once. This and the fact that there is often considerable interindividual variation in the intensity of nest defence (Reid and Montgomerie, 1985) would introduce even

more variation into parental response scores. Since their sample sizes were small (<10 nests per sample period) significant trends would have been difficult to detect. Although the results of Knight and Temple's (1986a) study are intriguing, more careful controls are needed.

Other studies make it clear that increased parental experience or some form of behavioral habituation to a model predator are not the sole reasons for an increase in defence through a nesting cycle. Data on Stonechats (Greig-Smith, 1980) and Song Sparrows (Weatherhead, unpub.) show that during consecutive breeding episodes in the same season, the nest defence response of parents rose and fell in the same pattern. Simple habituation or increasing experience in these cases would have resulted in a steady rise in response across all three episodes. It is thus clear that nest defence behavior changes with offspring age in a way that is not determined solely by parental experience or habituation.

Offspring Number

Although the risks to the parent of defending its nest should vary independently of the number of eggs or nestlings being defended, the benefits of deterring a predator will increase with offspring number. Thus the intensity of nest defence should be positively correlated with offspring number (Fig. 1b). This prediction is nicely supported by an experimental study of American Goldfinches (*Carduelis tristis*) showing that a significant proportion of parents increased or decreased their alarm call rates when their clutches or broods were artificially increased or reduced, respectively (Knight and Temple, 1986c). Note, however, that in species with uniparental care such a correlation will not necessarily be observed if the type of defensive behavior used is particularly risky, because death of the parent will result in loss of the brood as well (Lazurus and Inglis, 1986).

By manipulating clutch sizes of Red-winged Blackbirds, Robertson and Biermann (1979) found some support for this prediction as parents defended more vigorously with increasing clutch size. They found, however, that the behavior of females defending different-sized broods did not differ and they suggested that this anomalous result was due to conflicting

demands on parents during the nestling period. They argued that the time and energy demands made on a female during the nestling period prevented her from optimally defending her young. It makes little sense, however, for a parent to defend its young in a manner that is less than optimal (as defined by parent and offspring survival probabilities) in order that the parent might forage for nestlings in an optimal manner (as defined by nestling growth rates). Nestlings lost to predators are of no value to parents regardless of their growth rate before predation. Most important, Robertson and Biermann's analysis of nest defence for different-sized broods pooled the data for chicks of various ages. Since an age effect is also expected, any real differences among data from females with different brood sizes would tend to be obscured. Nur (1983) has raised other important questions about this analysis (see Biermann and Robertson, 1983, for a response). At best the results of Biermann and Robertson's study seem to provide equivocal support for the influences of offspring number on nest defence behavior.

Data from observing Great Tits are also equivocal in that two studies by the same authors have come to different conclusions with respect to the predicted positive correlation between brood size and nest defence (Regelmann and Curio 1983; Curio and Regelmann, 1987). Moreover, natural rather than experimental variation in brood sizes was used in these studies. This is important because the value of a given number of nestlings may depend to some extent on the reproductive potential of the parents. Two nestlings may represent as large a proportion of the lifetime reproductive success of a parent that is capable of rearing only 2 as do 10 nestlings for a parent that is capable of rearing 10. Only by testing the effects of an experimental manipulation of clutches can this problem be avoided in field studies (e.g., Knight and Temple, 1986c).

In an interspecific comparison of tropical birds, Ricklefs (1977) found a positive correlation between the intensity of nest defence and clutch size. Although he suggested that larger clutches have higher reproductive value and are therefore worth greater risk, it is inappropriate to compare species. To a bird that only lays a small clutch, two eggs will be worth much more than would two eggs to a bird that

lays large clutches. Additionally, interspecific comparisons can potentially involve other confounding factors such as differences in parental armament or mobility. Ricklefs did recognize this problem and conceded that the correlation he obtained could be spurious.

Offspring Quality

Irrespective of the number and age of offspring in a nest, their value to a parent may vary in other ways. In a year when food availability is low, so that there is a reduced probability that the offspring would survive even if they fledged, a parent should risk less in defending those young since a given level of defence will result in lower benefits (Fig. 1b). Similarly, if young that fledge late in the season have a lower probability of surviving to the following year than young fledged earlier in the season (Curio, Regelmann, and Zimmerman, 1984), then late broods are worth less and should be defended less intensively than early broods. This prediction is clearly opposite to that predicted for defending early versus late broods based on reneating potential. Thus, a decline in offspring quality through a breeding season may counter any effect of reneating potential and could explain the relatively limited evidence available supporting the prediction that parents should increase risk-taking as reneating potential decreases. Wallin (1987), for example, found that the intensity of nest defence by Tawny Owl parents declined during the breeding season, irrespective of changes in brood size, as did the survivorship of the broods.

The genetic aspect of offspring quality may also influence parental nest defence. Females mated to relatively high-quality males may defend their young more vigorously than when mated to a low-quality individual, again because the lifetime fitness benefits are higher (Fig. 1b). Male parents might be expected to make the same distinction. These predictions could be tested by experimentally altering some feature known to be used in assessing mate quality (e.g., Andersson, 1982; Burley, Krantzberg, and Radman, 1982) and then measuring the nest defence behavior of the mate.

Offspring Vulnerability

In some situations, absence of the parent from the nest, while interacting with the pred-

ator, could affect offspring survival. An exposed shorebird nest on bare ground could be quite vulnerable to rapid overheating in the midday sun or to hypothermia in cold wet weather (Cartar and Montgomerie, 1985). Thus, when the young are more vulnerable (eggs vs. nestlings or ectothermic vs. endothermic nestlings), a parent should respond more aggressively to a predator because of the increased benefits of defence (Fig. 1b), allowing the parent to return more quickly to the nest.

Larson (1960) reported that Arctic shorebirds increase the intensity of their distraction displays in bad weather. Regelmann and Curio (1983) found that Great Tits (a hole-nesting species) also defended their nests more intensely during cold wet weather. They had predicted just the opposite result, primarily because they expected a parent to be more energy-stressed in cool weather. They suggested, however, that their results could be explained by the fact that the response of parents in warm weather is limited by heat stress; during cool wet weather heat stress would be less likely to occur, and more active responses would be possible. It seems to us that offspring are more likely to be vulnerable to cold than parents to heat stress but both hypotheses make the same prediction about the intensity of nest defence during bad weather. To distinguish between these two explanations, the response of the same parents should be examined at different stages of offspring vulnerability.

Nest Characteristics

Crypsis

A parent with a cryptic nest should engage in less vigorous nest defence than one with an exposed nest since the benefits of defending a cryptic nest are lower (Fig. 1b). This is so because the probability that a predator will find a cryptic nest is relatively low for any given level of nest defence by the parents. Thus when nest concealment varies with season, either increasing as trees leaf out in the spring or decreasing as the nestlings exhibit begging behavior, parents should adjust their response to predators. Harvey and Greenwood (1978) suggested that the increasing conspicuousness because of nestling begging behavior may, in fact, account for the often-observed seasonal increase in nest defence during a breeding cycle. Such an increase, however, has been observed even before the eggs hatch (Reid and

Montgomerie, 1985), so other factors are certainly involved. In addition, many parents use a specific call to silence nestlings (Greig-Smith, 1980; East, 1981; Knight and Temple, 1986c) rather than immediately engaging in nest defence when a predator is nearby.

The expected pattern has been found within a species in a study of American Robins—the response of parents to a model crow was more vigorous when their nest was poorly concealed (MacLean, Smith, and Stewart, 1986). In this study, however, nest concealment was not altered experimentally so it is unclear whether concealment alone was responsible for the variation in parental defence. It is possible, for example, that aggressive parents simply tend not to conceal their nests.

Ricklefs (1977) also provided some evidence in support of the predicted pattern among different species. In tropical passerines, the strength of the parents' nest defence response was directly related to the conspicuousness of the nest. Although these results may be confounded by the various intraspecific differences mentioned earlier (e.g., re-nesting potential, offspring vulnerability), there was still a negative correlation between adult response and nest concealment even when the type of food and the number of offspring were held constant (Ricklefs, 1977). These results are so suggestive that a detailed interspecific comparison of nest defence relative to nest conspicuousness is warranted.

Accessibility

Birds should also defend in a manner related to the accessibility of nests, regardless of the conspicuousness of the nests. If the predator is unlikely to gain access even if it locates the nest, the parent should not respond, because there are decreased benefits for a given level of defence (Fig. 1b). Hole-nesting birds would be interesting to study in this regard since the accessibility of their nests should vary substantially according to the size of potential predators.

Predator Characteristics

Predator-specific responses have been recorded for many species of birds (Armstrong, 1954; Buitron, 1983; Skutch, 1955, 1976; Kruuk, 1964; Curio, 1975; Gottfried, 1979; Gottfried, Andrews, and Haug, 1985). In his discussion of this phenomenon in shorebirds, Gochfeld

(1984) reviewed a number of studies that suggest that birds probably respond to broad classes of predators (e.g., ungulate, avian) according to the danger they pose to their nests. That danger should be directly related to both the mobility and the armament of nest predators.

Mobility

Since predators probably cannot find a nest until they are relatively close, there should be some threshold distance beyond which no response is given. The threshold will be the distance at which a parent can reduce the probability of the predator detecting the nest by sight, sound or smell (Fig. 3). If the predator is inside the threshold distance, nest defence should reduce the probability of the predator finding the nest by silencing the offspring, confusing the predator, or eliciting a group mobbing response from neighbors. This threshold will also be determined by the mobility of the predator and should be sufficiently distant from the nest that if the predator begins to move toward the nest the parents have adequate time to respond to and deter the predator. Thus, for a highly mobile predator like a bird, the threshold distance should be much greater than that for a mammalian predator.

There is ample evidence that nesting birds respond to predators as if there was a threshold distance that triggers their response

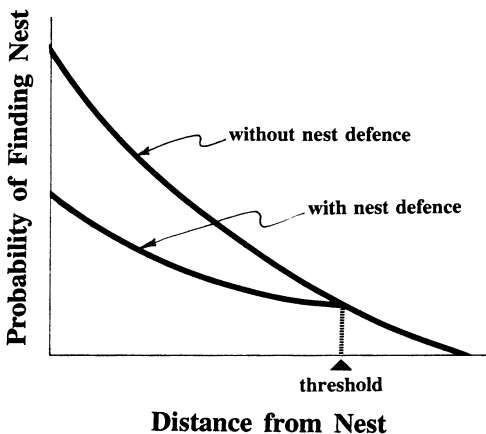


FIG. 3. PROBABILITY THAT A PREDATOR WILL FIND A NEST

This varies with the predator's distance from the nest and with the behavior of the parents.

(Kruuk, 1964; Ryden, 1970; Regelmann and Curio, 1983; Curio and Regelmann, 1985). Black-headed Gulls (*Larus ridibundus*), for example, responded to foxes at greater distances from their nests (10 m) than stoats (5 m) and to stoats at greater distances than hedgehogs (Kruuk, 1964). This suggests that both mobility and relative armament may affect the response of parents.

Armament

Any encounter between a parent and a nest predator involves potential costs and benefits for the predator as well as for the parent. The benefits for both are relatively straightforward: the parent can gain by the survival of its offspring; the predator, by consuming the nest contents. The costs of the interaction, however, will depend upon the nature of the threat that each poses to the other. The relative armament of predator and parent should therefore determine the intensity of nest defence. By armament we mean any feature such as bill, talons, or body size that poses a threat of injury to others.

When the predator is relatively well armed, the parent poses little direct threat to it (e.g., a small passerine defending against a large mammalian predator). In this case, parental response should remain constant or vary randomly with distance from the nest. To do otherwise would provide the predator with information on the nest location thereby increasing the likelihood of the nest being discovered without increasing the effectiveness of the parent's response. However, an increased response as the predator approaches the nest has been reported in Barn Swallows (*Hirundo rustica*; Shields, 1984) and is probably familiar to any naturalist who has searched for cryptic nests. This "geiger-counter effect" often facilitates nest-finding (pers. obs.) but it seems maladaptive for poorly armed parent birds and clearly warrants further study.

Why should parents provide predators with reliable information regarding nest location? If the parent is poorly armed relative to the predator, it is unlikely that the direct threat the parent poses to the predator will vary with response intensity. One possibility, suggested by Bourne (1977), is that an increase in the intensity of defence will increase the threat to the predator from third-party predators (i.e.,

predators dangerous to the animal threatening the nest) within hearing distance of the response of the nest owner. By the commotion that they create, the parents may also attract third-party predators dangerous to themselves. Thus American Robins mobbing a model crow near their nest attracted more crows, potential nest predators (MacLean, Smith, and Stewart, 1986) and crows (*Corvus corone*) mobbing a model owl attracted and were attacked by Goshawks (*Accipiter gentilis*; Slagsvold, 1982). The costs and benefits of attracting third-party predators will depend on their relative abundance in the local fauna.

When the parent is well armed relative to the predator and poses a direct threat to the predator (as might be the case, for instance, with raptorial parents), a response different from that described above is to be expected: the response of the parent should increase as the predator gets closer to the nest. By responding more vigorously as the predator approaches, the parent informs the predator of its willingness to attack if the predator continues to move toward the nest. Even when there is some danger from a direct attack on the predator, parents usually should be more willing than the predator to escalate the encounter because the nest contents should have greater relative fitness value to them (see Dawkins, 1983). Because parental responses also inform the predator of the nest location, the direction that the predator must move to reduce the likelihood of injury should be clear. We are unaware of any evidence relevant to the question of how well-armed parents vary their response to predators according to the distance of the predator from the nest. However, Gottfried, Andrews, and Haug (1985) have shown that American Robins signal their intention to attack a model predator using specific alarm vocalizations. It is possible, therefore, that response intensity could also be used to signal an intention to attack.

CONCLUSIONS

Two general conclusions emerge from this review. First it is clear that, at least in theory, there are a multitude of factors that should affect nest defence behavior. The empirical data available so far support this conclusion: nest defence behavior is highly variable both within and among species and often we can account

for only a small proportion of the variation. Regelmann and Curio (1983), for example, found that in Great Tits 11 of the 16 independent variables they examined affected the behavior of the parent birds. Equally impressive is the fact that collectively those 11 variables explained only 57 per cent of the variation in the parents' behavior. An important source of unexplained variation in defence responses could prove to be variation that is adaptive by virtue of being unpredictable (see Schall and Pianka, 1980).

The fact that nest defence behavior is likely to be influenced by many different factors also has important practical implications. For example, most studies have focused on only a few factors that might explain parental behavior. The amount of variation in nest defence behavior that will be explained by just a few variables, however, is likely to be small, and variables that are not monitored could well confound the results and lead to erroneous interpretations. In the future, researchers should attempt to monitor whatever independent variables are likely to be important, or to control those variables through experimental design.

The second general conclusion is that there is an obvious need for more research aimed at testing the assumptions involved in field experiments. Despite more than a decade of research on the adaptive significance of nest defence, few studies have examined the reliability of the methods used. There may therefore be some question whether results are comparable across studies and whether experiments have been properly controlled. Knight and Temple (1986a), for example, demonstrated that nest defence response of Red-winged Blackbirds was more intense to a live crow than to a mount, to a human looking at the nest rather than at the parent, and to a familiar human rather than to a stranger. These results underline the need for consistent and repeatable methods of minimizing the confounding variables and for detailed descriptions of experimental protocols so that the results of different studies can be evaluated and compared.

Studies of nest defence commonly use humans (e.g., Weatherhead, 1979a; Greig-Smith, 1980; Reid and Montgomerie, 1985) or model predators (e.g., Curio, 1975; Robertson and Biermann, 1979) in order to elicit defence re-

sponses. How birds classify humans or model predators probably depends on how similar these "predators" are to those real predators they normally encounter. Thus the parents' responses in an experiment must be interpreted in the light of the variety of natural predators to which they would normally respond. Some birds may respond to humans as they would to ungulates (as, for instance, when humans are rarely encountered); others may treat humans as they do other mammalian nest predators (especially where there has been a long history of egg harvesting).

The study of nest defence in birds is presently at about the same stage as the study of foraging behavior was a decade ago (Pyke, Pulliam, and Charnov, 1977): some simple optimality theory has been proposed and tested but rarely have the studies been comprehensive enough to convince skeptics that the theory is supported by the available data (see Knight and Temple, 1986a,b). As a result, much of the theory proposed to date is based on untested assumptions about the shapes of cost/benefit curves and the ability of parents to respond to variations in those costs and benefits. Although it is certainly true that some

of the parameters of our models are correct (e.g., the reproductive value of offspring increases with their age), we cannot yet be certain that a parent increasing the intensity of defence will always reduce the probability that its nest will be preyed upon while increasing the risks to itself. There may be some cases in which these models simply do not apply. In spite of these potential drawbacks, we have already seen that optimality modelling helps us focus our attention on testable predictions and that it can be a productive approach to understanding, rather than simply describing, the patterns in this important aspect of parental care.

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REFERENCES

- ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature (Lond.)*, 299:818-820.
- ANDERSSON M., C. G. WIKLUND, and H. RUNDGREN. 1980. Parental defence of offspring: a model and an example. *Anim. Behav.*, 28:536-542.
- ANDERSSON, S., and C. G. WIKLUND. 1987. Sex role partitioning during offspring protection in the Rough-legged Buzzard *Buteo lagopus*. *Ibis*, 129:103-107.
- ARMSTRONG, E. A. 1949. Diversionary displays—the nature and origin of distraction display. Parts I and II. *Ibis*, 91:88-97; 179-188.
- . 1954. The ecology of distraction display. *Anim. Behav.*, 2:121-135.
- . 1956. Distraction display and the human predator. *Ibis*, 98:641-654.
- BAKER, R. R., and G. A. PARKER. 1979. The evolution of bird coloration. *Phil. Trans. Roy. Soc. Lond. B.*, 287:63-130.
- BARASH, D. P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the Alpine Accentor. *Wilson Bull.*, 87:367-373.
- . 1980. Predictive sociobiology: mate selection in damselfishes and brood defence in white-crowned sparrows. In G. W. Barlow, and J. Silverberg (eds.), *Sociobiology: Beyond Nature/Nurture?*, p. 209-226. AAAS, Washington.
- BEECHER, M. D., and I. M. BEECHER. 1979. Sociobiology of Bank Swallows: reproductive strategy of the male. *Science*, 205:1281-1285.
- BELL, G. 1980. The costs of reproduction and their consequences. *Am. Nat.*, 116:45-76.
- BIERMANN, G. C., and R. J. ROBERTSON. 1981. An increase in parental investment during the breeding season. *Anim. Behav.*, 29:487-489.
- , and ———. 1983. Residual reproductive value and parental investment. *Anim. Behav.*, 31:311-312.
- BLANCHER, P. J., and R. J. ROBERTSON. 1982. Kingbird aggression: Does it deter predation? *Anim. Behav.*, 30:929-930.
- BOUCHER, D. H. 1977. On wasting parental investment. *Am. Nat.*, 111:786-788.
- BOURNE, W. R. P. 1977. The function of mobbing. *Br. Birds*, 70:266-267.
- BRUNTON, D. H. 1986. Fatal antipredator behavior

- of a Killdeer. *Wilson Bull.*, 98:605-607.
- BUITRON, D. 1983. Variability in the responses of black-billed magpies to natural predators. *Behaviour*, 88:209-235.
- BURLEY, N., G. KRANTZBERG, and P. RADMAN. 1982. Influence of color-banding on the conspecific preferences of zebra finches. *Anim. Behav.*, 30:444-455.
- BYRKJEDAL, I. 1987. Antipredator behavior and breeding success in Greater Golden plover and Eurasian Dotterel. *Condor*, 89:40-47.
- CARTAR, R. V., and R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the white-rumped sandpiper (*Calidris fusca*): A uniparental incubator in a cold environment. *Behaviour*, 95:261-289.
- COLEMAN, R. M., M. R. GROSS, and R. C. SARGENT. 1985. Parental investment decision rules: a test in bluegill sunfish. *Behav. Ecol. Sociobiol.*, 18:59-66.
- CRESSWELL, R. (translator). 1878. *Aristotle's History of Animals*. George Bell, London.
- CURIO, E. 1975. The functional organization of antipredator behavior in the pied flycatcher: a study of avian visual perception. *Anim. Behav.*, 23:1-115.
- . 1980. An unknown determinant of a sex-specific altruism. *Z. Tierpsychol.*, 53:139-152.
- . 1983. Begehen Kohlmeisen den "Concorde-Fehler"? *J. Ornithol.*, 124:196-198.
- CURIO, E., V. ERNST, and W. VIETH. 1978. The adaptive significance of avian mobbing. III. *Z. Tierpsychol.*, 48:184-202.
- CURIO, E., and K. REGELMANN. 1985. The behavior dynamics of great tits (*Parus major*) approaching a predator. *Z. Tierpsychol.*, 69:3-18.
- , and ———. 1987. Do Great Tit (*Parus major*) parents gear their brood defence to the quality of their young? *Ibis*, 129:344-352.
- CURIO, E., K. REGELMANN, and U. ZIMMERMAN. 1984. The defence of first and second broods by Great Tit (*Parus major*) parents: a test of predictive sociobiology. *Z. Tierpsychol.*, 66:100-127.
- DARWIN, C. 1872. *The Expression of the Emotions in Man and Animals*. Murray, London.
- DAWKINS, R. 1983. *The Extended Phenotype: The Gene as the Unit of Selection*. W. H. Freeman, Oxford.
- DAWKINS, R., and T. R. CARLISLE. 1976. Parental investment, mate desertion and a fallacy. *Nature (Lond.)*, 262:131-133.
- DEEVEY, E. S., JR. 1947. Life tables for natural populations of animals. *Q. Rev. Biol.*, 22:283-314.
- DEWAR, D. 1928. *Birds at the Nest*. John Lane, The Bodley Head Ltd., London.
- EAST, M. 1981. Alarm calling and parental investment in the Robin *Erithacus rubecula*. *Ibis*, 123:223-230.
- ERPINO, M. J. 1968. Nest-related activities of Black-billed Magpies. *Condor*, 70:154-165.
- FISHER, R. A. 1930. *The Genetical Theory of Natural Selection*. Clarendon, Oxford.
- FRIEDMANN, H. 1934. The instinctive emotional life of birds. *Psychoanal. Rev.*, 21 (3, 4):241; 381.
- GLADSTONE, D. E. 1979. Promiscuity in colonial monogamous birds. *Am. Nat.*, 114:545-557.
- GOCHFELD, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. In J. Burger and B. L. Olla (eds.), *Shorebird Breeding Biology and Populations*, p. 289-377. Plenum Press, New York.
- GOODMAN, O. 1974. Natural selection and a cost ceiling on reproductive effort. *Am. Nat.*, 108:247-268.
- GOTTFRIED, B. 1979. Anti-predator aggression in birds nesting in old-field habitats: an experimental analysis. *Condor*, 81:251-257.
- GOTTFRIED, B. M., K. ANDREWS, and M. HAUG. 1985. Breeding robins and nest predators: effect of predator type and defence strategy on initial vocalization patterns. *Wilson Bull.*, 97:183-190.
- GRAMZA, A. F. 1967. Responses of brooding night-hawks to a disturbance stimulus. *Auk*, 84:72-86.
- GREIG-SMITH, P. W. 1980. Parental investment in nest defence by stonechats (*Saxicola torquata*). *Anim. Behav.*, 28:604-619.
- GRIMES, S. A. 1936. "Injury Feigning" by birds. *Auk*, 53:478-480.
- HALLIBURTON, R., and L. R. MEWALDT. 1976. Survival and mobility in a population of Pacific coast Song Sparrows (*Melospiza melodia gouldii*). *Condor*, 78:499-504.
- HAMILTON, W. D. 1964. The genetical evolution of social behavior. I, II. *J. Theor. Biol.*, 7:1-52.
- HARVEY, P. H., and P. J. GREENWOOD. 1978. Antipredator defence strategies: some evolutionary problems. In J. R. Krebs and N. B. Davies (eds.), *Behavioural Ecology: An Evolutionary Approach*, p. 129-151. Blackwell, Oxford.
- HINDE, R. A. 1954. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). II. The waning of the response. *Proc. R. Soc. Lond. B*, 142:331-358.
- JOURDAIN, F. C. R. 1936. The so-called injury-feigning in birds. *Ool. Rec.*, 16:25-37, 62-70.
- . 1937a. The so-called injury-feigning in birds, III. *Ool. Rec.*, 17:14-16.
- . 1937b. Injury-feigning (so-called). *Ool. Rec.*, 17:37-38, 71-72.
- KNIGHT, R. L., and S. A. TEMPLE. 1986a. Why does intensity of avian nest defence increase during the nesting cycle? *Auk*, 103:318-327.
- , and ———. 1986b. Methodological problems in studies of avian nest defence. *Anim. Behav.*, 34:561-566.
- , and ———. 1986c. Nest defence in the American goldfinch. *Anim. Behav.*, 34:887-897

- KNIGHT, R. L., O. J. GROUT, and S. A. TEMPLE. 1987. Nest-defense behavior of the American Crow in urban and rural areas. *Condor*, 89:175-177.
- KREBS, J. R., and N. B. DAVIES (eds.). 1984. *Behavioural Ecology: An Evolutionary Approach*, 2nd ed. Sinauer, Sunderland.
- KRUUK, H. 1964. Predators and anti-predator behavior of the black-headed gull (*Larus ridibundus* L.). *Behaviour, Suppl.*, 11:1-129.
- LARSON, S. 1960. On the influence of the Arctic fox (*Alopex lagopus*) on the distribution of Arctic birds. *Oikos*, 11:277-305.
- LAZURUS, J., and I. R. INGLIS. 1986. Shared and unshared parental investment, parent-offspring conflict, and brood size. *Anim. Behav.*, 34:1791-1804.
- LEMMETYINEN, R. 1971. Nest defence behaviour of Common and Arctic Terns and its effect on the success achieved by predators. *Ornis Fenn.*, 48:13-24.
- . 1972. Nest defence behaviour in the Arctic Tern, *Sterna paradisaea*, towards stuffed nest predators on Spitsbergen. *Rep. Kevo Subarctic Res. Stn.*, 9:28-31.
- LYON, B. E., and R. D. MONTGOMERIE. 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? *Behav. Ecol. Sociobiol.*, 17:279-284.
- MACARTHUR, R. H., and E. O. WILSON. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- MACLEAN, G. L. 1974. Egg-covering in the Chadrarii. *Ostrich*, 45:167-174.
- MACLEAN, I. G., J. N. M. SMITH, and K. G. STEWART. 1986. Mobbing behaviour, nest exposure, and breeding success in the American robin. *Behaviour*, 96:171-186.
- MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1-9.
- MONTGOMERIE, R. D. In press. Seasonal patterns of mate guarding in the Lapland longspur. *Proc. 19th Internat. Ornithol. Congr.*
- NUR, N. 1983. On parental investment during the breeding season. *Anim. Behav.*, 31:309-311.
- O'CONNOR, R. J. 1984. *The Growth and Development of Birds*. Wiley, Chichester.
- PATTERSON, R. L., L. PETRINOVICH, and D. K. JAMES. 1980. Reproductive value and appropriateness of response to predators by White-crowned Sparrows. *Behav. Ecol. Sociobiol.*, 7:227-231.
- PETTINGILL, O. S., JR. 1976. Observed acts of predation on birds in northern Lower Michigan. *Living Bird*, 15:33-41.
- PIANKA, E. R., and W. S. PARKER. 1975. Age-specific reproductive tactics. *Am. Nat.*, 109:456-464.
- POWER, H. W., and C. G. P. DONER. 1980. Experiments on cuckoldry in the mountain bluebird. *Am. Nat.*, 116:689-704.
- PUGESEK, B. H. 1983. The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). *Behav. Ecol. Sociobiol.*, 13:161-171.
- PYKE, G. H., H. R. PULLIAM, and E. L. CHARNOV. 1977. Optimal foraging: A selective review of theory and tests. *Q. Rev. Biol.*, 52:137-154.
- RATCLIFFE, L. M. 1974. Nest defence behavior in the lesser snow goose. B. Sc. thesis, Queen's University, Kingston.
- REGELMANN, K., and E. CURIO. 1983. Determinants of brood defence in the great tit *Parus major* L. *Behav. Ecol. Sociobiol.*, 13:131-145.
- , and ———. 1986. How do great tit (*Parus major*) pair mates cooperate in brood defence? *Behaviour*, 97:10-36.
- REID, M. L., and R. D. MONTGOMERIE. 1985. Seasonal patterns of nest defence by Baird's sandpipers. *Can. J. Zool.*, 63:2207-2211.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.*, 9:1-48.
- . 1973. *Ecology*. Chiron Press, New York.
- . 1974. Fecundity, mortality and avian demography. In D. S. Farner (ed.), *Breeding Biology of Birds*, p. 366-435. Natl. Acad. Sci., Washington, D. C.
- . 1977. Reactions of some Panamanian birds to human intrusion at the nest. *Condor*, 9:376-379.
- ROBERTSON, R. J., and G. C. BIERMANN. 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol.*, 50:124-128.
- ROELL, A., and I. BOSSEMA. 1982. A comparison of nest defence by jackdaws, rooks, magpies and crows. *Behav. Ecol. Sociobiol.*, 11:1-6.
- ROHWER, S., S. D. FRETWELL, and D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am. Nat.*, 115:400-437.
- SARGENT, R. C., and M. R. GROSS. 1985. Parental investment decision rules and the Concorde Falcacy. *Behav. Ecol. Sociobiol.*, 17:43-45.
- SCHALL, J. J., and E. R. PIANKA. 1980. Evolution of escape behavior diversity. *Am. Nat.*, 115:551-566.
- SHIELDS, W. M. 1984. Barn swallow mobbing: self-defence, collateral kin defence, group defence or parental care? *Anim. Behav.*, 32:132-148.
- SIMMONS, K. E. L. 1952. The nature of the predator-reactions of breeding birds. *Behaviour*, 4:161-171.
- . 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape-, and brooding-drives. *Behaviour*, 8:130-173.

- SKUTCH, A. F. 1955. The parental stratagems of birds. *Ibis*, 97:118-142.
- . 1976. *Parent Birds and Their Young*. University of Texas Press, Austin.
- SLAGSVOLD, T. 1982. Mobbing: Goshawk attacking stuffed eagle owl. *Br. Birds*, 75:330-333.
- STEPHEN, W. J. D. 1963. Some responses of female Mallards to disturbance by man. *J. Wildl. Manage.*, 27:280-283.
- SWARTH, H. 1935. "Injury-feigning" in nesting birds. *Auk*, 52:352.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. In B. Campbell (ed.), *Sexual Selection and the Descent of Man 1871-1971*, p. 136-179. Aldine, Chicago.
- WALLIN, K. 1987. Defence as parental care in tawny owls (*Strix aluco*). *Behaviour*, 102:213-230.
- WEATHERHEAD, P. J. 1979a. Do savannah sparrows commit the Concorde Fallacy? *Behav. Ecol. Sociobiol.*, 5:373-381.
- . 1979b. Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. *Auk*, 96:391-401.
- . 1982. Risk-taking by Red-winged Blackbirds and the Concorde Fallacy. *Z. Tierpsychol.*, 60:199-208.
- WEATHERHEAD, P. J., and R. J. ROBERTSON. 1980. Sexual recognition and anticuckoldry behaviour in savannah sparrows. *Can. J. Zool.*, 58:991-996.
- WIKLUND, C. G., and J. STIGH. 1983. Nest defence and evolution of reversed sexual dimorphism in Snowy Owls *Nyctea scandiaca*. *Ornis Scand.*, 14:58-62.
- WILLIAMS, G. C. 1966. Natural selection, costs of reproduction and a refinement of Lack's principle. *Am. Nat.*, 100:687-690.