

REACTIONS OF SOME PANAMANIAN BIRDS TO HUMAN INTRUSION AT THE NEST

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Current thinking about variation in life-history patterns among species of animals stresses variation in the effort expended by parents to rear their young (Stearns 1976). Following Williams (1966), many authors have suggested that optimum reproductive effort is a compromise between augmenting any one year's productivity and increasing the probability of survival to the following breeding season. Reproductive effort presumably increases the risk of the parent's dying. If we assumed that the number of young reared is determined by both the level of parental effort and the availability of resources, tests of hypotheses concerning the optimization of effort would require the measurement of effort independently of resources and production. Adequate tests of such hypotheses have not been made, in part because reproductive effort is difficult to define and measure (Hirschfield and Tinkle 1975). Effort has many components, one of which may be the risk that parents assume to defend their offspring against potential predators. In this study, I report on the defensive behavior of adult birds near their nests and its relationship to other aspects of breeding behavior. Certainly behavior is not an adequate measure of risk, but if we assumed that the intensity of defense is a crude index to reproductive effort, we could test, at least tentatively, the hypothesis that effort and breeding productivity are directly related.

Although Alexander Skutch and others have reported the breeding biology of many species of tropical birds, certain aspects of breeding behavior, including the reactions of adults and nestlings to human intrusion at the nest, have received little attention. The results reported in this paper are based on observations made during a study on development rates in tropical birds (Ricklefs 1976).

STUDY AREA AND METHODS

I observed nests of passerine birds in the Panama Canal Zone and adjacent areas of the Republic of Panama between January and July 1968. I restricted field work to second-growth habitats, gardens, parks, and clearings because nests in such places are relatively conspicuous and successful. I visited nests between 1000 and 1600 h at intervals of one or two days. During each visit, young were weighed and

measured, nest structure and placement, clutch size, and incubation period were recorded, and the reactions of the adults to my approach to the nest and of the young to their being handled were noted.

The study included one to three nests of each of 17 species: PIPRIDAE—Red-capped Manakin (*Pipra mentalis*); TYRANNIDAE—Rusty-margined Flycatcher (*Myiozetetes cayanensis*), Vermillion-crowned (= Social) Flycatcher (*M. similis*), Fork-tailed Flycatcher (*Muscivora tyrannus*), Tropical Kingbird (*Tyrannus melancholicus*), Lesser Elaenia (*Elaenia chiriquensis*), Streaked Flycatcher (*Myiodynastes maculatus*); HIRUNDINIDAE—Mangrove Swallow (*Tachycineta albilinea*); TURDINAE—Clay-colored Robin (*Turdus grayi*); VIREONIDAE—Red-eyed Vireo (*Vireo olivaceus*); THRAUPINAE—Thick-billed Euphonia (*Euphonia lanirostris*), Plain-colored Tanager (*Tangara inornata*), Blue-gray Tanager (*Thraupis episcopus*), Palm Tanager (*T. palmarum*); FRINGILLIDAE—Variable Seedeater (*Sporophila americana*), Yellow-bellied Seedeater (*Sporophila nigricollis*), Green-backed (= Black-striped) Sparrow (*Arremonops conirostris*).

I determined the diets of the young from published accounts of each species or a close relative (primarily Skutch 1954, 1960), observations of food brought to the nest, and seeds and other plant remains in the feces. Abundant white matter (uric acid) in the feces was assumed to indicate a high-protein (insect) diet. I classified species according to the diet of the young as either (1) predominately fruit, (2) mixed, or (3) predominately insect. The seedeaters (*Sporophila*), which feed their young large quantities of grass seed, were included with fruit eaters (category 1).

I determined clutch size from my own observations and from published accounts. The average clutch, which ranged from two to four eggs, was rounded to the nearest 0.5 egg.

I assigned nests to three categories on the basis of structure and placement: (1) conspicuous, (2) intermediate, and (3) concealed. At one extreme, conspicuous nests, all belonging to flycatchers in this study, were bulky platforms or enclosed, grassy balls placed in conspicuous but relatively inaccessible locations, usually in dead trees or in trees with sparse foliage. At the other extreme, concealed nests were usually sparsely built or well-camouflaged and were placed among foliage. Concealed nests were difficult to find but readily accessible (to me, at least). I judged several species, including the Clay-colored Robin and most of the tanagers, to have nests of intermediate type.

I recognized four categories of response by adults to my intrusion at the nest: (1) not appearing or quietly leaving the vicinity of the nest, (2) perching quietly a short distance from the nest, (3) scolding, from a variable distance, often from an exposed or conspicuous perch, and (4) directly attacking me, often with physical contact. Responses reported are those recorded during the second (and in some species third) week of the nestling period. The adults' response increased in many species during the nest cycle (cf. Snow 1962, Erpino 1968) and

TABLE 1. Aspects of the reproductive behavior of 17 species of passerine birds in the Panama Canal Zone.

Species	Food ^a	Clutch size	Nest ^b type	Adult ^c response	Defecation ^d response
<i>Pipra mentalis</i>	1	2	3	1	3
<i>Myiozetetes cayanensis</i>	2	3	1	2.5	2.5
<i>Myiozetetes similis</i>	2	3	1	3	2
<i>Muscivora tyrannus</i>	3	2.5	1	2.5	1
<i>Tyrannus melan-cholicus</i>	3	3	1	4	1
<i>Elaenia chiriquensis</i>	2	2	3	1	2.5
<i>Myiodynastes maculatus</i>	3	4	1	4	1.5
<i>Tachycineta albilinea</i>	3	4	2	4	1
<i>Turdus grayi</i>	2	3	2	3	1
<i>Vireo olivaceus</i>	2	3	2	3.5	1.5
<i>Euphonia lanirostris</i>	1	4	2	2.5	2
<i>Tangara inornata</i>	1	2	3	1.5	3
<i>Thraupis episcopus</i>	1	2	2	1	3
<i>Thraupis palmarum</i>	1	2	2	2	2.5
<i>Sporophila americana</i>	1	2.5	3	1	2
<i>Sporophila nigricollis</i>	1	2	3	1	2
<i>Arremonops conirostris</i>	2	2	3	1	1

^a 1 = fruit, 2 = mixed, 3 = insect.
^b 1 = conspicuous, 2 = intermediate, 3 = concealed.
^c 1 = weakest, 4 = strongest.
^d 1 = none, 2 = once, 3 = multiple defecation.

reached a peak during the latter part of the nestling period.

Nestlings of most passerines defecate when they are handled, although this response is by no means uniform. Reactions to me fell into three classes: (1) no defecation, (2) a single fecal mass produced when the young were first handled, and (3) repeated, often profuse defecation. Intermediates between the categories were used when the response varied from visit to visit.

RESULTS

Observations on each species are presented in Table 1. All aspects of behavior reported here were interrelated. For example, adult response was weakest where the defecation response of the young is strongest; adult response was strongest among species with conspicuous nests; large clutches tended to be

laid in conspicuous nests and by species that feed insects to their young. The statistical significance of these relationships was tested with a nonparametric measure, the Kendall rank correlation coefficient corrected for tied ranks (Siegel 1956), and a parametric measure, the product-moment correlation coefficient (Table 2). I used the UCLA Biomedical Computer Programs BMDP3S and BMD03R to calculate the coefficients. All the relationships involving simple correlations are significant ($P < 0.05$) except for the product-moment correlation between defecation and nest type.

The correlations summarized in Table 2 are open to a variety of interpretations. For example, if adult response were assumed to be an index to reproductive effort, the inverse relationship between defecation response and adult response could lead us to conclude that young defend themselves more vigorously when parental defense is weaker and vice versa. But both the defecation response and parental response also are related to each of the other factors.

In studies of correlation among many factors, the independent relationship between two variables is often obscured by the relationship of each to other factors. The independent relationship may be determined by calculating the partial correlation coefficient between two factors with other factors held constant statistically. Partial correlation coefficients were based upon the product moment correlations to take advantage of available computer programs. Partial correlations (Table 3) show that, whereas the relationship between defecation response and adult response had a simple correlation coefficient of -0.61, the partial coefficient with other factors including food type held constant was -0.15, indicating no relationship. The simple correlation between defecation response and food type (-0.74) remained, however, essentially unchanged (-0.61) when variation in clutch size, nest type, and adult response were accounted for simultaneously.

TABLE 2. Kendall rank correlation coefficients (lower left) and product moment correlation coefficients (upper right) between aspects of reproductive behavior.

Dependent variable	Food type	Clutch size	Nest type	Adult response	Defecation response
Food type	-	0.53	-0.64	0.74	-0.74
Clutch size	0.50	-	-0.57	0.82	-0.49
Nest type	-0.56	-0.54	-	-0.76	0.36
Adult response	0.63	0.74	-0.65	-	-0.61
Defecation response	-0.64	-0.44	0.30	-0.49	-

TABLE 3. Partial product moment correlation coefficients between each aspect of reproductive behavior and all others.¹

Dependent variable	Food type	Clutch size	Nest type	Adult response	Defecation response
Food type	—	-0.22	-0.32	0.30	-0.61**
Clutch size	-0.22	—	0.05	0.69**	-0.10
Nest type	-0.32	0.05	—	-0.47*	-0.34
Adult response	0.30	0.69**	-0.47*	—	-0.15
Defecation response	-0.61**	-0.10	-0.34	-0.15	—

¹ Levels of significance are: * $P \approx 0.05$; ** $P < 0.01$.

Partial correlation analysis revealed only three significant relationships between the factors reported in this study:

(1) the strength of the defecation response is directly related to the proportion of fruit in the diet of the young;

(2) the strength of the adult response is directly related to the size of the clutch; and

(3) the strength of the adult response is directly related to the degree of conspicuousness of the nest. Connectives between the factors do not, however, prove cause and effect. Nor can we be certain that any of the relationships are independent of aspects of reproduction and life history not measured in this study.

DISCUSSION

The relationships discovered in this study can be used to test hypotheses about the evolution of reproductive patterns only if we are willing to tie one or more of the factors directly to the environment and interpret the others as evolved adaptations of reproductive behavior. A conservative interpretation would relate all factors directly to the environment and write off correlations among them as the fortuitous result of correlations among the environmental factors that influence each factor separately. A liberal interpretation would relate only one factor directly to the environment; evolutionary influence would be viewed as being transmitted from that factor to the others through a chain of casual relationship.

The factors reported in this study could be related to each other and to the environment by a variety of schemes. The number of such schemes could be reduced greatly if we determined cause and effect for one or more of the relationships. It would be absurd to believe that defecation response influenced food type (defecation \rightarrow food); causality of opposite direction (food \rightarrow defecation) could, however, easily be related to the bulk of food, much of it indigestible, that frugivores and granivores must consume to obtain adequate nourishment (White 1974). The relationships

between nest type, adult response, and clutch size are not so readily interpreted, but I cannot imagine how the environment could influence the response of adults to intruders at the nest more directly than it could influence nest construction. Nest type and adult response are likely related to the extent that a strong response from the adult might reveal the position or proximity of a well-concealed nest. For species with conspicuous but relatively inaccessible nests, scolding or attacking an intruder might dissuade a potential predator from robbing the nest. If causality were established as nest type \rightarrow adult response and food \rightarrow defecation, only two schemes of relationships, distinguished by the role assigned to clutch size, would be possible. In one, clutch size would be determined directly by the environment; in the other, it would be determined secondarily by some other attribute of reproductive behavior, perhaps the commitment of adults to the defense of their young.

The causal relationship of adult response \rightarrow clutch size has been predicted by theory which states that fecundity is influenced, independently of the environment, by variation in reproductive effort (e.g., Williams 1966, Gadgil and Bossert 1970, Cody 1971). We should not, however, accept the positive relationship between adult response and clutch size as compelling evidence for the demographic optimization of fecundity. This view carries with it several difficulties. First, adult response to intruders at the nest is not a complete measure of reproductive effort, particularly as it does not include foraging effort. Second, one demographic model of the optimization of reproductive effort in birds (Ricklefs 1977) has shown that, although effort should be inversely related to adult survival rate, variation in effort has little influence on fecundity. Third, a reasonable alternative explanation for the relationship between clutch size and adult response relates the effort expended in nest defense to the number of young raised in the brood, hence to the potential reproductive

value of the nesting attempt (clutch size \rightarrow adult response). At age 0 (the freshly laid egg), the reproductive value of all individuals is 1 (Lotka 1956), hence a clutch with four eggs has twice the reproductive value of a clutch of two. The reproductive value of eggs and chicks increases with age as the inverse of their survival probability. If, among a variety of species, egg and nestling survival were independent of clutch size, the reproductive value of a brood during the nestling period would remain directly proportional to clutch size and we would expect, therefore, that parents would defend large broods more vigorously than small broods. Unfortunately, there are too few nest success data for species with large clutches to test the independence of clutch size and nesting success.

A third explanation for the relationship between clutch size and adult response is that both are fortuitously associated with some other factor not recorded in this study. Strong reactions by adults to intruders may be characteristic of species with strong, highly maneuverable flight and that live in open habitats. Such species, which are mostly aerial feeders, have the skill required to attack intruders directly without incurring great risk to themselves. Other aspects of open habitats may lead to large clutches. The only species that struck me in reaction to my approaching their nests were the Tropical Kingbird, the Streaked Flycatcher and the Mangrove Swallow, all of which are powerful fliers. High marks for adult response were also won by the Clay-colored Robin and the Red-eyed Vireo, also strong fliers and characteristically aggressive species.

The relationships alluded to in this study are tenuous because they are based upon few species and they do not provide a complete description of reproductive behavior. These relationships nonetheless suggest some of the constraints that may limit the evolution of reproductive modes and they indicate a potentially fruitful area of research.

SUMMARY

Observations on food type, nest type, clutch size, and the response of adults and young to a human intruder at their nests were recorded for 17 species of passerine birds found in open and edge habitats in the Panama Canal Zone. Statistical analysis revealed significant positive

correlations between (1) defecation by the young when handled and proportion of fruit in the diet, (2) clutch size and strength of nest defense by the adult, and (3) concealment of nests and weakness of nest defense. These correlations are interpreted as resulting from the following causal relationships: food type \rightarrow defecation response, nest type \rightarrow adult response, and, possibly, clutch size \rightarrow adult response.

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LITERATURE CITED

- CODY, M. L. 1971. Ecological aspects of reproduction, p. 461-512. In D. S. Farner and J. R. King [Eds.], Avian biology. Vol. 1. Academic Press, New York.
- ERPINO, M. J. 1968. Nest related activities of Black-billed Magpies. *Condor* 70:154-165.
- GADGIL, M., AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1-24.
- HIRSCHFIELD, M. F., AND D. W. TINKLE. 1975. Natural selection and the evolution of reproductive effort. *Proc. Natl. Acad. Sci. U.S.A.* 72:2227-2231.
- LOTKA, A. J. 1956. Elements of mathematical biology. Dover, New York.
- RICKLEFS, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *Am. Nat.* 111:453-478.
- RICKLEFS, R. E. 1976. Growth rates of birds in the humid New World tropics. *Ibis* 118:179-207.
- SIEGEL, S. 1956. Nonparametric statistics. McGraw-Hill, New York.
- SKUTCH, A. F. 1954. Life histories of Central American Birds. *Pac. Coast Avifauna* 31:1-448.
- SKUTCH, A. F. 1960. Life histories of Central American birds. Vol. 2. *Pac. Coast Avifauna* 34:1-593.
- SNOW, D. W. 1962. A field study of the Black-and-White Manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47:65-104.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3-47.
- WHITE, S. C. 1974. Ecological aspects of growth and nutrition in tropical fruit-eating birds. Ph.D. diss., Univ. of Pennsylvania, Philadelphia.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100:687-690.

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