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CHAPTER 3

THE EFFECTS OF INVESTIGATOR DISTURBANCE ON NESTING BIRDS

FRANK GÖTMARK

1. INTRODUCTION

To learn about the behavior and ecology of nesting birds, we often study them when they occupy nesting territories. But by visiting territories or nests, the investigator may to a greater or lesser extent disturb the birds and affect the parameters being studied. Thus, we want to learn about the behavior or performance of birds under natural conditions, but may alter these conditions by our presence in the field. This has been called the "uncertainty principle" in field biology (Lenington, 1979).

In many cases, the effects of an observer may be negligible. For instance, repeated visits to a nest may mean only that the incubating bird is flushed, and perhaps mobs or tries to distract the observer. This disturbance might not affect individual survival or nesting success. In other cases, the effects of disturbance may be irrelevant to the question posed. For example, in comparisons of different groups or treatments, disturbance might not be a problem as long as all groups receive the same amount of disturbance. However, I show below that nesting suc-

FRANK GÖTMARK • Department of Zoology, University of Göteborg, S-400 31 Göteborg, Sweden.

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cess and behavior sometimes are affected by disturbance; therefore, when an unbiased estimate of nesting success or behavior is sought, investigator disturbance is a potential problem. Avian research in life history theory, demography, population dynamics, and conservation biology usually require unbiased estimates of fecundity, and behavioral studies may require that behavior is not affected by investigators. Statements such as "possibly the lower success rates . . . found in most passerine studies (Ricklefs, 1973) partly result from disturbance by observers" (Stobo and McLaren, 1975:52) motivated this review. In addition, knowledge of and attempts to minimize investigator impacts are desirable for ethical reasons (e.g., Taylor, 1986; American Ornithologist's Union, 1988).

Although ornithologists have long been aware of the disturbance problem (e.g., Stoddard, 1932; Kalmbach, 1938; Johnson, 1938; Skutch, 1966), studies designed to evaluate the problem have appeared only recently (e.g., Evans and Wolfe, 1967; Grier, 1969; Newton and Campbell, 1975; Ellison and Cleary, 1978; Gottfried and Thompson, 1978; papers in *Colonial Waterbirds*, vol. 4, 1981; Westmoreland and Best, 1985). To date, no comprehensive review of this literature has been published (but see Anderson and Keith, 1980; Boyle and Samson, 1983; Grier and Fyfe, 1987). To examine the problem, I reviewed papers with original data on the effects of observers. The specific objectives were (1) to examine the methods used to detect an observer influence, (2) to compare observer influence on nesting success in different groups of birds, (3) to identify the proximate reasons for reduced nesting success, (4) to determine how observer influence varies with stage in the nesting cycle and nesting density, and (5) to identify effects of observer visitation on behavior. I also review some methods that mitigate disturbance effects, discuss the ultimate reasons for differences in sensitivity among species, and suggest some future research.

The study was initiated during a review of the effects of recreational disturbance on birds (Götmark, 1989). Papers on researcher disturbance were gathered in several ways. I found most of them by scrutinizing studies of breeding biology and checking literature lists. I also searched avian studies (published 1960–1987) in Biological Abstracts, using the BIOSIS PREVIEWS® (Philadelphia, PA) system at the Biomedical University Library in Gothenburg, Sweden. The key words I used were "disturbance" and "interference" combined with "nesting," "breeding," and "reproduction." The output listed 126 papers; many of these I had already found, and some were not relevant. Most papers (88%) cited below were not included in the output. I believe I have found the most important papers, and that no particular group of birds has been over-

looked. Of 225 studies included in the review, 71% were from North America, 22% from Europe, and 6% from other parts of the world.

Studies concerned with effects of special methods used to capture, mark, or observe adults or nestlings (e.g., Blokpoel, 1981; Brubeck *et al.*, 1981; Nisbet, 1981; Hamilton and Martin, 1985; Kålås *et al.*, 1989; Kinkel, 1989; Wilson *et al.*, 1989; and references therein) were not included, as the aim was to review effects of "normal" field research. In the 100 studies included in Table I, nests or nesting areas were visited in all studies, chicks were banded or handled in at least 38 studies (probably more), and adults were trapped and banded in 26 studies (perhaps more).

2. METHODS USED TO EXAMINE EFFECTS OF INVESTIGATOR DISTURBANCE

A common claim in the older literature (see also Lenington, 1979) is that it is difficult or impossible to investigate observer influence in a nesting study. I found that a scientific approach is possible, although the strength of inferences and conclusions varied among papers. I identified at least seven methods used to study disturbance effects (Table I). Below, I comment on the problems of each method (see also Grier and Fyfe, 1987, for an excellent discussion). The papers in Table I concern nesting success or nest predation, or in a few cases nest site selection or behavior (see below). Studies of artificial nests were not included here (or in Table III) but are discussed in section 5.3 (I did include Gottfried and Thompson, 1978, as they also presented relevant data for natural nests). Bart (1977) was included in Table I but not in any analyses below because the conclusions were later questioned (Bart and Robson, 1982).

1. *Experimentally disturbed areas/nests and undisturbed controls.* Several authors compared experimentally disturbed areas and undisturbed control areas, but of these only Grier (1969), Grier *et al.* (1972), Westmoreland and Best (1985), and Grier and Fyfe (1987) stated that they chose experimental and control nests randomly from the population. Controls may be established by observing nests or nesting pairs from a distance. Incubating adults do not flush and no serious disturbance is created. This approach has been applied to raptors with large nests that can be seen from a distance (e.g., Grier, 1969; Poole, 1981; Fraser *et al.*, 1985; Grier and Fyfe, 1987) as well as shorebirds (Pienkowski, 1984; Galbraith, 1987), doves (Westmoreland and Best, 1985), and antbirds (Willis, 1973). In some studies control nests were disturbed on the day they were found, but not later (e.g., Westmoreland and Best, 1985),

TABLE I
Methods Used to Examine Effects of Investigator Disturbance
on Nesting Birds in 100 Studies^a

Method ^b	Number of Papers	References ^c
Experimentally disturbed areas/nests and undisturbed controls	27	3, 15, 22, 32, 52, 56, 58, 60, 61, 70, 74, 76, 77, 77a, 108, 109a, 111a, 125, 133, 139, 141, 165, 169, 172, 187, 189, 191
Correlational study (≥ 3 samples; differentially disturbed)	12	4, 34, 53, 57, 62, 67, 88, 97, 123, 130, 150, 160
Comparison of two samples (more and less disturbed)	33	1, 26, 29, 36, 38, 39, 45, 52, 56, 58a, 64, 65, 68, 80, 81, 82, 85, 95, 107, 111, 118, 126, 128, 129, 136b, 138, 153, 154, 156, 158, 159, 164, 181
Comparison of samples from different years or different studies	7	40, 53, 54, 106, 111, 141, 142
Comparison of visited active nests and nests that were terminated when detected	9	25, 50, 96, 97, 99, 109, 152, 171, 173
Other comparisons	9	12, 48, 50, 79, 99, 157, 166, 173, 179
"Dramatic effects"	11	20, 37, 41, 86, 92, 117, 122, 135, 145, 183, 193

^aEight studies used two methods and hence occur twice.

^bSee text for more detailed description.

^cThe numbers refer to papers in the reference section.

whereas in other studies control nests were never disturbed (e.g., Willis, 1973). The former nests might not be regarded as true controls, but the two types of studies were pooled in this review. Method 1 assumes no negative effects of distant observations, which may be determined from the behavior of adults. The assumption can also be evaluated by use of automatic cameras to monitor the behavior of adults before, during, and after distant observations by humans. Indeed, cameras can replace distant observers if they can be run for long periods.

In other cases, investigators visited an experimental area repeatedly and made the final visit to this area when the undisturbed control was first visited. They usually assumed they detected all nest losses and other effects in controls, which may not always be true (Duffy, 1979). The assumption can be justified to a greater or lesser extent depending on the

species and situation. For example, gull and tern nests may be visited during incubation (disturbance effects are less likely then), and as the number of pairs with eggs is known just before hatching, production of young in an undisturbed area may be assessed in one late visit and compared to that of a disturbed area (e.g., Feare, 1976; see also Fetterolf, 1983). Some late pairs may begin egg laying after other pairs have hatched, but their proportion of the population is usually small, and they might be detected on the final visit if nests were marked before the hatching period. In some waterfowl, destroyed nests may be visible for many days after failure and the proportion of such nests may be compared for disturbed and undisturbed areas late in incubation (Newton and Campbell, 1975; Götmarm and Åhlund, 1984). One potential problem in areas with high nesting density is that females may lay eggs in previously depredated nests (Newton and Campbell, 1975). Finally, differences in average clutch size, potentially reflecting egg predation (partial nest predation), may be evaluated by one visit late in incubation to a repeatedly disturbed and an undisturbed area (Cooch, 1965; Götmarm and Åhlund, 1984).

2. *Correlational study (≥ 3 samples)*. These studies compared areas or nests that were differentially disturbed. In all cases, at least three categories (e.g., "low-," "intermediate-," and "high-disturbance areas") were compared. No undisturbed area was included and for the objective of this review the conclusions are therefore weaker than for method 1 since one or a few visits also may reduce nesting success (note that original conclusions may not be "weak" if other hypotheses about disturbance were being tested). Nevertheless, in some studies the conclusions appear to be almost as strong as for method 1 (e.g., Fetterolf, 1983). No authors using this or the following methods stated that they chose nests for treatments randomly from the population.

3. *Comparison of two samples (more and less disturbed)*. This was the most common method used. It is subject to the same considerations as method 2. The fewer the visits to the "control," the closer to undisturbed conditions, and method 1 (assuming that the parameter studied is related to number of visits, and not just presence or absence of disturbance). In this category, I also included one study of effects of different numbers of observers simultaneously visiting nests (Livezey, 1980; see also Ollason and Dunnet, 1980).

4. *Comparison of samples from different years or different studies*. These papers compare years or studies where the degree of disturbance differed. However, other variables may also differ between years and between studies. If much information is available on other important

variables, and if the differences between years or studies are striking, relatively strong inferences could still be made (e.g., Fetterolf, 1983).

5. *Comparison of visited active nests and nests that were terminated when first detected.* In waterfowl, gallinaceous birds, and some other groups, terminated nests remain visible for many days and one can usually assess from the remains of egg shells if they were successful or not. Several studies compared the success of unvisited, terminated nests with that of active nests visited one or several times. There are several problems with this approach (some of them might apply to the other methods as well). First, although some nests were not visited when active, incubating birds at these nests may have been disturbed when the investigator visited other nests, as all nests usually were in the same area. Thus, ideally only terminated nests found on the first visit should be included. Second, if the unvisited group contained a higher proportion of nests that include the egg-laying period, the comparison could be biased because desertion and predation rates are often high during laying (see below). Thus, only nests found during laying should be included in the category of visited nests. If visited nests are only observed during part of their active period, the Mayfield method may also be used to estimate nest survival probability (Mayfield, 1961, 1975; Johnson, 1979; Hensler and Nichols, 1981). Third, if the visited group on average nested later, it may include a higher proportion of young or low-quality birds, or may be affected by seasonal changes in, for example, nest concealment. Fourth, it is possible that terminated nests that failed are more likely to be detected than hatched terminated nests (Kalmbach, 1938). For certain species, this bias might be avoided by using dogs to find nests (e.g., Keith, 1961).

6. *Other comparisons.* Each of the following methods are used in only a few studies. Four studies compared the success of nests where incubating birds were flushed versus not flushed by investigators (Hammond and Forward, 1956; Evans and Wolfe, 1967; Klimstra and Roseberry, 1975; Sugden, 1978). However, these two categories of birds may differ in condition or quality (Ollason and Dunnet, 1980). Also, incubating birds may flush more readily during laying than later on (Evans and Wolfe, 1967), so one should control for stage in nesting cycle, as Klimstra and Roseberry (1975) did. Sonerud (1985) compared predation of nests up to and after the first visit. Tiainen (1983) and Seding (1990) examined temporal patterns of predation after visits to nests (see also MacInnes and Misra, 1972; Bart, 1977; Bart and Robson, 1982; Vacca and Handel, 1988), and Eriksson (1980) compared number of visits made to successful and deserted nests.

7. *"Dramatic effects."* These studies found "dramatic effects" that

apparently were due to observer visits to nests. A paper was only included here if an effect of disturbance seemed likely and could be evaluated in some detail. Examples are intense predation on eggs and young during or after single, short visits to nesting areas (e.g., Paynter, 1951; DesGranges and Reed, 1981), nest predators following investigators and preying upon nests (e.g., Veen, 1977), and high rates of nest desertion after nest visits (Zwickel and Carveth, 1978; Myrberget, 1983).

3. DISTRIBUTION OF PAPERS AMONG ORDERS

Table II shows the distribution of 166 "disturbance papers" among 14 orders of birds. Here I included papers that found, or did not find, an effect of disturbance, and papers that only discussed the problem (the latter were not included in Table I). To examine if differences between orders reflected potential vulnerability to disturbance, or alternatively the extent to which their breeding biology had been studied, I also tabulated breeding biology papers in different orders published in 1970–1987 (key words used to search in BIOSIS PREVIEWS were "nesting," "breeding," and "reproduction"). Compared with the total number of breeding biology papers, studies of observer disturbance as defined above were overrepresented in the orders Pelecaniformes, Anseriformes, and Charadriiformes, but underrepresented in Passeriformes (Table II). Expected frequencies of disturbance papers for different orders, based on the BIOSIS PREVIEWS data, differed from observed frequencies ($p < 0.001$, χ^2 test). This implies that researchers studying certain taxa thought they might be vulnerable to disturbance, and examined or discussed this possibility. An alternative interpretation (J. Nichols, personal communication) is that nest success is easier to study in some groups (e.g., ducks) than others (e.g., passerines).

4. EFFECTS OF DISTURBANCE ON NESTING SUCCESS IN DIFFERENT ORDERS

To examine effects of disturbance on nesting success I divided the papers into two categories according to the strength of the conclusions. "Direct evidence papers" (DE papers; $n = 57$) applied methods 1–3 (Table I); "indirect evidence papers" (IE papers; $n = 12$) applied methods 4–7. In general, it is easier to exclude effects of confounding variables for DE than IE papers. For both categories of papers, "effects" refers to either reduced production of young per pair or reduced proportion of

TABLE II
Studies of Species in Different Orders Where Effects of Investigator Disturbance on Nesting Birds Were Examined or Discussed, Compared with Total Number of Breeding Biology Citations in These Orders^a

Order	Number of disturbance studies	Total number of citations	References ^b
Gaviiformes	3 (2%)	93 (1%)	47, 72, 73
Podicipediformes	2 (1%)	207 (1%)	38, 56
Procellariiformes and Sphenisciformes	5 (3%)	695 (4%)	1, 86, 129, 130, 145
Pelecaniformes	12 (7%)	474 (3%)	3, 15, 37, 41, 45, 93, 104, 114, 123, 146, 156, 192
Ciconiiformes	12 (7%)	771 (4%)	40, 58a, 68, 91, 105, 119, 133, 142, 159, 176, 177, 181
Anseriformes	30 (18%)	1,629 (9%)	7, 11, 18, 29, 32, 43, 44, 48, 60, 64, 66, 70, 79, 96, 97, 107, 109, 116, 117, 118, 125, 134, 135, 144, 157, 167, 172, 173, 180, 182
Falconiformes and Strigiformes ^c	21 (13%)	2,071 (12%)	2, 28, 55, 58, 59, 62, 76, 77, 108, 124, 140, 141, 158, 162, 164, 165, 166, 169, 184a, 188, 189
Galliformes and Gruiformes	14 (8%)	1,963 (11%)	16, 25, 49, 50, 83, 99, 122, 132, 137, 147, 154, 171, 190, 193
Charadriiformes	36 (21%)	2,616 (15%)	3, 20, 22, 26, 31, 35, 36, 46, 51, 53, 54, 61, 62a, 65, 67, 80, 81, 82, 84, 85, 92, 95, 109a, 110, 120, 121, 127, 136b, 138, 139, 143, 150, 153, 155, 160, 183
Passeriformes and Columbiformes ^d	33 (20%)	6,834 (39%)	4, 8, 9, 10, 12, 34, 39, 52, 57, 63, 74, 87, 88, 94, 101, 106, 107a, 111, 111a, 126, 126a, 128, 136, 152, 161, 163, 170, 178, 179, 184, 186, 187, 191
Total number of studies/citations	168 (100%)	17,353 (100%)	

^aBiological Abstracts 1970–1987; from BIOSIS PREVIEWS.

^bReferences for each order (see numbers in References).

^cOnly one study and species, Tengmalm's Owl (166).

^dOnly one species, Mourning Dove (8, 9, 126, 187).

successful nests, verified by statistical testing ($p < 0.05$; in cases where no test was reported, I included a study if effects of observers seemed obvious or if I was able to test the data). For both DE and IE papers, "no effects" refers to papers with no statistically significant effect. Four additional DE and 13 additional IE papers reported nest predation rates, but did not present data on nesting success; they are discussed in Section 5.1.

Overall, 33 (49%) of 68 nesting success papers reported effects (91% of these were DE papers), whereas 35 (51%) reported no effects of investigator disturbance (80% DE papers) (Table III). The results were similar when IE papers were excluded. Species in different orders seemed to differ in their degree of vulnerability to disturbance. Effects were reported in 88% of studies of Charadriiformes species (mainly larids and alcids; Table III), but in only 21% of studies of Passeriformes species (Table III); the result was similar when IE papers were excluded. Sample sizes (papers) for most groups were small, and differences in Table III should be treated with caution. Absence of effects in a given order does not necessarily mean that the species are insensitive to disturbance during the breeding season. In 7 of 11 studies of raptors, researchers found no effects of disturbance. One reason could be that the researchers were aware of the potential negative effects of disturbance (Fyfe and Olendorff, 1976; Steenhof and Kochert, 1982; White and Thurow, 1985) and made few visits or employed relatively harmless forms of disturbance (e.g., Grier, 1969; Grier and Fyfe, 1987; but see Snyder *et al.*, 1989). If raptors were studied with methods that are used for passerines, negative effects might be encountered more often.

The power of a statistical test (the probability of rejecting the null hypothesis of no difference when it is in fact false) generally increases with the sample size (e.g., Siegel, 1956). For some orders, such as Falconiformes and Passeriformes, effects of disturbance on nesting success might be hard to detect because of difficulties in collecting large enough samples of nests. I examined whether differences in sample size could account for the differences in Table III. Within orders, there were no apparent differences in average sample size between studies reporting effects on nesting success and those reporting no effects. Comparisons between orders showed larger average samples in studies of species of Anseriformes (276, SD = 274, $n = 7$) and Charadriiformes (282, SD = 179, $n = 16$) than in Falconiformes (124, SD = 126, $n = 10$) and Passeriformes (141, SD = 91, $n = 13$). The main reason for large samples in Charadriiformes was that researchers often used eggs or chicks as sample units, instead of nests. It is possible that larger average samples in Anseriformes and Charadriiformes facilitated detection of effects

TABLE III
The Influence of Investigator Disturbance on Nesting Success in Different Orders of Birds

Order	No. papers reporting effect ^a	(No. species studied)	References ^b	No. papers reporting no effect	(No. species studied)	References
Sphenisciformes	1 Pygoscelis adeliae (IE) ^c	(1)	145	2 Pygoscelis adeliae (DE)	(1)	1, 129
Podicipediformes	0	(0)		1 Podiceps grisegena (DE)	(1)	38 (0)
Procellariiformes	1	(1)	130	0		
Pelecaniformes	5 Fulmaris glacialis (DE) Pelecanus occidentalis (DE) P. erythrorhynchos (DE) Sula bassana (DE) Phalacrocorax auritus (DE)	(4)	3,156 15 123 45	0 —	(0)	
Ciconiiformes	2 Ardea herodias (DE) Nycticorax nycticorax (DE)	(2)	40 181	2 Bubulcus ibis, and other species (DE) Egretta tricolor (DE)	(>2)	68 58a
Anseriformes	2 Anas platyrhynchos (DE) A. strepera (DE) A. penelope (DE) A. discors, and other species (DE) Aythya fuligula (DE)	(>5)	125 125 125 107 125	6 Branta bernicla (IE) Anas platyrhynchos, and other species (DE) A. acuta (DE) A. discors (DE) Somateria mollissima (DE) Aythya valisneria (IE) A. affinis (DE)	(>9)	157 97 97 97 29, 64, 118 173 97
Falconiformes ^d	4 Accipiter cooperii (DE) Buteo jamaicensis (DE) B. buteo (DE) B. regalis (DE) Aquila chrysaetos (DE) Falco mexicanus (DE)	(6)	164 169 158 189 169 169	7 Pandion haliaetus (DE) Rostrhamus sociabilis (DE) Haliaeetus leucocephalus (DE) Buteo regalis (DE) Aquila verreauxii (DE) Falco mexicanus (DE)	(7)	77a, 141 165 58, 76 77 62 77
Galliformes	1 Fulica atra (DE)	(1)	154	0	(0)	
Gruiformes	0	(0)		—		
Charadriiformes	14 Haematopus moquini (DE) Larus delawarensis (DE) L. argentatus (DE) L. fuscus (DE) L. occidentalis (DE) L. glaucescens (DE) Sterna caspia (IE) S. fuscata (DE) Rhyncops niger (DE) Uria aalge (DE) Cephus grylle (DE) Fratrula arctica (DE) F. cirrhata (DE) Aethia pusilla (DE)	(14)	85 53 95 36 150 65 54 51 153 82 26 81 139 136b	4 Colinus virginianus (IE) Phasianus colchicus (DE, IE) 2 Vanellus vanellus (DE) Larus argentatus (DE)	(2) (2)	99, 171 25, 50 61 80

(Continued)

TABLE III (continued)

Order	No. papers reporting effect ^c	(No. species studied)	References ^b	No. papers reporting no effect	(No. species studied)	References
Passeriformes & Columbiformes ^e	3	(3)	187	11	(>17)	126
	<i>Zenaidura macroura</i> (DE)		111	<i>Zenaidura macroura</i> (DE)		191
	<i>Petrochelidon fulva</i> (DE)		106	<i>Gymnophis bicolor</i> (DE)		88
	<i>Agelaius phoeniceus</i> (IE)			<i>Anthus pratensis</i> (DE)		12
				<i>Troglodytes troglodytes</i> (IE)		74
				<i>Turdus migratorius</i> (DE)		111a
				<i>Catharus guttatus</i> (DE)		12, 57
				<i>Acrocephalus palustris</i> (DE, IE)		
				<i>A. arundinaceus</i> (IE)		12
				<i>Sylvia atricapilla</i> (IE)		12
				<i>Phylloscopus sibilatrix</i> (IE)		12
				<i>Spizella pusilla</i> , and other species (DE)		74
				<i>Cardinalis cardinalis</i> (DE)		74
				<i>Dendroica discolor</i> (DE)		128
				<i>D. kirtlandii</i> (DE)		4
				<i>Sturnella magna</i> (IE)		152
				<i>Sturnus vulgaris</i> (DE)		52
Total	33	(>37)		35		(>41)

^aEffect = decreased nest survival rate or reduced production of young per breeding pair ($p < 0.05$).

^bSee References.

^cIE = indirect evidence; DE = direct evidence (see text).

^dOne study (108) could not be categorized as regards effects.

^eOnly two studies, of Mourning Doves (126, 187). Doves and passerines were pooled because of ecological similarity.

(Table III), but on the other hand samples in all orders may be considered large (cf. Siegel, 1956). Given large samples, real differences might have been detected in most of the statistical tests.

For six species in Table III, both "effects" and "no effects" on nesting success were reported. In the Mallard (*Anas platyrhynchos*), Keith (1961) found no effects of disturbance, whereas Newton and Campbell (1975) did. A likely reason is that avian nest predators were much more common in the latter study (see below). Avian nest predators were also more common in a study of Mourning Doves (*Zenaidura macroura*) that reported effects (Westmoreland and Best, 1985) than in one that found no effects (Nichols et al., 1984), but the methods employed in the two studies also differed. Studies of Blue-winged Teals (*A. discors*) reported no effects of disturbance on nesting success (Keith, 1961) or decreased success and increased desertion of nest when more than one observer visited nests, an effect ascribed to "increased vegetational disturbance associated with 2 or 3 observers" (Livezey, 1980). In the Ferruginous Hawk (*Buteo regalis*), conflicting results were likely due to differential disturbance, either daily visits and effects (White and Thurow, 1985) or few visits and no effects (Grier and Fyfe, 1987). Finally, in the Herring Gull (*Larus argentatus*) (Harris, 1964; Kadlec and Drury, 1968) and Adelie Penguin (*Pygoscelis adeliae*) (Reid, 1968; Oelke, 1975; Ainley et al., 1983), conflicting results are not easily explained, but may be due to differences in the methods used.

To what extent was reproductive performance reduced in those studies that found an effect? I was able to estimate this for 28 of the 33 papers, but three different measures of success were used. The proportion of nests successfully producing fledged young was reduced by on average 39% (SD = 14%, range 23–62%, $n = 8$ papers) for disturbed compared to undisturbed nests. Production of fledged young per pair was reduced by 44% (SD = 26%, range 11–95%, $n = 17$). As the two measures are related, the similarity of the means is not surprising. Three studies (two of ducks, one of terns) only measured hatching success, which was reduced by an average of 24% (SD = 4%). Thus, the two measures of fledging success suggested a reduction of about 40%, but this is likely an underestimate as controls in many cases were not fully undisturbed. There seemed to be some differences between orders. Dramatic reductions of fledging success were found in pelicans, cormorants, and herons (33–83%), and in studies of shorebirds (95%), alcids (46–84%), and gulls (49%), whereas minor effects were recorded in three studies of passerines (14–34%). Although sample sizes are small, these figures support the indication in Table III that passerines are less sensitive to investigator disturbance. In general, it was unknown to what extent losses were compensated for by reneesting in the same season.

One factor that partly may explain the results of Table III is the frequency of nest visitation. If experimental nests are visited a few times, the degree of disturbance is low and it might be hard to detect an effect. I hypothesized that "no effect studies" involved fewer visits to experimental nests than "effect studies" and compared visitation rates for the two groups. Average visitation rate to control nests was low and did not differ between groups (Fig. 1); however, as predicted, experimental nests of "effect studies" had higher visitation rates than those of "no effect studies," although the difference was not significant (Fig. 1; $p = 0.11$, one-tailed Mann-Whitney U-test). This result may help to explain why some studies found no effect. Also, the possibility that an observer bias is as likely with one as with many visits seems to be contradicted; cumulative effects, rather than "all-or-none," seem more likely.

5. PROXIMATE REASONS FOR REDUCED NESTING SUCCESS

5.1. Relative Importance of Different Factors

The studies in Table III related nesting success to disturbance, but few of them examined why the success was reduced. However, all papers except four (Table IV) suggested one or more reasons for the reduced success, supported by at least some evidence. I sorted the suggestions into five categories (Table IV). Predation of eggs or young, noted in 22 (76%) of 29 papers, seemed to be the main reason for reduced nesting success. "Predation" includes also intraspecific killing of young, a common effect of disturbance in some colonial species. Desertion of

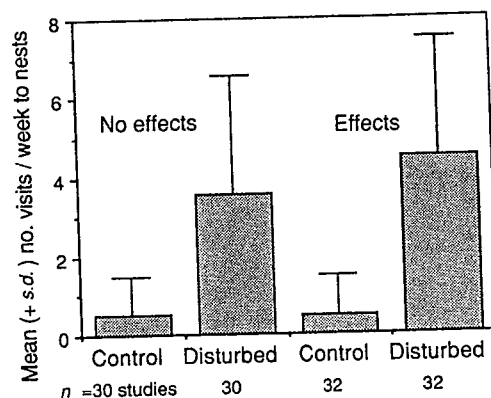


FIGURE 1. Observer visitation frequency to nests in studies that found no significant effects of investigator disturbance on nesting success ("No effects") and those that found reduced nesting success ("Effects"; see Table III). Sample sizes (papers) are given below treatment categories on the x axis. Visitation frequency tended to be higher to disturbed nests in "Effect studies" than in "No effect studies," although not significantly so ($p = 0.11$).

TABLE IV
Suggested Proximate Reasons for Reduced Nesting Success in Studies in Table III^a

Reason	No. papers	Reference ^b
Predation or killing of eggs or young	22	3, 15, 36, 40, 45, 51, 53, 54, 65, 85, 106, 123, 125, 145, 150, 153, 154, 156, 164, 181, 187, 189
Desertion of nest or offspring	11	3, 26, 45, 81, 107, 136b, 139, 145, 158, 169, 181
Extreme temperatures	5	3, 153, 156, 169, 189
Trampling on eggs or young by parents or other birds	3	26, 40, 156
Inadequate parental care or young leave nest too early	4	26, 136b, 153, 189

^aTwenty-nine papers included; papers 6, 49, 54, 65 could not be categorized; a study may appear in several categories.

^bSee References.

eggs or offspring (34% of papers) is another important reason, which may be underestimated, because deserted nests may be preyed on before they are detected by field workers (if so, predation will be overestimated). Other reasons (Table IV) were of minor importance.

Additional evidence for the importance of predation comes from the 4 DE and 13 IE papers that examined effects on predation rate rather than nesting success. These studies were of species of Pelecaniformes (2 papers), Ciconiiformes (1), Anseriformes (6), Strigiformes (1), Charadriiformes (5), and Passeriformes (2). Ten of the 17 papers (Johnson, 1938; Paynter, 1951; Drent et al., 1964; Buckley and Buckley, 1972; MacInnes and Misra, 1972; Mickelson, 1975; Veen, 1977; DesGranges and Reed, 1981; Quinney, 1983; Tiainen, 1983) found increased predation on nests or young as a result of disturbance, whereas six (Kalmbach, 1938; Coulson, 1958; Götmark and Åhlund, 1984; Pienkowski, 1984; Sonerud, 1985; MacIvor et al., 1990) were unable to find such differences (Hammond and Forward, 1956, could not be categorized).

5.2. Types of Predators and Their Impact

The predators were other birds, primarily larids and corvids. To illustrate this, I listed the predators that were mentioned as predominant in the 22 nesting success studies and the 10 predation studies that found increased predation due to investigator disturbance (Lenington, 1979, and White and Thurow, 1985, did not specify predominant predators). In five studies, two or more predominant species of predators were men-

tioned, and I included all species in these cases. Larids (especially larger gulls) were predominant predators in 22 studies, corvids in 13 studies, and people in one study (Snyder and Snyder, 1974) (Table V). Avian predators in some cases respond to or follow field workers, preying on nests visited by the investigators (e.g., Veen, 1977; Strang, 1980; Götmark et al., 1990). Alternatively, they are not attracted to people but predation increases simply because eggs or young are not attended or defended for some time after disturbance (e.g., Westmoreland and Best, 1985).

Many authors assumed or emphasized that mammalian predators would pose a great threat to nests visited by researchers (e.g., Earl, 1950; SOWLS, 1955; Snelling, 1968; Willis, 1973; Reed, 1975; Bart, 1977; Gottfried and Thompson, 1978; Lenington, 1979; Poole, 1981; Nol and Brooks, 1982; Nichols et al., 1984; Gawlik et al., 1988; Yahner et al., 1989; Reitsma et al., 1990). Surprisingly, I found no evidence for increased predation by mammals. They are believed to follow tracks in the vegetation made by observers, and to respond to human scent at nests and along trails and to the scent of feces at nests (in some species, incubating birds defecate when flushed by observers). Note that this requires that mammalian predators must first learn to associate the tracks or the scent

TABLE V
Nest Predators Mentioned as Predominant in 22 "Nesting Success" Studies and 10 "Predation Studies" in Which Increased Nest Predation Due to Investigator Disturbance Was Recorded^a

Larids (no. of studies)	Corvids (no. of studies)	Others (no. of studies)
<i>Sterna caspia</i> (1) ^b	<i>Corvus monedula</i> (2)	<i>Lanius collurio</i> (1)
<i>S. fuscata</i> (1) ^b	<i>C. corone</i> (2)	<i>Homo sapiens</i> (1)
<i>Rhyncops niger</i> (1) ^b	<i>C. ossifragus</i> (1)	
<i>Larus ridibundus</i> (1)	<i>C. brachyrhynchos</i> (3)	
<i>L. atricilla</i> (1)	<i>C. caurinus</i> (1)	
<i>L. delawarensis</i> (2) ^b	<i>C. corax</i> (1)	
<i>L. fuscus</i> (1) ^b	<i>Pica pica</i> (1)	
<i>L. argentatus</i> (5)	<i>Garrulus glandarius</i> (1)	
<i>L. occidentalis</i> (2) ^b		
<i>L. dominicanus</i> (1)		
<i>L. glaucescens</i> (1) ^b		
<i>L. marinus</i> (3)		
<i>L. hyperboreus</i> (1)		
<i>Stercorarius parasiticus</i> (1)		
Total (22)	(13)	(2)

^aIn five studies, two or more predators were mentioned; they were included, so the sum of studies exceeds 32.

^bOne study for each species concerns intraspecific nest predation.

with food. Seven studies examined these ideas in more detail. In an area where mammalian predators were common, Hammond and Forward (1956) found higher predation on nests from which females were flushed than on nests where the female was absent or not flushed, but no statistical test was presented for this comparison. Experiments with eggs scented with duck feces and control eggs showed "significant evidence" ($0.05 < p < 0.1$) of higher predation on scented eggs in one of six trials, but not for the combined data ($p = 0.7$) (Hammond and Forward, 1956). Keith (1961) found no effects of duck feces or human scent on the survival of chicken eggs in a study in which mammalian predators predominated. Two studies compared natural nests with regard to presence of feces but did not find increased predation if feces were present (Townsend, 1966; Livezey, 1980). In fact, duck feces may reduce egg predation by ferrets and rats (Swennen, 1968) as well as egg predation by crows but not gulls (McDougall and Milne, 1978). Livezey (1980) found no evidence that tracks from vehicles or humans attracted nest predators (but see Bowen et al., 1976, for effects of vehicle tracks). In a study of plovers (MacIvor et al., 1990), foxes did not follow researcher tracks to nests. In fact, nest predation was significantly lower for nests that were monitored from distances of < 3 m compared to nests monitored from 3–15 m; possibly, foxes avoided nest sites with human scent. Thus, there is no or very little evidence for increased nest predation by mammals as a result of researcher disturbance.

To further analyse the potential impact of mammalian nest predators, I classified all 61 DE and 25 IE studies ("nesting success" studies and "predation" studies) according to predator regime, that is, as to whether mammals or birds predominated as nest predators. Authors often presented information on the abundance of different predators or on numbers of nests preyed upon by different (usually presumed) predators. Papers where mammalian and avian predators appeared to be equally abundant were omitted. In sum, avian predators predominated in 40 studies and mammalian predators in 17. Decreased survival or increased predation rate of disturbed nests were recorded in 31 (78%) studies where avian predators predominated, but only in two or three (18%) studies where mammalian predators predominated ($p < 0.001$, χ^2 test). One of these concerned human predators (Snyder and Snyder, 1974; see below); the other two presented indirect evidence of increased mammalian predation (Lenington, 1979, who found increased nest predation in the second year of several studies, and signs of mammalian predation; and Hammond and Forward, 1956, described above). In addition, in three studies where snakes were the major nest predators, disturbance did not increase nest predation (Gottfried and Thompson,

1978; Nichols *et al.*, 1984; see also Thompson, 1978) or was considered unlikely to have done so (Petrinovich and Patterson, 1983). However, studies where avian predators predominated included a much higher proportion of studies of colonial birds, which were more vulnerable to disturbance (see below). I therefore repeated the comparison including only studies of solitary species (< 5 nests/ha). The result was similar: decreased survival or increased predation rate of disturbed nests was recorded in six of nine studies where avian predators predominated, but only in 2 of 15 studies where mammals predominated ($p = 0.02$, Fisher's exact test).

These results strengthen the conclusion that mammalian predators do not pose a threat to nests visited by researchers, whereas avian predators sometimes do. Possibly, human scent along trails or at nests disappear rapidly, making it difficult for mammalian predators to learn to use this clue to find nests (S. A. Rohwer, personal communication). Alternatively, researchers may have reduced the likelihood of an effect by various precautions (e.g., Bennett, 1938; see also Stoddard, 1932:195). If precautions like avoiding the creation of trails in the vegetation are effective and generally used in studies where mammalian predators predominate, this might partly explain the absence of an effect. Another factor is the relationship between predators and man. If mammalian predators are persecuted or hunted, they may avoid humans and especially human scent, which could lead to reduced impact of mammals on nesting success and even improved success of disturbed nests (Buss, 1946; MacIvor *et al.*, 1990). Avian predators such as crows also sometimes avoid investigators or disturbed nesting areas (Götmark and Åhlund, 1984; Shields and Parnell, 1986).

5.3. Predation on Artificial Nests

Some studies examined whether predation on artificial nests is affected by observer visitation. I treat these studies separately because they differ from the others in one respect: no parents would have attended or defended eggs or young. Parents potentially could attract, or in case of aggressive species (e.g., Galbraith, 1987) deter predators that prey on disturbed nests. Thus, conclusions from studies of artificial nests are not necessarily applicable to natural nests (but see Gottfried and Thompson, 1978; Götmark *et al.*, 1990)

Four studies of artificial ground nests with chicken or quail eggs [Bowen *et al.*, 1976; Gottfried and Thompson, 1978 (plus Thompson, 1978); Erikstad *et al.*, 1982; Hoi and Winkler, 1988] found that visited nests (5–21 visits) suffered no more predation than control nests visited

once (when laid out). During part of the season, Hoi and Winkler (1988) found lower predation for visited than for unvisited nests. Nilsson *et al.* (1985) recorded no difference in nest predation rate between visited (1–2 visits) and unvisited artificial tree nests of *Turdus*. For artificial goose nests in tundra habitat, nest predation was concentrated in periods after visits (Vacca and Handel, 1988), so predators [primarily Glaucous Gulls (*Larus hyperboreus*)] apparently were attracted to people, as in two earlier studies at the same site (Mickelson, 1975; Strang, 1980). Interestingly, this result applied to artificial nests that were uncovered but not to those that were covered with down, indicating that if nests are covered there may be no investigator bias. Similar results were also reported for eiders (Götmark and Åhlund, 1984). If possible, investigators should cover nests from which incubating birds are flushed, and in their papers should make clear whether nests were covered or not (in waterfowl papers, this information is often lacking).

Four studies tested whether predators were attracted to artificial nests marked with conspicuous marker stakes or flags. Higher predation on marked than on unmarked nests was noted when dispersed, cryptic nests were studied (Picozzi, 1975; Bowen *et al.*, 1976). No differences were reported in a study with high nest density (Newton and Campbell, 1975) or in case of dispersed but conspicuous nests (Vacca and Handel, 1988). In the two latter studies, predators apparently could find unmarked nests as easily as marked nests. In addition, O'Reilly and Hannon (1989) found no influence of distance between nest and nest marker stakes (7–20 m) on predation rate. Nilsson *et al.* (1985) placed small flags 10 m from artificial *Turdus* nests in trees; predation of these nests was similar to that of unmarked nests. Two studies concerned natural nests: one suggested that predators (cranes) were attracted to marked dispersed and cryptic nests of shorebirds (Reynolds, 1985), the other found similar survival rates for marked and unmarked Northern Lapwing (*Vanellus vanellus*) nests and attributed this to parental nest defense (Galbraith, 1987).

5.4. Desertion of Nests

It is often stated that birds tend to desert nests when disturbed early, during nest building, egg laying, or early incubation. In five studies, the proportion of successful nests was lower for nests visited early than for control nests; no or little predation was noted, and nest desertions seemed to be the main reason for the reduced success rate (Tremblay and Ellison, 1979; Steenhof and Kochert, 1982; Harris and Wanless, 1984; Pierce and Simons, 1986; Piatt *et al.*, 1990; for less direct evidence, see

Reid, 1968; Anderson and Keith, 1980; Cairns, 1980; Gaston et al., 1988; Selås, 1988). However, five studies that included the laying period found no effects of disturbance, indicating that desertion of nests does not always occur after disturbance or that it depends on the amount of disturbance (Gargett, 1977; Sugden, 1978; Fraser et al., 1985; Grier and Fyfe, 1987; Snyder, et al., 1989:314).

Nolan (1978) netted female warblers at the nest and recorded desertion rates; 48% ($n = 27$) during nest building and laying, 5% ($n = 19$) during incubation, and 0% ($n = 37$) during the posthatch period (see also Lombardo, 1989, and references therein). Several authors reported a high rate of nest desertion (and also high predation rate) during the laying period and assumed it was due to observer disturbance. This is possible, or even likely (Zwicker and Carveth, 1978; Myrberget, 1983), but control nests are required for firm conclusions since desertion rates can be high also in the absence of human disturbance (Knopf, 1979).

F. C. Rohwer (personal communication) found differences in nest desertion rates among three species of ducks. All nests were discovered by flushing females from nests, and analyses were based on the first check after discovery of nests. Mallards had higher desertion rates than Northern Shovelers (*Anas clypeata*), which had higher desertion rates than Blue-winged Teals ($p < 0.001$). These differences are thought to be related to differences in life expectancy in the three species (F. C. Rohwer, personal communication), a hypothesis discussed in Section 10.

5.5. Extreme Temperatures

If incubating or brooding adults are disturbed, eggs and young may die because of exposure to heat or cold. Only five studies suggested this proximate reason for reduced success (Table IV), presumably reflecting the fact that the data were mainly from temperate areas. The importance of extreme temperatures probably depends on latitude, habitat, nesting cover, and time of day of nest visit.

6. RELATIONSHIPS TO STAGE OF BREEDING AND NESTING DENSITY

To examine the common assumption that nesting birds are susceptible to disturbance early in the nesting cycle, I classified all DE and IE studies according to when they were initiated; either in period 1 (prelaying or laying; $n = 49$ papers), period 2 (incubation; $n = 26$), or period 3

(posthatching, $n = 7$). I then compared the proportion of papers reporting effects (reduced nesting success or increased predation) in each period. Effects were found in 59% of period 1 papers, in 46% of period 2 papers, and in 29% of period 3 papers ($0.1 > p > 0.05$, one-tailed χ^2 test, periods 2 and 3 combined), suggesting a weak trend for birds to be more susceptible to disturbance early in the breeding cycle. At that time, territories or nests may more often be deserted (see above), and lower nest attendance and weaker parental defense of nests may lead to increased predation of nests of disturbed pairs. As it is easy to overlook nests that are deserted during nest building and egg laying, it is possible or likely that the negative impact in period 1 was underestimated.

For period 3, effects on chick growth rates are also relevant, as fledging weights may influence future survival and fitness (Richner et al., 1989, and references therein). Two studies of alcids reported decreased growth rates of disturbed chicks (Harris and Wanless, 1984, and Birkhead cited therein). Pierce and Simons (1986) found lower weights of disturbed than of undisturbed chicks, and attributed this to an age difference resulting from prolonged incubation in disturbed areas. In four other studies, no effects on growth rates were found (Cairns, 1980; Parsons and Burger, 1982; Hedgren cited in Harris and Wanless, 1984; Feare, 1984).

To examine the influence of nesting density, I classified papers as to whether solitary (< 5 nests/ha) or colonial species (≥ 5 nests/ha) were studied. The specified densities meant that a few species that are not normally regarded as colonial were classified as such (four studies of ducks, one of a shorebird, and one of a passerine). For the papers in Table III, effects of disturbance on nesting success were noted in 26 (74%) of 35 studies of colonial species, but only in 7 (21%) of 33 studies of solitary species ($p < 0.001$, χ^2 test, two-tailed). Similarly, among studies examining nest predation, effects of disturbance were noted in seven of ten studies of colonial species, but only in one of four studies of solitary species. These comparisons might be biased by smaller sample sizes in studies of solitary than in colonial species, leading to reduced power of statistical tests in the former studies (see Section 4 for a discussion). Nonetheless, I believe the results suggests that, with regard to nesting success, colonial species are especially susceptible to disturbance. The result may reflect differences between taxonomic groups rather than variation in nesting density per se. To examine this, I repeated the analysis, including only passerines. Effects of disturbance on nesting success were noted in two of three studies of colonial passerines, but only in 1 of 11 studies of solitary passerines. Although the difference in this smaller sample was not significant ($p = 0.19$, Fisher's exact test,

two-tailed), it suggests that nesting density is an important factor also within orders. Aggregations of nests provide a rich, clumped food source that is easy to locate for predators that nest in or close to them. Colonial birds may actively defend their nests (Götmarm and Andersson, 1984; Wittenberger and Hunt, 1985) but human disturbance may disrupt their normal behavior and increase desertion rates and predation or intraspecific killing of eggs and young.

7. EFFECTS OF DISTURBANCE ON BREEDING DENSITY AND NEST SITE SELECTION

Several studies suggested that nesting density may decline in study areas because of disturbance. Settlers may choose to nest away from disturbance and pairs with nests in which incubation has not begun may desert (see above) and move elsewhere. Effects on density were found in Double-crested Cormorants (*Phalacrocorax auritus*) (Ellison and Cleary, 1978), Black-crowned Night-Herons (*N. nycticorax*) (Tremblay and Ellison, 1979), Black Skimmers (*Rhynchops niger*) (Safina and Burger, 1983), Tufted Puffins (*Fratercula cirrhata*) (Pierce and Simons, 1986), and apparently in Jackass Penguins (*Spheniscus demersus*) (Hockey and Hallinan, 1981).

Abandonment of nest sites and changes in nest site selection because of disturbance were documented also between years. Changes in nest tree selection were found in Black-billed Magpies (*Pica pica*) (Knight and Fitzner, 1985; see also Dhindsa et al., 1989), and pairs of Ferruginous Hawks (*Buteo regalis*) that deserted nests after disturbances shifted to different territories the following year more often than undisturbed control pairs (White and Thurow, 1985). In Gyrfalcons (*Falco rusticolus*) (Platt, 1977), helicopter overflights did not reduce nesting success, but disturbed pairs changed nest site in the following year more often than undisturbed pairs (observed from the ground at some distance). No between-season effects of disturbance were recorded for Bald Eagles (*Haliaeetus leucocephalus*) in studies with few and late nest visits (Grier, 1969; Fraser et al., 1985). Long-term studies of Adelie Penguins indicate that heavily disturbed areas are avoided, with declining nest densities there (Reid, 1968; Ainley et al., 1983; Wilson et al., 1989, and references therein). Finally, during several years, nesting Ring-billed Gulls (*Larus delawarensis*) were observed to desert areas of the colony where investigators studied them the year before (Conover and Miller, 1978).

8. EFFECTS OF DISTURBANCE ON BEHAVIOR

8.1. Parental Behavior

Some changes in avian behavior during investigator disturbance are obvious, others are less apparent. For instance, reduced nest attendance while observers check nests is a trivial observation. However, in gulls other changes in behavior also occur. The equal sharing of incubation duties between the sexes may be disrupted, with males incubating more after disturbance (Burger, 1981). Further, when disturbed, gulls engage in more aggression of a higher intensity, and fights with neighbors may lead to exposure of eggs or young to predators, cannibalistic gulls, or attacking neighbors (Burger, 1981; Fetterolf, 1983).

In Pied-billed Grebes (*Podilymbus podiceps*), during egg laying, average time spent off nests was higher after a disturbance than during undisturbed nest reliefs; the reverse applied to the hatching period (Forbes and Ankney, 1988). In Arctic Loons (*Gavia arctica*), a short disturbance of incubating birds increased the time they were off nests compared with nest reliefs during undisturbed conditions, but this did not seem to increase nest predation (Götmarm et al., 1989, 1990).

Different responses to investigators in different populations of nesting birds complicate comparisons of these populations if nesting success is affected by investigators only in certain areas. Corvids and raptors tend to be shy at nests in areas where they are persecuted and are more fearless or aggressive in areas where they are not persecuted (Olson and Olsen, 1980; Knight, 1984; Knight et al., 1987, 1989). Possibly, shy populations of these species are more susceptible to investigator disturbance.

Knight and Temple (1986) highlighted a potential problem in testing parental investment theory. When the observer uses him- or herself to examine seasonal antipredator behavior of parents, he or she repeatedly poses a threat but always withdraws. By positive reinforcement, the birds' responses might with time become inordinately bold, thereby skewing conclusions about seasonal predator harassment. Even though Knight and Temple's argument is compatible with theory in this field and apparently is not the only reason for increased seasonal nest defense (Redondo and Caranza, 1989:370; Westmoreland, 1989), they illustrate that it is important to realize that investigator behavior may influence avian behavior in various and unexpected ways.

In two studies, parents laid eggs outside nests, apparently because they were kept off nests by investigators (Feare, 1976; Wackenhut et al., 1983).

8.2. Behavior of Young and Habituation to Field Workers

In many colonial birds, disturbance leads to higher mobility of chicks, which may affect their survival. Herring Gull chicks handled daily ran farther away from their nests when approached than those handled weekly; thus, they did not habituate to observers. Weekly handling of chicks did not result in higher chick mobility than disturbance without handling (Burger, 1981). In Ring-billed Gulls, disturbance increased the number of running chicks, adult attacks on chicks, and pecks per attack (Fetterolf, 1983). Chick running in response to handling seems to vary with chick age, intensity of handling, weather, and species [Black Skimmers responded more strongly than Common Terns (*Sterna hirundo*)] (Gochfeld, 1981). In tree-nesting Black-crowned Night-Herons, chicks that were handled and weighed from hatching onward stayed in nests during visits, whereas those that were handled and weighed at an age of three weeks moved some distance (< 4 m) away from nests, indicating that experimental chicks habituated to investigators (Parsons and Burger, 1982).

Several authors concluded that adults and chicks to some extent habituated to the presence of investigators; responses of disturbed birds to people seemed to be weaker than those of undisturbed birds (Robert and Ralph, 1975; Schreiber, 1979; Parsons and Burger, 1982; Ainley *et al.*, 1983; see also Cooke, 1980; Burger and Gochfeld, 1981, 1983; McNicholl, 1983). The degree of habituation may increase gradually during a nesting season, and this pattern may be repeated each season (Schreiber, 1979), but banding and handling of chicks may change their response and result in lifelong habituation to people (Ainley *et al.*, 1983; Snyder and Snyder, 1974; see below). Banded and unbanded Black-billed Magpies, however, did not differ in flushing distance when approached by a human observer (Dhindsa and Boag, 1989). Even though habituation sometimes occurs, this does not mean that observer effects can be excluded; in fact, negative effects were found in most studies cited in this paragraph.

9. METHODS THAT MITIGATE DISTURBANCE EFFECTS

Sometimes one can guess (Stoddard, 1932; Reed, 1975) or observe (Götmark *et al.*, 1989, 1990) which nests failed because of observer disturbance, and these can be excluded in analyses. Many procedures for reducing a negative impact, however, were suggested in the literature, and these should be used if possible. For reviews concerning raptors, see

Fyfe and Olendorff (1976), Steenhof and Kochert (1982), and Grier and Fyfe (1987); the journal *Colonial Waterbirds*, volume 4 (1981), provides information on several colonial species. Below, I summarize some useful low-disturbance methods for studying nesting birds.

In colonial species, four visits with a simple "capture-recapture" count of marked (dyed) chicks may suffice to assess chick production (Mineau and Weseloh, 1981). If observations of colonial birds at close range are required, tunnels providing hidden access to blinds minimize disturbance effects (Shugart and Fitch, 1981; Cairns *et al.*, 1987). Whenever feasible, distant observations of nests with spotting scopes (e.g., Knopf, 1979; Fetterolf and Blokpoel, 1983) or cameras are preferred over visits to colonies. This method can be applied also to solitary species with large, conspicuous nests. Observations may also be made from airplanes or helicopters, but knowledge of species' responses to aircraft is important (White and Sherrod, 1973; Carrier and Melquist, 1976; Platt, 1977; Kushlan, 1979; Bunnell *et al.*, 1981; Fraser *et al.*, 1985; Boellstorff *et al.*, 1988; Andersen *et al.*, 1989).

Visits to territories or nests before or during egg laying should be avoided if possible; laying dates could be obtained from hatching dates (if the length of the incubation period is known) or from indices on egg density (van Paassen *et al.*, 1984; Collins and Gaston, 1987; and references therein). Field workers should cover nests with down or vegetation if the species studied covers its eggs. In some colonial species, prior to hatching fences could be erected around representative or randomly chosen nests or groups of nests. Posthatching visits to the colony should then be made when as many chicks as possible are large enough to successfully return to the natal territory without getting lost or killed by neighbors or predators (Fetterolf and Blokpoel, 1983).

For burrow-nesting puffins, Pierce and Simons (1986:215) concluded "sensitive colonies should not be disturbed at all during the incubation period, and estimates of reproductive success should be made by combining data from several similar subcolonies that are visited at progressively later intervals during the season." For Ancient Murrelets (*Synthliboramphus antiquus*), there are several methods of monitoring breeding populations without causing disturbance and nest desertion (Gaston *et al.*, 1988). Several authors emphasize that the approach to nest sites should be slow and in full view of the birds, giving them an opportunity to detect one's presence and leave the nest in an orderly fashion (sudden departures could damage eggs or nestlings) (Grier and Fyfe, 1987; Schreiber, 1979). Also, knowledge of the susceptibility of eggs and chicks to extreme temperatures is useful (Hunter *et al.*, 1976; Webb, 1987; Kirkley and Gessaman, 1990).

The fact that avian predators may learn to associate nest markers or field workers with prey (eggs) have led many researchers to extreme precautions during fieldwork. For example, in studies of artificial nests, nests are often placed out without markers and in darkness, and rubber boots and gloves are used to minimize human scent. This is good but in many cases probably unnecessary, judging from studies cited in Sections 5.2 and 5.3. Effects of nest markers were recorded only for large, conspicuous markers and dispersed cryptic nests. Small, inconspicuous markers probably present no problem (natural objects of various sorts are especially useful for marking nests, if carefully described in the notebook). Also, in no case have mammalian predators been shown to follow observers to nests, and such behavior in avian predators has rarely been demonstrated (e.g., Veen, 1977; Strang, 1980; Vacca and Handel, 1988; Götmarm et al., 1990). Open habitats, high local nest density, and many repeated visits to the same nests increase the opportunities for avian predators to learn to follow observers, but I believe that, in most cases, increased avian predation during disturbance results from increased opportunities for predators (unattended nests or young) rather than responses to observers per se.

Some other suggestions to reduce the effects of disturbance in individual species can be found in the papers in the reference section (Table II may be helpful in searching by order). Anyone who wants to study a sensitive species should carefully consult the literature and contact people already studying the species, because disturbance effects are probably not always mentioned in the papers.

10. GENERAL DISCUSSION

This review suggests that an impact of investigators on avian nesting parameters may be quite common. About half of the 69 papers I investigated concluded that disturbance lowered productivity, but certain groups (particularly colonial birds) seemed more susceptible than others (Table III). However, it is doubtful that the proportions of studies reporting effects in different groups (Table III) are representative of investigator effects in nesting studies of these groups in general. Possibly, certain sensitive species or situations were overrepresented; certain study areas or nests were also visited more frequently than others (Fig. 1). On the other hand, I excluded special trapping or marking techniques in this review, and they may affect nesting success, as well as adult and chick survival. Avian predators often preyed on disturbed nests, but, contrary to common belief, there was little evidence that mammalian

predators increased the predation on disturbed nests. Desertion of territories or nests contributed to lowered nesting success, and sometimes affected nesting density and habitat or nest site selection in disturbed areas.

Studies that recorded an effect of disturbance on fecundity showed a reduction in fecundity by an average of at least 40%. This would bias estimates in life tables and models of population dynamics. Fecundity is used in the calculation of, for instance, net reproductive rate (R_0), generation time (T), reproductive value (v_x), and intrinsic rate of increase (r) (Pianka, 1983). These parameters will be underestimated in cases where investigator disturbance lowers fecundity. For example, in a stable population R_0 is 1.0, but a 40% reduction in fecundity caused by observers will shift R_0 to 0.6, unless survivorship increases as a result of disturbance, which is unlikely in most cases. The false conclusion is that the population is decreasing or will decrease. In some species, renesting within the same season may occur following failure due to observers, and this could to some extent compensate earlier losses. This applies for pairs nesting early in the season; for late pairs, renesting is less likely. In some species, only pairs that fail during laying and early incubation renest (Custer and Pitelka, 1977). For double-brooded species studies (disturbed) throughout the nesting season, there is no opportunity for breeders to compensate losses, unless they leave and attempt to nest outside the study area, which is difficult for investigators to detect.

Could postfledging survival to reproductive age be affected by investigator disturbance? In Ring-billed Gulls, Fetterolf (1983) suggested it could through changes in mortality patterns of chicks. First, gull chick mortality could be random during disturbance, and not a result of natural selection; second, it could be nonrandom if there is selection against chicks behaving in a "life-threatening" manner during disturbance; and third, brood reductions could enhance survivorship of remaining chicks, but have the opposite effect in broods where parents adopt a chick from a neighboring nest. Some studies found reduced weights of disturbed chicks at fledging (Section 6), which potentially could decrease postfledging survival. More direct evidence comes from a study of Cooper's Hawk (*Accipiter cooperii*) in which some nests were visited every two or three days, and other nests only one to three times each season (Snyder and Snyder, 1974). According to recoveries of banded birds, chicks in the former nests had a significantly lower survival rate than those in the latter nests. Several recovered birds that had been subjected to intense disturbance were killed by people, and the authors suggested that familiarity with people may render a hawk more

likely to die from shooting or other forms of persecution. Similar effects cannot be excluded in other species that are hunted or persecuted by humans.

Visitation frequency to nests likely influences the degree to which nesting success is reduced by disturbance (Fig. 1; Fetterolf, 1983). Because visitation rates vary, it may be misleading to make comparisons between studies of species unless the data can be corrected for the influence of visitation rate. Also, comparisons between species, families, or orders may be biased because of differential sensitivity to disturbance (Table III). Thus, apart from biasing nesting parameters, researcher disturbance complicates comparisons within and among species. A third problem is that the relationship between habitat type, nest concealment, and nesting success may be confounded (Westmoreland and Best, 1985, and references therein). Finally, a fourth problem is ethical or political; because of the effects of disturbance, landowners and managers might be unwilling to allow research in natural areas or reserves (Duffy, 1979; Seding, 1990). This problem could partly be overcome by information and, as in the case of the other problems, by mitigation techniques.

Differences in sensitivity to disturbance among orders relate to differences in nest density, conspicuousness of adults and nests, and availability of nest predators. It also seems that species or taxa differ in the extent to which nests or territories are deserted in response to disturbance, although I was unable to quantify this. Nest desertion during prelaying, laying, or incubation may be frequent among, for instance, certain raptors, gallinaceous birds, and colonial birds, whereas I think that most ornithologists would agree that many passerines withstand relatively extensive disturbance without desertion early in the nesting cycle. There may be several reasons for such differences. First, susceptibility of raptors may partly be an effect of persecution by humans (Biljeveld, 1974; Newton, 1979); the birds simply avoid areas inhabited or visited by people (e.g., Speiser and Bosakowski, 1987; Andrew and Mosher, 1982). In contrast, passerine birds (except corvids) are not often persecuted. Persecution might also influence the behavior of some colonial birds, but nest desertion in this group is more likely related to the selection of inaccessible or protected nest sites (islands, trees, cliffs); if such a site can be reached by mammalian predators (including humans), the birds may sometimes consider it unsafe and desert it. Second, life history traits may account for some of the differences between orders. Most passerines are short-lived and may be selected to take greater risks when reproducing (cf. Clark and Ydenberg, 1990); interrupting a nesting attempt may have dramatic effects on

fitness in species that breed only a few years. Raptors and many colonial birds, on the other hand, live longer and reproduce several or many times. In these cases, interrupting a nesting attempt because of human disturbance would involve a smaller reduction in fitness, and therefore selection may not have disfavored nest desertions to the same extent in these species, compared with the passerines. Data for a test of this hypothesis are not available, or are too indirect, but experiments are possible (see Section 11).

One important message of this review is that researchers seeking unbiased estimates of nesting parameters should measure their own impact. This, of course, applies to sensitive species (Table III) but also to other species, since it is difficult to predict effects (e.g., six species in Table III occurred both under "effects" and "no effects"). Editors and referees should encourage field workers to examine the effects of disturbance in nesting studies. Authors should make clear whether they examined disturbance effects; if they did not, they should explain why.

11. SUGGESTIONS FOR FUTURE RESEARCH

Issues of interest for future research include (1) the influence of disturbance on nesting success, (2) proximate mechanisms causing lowered nesting success, (3) influence of disturbance on nest site selection and nesting density, and the mechanisms involved, (4) the potential for habituation to investigators, (5) influence on postfledging survival to reproductive age, and (6) techniques that mitigate disturbance effects. Regarding point (1), I made a broad taxonomic overview (Table III), but detailed comparisons of species or taxa and additional analyses of the influence of ecological factors require more studies. It is of interest to assess whether reneeding in the same season compensates losses of eggs or young due to disturbance. Procedures in setting up studies deserve mention at this point. If nests or study areas are assigned to treatments arbitrarily, it is useful if they can be studied before the experiment to evaluate differences between them. Even better, control and experimental areas may be paired with regard to similarity (James and McCulloch, 1985:24–25) and they may be shifted between years (Ellison and Cleary, 1978; Tremblay and Ellison, 1979; DøRoos and Schaafsma, 1981). Also, use of Mayfield-type estimators of nesting success is recommended in studies in which all nests are not found on day 1 of laying (Mayfield, 1961, 1975; Johnson, 1979; Hensler and Nichols, 1981; Bart and Robson, 1982; Erwin and Custer, 1982; Pollock and Cornelius, 1988; Johnson and

Shaffer, 1990). Finally, in studies that fail to reject a null hypothesis, it is useful if authors report the power of their test (e.g., Nichols *et al.*, 1984; Forbes, 1990, and references therein).

In the case of point (2), proximate mechanisms, we have no precise or good estimate of the degree to which disturbance increases territory and nest desertions, and this may be examined in a study of nest site selection (see below). One problem is that nests are not always attended during laying and thus they may fail before being detected. However, species with large or clumped nests may be observed from a distance. Further, whether nesting is interrupted or not might be possible to judge from the behavior of adults (e.g., Willis, 1973). I suggested above that, among species, both degree of human persecution and life expectancy should influence territory and nest desertion. These ideas could be tested by experimentally disturbing closely related species that differ in life expectancy or with regard to persecution.

Regarding point (3) pertaining to nest site selection and density, point (4) on habituation, and point (5) on postfledging survival, there are only a few relevant studies, and more work, especially long-term studies, is needed. The fact that disturbance effects may vary between nesting seasons, because of differences in food supply (White and Thurow, 1985) or other unknown factors (Ellison and Cleary, 1978), also suggests that long-term studies (three or more nesting seasons) are important. With regard to nesting density, one may predict either decreased or unchanged density in disturbed plots over several years of study. No change is predicted if there are no or minor effects on nesting success, and habituation to field workers. Reduced density is predicted if nesting success decreases and perhaps also if there are negative physiological effects of disturbance that do not necessarily influence nesting success (e.g., stress effects: Gabrielsen, 1987; Wilson *et al.*, 1989; see also Platt, 1977, in Section 7 for a possible example). The predictions become more complicated when site tenacity is taken into account (van der Zande and Vos, 1984:239; van der Zande *et al.*, 1984:22). It tends to preserve present densities of breeders in a disturbed area, but newcomers might avoid it, and in the long run density may decrease. However, this might not be the case if there is a surplus of nesters ("floaters") willing to settle. Another problem that should not be overlooked is that birds may desert disturbed areas and settle in control sites, artificially increasing density there (Safina and Burger, 1983). With regard to point (5), a long-term study of disturbance and nest site selection also has the potential to examine postfledging survival of chicks in disturbed and undisturbed areas. Survivorship might be estimated from recoveries of banded birds or from resightings of nestlings

tagged with individually identifiable patagial tags (Krementz *et al.*, 1989).

Point (6) concerns mitigation techniques. Here we need to (1) assess the degree to which different methods reduce biases caused by "normal" visitation rate to nests or territories, and (2) assess the precision of estimates of nesting parameters derived from alternative methods and evaluate whether the estimates are sufficient to meet various objectives of ornithological research.

A study of effects of investigator disturbance on nesting birds might not have high priority among researchers or funding agencies in a competitive scientific community, but it is easy to combine with any short- or long-term study of other aspects of avian ecology or behavior. If researchers are willing to study disturbance problems, we may improve our knowledge and correct for biases caused by our activities.

12. SUMMARY

Disturbances of nesting birds by investigators may bias estimates of breeding parameters. A review of the literature showed that this problem was discussed especially in studies of species of Pelecaniformes, Anseriformes, and Charadriiformes, but less often for species of Passeriformes. I identified more than seven methods used to study the problem. Overall, 33 of 68 papers reported reduced nesting success as a result of disturbance; however, such an effect was recorded in 14 of 16 studies of Charadriiformes, but only in 3 of 14 studies of Passeriformes and Columbiformes. In studies that found an effect, nesting success of disturbed pairs was reduced on average at least 40%. In addition to these studies, ten studies reported increased predation of nests as a result of disturbance, whereas six studies found no such effect (these papers were analyzed separately because a significant increase in nest predation does not necessarily lead to a significant decrease in overall nesting success). Visitation frequency to disturbed nests was slightly higher in studies that reported decreased nesting success than in those that reported no effect. The earlier in the season a study was initiated, the higher the probability of an investigator-induced reduction of nesting success. Increased predation by avian predators was the main reason for reduced nesting success of disturbed pairs, but desertion of nests was also an important factor. Many authors assumed mammalian predators are attracted to nests visited by observers, but I found no or little evidence in the literature that researcher disturbance increases nest predation by mammals. Some studies showed that breeding density

declined in disturbed areas, apparently because of territory or nest desertion. Densely nesting species (mainly colonial ones) were more often affected by disturbance than solitary species, and behavioral changes other than disturbance occurred in several colonial species. Differences between species in degree of susceptibility to disturbance relate to ecology, life history traits, and human persecution. More research is needed especially on the effects of disturbance on territory or nest desertion, nesting density, and postfledging survival. Also, methods that mitigate disturbance effects need to be developed.

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CHAPTER 4

ANALYZING QUANTITATIVE RELATIONSHIPS BETWEEN SEABIRDS AND MARINE RESOURCE PATCHES

J. CHRISTOPHER HANEY
and ANDREW R. SOLOW

1. INTRODUCTION

Spatial relationships in the ocean form the bases for interpreting many aspects of seabird ecology. Spatial characterization enables the detection of foraging segregation among seabird species (e.g., Trivelpiece *et al.*, 1987; Weimerskirch *et al.*, 1988). Distances that seabirds commute to obtain food for their young (Adams and Wilson, 1987) and the proximity of suitable foraging zones to colonies (Anderson and Ricklefs, 1987) have implications for a large suite of seabird life history parameters: activity and energy budgets of adults (Prince and Francis, 1984; Cairns *et al.*, 1987a), colony attendance (Gaston and Nettleship, 1982; Piatt *et al.*, 1990), meal delivery to chicks (Ricklefs *et al.*, 1985), chick growth rates (Shea and Ricklefs, 1985; Nelson, 1987), breeding success (Schaffner,

J. CHRISTOPHER HANEY and ANDREW R. SOLOW • Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

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no help in correctly maintaining an animal from a selected area.

Even with these problems, this book would have been an acceptable and even welcome attempt to present data on these animals, except for the deplorable job done by the publisher. The photographs are often upside down or sideways, including the front cover! The type size, credits and cropping of correctly oriented figures are so poorly done that they are also irritating to look at. The computer generated figures are printed with a dot-matrix printer and assault the eye. Wording in the text is sometimes stilted, and one wonders if the publisher's editors helped the author at all. It is a shame that such a significant amount of information is so poorly displayed. For the cost, it is difficult to recommend this book except to the serious student of Southeast Asian herpetology.

NEIL B. FORD, *Biology, University of Texas, Tyler, Texas*

THE RUSSIAN JOURNAL OF ORNITHOLOGY. Volume 1, Number 1.

Edited by Alexander Bardin. Alga Publishers, St. Petersburg; subscription orders: E. Potapov, c/o EGI, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom. £27 (paper). 120 p.; ill.; no index. ISSN: 0869-4362. [Written in Russian.] 1992.

A new ornithological journal has been born in Russia. This is truly good news: Ornithological research has long and strong traditions in Russia, extending back to the mid-19th century (and even further if the 18th-century explorations to the Eurasian continent are considered), and the traditions remained in good shape in the Soviet Union, but there has been a chronic lack of publication forums. Russian ornithological literature has mainly appeared in a series of volumes called *Ornitologiya* (Ornithology), published almost annually by Moscow University, and in various *Storniks* (article collections), published irregularly by universities and institutes, which are very difficult to learn about and practically impossible to obtain.

The first number is published in Russian, with English abstracts attached to both articles and short communications. In his introductory text, however, the editor in chief sets the publication of papers in English as a future goal. The first number contains 8 articles, 3 short communications, 1 review, and 1 meeting chronicle. The first two articles deal with paleontology: Nesov of St. Petersburg University reviews the known localities of Mesozoic and Paleogene birds of the former USSR, and Irisov of the Biological Institute of the Novosibirsk Branch of the Academy of Sciences describes a new hypothesis about the origin of birds in high-

altitude environments. The rest of the articles deal with a variety of subjects ranging from circadian rhythm in the chaffinch, and variation in the wing-shape in swallows and sand martins, to population structure in pied flycatchers according to blood parasite data, and commensalism in winter feeding between tits and red squirrels.

Because of the wide range of topics covered, it is impossible to summarize the number in more detail. Some of the articles share the problem that is typical of Russian biological research and due to the insulation from international exchange: Russian scientists have been suffering for decades. They are overtly descriptive, without any clear theoretical context. Descriptiveness per se is no problem, but the lack of context is. Increasing publication frequency is the correct way to make scientists more context-conscious; this is yet another reason to welcome this new journal.

The first number is technically adequate, but the reader gets curious about publisher details: One learns that the editor in chief is Aleksandr Bardin, and the publication is sponsored by "The Alga Association," which is characterized as "a scientific-industrial complex." There is no mention of an advisory board, or of any referee procedure used for evaluating the submissions. These are details I would like to see corrected in future issues. It is hoped that it will be the contents that ultimately matter, but a better substantiated scientific background would increase confidence in the survival of this very valuable and timely enterprise.

YRJÖ HAILA, *Satakunta Environmental Research Centre, University of Turku, Turku, Finland*

CURRENT ORNITHOLOGY. Volume 9.

Edited by Dennis M. Power. Plenum Press, New York. \$69.50. xiv + 247 p.; ill.; index. ISBN: 0-306-43990-5. 1992.

Volume 9 maintains a standard set by this series, making a significant contribution to ornithology. Its six papers review diverse aspects of avian biology and, without exception, raise important questions for future research.

Bucher's is a convincingly argued account (Chapter 1) of extermination, through loss and fragmentation of forest habitat, of a nomadic specialist, the passenger pigeon. His paper also raises important conservation issues, in the context of landscape scale, for many species, particularly those with colonial and flocking habits.

Cairns's discussion (Chapter 2) of population regulation in seabird colonies suffers, in my opinion, from imprecision in the use of terms: "regulate" seems to be used synonymously with "influence," "affect," and "control." Thus we read "Food supply could affect populations . . ." (p. 40). "The clearest examples of food-based population regula-

tion during nonbreeding come from the El Niño-Southern Oscillation (ENSO) . . ." (p. 41). ". . . food shortages . . . would also influence colony size . . ." (p. 42), and "breeding site limitations may control colony populations . . ." (p. 42). Surely regulation implies a negative feedback system in which individuals in a population show appropriate reproductive responses (increase, no change, decrease) to a given set of environmental conditions. Control implies no such system and is usually manifested only in lowered population size. Thus the ENSO, causing mass starvation, would seem not to be a form of regulation.

Götmarm's paper (Chapter 3) is a very timely discussion of the researcher's impact on the nesting success of birds, a subject made complex by variation in bird species studied, predator community involved, and researcher behavior. That Götmarm could find "no or very little evidence for increased nest predation by mammals as a result of researcher disturbance" (p. 79) should be viewed with caution and become a prime subject for investigation.

Haney and Solow's chapter (4) on analysing quantitative relationships between seabirds and marine patches will become required reading for all students of marine ornithology as they embark on studies of seabird population ecology. I suspect that many of the principles enunciated would apply equally to other flocking and nomadic species.

Martin describes (Chapter 5) an interactive model that links nest predation, food limitation, and reproductive strategies of birds. This model is based on a number of assumptions, many needing validation, particularly the impact of the research on nest predation. That Martin has not cross-referenced Götmarm's paper in the same volume is surprising; it throws considerable doubt on the validity of a key assumption.

Spector reviews (Chapter 6) the singing behavior of wood warblers and the nature of their song systems. In so doing he raises a number of interesting hypotheses about song function and phylogenetic relationships.

The editor, to be commended for drawing upon an international authorship (3 of 7), has, however, failed to present for his readers the published literature in languages other than English. Of the 997 citations, only 11 are in a foreign language. Are we to interpret this to mean that 99 percent of the pertinent literature is in English? Or is this a sad comment on the arrogance of the English-speaking scientific community? With the exception of one chapter, the accounts are well written (split infinitives seem to have been accepted by the editor) and relatively free of jargon. Typographical errors are few (I counted 7) and in Table III (p. 73) *Galliformes* and *Gruiformes* are interchanged.

DAVID A. BOAG, *Zoology, University of Alberta, Edmonton, Alberta, Canada*

STORKS, IBISES AND SPOONBILLS OF THE WORLD.
By James A. Hancock, James A. Kushlan, and M. Philip Kahl; illustrated by Alan Harris and David Quinn. Published with the support of the Brehm Foundation by Academic Press, London and San Diego (California). \$139.00. vi + 385 p.; ill.; index. ISBN: 0-12-322730-5. 1992.

Storks, ibises, and spoonbills comprise a diverse group of wading birds that range in appearance from the grotesque to the beautiful, in social habits from solitary to highly colonial, and in demographics from small, isolated populations to continent-wide distributions. Additionally, whereas some species have been studied for centuries, the natural history of others remains virtually unknown. The authors, each having extensive experience with this avian group, have teamed up to produce a comprehensive yet detailed volume that not only presents what is known of this group but also emphasizes what is currently *not* known. The text, numerous illustrations, and large format (9 1/2" x 12") make *Storks, Ibises and Spoonbills of the World* both informative and attractive, much in keeping with Hancock and Elliott's earlier work, *The Herons of the World* (Harper & Row, New York, 1978).

The book is organized into five photo-illustrated chapters—Introduction, Classification, Conservation, Courtship and reproduction, Feeding behaviour and ecology—followed by the 49 species accounts. Each species account discusses identification, distribution, ecology, breeding, taxonomy, and conservation, and includes a range map and a full-page color plate. The artwork, by the way, exhibits some of the best bird portraits in a book of this kind. A 44-page Appendix lists body measurements, egg measurements, and egg-laying months in different geographic areas for each species, and an extensive bibliography contains over 4,000 references.

Throughout the book the authors stress the need for conservation. It is disheartening to learn that over 20 percent of the species are endangered or vulnerable, and that in the past five decades "populations of most storks, ibises and spoonbills have been reduced by at least a half, and in many species by more" (p. 16). Some, such as the Waldraup Ibis (*Geronticus eremita*) and Storm's Stork (*Ciconia stormi*), may soon be lost from the wild. Thus certain species and their associated habitats require immediate attention to avoid extinction. Unfortunately, the cost of the book may keep it out of the hands of wildlife managers in those countries that could benefit most from the information it offers.

Some readers may take issue with several taxonomic arrangements. For example, the White Ibis (*Eudocimus albus*) and Scarlet Ibis (*E. ruber*), originally considered distinct species of a superspecies, are here considered subspecies of a polytypic spe-