NESTING SUCCESS IN ALTRICIAL BIRDS

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NEARLY 20 years ago I presented a table in which it was shown that the percentage of success in 10 studies of open-nesting altricial birds averaged 43 for the eggs and 46 for the nests. I also pointed out that nesting success in hole-nesting altricial birds had been found to average about 66 per cent (1937: 143). This table on the open-nesters has been referred to by many workers; it seems high time to bring the subject up to date.

In Table 1, 35 studies are summarized on the success of altricial species that build open nests. Three of the papers in the 1937 table are omitted: Clabaugh (1926) because no information is given as to the species involved, Nice (1923) because most of this material is included in Nice (1931), and Walkinshaw (1936), since this study on 46 nests of the Field Sparrow is replaced by unpublished notes on 593 nests. The figures in Potter (1915) and Clabaugh (1925) have been altered by the omission of hole-nesting altricials and of precocial species. Because of the wealth of material a lower limit of 30 nests was set for this table. No nest is included unless at least one egg was laid in it; this rule necessitated recalculations with Howell's (1942) and Kendeigh's (1942) papers. Twenty-eight of the studies were carried out in the United States, six in Great Britain, and one in Germany.

Success of 7,788 nests was 49 per cent. Hatching success of 21,040 eggs was 60 per cent, while fledging success of 21,951 eggs came to 46 per cent. The corresponding figures in 1937 were: success of 814 nests, 46 per cent; hatching success of 1,994 eggs, 61 per cent; fledging success, 43 per cent. Now, with 10 times as many nests and eggs, the success of nests and fledging of eggs prove to be 3 per cent higher than before. The hatching success of eggs has dropped 1 per cent.

The success of hole-nesting birds averages distinctly higher than that of open-nesters. Table 2, largely taken from Table 9 in Allen and Nice (1952), summarizes hatching and fledging success in 20 studies in the New World and 13 in the Old. I have not included Creutz's (1949) study of the Tree Sparrow (*Passer montanus*), where only 379 young were fledged from 855 eggs (44.3 per cent), since the examination of the nests caused a considerable amount of desertion.

Hatching success of 34,000 eggs was 77 per cent; fledging success of 94,400 eggs was 66 per cent.

A further check on the validity of these figures may be obtained

TABLE 1

SUCCESS OF OPEN NESTS OF ALTRICIAL SPECIES

Species	*Reference*		*Years*	*Nests* *Total*	*Successes* *Number*	*Per cent*	*Eggs* *Laid*	*Hatched* *Number*	*Per cent*	*Fledged* *Number*	*Per cent*
Mourning Dove	Nice	1931	8	249	130	52.8	500			213	42.6
Zenaidura macroura	Pearson	1939	3	592	309	52.2					
	McClure	1946	6	4273	2043	47.9	8018	4379	54.6	3734	46.6
	Monk	1949	9	235	122	52.0					
	Cowan	1952	4	204	142	69.6	398	310	77.8	274	68.8
Horned Lark	Pickwell	1931	2	30	18	60.0	102	79	77.4	46	45.1
Eremophila alpestris											
American Robin	Howell	1942	2	136	78	57.3	259	157	60.6	131	54.4
Turdus migratorius	Koehler	1945	1	64	49	76.6					
	Young	1955	3	176	86	48.8	548	316	57.8	246	44.9
Whinchat	Schmidt	1954	1	129	57	44.4					
Saxicola rubetra											
Cedar Waxwing	Putnam	1949	6	60	46	76.7	245	189	77.1	171	69.8
Bombycilla cedrorum											
Yellow Warbler	Schrantz	1943	2	41			168	119	70.8	91	54.2
Dendroica petechia											
Redwing	Williams	1940	1	67			214	156	72.9	105	49.1
Agelaius phoeniceus	Smith	1943	1	356			1140	823	72.2	675	59.2
Yellow-headed Blackbird	Fautin	1941	1	128			443	314	70.9	99	22.4
Xanthocephalus xanthocephalus											
Brewer Blackbird	LaRivers	1944	1	107	53	49.5	521	327	62.7	205	39.3
Euphagus cyanocephalus											
Bronzed Grackle	Petersen	1950	3	62	34	54.8	288	209	72.6	135	46.9
Quiscalus quiscula											
Goldfinch	Walkinshaw	1939	5	35	21	60.0	161	113	70.2	80	49.7
Spinus tristis	Stokes	1950	3	239			696	455	65.3	338	48.6
McCown's Longspur	Mickey	1943	3	45	27	60.0	153	92	60.1	71	46.4
Rhynchophanes mccownii											
Corn Bunting	Ryves	1934a	1	54			207			126	60.9
Emberiza calandra	Ryves	1934b	1	53	40	76.7	204			144	70.6

TABLE 1—*Continued*

Species	*Reference*	*Years*	*Nests*			*Eggs*				
			Total	*Successes*		*Laid*	*Hatched*		*Fledged*	
				Number	*Per cent*		*Number*	*Per cent*	*Number*	*Per cent*
Chipping Sparrow *Spizella passerina*	Walkinshaw 1952	12	88	55	62.5	277	185	66.8	170	61.4
Field Sparrow *Spizella pusilla*	Walkinshaw (males)	10	593	226	38.1	1738	888	51.1	620	35.7
Song Sparrow	Nice 1937[1]	3	147	77	52.4	585	389	66.5	243	41.5
Melospiza melodia	Nice 1937[2]	4	76	30	39.5	321	147	45.8	80	24.9
7 Species—New Jersey	Potter 1915	4	43	18	41.9					
8 Species—Scotland	Praeger 1921	1	240	99	41.2					
10 Species—California	Clabaugh 1925	1	30	20	66.6	145	93	64.1	70	48.3
? Species—Scotland	Nicholson 1929	1	156			687	420	61.1	300	43.7
11 Species—England	Baron 1934	1	71			265	160	60.4	124	46.7
6 Species—England	Steuart 1939	1	113			428	295	68.9	248	55.6
11 Species—Ohio	Kendeigh 1942	19				2151	1317	61.2	1010	46.9
6 Species—Wisconsin	Young 1949	1	121	57	47.0	421	257	61.0	170	40.4
13 Species—Pennsylvania	Norris 1947	2	237			668	383	57.3	252	37.7
24 Studies: nest success			7788	3837	49.3					
26 Studies: hatching success of eggs laid						21040	12572	59.8		
29 Studies: fledging success						21951			10071	45.9

[1] First 3 years when the environment was favorable.

[2] Last 4 years when the environment was badly disturbed.

TABLE 2

SUCCESS OF SOME HOLE-NESTING ALTRICIAL SPECIES

Species	*Reference*		*Years*	*Nests*	*Eggs*	*Hatched*		*Fledged*	
						Number	*Per cent*	*Number*	*Per cent*
Tree Swallow	Chapman	1939[1]	9	219	1123	928	83.4	679	61.0
Iridoprocne bicolor	Low	1934	3	352	1759	1424	81.0	857	48.7
	Kuerzi	1941[2]	3	80	430	310	72.1	303	70.5
	Shelley	1937	2	37	184	163	88.6	123	66.8
	Weydemeyer	1935	8	60	363	358	98.6	340	93.7
Pied Flycatcher									
Muscicapa hypoleuca	Haartman	1951	8	221	1074			789	73.5
	Creutz	1955	13	606	3724	2632	70.7	2315	62.2
Black-capped Chickadee	Odum	1941	2	11	74			53	71.6
Parus atricapillus									
Great Tit	Gibb	1950[3]	5	202	1936	1653	85.4	1416	73.1
Parus major	Kluijver	1951[4]	19	5011	45466			29529	64.9
	Mackensie	1950	2	66	460	425	92.4	340	72.4
	Wolda	1929	2	623	6012	4579	76.2	3938	65.6
Blue Tit	Gibb	1950[3]	5	183	1887	1548	82.0	1453	77.0
Parus caeruleus	Huxley	1938	2		247	185	75.0	168	68.0
	Kenrick	1940	4	37	286	187	65.0	128	44.7
	Mackensie	1950	2	46	413	366	88.6	327	79.2
Coal Tit	Mackensie	1950	1	18	161	153	95.0	131	81.4
Parus ater									
House Wren	Kendeigh	1942[5]	19	1056	6773	5576	82.3	5351	79.0
Troglodytes aëdon	Kuerzi	1941	3	34	211	135	64.0	118	55.2
	McAtee	1940	6		469			399	83.7
	Walkinshaw	1941	21	64	333	199	59.7	161	48.3
Bewick Wren	Laskey	1946	15	21	129			79	56.8
Thryomanes bewickii									
Bluebird	Laskey	1943[6]	11	1401	6260	3943	63.0	2786	44.5
Sialia sialis	Low	1933	2	86	377	302	80.1	274	72.7
	Musselman	1935[7]	3	301	1290			839	65.0
	Thomas	1946	9	67	272	213	78.3	172	63.2
	Walkinshaw	1941	20	50	203	131	64.5	127	62.5

TABLE 2—*Continued*

Species	*Reference*		*Years*	*Nests*	*Eggs*	*Hatched*		*Fledged*	
						Number	*Per cent*	*Number*	*Per cent*
Starling	Lack	1948b			10557			7923	75.1
Sturnus vulgaris	McAtee	1940	6		472			410	84.5
Prothonotary Warbler	Walkinshaw	1941	11	121	413	159	38.5	106	25.7
Protonotaria citrea	Walkinshaw	1941	2	36	163	100	61.3	100	61.3
House Sparrow	McAtee	1940	6		114			97	78.5
Passer domesticus									
Five Species	Wolda	1929[8]	2		775			500	66.2
23 Studies (8 species) on hatching success					34000	26169	77.0		
33 Studies (13 species) on fledging success					94400			62331	66.0

[1] Records for 1938–1943 given in letter by L. B. Chapman.
[2] Number of "nests" in Kuerzi's table XVI should read "Pairs"; 11 repeat nests are cited in Table V and a second brood mentioned; total 80 nests.
[3] Totals for 1947–1951 given in letter by J. A. Gibb.
[4] Totals for 4 localities given in letter by H. N. Kluijver, observed for 12, 13, 14, and 19 years.
[5] See Nice, 1942.
[6] Totals for 1938–1949 given in letter by Amelia Laskey.
[7] With the addition of 67 eggs in 33 sets destroyed by April freeze, p. 120.
[8] Great Tit, Blue Tit, Coal Tit, Redstart (*Phoenicurus phoenicurus*), and Wryneck (*Jynx torquilla*).

by an examination of the frequencies of percentages of success as shown in Table 3.

TABLE 3

DISTRIBUTION OF PERCENTAGES OF HATCHING, FLEDGING, AND NESTING SUCCESS FROM TABLES 1 AND 2

	Open nests			*Hole nests*	
		Success of eggs		*Success of eggs*	
Percentage	*Success of nests*	*Hatching*	*Fledging*	*Hatching*	*Fledging*
20–29			2		1
30–39	1		3	1	
40–49	7	1	14		4
50–59	7	4	5		2
60–69	5	12	3	6	11
70–79	4	9	2	5	11
80–89				8	3
90–99				3	1
Median	52.5	64.7	46.9	78.3	66.8

With eggs in open nests, half the cases of hatching success fell in the sixties and half of those of fledging success in the forties. With the hole-nesting birds the largest percentages of hatching success of the eggs were in the sixties to eighties; of fledging, in the sixties and seventies.

As to success of nests, in the 24 studies of open nests where these figures are given, the majority fell in the forties and fifties. From these data it appears that about half the open nests of altricial birds in the North Temperate Zone succeed. This is five times the figure suggested by A. A. Allen (1930: 160). In all these studies in Table 1 nests were more successful than eggs, owing to the many partially successful nests. Egg success could exceed nest success in case of a high rate of desertion of incomplete sets, coupled with a high percentage of completely successful nests.

Eggs in partially enclosed nests—either domed or placed in niches—may have an intermediate rate of success, as pointed out by May (1947: 11) for the Willow Warbler (*Phylloscopus trochilus*) and Lack (1946: 130) for the European Robin (*Erithacus rubecula*). There are three studies on birds with domed nests. Of 244 Willow Warbler eggs, 213 (86.9 per cent) hatched and 138 (56.5 per cent) were fledged (May, 1949). During the three seasons, "human interference was in no year considerable" and the "weather showed no extremes." With the Chiffchaff (*Phylloscopus collybita*), of 235 eggs, 138 hatched (58.7 per cent) and 103 fledged (43.8 per cent) (Geissbühler, 1954).

Ovenbirds (*Seiurus aurocapillus*), studied for two seasons by Hann (1937), also showed no higher rate of success than open-nesters. Of 36 nests, 20 fledged young (55.5 per cent); of 161 eggs, 102 hatched (63.4 per cent) and 70 were fledged (43.5 per cent). A heavy loss—18 per cent—of eggs and young was due to parasitism by the Cowbird (*Molothrus ater*).

As to nests in niches, two cooperative studies by the British Trust for Ornithology have been published. With the Robin 71 per cent of 1,426 eggs hatched, and 77 per cent of 1,865 young were fledged. The "average success from egg to leaving nest" was 55 per cent (Lack, 1948c: 102). With Spotted Flycatchers (*Muscicapa striata*) 819 eggs hatched out of 1,052 laid (78 per cent), and of 749 hatchlings, 609 flew (81 per cent): hence over-all success is calculated as 63 per cent (Summers-Smith, 1952). With the House Finch (*Carpodacus mexicanus*) in Colorado, 166 young fledged from 283 eggs—59 per cent (Bergtold, 1913).

A study that is somewhat hard to classify is that on Orchard Orioles (*Icterus spurius*) on a refuge in Louisiana; of 157 eggs in 50 nests, 131 hatched (84 per cent) and 126 young were fledged (80.3 per cent). In these well-woven, semi-pensile nests, destruction of eggs and young "through predation constituted a very low percentage." But after leaving the nest at 12 to 14 days of age, the noisy fledglings, unable to fly, are highly vulnerable to raccoons, reptiles, and birds of prey (Dennis, 1948).

Success of nesting with passerines is influenced by the safety of the nest site; the percentage of eggs that hatch and are fledged typically falls in the sixties with hole-nesting species, perhaps in the fifties with birds with partially enclosed nests, and in the forties with those nesting in the open.

All these studies were made in the North Temperate Zone. The only paper I have found dealing with the success rate of more than 100 eggs in the South Temperate Zone is Bull's (1946) on two introduced species in New Zealand; their very low rate of success might be explained by an over-abundance of predators as discussed below. As to the tropics, the Moreaus (1940) speak of "the very high mortality in the nest" in Africa. In Central America, Skutch (1945) writes:

"Of 35 nests that I attempted to follow through in lowland forest in Panama, in 1935, only five, or 14.3 per cent, came to a conclusion—that is, produced at least one fledgling. In other forested regions of the lowlands, my luck has been scarcely better. But in the Guatemalan highlands, between 8,000 and 9,000 feet above sea level, 37 of 67 nests, or 55.2 per cent, were successful."

These nests were both open and enclosed. In another paper (1940) Skutch attributes this "astounding mortality of nests in the lowland forests . . . chiefly to snakes," although losses are also caused by Swainson's Toucan (*Ramphastos swainsonii*), Swallow-tailed Kite (*Elanoides forficatus*), and monkeys.

The site and architecture must afford some protection from the vicissitudes of the weather and from predators.

Is ground nesting more dangerous than bush or tree nesting? Kalmbach (1939) thought so. Examination of his sources, however, reveals that his tables are badly confused. Precocial and altricial species are mixed indiscriminately in his Table 1; sometimes hatching success is used, sometimes fledging, and even, in one case, fledging *failure* as "Per cent productive." Tables 2 and 3 are scarcely better. (See Nice, 1940.) Only in Table 4, "Nesting Success—Waterfowl," are we on surer ground, but even here the author does not discriminate between nests and eggs.

In Table 1 of the present study, the eggs of the 3 ground-nesting species had the following percentages of success: Horned Lark, 45; McCown's Longspur, 46; Corn Bunting, 66. For the 3 species building domed nests on the ground, the percentages were 44 for the Ovenbird and Chiffchaff and 57 for the Willow Warbler.

Smith suggested that the high success rate of his and Williams' Red-wings—59 and 49 per cent respectively—might be explained by their comparative safety from ground predators due to nesting over water. But Fautin's Yellow-headed Blackbirds were markedly unsuccessful, largely because of severe storm damage.

Weather conditions may be disastrous—especially wind, rain, flood, drought, or excessive cold or heat. Here the hole-nesters have a great advantage in security of nest sites, although swallows and swifts may perish from starvation during cold, rainy periods. Drought can bring disaster to young waterfowl through the drying up of ponds and to passerine nestlings through diminishing the supply of insects. Storms have been responsible for heavy losses among Mourning Doves and Yellow-headed Blackbirds, while drought and flood wrought havoc with my nestling Song Sparrows. Early in the season eggs of Bluebirds, House Finches, and Horned Larks may be frozen.

A wide variety of enemies might be included under "predators" in the broadest sense of the term: typical predators—reptilian, avian, and mammalian, native and introduced—that eat the eggs and young; nest competitors that drive off the parents and sometimes destroy eggs or young; brood parasites, such as the Cowbird and Cuckoo (*Cuculus canorus*); arthropod parasites that prey on the nestlings;

man with his destruction of habitat and of the parents, eggs, and young, although at times his activities are helpful in the provision of nest sites and elimination of some predators.

Open-nesting passerines typically lose some 55 per cent of their eggs or young. Predators in the restricted sense of non-human animals, excluding the Cowbird, have been found to account for the following percentages of the total eggs: 24 (Young, 1949, for 6 species), 30 (Smith, 1943, Red-wings), 36 (Nice, 1937, Song Sparrows). The Ovenbird, despite its domed nest, suffered a 24 per cent loss from this source (Hann, 1937). Lack (1954: 77) thinks it likely that "in open-nesting song-birds over three-quarters of the losses of eggs and young are due to predation." In the above studies predation loss came to the following percentages of total loss: 40, 73, 55 and 43, respectively.

High incidence of predation decreased the rate of success in my Song Sparrows and La Rivers' Brewer Blackbirds. A striking example of this situation is afforded by the New Zealand study by Bull (1946) on the introduced Song Thrush (*Turdus philomelus*) and European Blackbird (*Turdus merula*). With the former, of 474 eggs, 172 hatched (36 per cent) and 105 were fledged (22 per cent); with the latter, of 201 eggs, 69 hatched (34 per cent) and 61 were fledged (30 per cent). Rats, stoats, cats, Starlings, children, wind, and hedge trimming were cited as inimical factors. In Great Britain, on the contrary, high success was found for the Song Thrush: of 739 eggs, 525 hatched (71 per cent); of 1034 hatched young, 808 were fledged (78 per cent); hence the percentage of eggs which produced young is calculated as 55 (Silva, 1949). These birds build secure nests reinforced with mud, as do American Robins, whose success proved high in two of three studies (Howell, 1942; Koehler, 1945).

As to hole-nesters, Lack (1954: 75) considers their high rate of success in comparison to open-nesters as "mainly due to the much smaller losses from predation." In Table 2 the two lowest percentages reflect severe predation and severe competition. In regard to the 44.5 per cent fledging success of 6,260 eggs of the Bluebird, "predators are chiefly responsible for the loss of eggs, young, and brooding females. Cats and snakes regularly climb to the boxes; there has been some depredation by boys" (Laskey, 1943: 39); while fire ants (*Solenopsis*) have also caused losses (Laskey, letter). The very low figure for the Prothonotary Warbler in Michigan—25.7 per cent for 413 eggs—was due to competition with an over-population of House Wrens. In Tennessee, without House Wrens, the success rate of 163 warbler eggs was 61.3 (Walkinshaw, 1941: 13).

The three studies of open-nesters where Cowbird parasitism was high show low fledging success of the host species: 35 per cent of 906 Song Sparrow eggs during 7 years (Nice, 1937), 36 per cent of Walkinshaw's Field Sparrows and 38 per cent for Norris' 13 species. The Ovenbirds with their covered nests should have had more than 44 per cent success.

As to nesting studies with higher success than usual, a variety of factors suggest themselves. Predation may have been lessened through human protection, as with Steuart's population in Essex, Kendeigh's House Wrens, and McAtee's Starlings and House Sparrows. This might also be the case with some of the marked successes of titmice in Great Britain.

Evergreens as nesting sites afford protection from storms and predators, as is evidenced by the high success rate of Walkinshaw's Chipping Sparrows and the Koehlers' Robins, as well as favoring an over-population of Bronzed Grackles (Sherman, 1928). Late nesters seem to be less harried by predators and sometimes by weather, as shown by the Goldfinches, Cedar Waxwings, and Corn Buntings. September nesting was far more productive with my Mourning Doves than spring nesting.

Parental devotion may also have an influence. Putnam (1949: 178) believed that the great success of his Cedar Waxwings was partly due to the constant attendance of one or both parents at the nest. Robins and Red-wings are bold in defense of their nests.

When nesting success proves to be markedly higher or lower than the norms found in these tables, it would seem advisable to search for especially favorable or unfavorable factors affecting the population. Ideally such a study should be carried on for a number of years. Fledging success of my Song Sparrows ranged from 19 to 46 during 7 years. It should be noted that only in one year—1930, which showed a success of 43 per cent—was I able to carry observations to the end of the nesting season; if this had been possible for the other years, nesting success would probably have been higher. Walkinshaw did pursue his studies throughout the season; the success rate of his Field Sparrows ranged from 30 to 48 per cent in 9 years. Lack (1946) reports fledging success of European Robins as ranging from 30 to over 70 per cent in different localities.

Since hole-nesting is so much more successful than open-nesting, one would expect hole-nesters greatly to outnumber open-nesters. Hole-nesting, however, presents difficulties, chiefly because of the limited number of holes. This may mean severe competition, with destruction of the eggs and young of less aggressive species by House

Wrens, Tree Swallows, Starlings, House Sparrows, European Tree Sparrows, and Wrynecks. Great Tits may even kill adult Pied Flycatchers (Haartman, personal communication). Or there may be intra-specific strife, as when first-year females arrive late in a nesting colony of Tree Swallows and break up mated pairs (Shelley, 1935). In a flock of "many thousands of Grey Starlings, *Sturnus cineraceus*," quarrels were staged between pairs for a nesting hollow "and almost ¼ of the flock seemed to have psychologically returned to non-breeding condition by lack of nesting site" (Kuroda, 1955). The dependence of the Purple Martin (*Progne subis*) on its highly specialized multiple nesting site, for which competition is keen, may be a reason for its very early and at times disastrous return from its wintering grounds in Brazil.

Hole-nesters spend more time fledging a brood than do open-nesters; clutches are typically larger, incubation is slightly longer and fledging as a rule markedly longer. For discussion of these subjects see Nice (1943: 70–71) and Lack (1948a: 29–41). Hole-nesting passerines leave the nest at a more advanced stage than do open-nesters; the former are able to fly from the nest, while the latter hop from it. Hence, hole-nesters are even more successful in comparison to open-nesters than the percentages indicate; 6 days after leaving the nest, the 46 per cent of fledged open-nesters have diminished to some extent.

TABLE 4

SIZE OF CLUTCH, LENGTH OF INCUBATION AND FLEDGING IN HOLE-NESTERS AND OPEN-NESTERS

	Locality	*Number of species*	*Average clutch*	*—Average Duration of—* *Incubation*	*Fledging*	*Total days*
Hole-Nesters	Europe[1]	18	6.9	13.8	17.3	38
	U. S. A.[2]	10	5.4	13.8	18.8	38
Open-Nesters	Europe[1]	54	5.1	13.1	13.2	31.4
	U. S. A.[3]	11	4.0	12.0	11.0	27

[1] Lack (1948a), Table 3.

[2] Species from Table 2, this study, with addition of 3 more swallows.

[3] Species from Table 1, this study.

As shown in Table 4, for 18 European and 10 North American hole-nesting passerines the brood is vulnerable for an average of 38 days. For 54 European and 11 North American open-nesting passerines the brood is vulnerable for an average of 31 and 27 days respectively. The average loss of eggs or young to hole-nesters in Table 2 is 34

per cent, to open-nesters in Table 1, 54 per cent. A loss of 34 per cent in 38 days gives an average loss of 0.9 per cent of eggs or young per day. A loss of 54 per cent in approximately 29 days gives an average loss of 1.9 per day, twice the loss suffered by hole-nesters. Loss of nests, for open-nesters, averages 1.8 per cent per day.

On what basis can we compare nesting success of altricial and precocial birds? A precocial bird passes its whole nest-life within the egg, while an open-nesting altricial spends about half this period in the egg and half out of it. At leaving the nest, both birds have reached a somewhat comparable stage of development. Both are strong on their feet and both respond to parental notes of alarm. One is covered with down, the other with feathers. Peeking at food and drinking will come in a day or two for both. Both need parental care—the precocial must be brooded, and the altricial must be fed (Nice, 1943: 73).

Let us consider very briefly, with no pretense of covering the voluminous literature since Kalmbach's paper, the success rate of some precocial birds in comparison to altricials. Hickey (1955: 337), in a review of population problems in gallinaceous birds, found a hatching success of 35.5 per cent for 3,299 Phasianinae nests in 11 studies, and 51 per cent for 865 nests of Tetraoninae in 6 studies. "Nice's figure [of 46 per cent of 814 open nests of altricials] is almost matched by 44.5 per cent for 5,597 galliform nests."

If the galliforms in Hickey's table average a clutch of 11 eggs and an incubation period of 24 days, then a 55 per cent loss would mean a 1.6 per cent loss per day—much the same as with open-nesting passerines.

To judge from Kalmbach's Table 4 and Kiel's (1955) 4-year study in pot-hole country in Manitoba, waterfowl—at least diving ducks—would seem to have better success than galliforms. Kalmbach summarizes 28 studies on more than 7,600 nests of 13 species of ducks and the Canada Goose (*Branta canadensis*); the rate of success ranged from 29 to 85 per cent, averaging 60. Kiel found 73 per cent success with 227 nests of diving ducks and 50 per cent success with 149 nests of dabbling ducks. If we estimate 9 eggs per clutch for all the ducks and 26 days of incubation for the divers and 23 for the dabblers, we find 0.8 per cent daily loss for the former and 1.6 for the latter—the same as for the gallinaceous birds. The dabblers nest on the upland, the divers over water. In pot-holes, writes Kiel, "nesting over water is a distinct advantage because nests are largely protected against land-dwelling mammals and yet are not subjected to danger of destruction by wave action." Also these nests were safe from

sudden changes of water level occurring in connection with irrigation projects.

We must remember that all these percentages of success refer to nesting *attempts;* low percentages are usually compensated by an increase of attempts. Hickey suggests that "the larger clutch size of the single-brooded gallinaceous birds at least is in part counterbalanced by the multi-broodedness of passerine species." Some pairs of altricial species occasionally *raise* 3 or 4 broods, or even very rarely, 5 or 6—e.g., Mourning Doves (Cowan, 1952: 514; Monk, 1949: 4)—in a season. Such broods overlap, the father often caring for one brood until it reaches independence, while the mother incubates the next set. As a rule, multi-broodedness is more common with open-nesters than with hole-nesters. But this is not always so.

When a species consistently enjoys a high rate of nesting success, we can suspect that population increase may be limited in other ways. Or such over-success may lead to over-populations, as with House Sparrows, House Wrens, Starlings, Chipping Sparrows, Redwings, Grackles, and others.

The subject of nesting success has endless ramifications in the ecology and biology of each species, especially its longevity (Lack, 1950: 432) and its capacity to meet changing conditions. The wide range in the figures found by different workers for one species reflects the many variables that affect these aspects of a bird's life history.

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SUMMARY

The success rate of open nests of altricial birds in the North Temperate Zone has been found in 24 studies on 7,788 nests to range from 38 to 77 per cent, averaging 49. In 29 studies involving 21,951 eggs, fledging success ranged from 22 to 70 per cent, averaging 46.

For hole-nesting altricial birds, fledging success of 94,400 eggs in 33 studies ranged from 26 to 94 per cent, averaging 66.

Fledging success in 6 studies on species with partially enclosed nests averaged 44, 44, 55, 57, 59 and 63 per cent.

Various favorable and unfavorable factors for nesting success are discussed.

In 18 European and 10 North American hole-nesting passerines, the brood is vulnerable for about 38 days; a loss of 34 per cent of the eggs and/or young would average 0.9 per cent per day.

In 54 European and 11 North American open-nesting passerines, loss of eggs and/or young would average 1.9 per cent per day for about 29 days, while the loss of nests would average some 1.8 per cent per day.

A newly-hatched precocial bird corresponds in some respects to a passerine that has just left its open nest. A success rate of 45 per cent was found in 5,597 galliform nests; the loss here might average 1.6 per cent per day. An average loss of 0.8 per cent of the nests per day was found for diving ducks nesting over water in pot-holes, and of 1.6 per cent per day for dabbling ducks nesting on the uplands.

The figures for nesting success refer to nesting attempts; low percentages are usually compensated by a larger number of attempts.

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