THE CONSTANCY OF INCUBATION

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IN an earlier paper (1957) I briefly surveyed the bewildering variety of incubation patterns which birds exhibit and attempted to correlate their incubation habits with their coloration, the form of their nests, their environment, and other factors that seemed to be pertinent. From this survey, it appeared that many modifications in the incubation pattern, especially those involving the participation of the sexes, are non-adaptive, in the sense that they are not more conducive to the reproductive efficiency of a particular species than some alternative pattern might be. The best than can be said in their favor, in the light of our present understanding, is that they are not deleterious.

Even within a single incubation pattern, such as those classified in the above-mentioned paper, the student of the incubation habits of birds discovers bewildering diversity, caused principally by the varying lengths of the birds' continuous sessions on the eggs. Some birds sit for hours or even days at a stretch, others rarely cover their eggs uninterruptedly for as long as half an hour in the daytime. In some species of which only a single parent incubates, its absences are far shorter than its sessions, so that a high constancy of incubation is achieved; in others, the absences are of about the same length as the sessions with which they alternate, so that the eggs are covered only about half of the day. What causes these differences? Can we correlate them with differences in the birds themselves or in their environments—with factors such as size, diet, weather, type of nest, and the like? As, over the years, I have given attention to the incubation habits of a great variety of birds and have tried to explain what I found, these questions have occurred to me again and again. The present paper is a preliminary attempt to answer them.

NOMENCLATURE, METHODS OF OBSERVATION AND COMPUTATION

Scientific names of most species mentioned in the text are given only in the tables.

The rather ponderous terms "attentive period" and "inattentive period" have in the last few decades come into rather general use in the description of the breeding behavior of birds. These designations were introduced by Baldwin and Kendeigh (1927) to serve the theory that at every stage of their reproductive cycle birds devote alternate periods to reproductive activities and self-maintenance. Thus the male sings for a while to advertise his possession of a territory and attract a mate, then eats or preens in silence. During nest construction, periods of active building alternate with intervals dedicated to feeding, bathing, or rest. Later, spells of incubation are separated by absences for foraging or preening; and while in charge of dependent young, the parents alternate between periods devoted to the service of their offspring and those taken up with filling their own vital needs or with resting.

While it is true that birds cannot wholly neglect their own welfare while reproducing their kind, and most small birds shift many times in the course of a day from activities that serve their progeny to those which preserve themselves, in most phases of the nesting operations it is in practice scarcely possible to delimit these alternating periods of attention and inattention. A building bird may indeed bring material to the nest a number of times in quick succession, then remain away for many minutes. But often its visits are so irregularly spaced that it is difficult for the watcher to recognize rhythmically alternating periods of attentiveness and inattentiveness, so that he usually counts visits to the nest, not spells of work. So, too, in feeding nestlings, there are spurts of active food-bringing when the young are hungry and rather long periods of neglect when they are satiated; but between these extremes there are visits with food spaced at all intervals. The observer tries in vain to analyze his record into alternating periods of attention and neglect, and in the end he expresses his data as feedings per hour, or some other unit of time. Only during incubation are periods of attention to the nest and of inattention sharply delimited and accurately measurable. But in this case an attentive period is a continuous spell of sitting and an inattentive period the whole of each absence; and if we call these more briefly "sessions" and "recesses," everyone who has been to school will understand what we mean.

It is of interest to know not only the lengths of the sessions and recesses, or the number of the bird's comings and goings per hour or per day, but the proportion of the day that the eggs are kept covered. Information of the first sort tells us at once whether a bird is a quiet or a restless sitter, which may be an expression of temperament; but the percentage of the daylight hours spent in the nest gives us a better index of the amount of heat applied to the eggs. If we decide to calculate the percentage of time devoted to sitting, we must give careful thought to the methods we shall employ. First of all, how shall we collect our data? Automatic instruments, usually electrical, have been used in both Europe and America for making continuous records of activity at a nest for days together, or even for the entire period of incubation; and in Africa, R. E. Moreau gathered a vast bulk of data by using a relay of native observers who were not trained ornithologists. But most students of breeding behavior watch their nests in person, and this reveals intimate details not to be discovered by any other method.

Ideally, for learning the percentage of time devoted to incubation the watch should begin at daybreak, before the bird becomes active, and continue until after it has settled down to rest for the night. A lone observer will find that this makes a strenuous day, and may prefer the almost equally satisfactory practice of beginning his vigil at about noon, continuing until nightfall, then resuming his watch at daybreak and carrying on until the hour at which he began on the preceding day. If his bird is strictly diurnal, he will then have a continuous record of all its activities in a period of 24 hours, made in two watches rather than in one far more exhausting vigil. In a study of this sort, it is hardly necessary to emphasize the great importance of the observer's being well concealed, if there is the least suspicion that his presence influences the movements of the birds he is watching.

When we have made a continuous dawn-to-nightfall record, or a noon-to-noon record, we can add all the sessions together and all the recesses together to learn how many minutes in the day have been devoted to incubation and how many to absences. From this the percentage of time on the eggs might be calculated. But a perplexity as to the correct mode of procedure is likely to arise. After awaking on her eggs in the morning, the incubating bird may remain sitting after her mate and others of her kind have become active, not starting her first recess until many minutes after it has become light. At the other end of the day, she may end her last absence long before nightfall. I have known birds which most of the day had been taking recesses at less than hourly intervals to settle on their eggs in the middle of the afternoon and stay until the next morning. If we do not include with the diurnal sessions these portions of the long nocturnal session which fall between the afternoon's last return to the nest and nightfall, and between daybreak and the first morning departure, we shall give too low a value to the percentage of the day spent on the eggs. But if we decide to add to the diurnal sessions these extensions of the nocturnal session into the early morning and late afternoon, we shall be puzzled as to how to assess them. In theory, we might delimit the strictly nocturnal period by noting the time when other, non-incubating individuals of the same species begin and end their active day; but in practice we shall find this point hard to determine.

It often happens that we are not able to make an all-day record of events at a nest, but can only watch for a few hours at a stretch. These shorter periods of observation are never so informative as the longer ones; but if long enough to include several sessions and recesses that are complete in the sense that they began and ended spontaneously, and if on different days they come at different hours, so that together they cover most of the daylight period, they can yield much valuable information. Since we often arrive while the bird is absent from the nest and we may be obliged by other duties to leave while it is still sitting, the records of these shorter watches will include incomplete sessions and recesses, which in most cases it is best to omit from the calculations. After the rejection of these fragments, the records may still contain unequal numbers of sessions and recesses, so that if we compute percentage from their totals, we may derive a false notion of the bird's constancy in incubation; for the numerical value will be seriously influenced by whether we happened to watch a greater number of sessions or of recesses. We may overcome these irregularities by computing the average length of the sessions (S), the average length of the recesses (R), then deriving the percentage of time on the nest (T) by the formula

$$T = \frac{100\,S}{S + R}$$

The value of T is then controlled by the ratio of the length of the sessions to the length of the recesses, which in small birds incubating alone seems to be determined by, among other things, the time they require to satisfy their hunger and the rapidity of their digestion, so that it is not an arbitrary value.

The incubating bird's active day begins and ends with a recess, so that if we have watched the nest throughout the day we shall have timed one more recess than session. When we have made such a comprehensive record, it might be held that our result will be more accurate if we compute the percentage of constancy on the basis of the totals of the sessions and of the recesses rather than on the basis of their averages. But the use of the formula will help to compensate for the extensions of the nocturnal session into the species' period of daylight activity at both ends of the day, which are otherwise difficult to handle. For most small birds which take a fairly large number of sessions each day, the two methods of calculation will in this case yield values substantially the same.

A few examples will show the closeness of agreement. I have an all-day record of an incubating White-crested Coquette which began her active day at 5:31 AM and ended it at 5:21 PM. In this interval of 11 hours and 50 minutes, she took 37 sessions, which ranged from less than 1 to 78 minutes and averaged 13.4 minutes. Her 38 recesses varied in length from less than 1 to 22 minutes and averaged 5.7 minutes. Her sessions totaled 494 minutes and her recesses totaled 216 minutes. As computed by the formula, she incubated with a constancy of 70.2 per cent. If we calculate her constancy from the totals of her sessions and recesses, it comes to 69.6 per cent. A Yellow-browed or Speckled Tanager, likewise watched for an entire day, first left her eggs at 6:15 AM and settled down for the night at 5:55 PM, making an active day of 11 hours and 40 minutes. She took 14 sessions, ranging from 20 to 77 minutes, totaling 529 minutes, and averaging 37.8 minutes. Her 15 recesses varied from 3 to 23 minutes, totaled 171 minutes, and averaged 11.4 minutes. By the formula, her constancy was 76.8 per cent; on the basis of total times, it was 75.6 per cent. Less close is the agreement of the two methods of computation in the case of a Thrush-like Manakin whose rhythm of incubation was far slower. Between 6:00 AM and 5:51 PM she took four sessions, which ranged from 97 to 151 minutes, totaled 454 minutes, and averaged 113.5 minutes. Her five recesses varied from 14 to 82 minutes, totaled 257 minutes, and averaged 51.4 minutes. By the formula, her constancy in incubation was 68.8 per cent; calculated from her total times on and off the nest during her active period, it was only 63.9 per cent.

RANGE OF CONSTANCY

When the parents share incubation, they may keep their eggs almost continuously covered, from the day the last or even the first is laid until they

TABLE 1

INCUBATION PATTERNS OF PAIRS OF BIRDS OF 23 SPECIES AT 27 NESTS*

Species	Hours watched	Sessions in minutes No.	Sessions in minutes Range	Sessions in minutes Average	Intervals of neglect in minutes Range	Intervals of neglect in minutes Average	Constancy %
Rufous-tailed Jacamar (*Galbula ruficauda*)	10	3 2	100–113 84–101	108.3 92.5	1–19	5.8	95
Black-breasted Puffbird (*Notharchus pectoralis*)	7	5	7–162	58.2	17–46	25.2	70
Fiery-billed Araçari (*Pteroglossus frantzii*)	8	12	2–102	25.6	2–53	15.9	64
	5	7	12–53	28.1	2–31	14.6	66
Blue-throated Toucanet (*Aulacorhynchus caeruleogularis*)	6	8	<1–81	33.3	1–18	11.9	74
Golden-olive Woodpecker (*Piculus rubiginosus*)	12.5	2 3	82–118 51–297	100.0 146.3		0	100
Red-crowned Woodpecker (*Centurus rubricapillus*)	12	4 6	22–105 2–80	62.0 57.7	1–12	5.2	96
Golden-naped Woodpecker (*Tripsurus chrysauchen*)	10	12 10	4–38 4–44	19.3 25.5	2–16	4.8	90
	12.5	21 22	5–39 2–51	17.0 13.4	1–7	3.4	89
Olivaceous Piculet (*Picumnus olivaceus*)	11	5 5	40–112 30–69	66.2 50.2		0	100
	12	5 5	2–76 7–89	44.4 55.2	17–35	27.0	88
Streaked-headed Woodcreeper (*Lepidocolaptes souleyetii*)	12	8 11	6–37 5–57	16.4 26.9	4–41	16.9	60
	15	3 13	15–42 7–72+	28.3 37.5	2–41	21.2	66
Buff-throated Automolus (*Automolus ochrolaemus*)	18	6	62–138+	96.8	32–122	69.2	58
Plain Xenops (*Xenops minutus*)	11	9	12–118	49.8	25–51	43.5	72
Slaty Castlebuilder (*Synallaxis brachyura*)	17.5	28	2–120	25.2	1–48	13.0	82

* When the sexes could be distinguished, the alternating sessions of the male and female are given in consecutive lines, those of the male above; when they could not be distinguished, the sessions of the two partners are given in the same line. Constancy was computed from total time in the nest rather than by the formula.

TABLE 1 *(Continued)*

Species	Hours watched	No.	Sessions in minutes Range	Sessions in minutes Average	Intervals of neglect in minutes Range	Intervals of neglect in minutes Average	Constancy %
Great Antshrike (*Taraba major*)	11.5	2 2	146–238 34–188	192.0 111.0	17	17.0	96
Plain Antvireo (*Dysithamnus mentalis*)	17	5 4	100+–137 41–79	117+ 65.2	1–18	5.6	95
White-flanked Antwren (*Myrmotherula axillaris*)	13	4 2	3–174+ 98–140	83+ 119.0	11–94	35.6	76
Slaty Antwren (*Myrmotherula schisticolor*)	6	3 2	33–142 53–66	73.0 59.5	11+	11+	94
Tyrannine Antbird (*Cercomacra tyrannina*)	14	7 3	11–153 79–124	57.3 97.0	1–59+	22+	82
Chestnut-backed Antbird (*Myrmeciza exsul*)	12	3 2	45–95 92–136	69.3 114.0	1–39	18.0	88
Spotted Antbird (*Hylophylax naevioides*)	13	3 3	44–217 36–164	112.7 109.0	8–22	13.5	92
Blue-and-White Swallow (*Pygochelidon cyanoleuca*)	9	25	3–50	18.6	1–14	6.9	86
Black-eared Bushtit (*Psaltriparus melanotis*)	12.5	30 22	1–31 1–22	8.5 8.8	1–34	8.3	60
Tropical Gnatcatcher (*Polioptila plumbea*)	10	7 6	19–55 27–34	39.3 29.8	2–21	9.9	82
Long-billed Gnatwren (*Ramphocaenus rufiventris*)	12	5 4	14–95 60–90	67.0 79.8		0	100

hatch (Table 1); although in some species both parents together devote less time to the nest than do other birds incubating alone. When a single parent incubates, the percentage of the day that it covers the eggs fluctuates widely from species to species and even within a single species. Is it possible to assign limits to this variation, so that we may designate an "average" oı "normal" constancy in incubation? I have tables showing the constancy in incubation of 137 individuals of 82 species in which the female incubates alone without receiving much food from her mate or other attendants. They represent 15 families of passerine birds and six species of hummingbirds. These tables were drawn up from data gathered chiefly by myself but in a few cases with the help of students, mostly in Central America but in a few instances in the United States. Each of the birds was watched for five to 20 hours, for the most part in one continuous vigil or a few long periods of observation. Although these records do not cover sufficient time to permit an exhaustive analysis of the rhythm of incubation of any individual bird, they seem to provide a fair "random sample" of the constancy in incubation of a number of avian families as represented in Central America. (Table 2 gives a selection of these records.)

TABLE 2

INCUBATION PATTERNS OF FEMALE BIRDS OF 66 SPECIES AT 119 NESTS

Species	Hours watched	No.*	Sessions in minutes Range	Sessions in minutes Average	Recesses in minutes Range	Recesses in minutes Average	Constancy %
Little Hermit Hummingbird	12	9	16–92	60.7	10–25	18.3	77
(*Phaethornis longuemareus*)	12	14	9–59	27.9	9–29	15.1	65
Cuvier's Hummingbird	12	13	4–99	38.5	1–34	9.3	81
(*Phaeochroa cuvierii*)	12	35	<1–103	14.3	<1–23	6.0	70
Violet-headed Hummingbird (*Klais guimeti*)	11	11	15–77	40.6	6–28	15.2	73
White-eared Hummingbird	12	49	<1–24	9.5	1–17	4.9	66
(*Hylocharis leucotis*)	12	59	<1–35	8.7	<1–20	3.3	73
White-crested Coquette	12	38	1–34	10.4	1–23	7.1	59
(*Paphosia adorabilis*)	12	37	<1–78	13.4	<1–22	5.7	70
Tawny-winged Dendrocincla	12	8	16–89	57.0	12–36	26.4	68
(*Dendrocincla anabatina*)	13	10	10–96	45.8	11–51+	29.3	61
Blue-crowned Manakin	8.5	3	74–171	120.7	14–34	25.5	83
(*Pipra coronata*)	9.5	4	44–197	103.8	15–21	18.2	85
Yellow-thighed Manakin	12	7	29–108	65.1	6–21	14.0	82
(*Pipra mentalis*)	6.5	2	98–214	156.0	26–34	30.0	84
Orange-collared Manakin	11	14	10–64	33.9	3–17	7.1	83
(*Manacus aurantiacus*)	12.5	8	17–258	71.4	3–25	12.2	85
Thrush-like Manakin	11	4	44–134	95.5	34–97	75.0	56
(*Schiffornis turdinus*)	12	4	97–151	113.5	14–82	51.4	69
Turquoise Cotinga (*Cotinga ridgwayi*)	12	4	36–156	114.0	35–88	51.0	69
White-winged Becard (*Pachyramphus polychopterus*)	10	17	6–38	15.2	8–35	18.9	45
Rose-throated Becard (*Platypsaris aglaiae*)	17	49	3–38	11.6	2–19	9.0	56
Masked Tityra (*Tityra semifasciata*)	10	8	24–49	37.1	13–29	19.6	65
Yellow-bellied Elaenia	7	19	8–22	13.2	4–12	8.2	62
(*Elaenia flavogaster*)	10	27	4–49	15.6	4–13	6.9	69
Bellicose Elaenia	7	41	2–21+	5.6	2–8	5.0	53
(*Elaenia chiriquensis*)	12	42	2–60	13.3	<1–7	3.3	80
Yellow Flycatcher (*Capsiempis flaveola*)	7	9	12–40	27.8	13–42	21.5	56
Golden-crowned Spadebill	5	16	3–23	10.6	2–19	8.3	56
(*Platyrinchus coronatus*)	5	10	8–27	16.3	9–20	12.3	57
Bran-colored Flycatcher	6	28	3–14	6.6	2–16	6.5	50
(*Myiophobus fasciatus*)	5	25	<1–18	7.7	<1–9	4.6	63
Tropical Kingbird	8	7	10–56	32.4	9–20	12.1	73
(*Tyrannus melancholicus*)	10	5	19–92	50.8	15–47	24.6	67
Boat-billed Flycatcher	6	5	27–68	44.6	5–20	13.3	77
(*Megarhynchus pitangua*)	10	16	15–77	30.2	2–19	8.3	78
Torrent Flycatcher	5	25	3–13	6.7	1–13	5.2	56
(*Serpophaga cinerea*)	4.5	17	1–14	7.2	2–17	9.1	44
Streaked Flycatcher (*Myiodynastes maculatus*)	12.5	13	15–72	30.3	8–18	12.6	71
Gray-capped Flycatcher	12	22	7–42	20.0	7–20	11.8	63
(*Myiozetetes granadensis*)	6	15	6–50	15.5	4–14	8.0	66
Vermilion-crowned Flycatcher	9	25	4–32	12.8	4–27	10.2	56
(*Myiozetetes similis*)	10	12	9–72	30.4	11–31	18.5	62

TABLE 2 *(Continued)*

Species	Hours watched	No.*	Sessions in minutes Range	Sessions in minutes Average	Recesses in minutes Range	Recesses in minutes Average	Constancy %
Piratic Flycatcher	7	8	20–49	34.0	5–18	12.9	73
(*Legatus leucophaius*)	9	13	13–40	26.0	6–22	11.3	70
Paltry Tyranniscus	5	6	8–75	32.5	10–18	12.5	72
(*Tyranniscus villissimus*)	6	8	22–35	27.4	10–24	13.3	67
Slate-headed Tody-Flycatcher	6	10	10–22	17.2	13–25	17.9	49
(*Todirostrum sylvia*)	6	11	14–33	21.0	9–16	12.7	62
	7	11	13–38	20.0	11–29	20.3	50
Sulphury Flat-bill	5.5	9	10–36+	19.7	8–52	18.1	52
(*Tolmomyias sulphurescens*)	7	14	10–28	17.4	7–28	13.5	56
Royal Flycatcher	12	19	4–52	22.4	3–33	13.6	62
(*Onychorhynchus mexicanus*)	6	10	9–32	17.9	4–18	12.0	60
Sulphur-rumped Myiobius	12.5	22	7–33	14.1	8–28	15.6	48
(*Myiobius sulphureipygius*)	5.5	7	15–30	23.1	14–47	24.6	49
Southern House Wren	6	12	8–20	14.1	11–24	15.7	47
(*Troglodytes musculus*)	9.5	14	14–44	25.8	8–29	14.4	64
	6	11	5–26	19.6	6–18	11.4	63
Highland Wood Wren (*Henicorhina leucophrys*)	9	15	8–28	16.4	7–40	16.8	49
Catbird (*Dumetella carolinensis*)	13.5	24	5–61+	23.8	3–12	6.9	78
White-breasted Blue Mockingbird (*Melanotis hypoleucus*)	14	28	8–42	20.8	1–23	7.1	75
Gray's Thrush (*Turdus grayi*)	5	4	34–84	59.0	11–28	20.3	74
	7	5	29–188	73.6	10–14	12.0	86
Orange-billed Nightingale-	6	10	11–39	25.6	8–19	11.9	68
Thrush	11	26	5–56	12.6	5–24	13.2	49
(*Catharus aurantiirostris*)	5	9	7–32	17.2	11–19	15.1	53
Russet Nightingale-Thrush (*Catharus occidentalis*)	8	12	13–42	26.6	8–21	12.4	68
Yellow-green Vireo	6	9	15–61	28.1	6–18	8.5	77
(*Vireo flavoviridis*)	6	4	40–56	49.3	10–55	24.2	67
Gray-headed Greenlet (*Hylophilus decurtatus*)	10	20	7–25	15.3	7–26	14.0	52
Slaty Flower-piercer (*Diglossa baritula*)	12.5	22	4–62	19.1	4–24	10.5	65
Green Honeycreeper (*Chlorophanes spiza*)	10	8	32–149	54.9	6–20	12.2	82
Blue Honeycreeper	5.5	8	16–53	28.6	9–22	13.9	67
(*Cyanerpes cyaneus*)	7.5	11	12–44	27.7	6–19	11.2	71
Turquoise Dacnis (*Dacnis cayana*)	12	20	11–55	23.6	6–18	11.7	66
Bananaquit (*Coereba flaveola*)	12.5	7	47–82	60.7	12–29	17.0	78
Crescent-chested Warbler	6	12	5–37	18.8	2–13	8.1	70
(*Vermivora superciliosa*)	5.5	9	14–28	23.0	7–24	11.8	66
Slate-throated Redstart (*Myioborus miniatus*)	12	11	26–49	37.6	10–37	18.2	67
Pink-headed Warbler (*Ergaticus versicolor*)	13	24	13–35	20.1	4–13	8.3	71

TABLE 2 *(Continued)*

Species	Hours watched	No.*	Sessions in minutes Range	Average	Recesses in minutes Range	Average	Constancy %
Chestnut-capped Warbler (*Basileuterus delattrii*)	12	9	27–70	44.6	16–35	23.3	66
Buff-rumped Warbler	6	5	5–97	38.8	8–30	18.5	68
(*Basileuterus fulvicauda*)	6	3	78–90	85.3	24–37	30.7	74
Scarlet-rumped Black Tanager	12	16	8–102+	29.3	5–32	11.8	71
(*Ramphocelus passerinii*)	16	21	12–104+	33.6	7–19	11.6	74
Crimson-backed Tanager (*Ramphocelus dimidiatus*)	10	10	16–89	39.0	11–36	21.9	64
Red Ant-Tanager	7.5	3	88–142+	117+	21–51	32.7	78
(*Habia rubica*)	7.5	4	40–140+	80+	23–44	32.5	71
Golden-masked Tanager	6	6	10–64	29.3	6–29	16.0	65
(*Tangara larvata*)	7	15	6–51	18.9	2–17	7.9	71
	10	20	2–47	22.6	2–11	7.3	76
Speckled Tanager	12.5	14	30–53	39.7	2–27	10.1	80
(*Tangara chrysophrys*)	12.5	14	20–77	37.8	3–23	11.4	77
Silver-throated Tanager	6	12	8–48	21.1	5–12	8.3	72
(*Tangara icterocephala*)	5	10	17–33	24.1	4–14	7.2	77
Gray-headed Tanager	6	4	45–97	60.8	20–55	29.3	68
(*Eucometis penicillata*)	6	3	66–97	76.3	25–66	45.5	63
Tawny-bellied Euphonia	10	5	77–108	86.8	13–43	29.8	74
(*Tanagra imitans*)	4.5	3	55–78	66.5	27–38	31.7	68
Variable Seedeater	8	12	12–33	22.5	7–22	14.4	61
(*Sporophila aurita*)	8	14	2–99	24.9	2–26	8.3	75
	9	5	29–148	74.2	8–22	17.2	81
Yellow-faced Grassquit	9	5	18–89	50.2	22–39	28.2	64
(*Tiaris olivacea*)	6	6	15–61	42.2	9–25	17.8	70
Blue-black Grosbeak	18	7	48–203	105.0	17–70	37.8	74
(*Cyanocompsa cyanoides*)	7.5	3	64–160	107.7	22–57	36.0	75
	12.5	3	99–364	227.7	18–19	18.5	95
	8	2	135–254	194.5	44	44.0	82
Buff-throated Saltator	12	18	6–52	25.7	6–34	13.2	66
(*Saltator maximus*)	6	12	2–39	19.1	2–16	9.7	66
Streaked Saltator	9	21	6–65	18.3	5–12	8.4	69
(*Saltator albicollis*)	4	4	7–108	43.3	7–30	14.2	75
Gray-striped Brush-Finch	9	6	41–70	52.8	21–68	34.0	61
(*Atlapetes assimilis*)	6.5	3	52–128	81.7	31–71	44.7	65
Orange-billed Sparrow	12.5	6	14–102	77.7	29–52	39.1	67
(*Arremon aurantiirostris*)	8.5	3	70–210	128.7	32–52	39.7	76
Black-striped Sparrow	11	7	33–99	59.4	12–25	19.4	75
(*Arremonops conirostris*)	12	7	47–94	70.3	13–35	21.9	76

* Number of sessions. The number of recesses is approximately the same.

Of these 137 birds incubating without help from a mate, 101 kept their eggs covered for from 60 to 80 per cent of the time they were observed, as calculated by the formula given above. Could one infer from this that 60 to 80 per cent of each individual's active day represents "normal" constancy for birds incubating alone and given at most a few billfuls of food by their mates? I began years ago to pay attention to this point in the published reports of other students, but since a large share of the pertinent data in these studies has been summarized in tabular form by Kendeigh (1952), we may most conveniently refer to his tables for the information we need. Tables 44 to 50 provide information on the incubation behavior of 165 individuals of passerine birds representing nearly as many species. Excluding those birds for which I supplied the information and which are accordingly included in the foregoing statements, in 50 cases the female is said to incubate alone receiving little or no food from her mate, and the average length of the sessions and recesses is given. The percentage of time these birds spent on the nest is not directly stated, but from these averages it is possible to pick out by simple mental arithmetic the cases in which this percentage falls below 60 or exceeds 80, if we recall that at 60 per cent constancy the sessions are 1.5 times as long as the recesses, and at 80 per cent constancy they are four times as long. Of these 50 birds, 11 incubated more than 80 per cent of the time and six incubated less than 60 per cent of the time, leaving 33, or approximately two thirds of the total number, that fall within the range of 60 to 80 per cent. Of the 11 birds that incubated more than 80 per cent of the time, five are said to have received a small amount of food from their mates (indicated by a single + in the tables); but possibly the quantity given to them was sufficient to cause a significant reduction in the time these females devoted to foraging. Three of these five individuals were American Redstarts (*Setophaga ruticilla*) that were fed by their mates. A fourth redstart which received no food on the nest incubated only 73 per cent of the time.

In addition to these small birds which take numerous recesses in the course of the day, in many larger species incubation is carried on by a single parent which receives no food from the mate, but takes only one or two recesses each day, so that the time on the nest cannot well be calculated by the formula we have been using. However, it should not be difficult to decide whether they are conspicuously more or less assiduous in incubation than the birds we have been considering. In the Little Tinamou (*Crypturellus soui*), the single bird that attends the nest, probably the male, takes each day one long absence, beginning early or late in the morning and leaving the eggs exposed for four or five hours continuously, so that often it incubates only about 60 per cent of the little more than 12 hours of daylight in Costa Rica. Presumably it sits uninterruptedly through the night. The Marbled Wood Quail (*Odontophorus gujanensis*) likewise takes each morning a single long recess, usually lasting from one hour and 40 minutes to three hours, so that on many days its constancy falls within the 60 to 80 per cent range, although as the eggs near hatching it is likely to exceed 80 per cent of the daylight period.

Although these and some other fairly large birds fail to cover their eggs a greater proportion of the time than do many small passerines that come and go far more frequently, among the non-passerines there are a number of species which incubate much more constantly. Since in most non-passerine families with altricial young both sexes incubate, these constant sitters are nearly all the parents of nidifugous chicks. Among them are a few species (IIA3a and IIB3 in my classification, 1957:72–73) of which the female or less often the male sits without taking food for much or all of the period of incubation. These pheasants, ducks, and emus are big birds which can live for weeks on their internal reserves, in a manner impossible for small passerines; and what is equally important, after the eggs hatch they do not engage in the strenuous occupation of hunting many billfuls of food which they must carry to the nest from a distance. On the contrary, their precocial chicks follow them and pick up the food where it is found. Hence it seems less important for them to pass through the incubation period with weight and strength unimpaired than in the case of parents who, after the eggs hatch, must throw themselves into a protracted course of the most strenuous activity of the whole reproductive cycle.

The attempt to hatch the eggs without taking food may, however, prove too much of a strain, as is evident from Tinbergen's (1958:246–248) observations on Eider Ducks (*Somateria mollissima*). During the four weeks of incubation, the duck leaves her nest for 10 or 15 minutes on every second or third day, to drink but not to seek food. This regimen is so exhausting that the emaciated females are sometimes forced to desert their nests and stagger to the water; they may even abandon eggs on the point of hatching in order to preserve their own lives. Domestic hens (*Gallus gallus*) usually leave their nests for a brief interval each day for food and water, yet even they show the effects of protracted incubation. Three broody hens generally ate one-fifth of their usual ration and took more water than solid food, on which diet they lost from 4 to 20 per cent of their body weight. A cock who was given no more than a broody hen ate died when she, and consequently he, passed three days fasting, while another cock and a non-broody hen lost from 23 to 33 per cent of their weight on the broody hen's diet (Wood-Gush, 1955 : 105).

Apparently the only altricial bird which incubates continuously without taking nourishment is the Emperor Penguin (*Aptenodytes forsteri*). But soon after the egg hatches, the emaciated male Emperor relinquishes the chick to a female, who for months has been away at sea eating and growing fat, and himself walks off to the water to recover from the effects of his long fast before returning with food for the young (Stonehouse, 1953).

In a number of birds, especially penguins and Procellariformes, the parent of either sex may fast for many days, up to 40 in the Adelie Penguin (*Pygoscelis adeliae*) and 32 in the Laysan Albatross (*Diomedea immutabilis*). These sea fowl seem to flout our generalization that in altricial birds incubating individuals not nourished by their mates require in most instances at least 20 per cent of the daily period of activity for finding food. But after fasting on the eggs for a number of days, these birds enjoy an interval of about the same length for rest and recuperation while the mate takes charge of the nest. Thereby they remain in fairly good condition for the strenuous task of nourishing the young with food which must often be brought from a great distance.

I believe that we may fairly conclude that, with the conspicuous exception of some nidifugous species, the great majority of birds which incubate alone, receiving no food from their mates or at most token feedings, cover their eggs from 60 to 80 per cent of the daytime. If they greatly exceed this upper limit, as in the Emperor Penguin, they require a long period of recuperation before they begin to feed their young. In species of which the sexes share incubation, in no case known to me does either partner sit for more than 80 per cent of the day, except in certain penguins, Procellariformes, and a few others, in which one or several days of continuous incubation is followed by an approximately equal period of freedom and foraging. The upper limit of constancy seems to be set by the requirement of self-maintenance in birds whose approaching parental activities demand that they pass through the period of incubation with no impairment of health and strength; for when well nourished by their mates, many birds sit far more continuously; and where precocial chicks can be fed with less strenuous exertion, large birds with considerable internal reserves have in a few instances evolved the habit of incubating continuously without taking food. The lower limit of constancy in incubation is apparently set by the heat requirements of the developing embryo.

Discussion of some extreme cases.—It should be instructive to consider some cases of passerine birds which depart from the 60 to 80 per cent range in one direction or the other. The most numerous examples of less than 60 per cent constancy in my records are provided by the smaller American flycatchers (Tyrannidae), many of which covered their eggs for only 50 to 60 per cent of the five to 12 hours that they were watched, while a few were even less attentive. Included among these flycatchers are two Sulphur-rumped Myiobiuses, one of which sat for 47.5 per cent of 12.5 hours and the other for 48.5 per cent of 5.5 hours; two Slate-headed Tody-Flycatchers, one of which incubated for 50 per cent of seven hours and the other for 49 per cent of six hours; two Golden-crowned Spadebills, of which the first sat for 56 per cent of five hours and the second for 57 per cent of five hours; two Sulphury Flat-bills, of which one incubated for 56 per cent of seven hours and the other for 52 per cent of 5.5 hours; a Yellow Flycatcher which incubated for 56 per cent of seven hours; two Torrent Flycatchers which sat for 56 per cent of five hours and for 44 per cent of 4.5 hours; a Bran-colored Flycatcher which incubated for 50 per cent of six hours; and a Bellicose Elaenia which occupied her nest for 53 per cent of seven hours. Other individuals of some of these species incubated slightly more constantly: a Slate-headed Tody-Flycatcher for 62 per cent of six hours; a Bran-colored Flycatcher for 63 per cent of five hours; and an exceptionally attentive Bellicose Elaenia for 80 per cent of 12 hours.

With the exception of the elaenia, which includes berries and other fruits in its diet, all of these little flycatchers are largely if not wholly insectivorous, and they need much time to catch enough small volitant insects to nourish themselves. Since at the season when these birds chiefly nest in Costa Rica hard afternoon rains are frequent, they must make the best of the sunny hours when flying insects are most active; and in fair weather, when chiefly they were watched, they rarely devote much over half the time to their eggs. That their inconstant incubation is caused by their diet rather than by their diminutive size is suggested by the fact that the Paltry Tyranniscus, one of the smallest of the flycatchers, which includes many mistletoe berries in its diet, incubates far more constantly—one for 67 per cent of six hours and another for 72 per cent of five hours. Even much bigger flycatchers which subsist largely on flying insects, like species of *Myiozetetes*, *Myiodynastes*, and *Tyrannus*, rarely exhibit a constancy in incubation exceeding 70 per cent; and one Vermilion-crowned Flycatcher sat for only 56 per cent of nine hours. But the big Boat-billed Flycatchers, which in the breeding season catch such substantial insects as cicadas, spend in the neighborhood of 80 per cent of the time on their eggs; the most constant in my records covered them for 88 per cent of 4.5 hours.

Among the cotingas, becards are most inconstant sitters. A Rose-throated Becard was in her nest only 56 per cent of 17 hours, and a White-winged Becard sat for only 45 per cent of 10 hours. The latter nested in the Tropical Zone, but the former was in the highlands at about 8,500 feet, in the chill and gloomy weather of the wet season. The thick walls of the bulky closed nests of these becards help to conserve heat and allow the birds to enjoy outings that do not differ much from their sessions in length.

Swallows also tend to spend much time away from their eggs, and their constancy in incubation is likely to fall below 60 per cent. Of the five species in which the female alone incubates for which incubation records are summarized by Allen and Nice (1952, Table 5), two, the Wire-tailed Swallow (*Hirundo smithii*) and the Rough-wing Bank-Martin (*Psalidoprocne holomelaena*) sat for less than 60 per cent of the time. Both are species of tropical Africa watched for many hours by Moreau (1939, 1940) and his helpers. The low constancy of swallows is apparently related to their fare of volitant insects, as with the American flycatchers. Since in the swifts, whose dietary habits are similar, the sexes seem to share incubation rather equally, it is unlikely than one individual will attend the nest much more than half the time. Hummingbirds also eat many tiny insects and spiders, which they either pluck from flowers and foliage or snatch deftly from the air. But, as a rule, they supplement this by much nectar, and this combination forms a very sustaining diet; so that, despite their diminutive size, and the fact that in the morning they often neglect their eggs while seeking cobweb and down to add to their nests, their constancy in incubation rarely falls below 60 per cent, and they sometimes sit an hour at a stretch.

Aside from the foregoing, my records contain only a scattering of instances of less than 60 per cent constancy and some are difficult to explain. One Orange-billed Nightingale-Thrush sat for only 49 per cent of 11 hours and another for 53 per cent of five hours; but a third incubated for 68 per cent of six hours. A Southern House Wren covered her first set of eggs for only 47 per cent of six hours; but while incubating her third set of the same season, this bird sat for 64 per cent of 9.5 hours. A Highland Wood Wren incubated for 49 per cent of nine hours. Kendeigh's (1952:40) very extensive records of incubation in the House Wren (*Troglodytes aedon*), obtained on 30 females over a total of 332 days, showed an average constancy of only 58.2 per cent (or 58.7 per cent if calculated from his data by my formula). But the Carolina Wren (*Thryothorus ludovicianus*) studied by Nice and Thomas (1948) covered her eggs for 73.4 per cent of 92 hours; perhaps this higher constancy was due to the fact that, unlike the other wrens mentioned, she was fed fairly often by her mate. Of my 46 records of incubating tanagers and finches, only one shows a constancy of less than 60 per cent. This was a Turquoise-naped Chlorophonia (*Chlorophonia occipitalis*), which incubated for only 57 per cent of five hours.

Of birds whose constancy exceeded 80 per cent, we need not pause to discuss the goldfinches (*Spinus*), which are fed liberally on the nest by their mates, nor the jays (*Psilorhinus* and *Calocitta*), which are often supplied with food by a number of attendants. Aside from these, the first important examples of extraordinary constancy in my tables are the tiny manakins. One Yellow-thighed Manakin incubated for 82 per cent of 12 hours and another for 84 per cent of 6.5 hours. A Blue-crowned Manakin sat for 83 per cent of 8.5 hours and another incubated for 85 per cent of 9.5 hours. One Orange-collared Manakin covered her eggs for 85 per cent of 12.5 hours, while another did so for 83 per cent of 11 hours. In contrast to these birds, one far larger Thrush-like Manakin sat for only 69 per cent of 12 hours and a second for 56 per cent of 11 hours. Manakins eat many fruits as well as small invertebrates; and in the tropical forest with its many predators, the long periods of immobility of the olive or greenish females on their very slight nests doubtless decrease the probability of drawing attention to them by their approach or departure.

A Blue-black Grosbeak incubated for 95 per cent of 12.5 hours, and another did so for 82 per cent of eight hours. The first was fed at long intervals by her mate. The second was not given food in our presence, although possibly she was fed away from the nest. Since she was within a short flight of a corn granary, where she helped herself to sustaining maize, she could quickly satisfy her appetite. In contrast to these two grosbeaks, another incubated for 73.5 per cent of 18 hours and a fourth for 75 per cent of 7.5 hours. A Variable Seedeater covered her eggs for 81 per cent of nine hours, but three other individuals of the species were considerably less attentive. A Scarlet-rumped Black Tanager incubated for 84.5 per cent of six hours, apparently held to her eggs by mistrust of another of her kind who was actively building only 4 inches away; for all my other Scarlet-rumped Black Tanagers were far less constant. A Green Honeycreeper incubated for 82 per cent of ten hours, and a Gray's Thrush for 86 per cent of seven hours. Leaving aside birds fed by their mates, only 12 of the 137 individuals of 82 species in which one parent incubates that are included in my records covered the eggs for more than 80 per cent of the observation period.

Obviously in an extensive sampling inexplicable extremes will be met. Some of the instances of unusually constant incubation are probably due to the presence of exceptionally favorable sources of food, as some of the cases of outstanding inconstancy may be the result of scarcity. Probably some of the birds which showed extremely high or low attentiveness on the day they happened to be watched would on other days have exhibited more conservative behavior. When we consider all the causes of variability, it is surprising that so large a majority of the recorded instances fall within the relatively narrow range of 60 to 80 per cent constancy. This is the more remarkable when we reflect that the 101 birds which came within this range showed a variation in the lengths of their sessions from less than one minute to 210 minutes, and even the averages of their sessions varied from 7 minutes to 129 minutes. The recesses ranged from less than one minute to 88 minutes, and the averages of the recesses from 3 to 51 minutes. (Longer sessions and recesses were recorded for birds whose constancy exceeded 80 per cent or fell short of 60 per cent.) But in all these so varied birds, with such contrasting rhythms of coming and going, the recesses were so adjusted to the sessions that the average session was not less than 1.5 times nor greater than four times the average recess, corresponding to a constancy in incubation of 60 to 80 per cent of the active period of the day.

ADDITIONAL FACTORS THAT INFLUENCE INCUBATION

In my earlier paper (1957) I searched, largely in vain, for radical changes in the pattern of incubation, involving the acquisition or loss of the habit of sitting on the eggs by one of the sexes, which seemed clearly attributable to the birds' mode of life. Only in the cases of the Emperor Penguin and of Gould's Violet-ear Hummingbird (*Colibri coruscans*) did such an alteration appear to be related to peculiar environments, which caused the male penguin to incubate without his mate's help, and the male hummingbird to take turns on the eggs, although in this family he usually remains aloof from the nest. But I recognized several factors which, although not changing the participation of the sexes in incubation, profoundly modified their movements. A wide separation of the breeding and feeding areas causes each incubating bird to take long sessions on the eggs, amounting to weeks together in some of the penguins and Procellariformes. Danger in approaching the nest also diminishes the frequency of changeovers, as in some of the small petrels; and perhaps the reduction of movement effected by very long sessions increases the security of exposed but inconspicuous nests, as in the diminutive, neutrally colored female manakins of the tropical forest. The necessity to guard the nest against neighbors eager to carry off its materials or to protect the eggs from predators causes each parent to remain on duty until relieved by its mate, as in gulls and many other fairly large birds that nest in colonies; and in a few birds whose exposed nests are solitary, the male guards during his mate's absences although he does not incubate, as in some jays. But when the nest is inconspicuous or well concealed, the two sexes together may fail by a good deal to keep it constantly attended, as in toucans, some antbirds, and a number of ovenbirds (Furnariidae). (See Table 1.)

As we have just noticed, the character of a bird's diet strongly influences the frequency of its comings and goings during incubation. Birds which subsist largely upon small volitant insects, as some of the American flycatchers and swallows, are the most impatient sitters; but if tiny insects and spiders are supplemented by copious draughts of nectar, as with hummingbirds, the more sustaining fare permits more constant incubation. It appears that the more substantial a bird's food, the longer its sessions on the eggs. Females liberally supplied by their mates or other attendants can incubate almost continuously, as do hoopoes, jays, goldfinches, siskins, and waxwings, or even quite uninterruptedly, as do hornbills. All of the foregoing factors may be considered constant, because they are integral parts of a bird's life history and influence it rather equally from day to day. In addition to these, a few other constant factors, such as the bird's size and temperament, seem worthy of our examination; and then there are the variable factors whose intensity often changes from day to day or hour to hour, like temperature and rainfall.

Size of the birds.—When we survey the incubation habits of birds as a whole, we find many of the larger kinds remaining on the nest without taking food for periods which would be fatal to the smaller kinds. The shorter sessions of the latter, their more frequent comings and goings, reflect their more rapid metabolism and their inferior capacity for storage, whether of reserves of fat in their tissues or undigested food in stomach or crop. But the biggest birds are hundreds of times as heavy as the smallest; and we cannot deduce from these facts, without further investigation, that less striking contrasts in size, as between members of the same family, have much effect upon the rhythm of incubation. Yet the discovery by Gibb (1954) that in titmice the time devoted to feeding varies inversely with body weight suggests that even in a single family there may be a positive correlation between size and constancy of incubation. In an investigation of this sort, it is desirable to know the weights of the birds; but since in many cases this information is lacking, I shall use their lengths as given in Ridgway's "Birds of North and Middle America." The dimensions of the eggs will also be employed as an indication of the birds' relative bulk and weight. Amadon (1943) demonstrated that, in a homogeneous taxonomic group, the weight of a bird may be calculated from the measurements of its eggs.

Of the birds whose nesting I have studied, the woodpeckers exhibit the greatest range in size. The largest is the Pale-billed Woodpecker (*Phloeoceastes guatemalensis*), about 32 cm in length. I spent all of one afternoon and all of the following morning watching a nest of this big woodpecker that contained two eggs. The female sat continuously for 266 minutes in the forenoon. The male, who was in the hole nearly all the rest of the time and took charge by night, remained at his post continuously for 1174 minutes (19 hours, 34 minutes), which is the longest period of attendance that I have timed for any woodpecker. But the single session which the female took in the course of the day was exceeded by a session of a female Golden-olive Woodpecker, a bird only 20 cm long, which sat for 297 minutes (nearly five hours) continuously, although all the other diurnal sessions by both sexes were much shorter. In contrast to the Pale-billed Woodpecker, the far larger Ivory-billed (*Campephilus principalis*), about 46 cm long, exchanged places on the eggs about eight times a day, thus taking sessions that averaged less than two hours (Tanner, 1941). Leaving aside the relatively huge Pale-billed Woodpecker, my records reveal no correlation between the bird's size and the length of its sessions in this family. The Olivaceous Piculet, a pygmy woodpecker only 8.5 cm long, frequently sits for over an hour at a stretch and sometimes remains in the hole for nearly two hours. In sharp contrast to this, in 38 hours of watching at five nests of the Golden-naped Woodpecker, whose length is about 17 cm, the longest session that I observed lasted only 51 minutes, and sessions exceeding 40 minutes in length were rare. In the slightly smaller Red-crowned Woodpecker each sex may take sessions which average about an hour, but some pairs incubate much less constantly.

The pigeons and doves show a considerable range in size. Of those that I have watched, the largest, the Band-tailed Pigeon (*Columba fasciata*) is about 35 cm long and lays eggs about five times the volume of those of the smallest, the Ruddy Ground-Dove (*Columbigallina talpacoti*), which is about 16.5 cm long. Yet these two pigeons and all those intermediate in size incubate in essentially the same fashion, the male sitting continuously for seven to nine hours each day, and the female normally covering the eggs all the rest of the time.

In the American kingfishers, on the contrary, the larger and smaller species have radically different incubation patterns. A pair of big Ringed Kingfishers (*Ceryle torquata*), whose length is about 38 cm, replaced each other once daily, in the morning, so that the male and female sat through alternate days and nights. In the smaller Amazon Kingfisher (*Chloroceryle amazona*), length 27.5 cm, and Green Kingfisher (*C. americana*), length 19 cm, I found that the mates changed places in the burrow several times daily and the females incubated every night. But the big Ringed Kingfishers seemed unable to take their 24-hour periods in charge of the eggs in a single unbroken session, and each afternoon the member of the pair on duty sallied forth from the burrow for refreshment. The longest uninterrupted diurnal sessions that I timed lasted from five to seven hours, which is about the same as the longest sessions of the far smaller Amazon Kingfisher. Moreau (1944) found that the Half-collared Kingfisher (*Alcedo semitorquata*) takes sessions an hour or two in length in tropical Africa.

Among the trogons, the largest species that I studied, the Quetzal (*Pharomachrus mocinno*) is 35 cm long without including the male's long upper tail-coverts, and it lays eggs about 2.5 times the volume of those of the smallest, the Black-throated Trogon (*Trogon rufus*), which is about 23.5 cm long. Yet the big Quetzal takes shorter sessions, for those that I watched divided the day into three shifts and rarely stayed in the nest as much as four hours at a stretch by daylight. The male Black-throated Trogon, on the contrary, may sit for about eight hours without a break. Most of the other trogons I have watched resemble the Black-throated Trogon in their pattern of incubation, except the Mexican Trogon (*T. mexicanus*), in which I found considerable variation from pair to pair. One female Mexican Trogon, after spending the night on the nest, sat continuously through the morning and until 1:10 PM. Her unbroken fast of 19 or 20 hours was far longer than any I recorded for the larger Quetzal. In this family, as with the pigeons, there seems to be no relation between the size of the birds and the lengths of their sessions on the eggs. Perhaps the more frequent changeovers of the highland Quetzal are caused by the lower temperatures and more rapid expenditure of energy at greater altitudes.

Of the antbirds I have studied, the largest, the Great Antshrike, 19 cm long, was watched for a whole day, during which the male's sessions averaged 192 minutes and the female's 111 minutes. One of the smallest was the White-flanked Antwren, whose length is only nine cm. In this species, the male's sessions averaged more than 83 minutes, the female's 119 minutes. The male antshrike's longest session was 238 minutes, his mate's 188 minutes; the corresponding figures for the little antwren are more than 174 minutes and 140 minutes. But the antshrikes kept their eggs covered 96 per cent of the time; while the antwrens, which took surprisingly long intermissions between the sessions of male and female, warmed theirs only 76 per cent of the day. An antbird of intermediate size, the Plain Antvireo, 10.5 cm long, was watched for 17 hours, in which the male's sessions averaged more than 117 minutes, the female's 65 minutes, and the eggs were covered 95 per cent of the time. A nest of the Spotted Antbird, very nearly the size of the last species, was studied for 13 hours, during which the male's sessions averaged 113 minutes, the female's 109 minutes, and the eggs were covered 92 per cent of the day. In this family my records show slightly more constant incubation by the larger species; but the differences are not so great as one might expect from the great disparity in the sizes of the birds, which is suggested by the fact that the eggs of the Great Antshrike are about 5.5 times the volume of those of the White-flanked Antwren, 2.7 times the volume of those of the Spotted Antbird.

Among the American flycatchers, the biggest species, the Boat-billed Flycatcher, 22.5 cm long, was by far the most steadfast sitter. One female took sessions which averaged 45 minutes and covered her eggs for 77 per cent of six hours; the sessions of another averaged 30 minutes, and she was on the nest for 78 per cent of ten hours. Some of the very small flycatchers are, as we have learned above, most inconstant sitters. On the other hand, some of the larger flycatchers are no more assiduous than others much smaller. During ten hours, one Tropical Kingbird, whose length is 21 cm, took sessions averaging 51 minutes and was in the nest 67 per cent of the time. During eight hours, another kingbird's sessions averaged 32 minutes and she was on her eggs 73 per cent of the time. Watched all day, a Streaked Flycatcher, 20 cm long, took sessions averaging 30 minutes and was in her nest box 71 per cent of the time. Turning now to the far smaller Paltry Tyranniscus, which is only 9.5 cm long, my records show that during five hours one female's sessions averaged 32.5 minutes and she was attentive 72 per cent of the time. In six hours, the sessions of a second tyranniscus averaged 27 minutes and she covered her eggs 67 per cent of the observation period. As already suggested, the tyranniscus's constancy, unusual for so small a flycatcher, is a consequence of her diet of mistletoe berries.

These and a number of other records of incubation that I have analyzed suggest some correlation between size or weight and the constancy of sitting of birds in the same family. The larger birds tend to take longer sessions and to keep their eggs covered a greater proportion of the day. But there are many irregularities and exceptions, and some small birds sit far more steadfastly than related species several times as big. Even in a single species in the same locality, some individuals may come and go twice as often as others, although the percentage of the day which they spend on the nest may be about the same. Differences in food, and perhaps also in temperament, seem to be in part responsible for these variations in attentiveness.

Number of participants.—Does a bird sharing incubation with its mate, and perhaps also with other individuals, take sessions longer or shorter than it would take if it had sole charge of the eggs? Because birds on the whole adhere so strictly to their hereditary pattern of incubation, it is difficult to find in a single species nests at which both sexes incubate and others where a single parent is in charge, which would provide the best material for investigating this point.

Only a few instances of such a radical departure from the normal pattern of incubation have been reported. One of the most interesting is that of a domestic pigeon (*Columba livia*) which undertook to incubate alone a set of eggs which had been fertilized by a male with whom she did not form a pair. She sat almost continuously and, except for brief absences for food and drink, remained covering her eggs during the middle hours of the day, when the male would ordinarily have been present (Goodwin, 1947).

In contrast to this, when two male Ring-necked Doves (*Streptopelia risoria*) formed a pair, built a nest in an aviary, and were given the egg of another pigeon to incubate, they sat side by side upon the nest all day, but at night left the egg exposed while they went to roost on a perch (Neff, 1944). The sex which does not normally incubate or brood the young by night scarcely ever does so in response to unusual circumstances. Although a male Mockingbird (*Mimus polyglottos*) assumed sole charge of four nestlings a few days old, whose mother had been eaten by a cat, and fed them faithfully, he neglected the maternal role of covering them by night, with the result that they soon died of exposure (Laskey, 1936). When a male Eastern Bluebird lost to a cat his mate which had been incubating for nine days, he did not himself attempt to hatch the eggs, but went off and on the second day returned with a new partner, who strangely enough took over the incubation of the eggs she had not laid, and despite their two days' exposure to chilling temperatures, hatched four of the set of six (Hamilton, 1943).

On the other hand, Walkinshaw (1944) reported on a male Field Sparrow (*Spizella pusilla*) which on one occasion brooded by night young a few days old; but sporadic sitting of this sort is most unusual. Almost unique in the annals of ornithology is the case of the male Tree Swallow (*Iridoprocne bicolor*) whose mate died three days after she started to incubate, and who then assumed full charge of the nest, hatching all five eggs on the fifteenth day (Kuerzi, 1941). Similar behavior is exhibited by the male Bobwhite, which, when his incubating mate is lost, may take over the eggs, attending them by day and night (Stoddard, 1946). Yet even if the hen does not die, the male Bobwhite may hatch the eggs; and this habit is evidently related to the simultaneous incubation by the male and female of a pair of Red-legged Partridges (*Alectoris rufa*) of two sets laid by the female. So, too, does Skead's (1954) observation that in the Cape Wagtail (*Motacilla capensis*) either sex may incubate by night become explicable when we recall that in other wagtails both parents regularly sleep on the nest (Moreau, 1949*a*).

But such departures from the normal routine of incubation and brooding the young are rare among birds, so that, when we wish to investigate the influence of the number of participants on the constancy of sitting, we must on the whole be content to compare different species of approximately the same size and diet, in one of which both sexes incubate and in the other a single sex; although this method leads to rather precarious conclusions, as the two species will probably differ in other ways.

When the sexes alternate on the nest, two factors are at work to modify the lengths of the sessions in contrary directions. On the one hand, the longer periods which one bird enjoys for feeding, while its mate takes charge of the eggs, should allow it to fortify itself well in preparation for a long session when it returns to the nest. One sometimes observes this effect at a nest where a single parent incubates, for often an unusually long session follows an exceptionally long recess, whereas a short session follows a short absence. On the other hand, the absent partner's eagerness to return to the eggs may curtail the session of its mate, who without this interruption would remain longer on the nest. When each bird stays at its post until relieved by its mate, the absent rather than the sitting partner usually determines the length of the session; but it is probable that over the generations the recesses of one partner have been nicely adjusted to the needs of its fasting mate. Thus, in the Paradise Flycatcher (*Tchitrea perspicillata*), Moreau (1949*b*) found that the most frequent duration of the sessions, 30 to 40 minutes, was the same whether the session was terminated by the arrival of the mate or the incubating bird left spontaneously without awaiting relief. This suggested that the birds' movements were regulated by an internal rhythm, whose tempo was the same whether they were on or off the nest.

In a number of ovenbirds and toucans, the incubating bird frequently leaves the nest before its mate's return, as though tired of sitting in the dimly lighted nest chamber; and the eggs are in consequence left unattended for many minutes each day, as in small birds of which a single sex incubates. In these cases there is no suspicion that the sessions have been curtailed by the partner's eagerness to take over the eggs. The sessions of toucans are short for such large birds, those of *Aulacorhynchus* and *Pteroglossus* rarely exceeding an hour and averaging about half an hour (Table 1). Van Tyne (1929) found that even the larger *Ramphastos sulphuratus* were during the first few days of incubation surprisingly restless and frequently stayed with their eggs only 20 minutes to an hour before being relieved, or went off leaving the nest unattended. The sessions of *Xenops, Automolus,* and *Sclerurus* among the ovenbirds are perhaps no longer than one would expect of birds of their size and habits if a single parent incubated. On the other hand, the very long sessions of some of the small antbirds, often lasting two or even three hours, suggest an increased capacity for fasting resulting from the long recesses each enjoys while the mate takes charge of the nest. One would not expect a small insectivorous bird, incubating alone, to sit continuously for such long periods. The long sessions of both male and female Long-billed Gnatwrens, averaging over an hour and sometimes continued for an hour and a half, point to a similar conclusion, for this is a very small insectivorous bird.

Instances of the opposite effect of incubation by both sexes, the shortening of sessions caused by the mate's eagerness to return, are less dubious; for we often witness the reluctance to leave of the bird who has been sitting. Golden-naped Woodpeckers and Olivaceous Piculets at times linger in the nest with the mate who has returned prematurely to take over the eggs. For a woodpecker, the Golden-nape takes short sessions, rarely exceeding half an hour and never in my experience continuing for an hour; and I believe that this is caused by their great attachment to their nest hole, which serves as their dormitory through much of the year, and to which each is eager to return after a short absence.

When more than two birds share incubation, as in the anis (*Crotophaga*) and the Acorn Woodpecker (*Melanerpes formicivorus*), the shortening of sessions may be still more pronounced; for when four or more individuals desire turns on the eggs, none is allowed to remain long. Moreover, in these highly sociable birds the urge to be abroad with their companions is strong and frequently drives them from the nest even before relief has arrived. At a high, inaccessible nest of the Acorn Woodpecker which I watched for nearly 12 hours, four or possibly five birds of both sexes were incubating, and one replaced another every few minutes. The average of 108 sessions by all the cooperating woodpeckers was only 5.1 minutes. Once three changeovers took place in slightly over a minute; and the longest continuous session that I timed lasted only 17 minutes. Yet these birds did not always remain in the nest until relief arrived, and the four or five of them together attended the eggs for only 80 per cent of the 12 hours—although in other kinds of woodpeckers a single pair achieves a higher constancy in incubation. In California, Leach (1925) found Acorn Woodpeckers equally restless when attending their eggs.

Influence of the male on his mate's constancy in incubation.—When only the female incubates, the male, if he brings abundant food, may, as we have seen, greatly increase his mate's time on the eggs. In the Pied Flycatcher (*Ficedula hypoleuca*), von Haartman (1958) found a positive correlation between the frequency with which the male fed his incubating partner and the time she spent on her nest. When the male of one pair was removed, both the sessions and the recesses of his mate became longer, but the latter increased more than the former, with the result that her constancy in incubation fell from 79 to 58 per cent; and despite the longer intervals which she devoted to foraging, she lost weight.

If the male frequently approaches the nest without bringing food, he may be responsible for decreasing his mate's constancy of sitting, for his calls may draw her from the nest to fly and forage with him. Without this disturbing influence, she would remain longer on the eggs. Even if he stays to guard the nest instead of accompanying his partner on her outing, his too prompt return to assume this duty may bring her away before she has sat her full period. An Orange-billed Nightingale-Thrush whose mate never came near the nest took longer sessions than a neighboring female whose mate through much of the day returned, after she had been sitting for ten minutes or so, to resume his guardianship of the nest, which was the signal for her to begin her recess. Likewise, a Streaked Saltator whose mate seldom came to watch over the nest took longer sessions than another saltator whose partner was more eager to perform this service. The longest morning sessions of the second female were made during an interval of two hours in the middle of the forenoon when the male stayed beyond sight and hearing. The shortest session of the first saltator was the fault of her mate, who called her from the nest only seven minutes after her return from an outing. Except in large, powerful birds like jays and the biggest flycatchers, the habit of guarding the nest is not equally developed in all males, nor consistently followed by the same individual. On this point, the testimony of Nice (1937) for the Song

Sparrow (*Melospiza melodia*) and of Mickey (1943) for McCown's Longspur (*Rhynchophanes mccownii*) is in accord with my experience with the Orange-billed Nightingale-Thrush, the Streaked Saltator, and the Bran-colored Flycatcher. In birds like these, the unpredictable behavior of the males is responsible for wide fluctuations in the constancy of their incubating mates.

Influence of the type of nest.—Birds which build extraordinarily large or elaborate nests are often poor sitters, spending short periods on their eggs. I found this true of the castlebuilders (*Synallaxis*) with their great strongholds of sticks, the becards (*Platypsaris* and *Pachyramphus*) in their relatively huge nests entered through a narrow orifice in the side or bottom, and the bushtits (*Psaltriparus*) with their exquisite, lichen-covered, downy pouches. These birds neglect their eggs while they seek new materials for their cherished edifices or carefully put them in order. But the eggs in these thick-walled containers doubtless retain their heat better than in open, cuplike nests. The birds apparently enjoy active building more than inactive sitting in the dim interior; and everything works out well in the end—unless, indeed, the bulky, conspicuous nest attracts the attention of some despoiler. Hummingbirds, too, devote much time to adding material to their nests when they might well be incubating. Their beautiful, little, lichen-studded chalices, no matter how well insulated on the bottom and sides, let the heat escape above when the bird is absent, and in this case the time lost to incubation by the bird's preoccupation with building is not compensated by the greater heat-retention of the nest. All these indefatigable builders bring additional materials chiefly during the sunny hours, when the eggs can best withstand exposure.

Temperament.—The constancy of incubation cannot be wholly accounted for by the birds' food, habits, and the number of cooperating partners. When all the obvious determining influences have been assessed, there remain inexplicable vagaries which we can attribute only to that mysterious factor in bird behavior which for want of a better term we call "temperament." Some birds are stolid and restful, others mercurial and restless. There seems to be no reason, either from size, diet, or mutual assistance, why the toucans should not incubate as constantly as their neighbors of the tropical forest, the trogons; but anyone who has watched those nervous, active, sociable, huge-billed avian clowns will understand that it must be more difficult for them to sit still for long periods than for the quiet, dignified, contemplative trogons. When suspicious of the watcher's blind, trogons bringing food to their nestlings will at times delay for seemingly interminable periods holding an insect in their bills.

When I studied the nesting habits of the Ringed Kingfishers along a Guatemalan river years ago, I marvelled that they could endure to pass such long, inactive periods at the end of their long tunnels in the sandy bank. But one day I watched a female who rested in a balsa tree with a large fish dangling crosswise in her heavy bill. For over two and a half hours, by my watch, she held it so, changing her position only from one limb to another of the same tree. The reason for this long period of abstention from her food I could not tell; but I knew then that extended intervals of inactivity were wholly in keeping with the kingfisher's nature—it is, after all, a typical angler!

On the other hand, some active, restless birds may take long sessions on their eggs. Among them are female jays, which while incubating are fed by their mates and sometimes also by other attendants, and jacamars of both sexes, which receive no food while in their burrows. Even in a single species, one finds individual differences in behavior of the sort that we ascribe to temperament. Thus Kendeigh (1952:67) noticed differences in the average rates of feeding the young of House Wrens which "must lie in the innate psychological or physiological constitution of the birds themselves."

Stage of incubation.—Do birds begin at once to incubate with the same assiduity they will display a few days later, or do they gradually "warm up" to their task? Are they more reluctant to stay away as their eggs near the point of hatching than they have been during the greater part of the incubation period? These, like so many others of the questions we have considered, have not yet been exhaustively investigated; yet answers are available for a growing number of birds. And as we might suppose, the answer varies with the kind of bird, and also the individual.

At times birds sit less constantly at the very beginning of incubation. Nice (1937:124) says of the Song Sparrow that in every case except K2's second record the longer periods off the nest came during the first two days of incubation. At a nest of the Scarlet-rumped Black Tanager, I watched for two hours in the middle of the morning and two in the middle of the afternoon during the period of egg laying and the beginning of incubation. On the day she laid her first egg, the female tanager sat for only 11 per cent of the four hours. On the next day, after she deposited the second egg, which completed her set, she incubated for 30 per cent of the four hours. On the following day, she was in the nest for 55 per cent of the same period, and five days later she incubated for 67 per cent of the four hours, which is almost full constancy for this tanager. But other Scarlet-rumped Black Tanagers worked up more rapidly to high constancy (Skutch, 1954:138). On the third or possibly fourth day after their set of four eggs was complete, a pair of Black-eared Bushtits together attended the nest for only 43.5 per cent of the first four hours of the morning. But nine days later, in the same period of the morning, they sat for 74.5 per cent of the time. The longest interval of neglect on the first morning was more than 78 minutes (I grew tired of waiting for their return), but on the later morning they were never absent more than 13 minutes at a stretch. They became far more attentive to their eggs as incubation advanced. In Honduras, I watched a pair of Groove-billed Anis (*Crotophaga sulcirostris*) that on the morning of the fifth day after their set was complete covered the eggs only 59 per cent of the time; but on the next-to-last and final days of incubation these same birds left their eggs unattended for only two minutes in the course of five hours. Davis (1940) found that the Smooth-billed Ani is similarly slow to begin incubation in earnest. On the other hand, Ruddy Ground Doves and other pigeons keep their two eggs almost continuously covered from the moment the second is laid.

In contrast to the slow increase in constancy of some tropical birds, northern birds often show a more rapid rise to full attentiveness after the completion of their set. Kendeigh's (1952) vast bulk of data on the House Wren revealed that although practically full constancy in incubation is attained by the day the last egg is laid, there is a slight increase in assiduity during the next three days, after which the female's total daily time on the nest remains fairly constant until the eggs hatch. Likewise in the Cedar Waxwing (*Bombycilla cedrorum*), Putnam (1949) found a slight increase in the percentage of time on the nest for the first three days after the completion of the set. On the other hand, Conder's (1948) study of the European Goldfinch (*Carduelis carduelis*) showed that practically full constancy was reached by the time the last egg was laid; and the same was found to be true of American Goldfinch, the Robin (*Turdus migratorius*), and the Yellow Warbler (*Dendroica petechia*) by Kendeigh, the American Redstart by Sturm (1945), and the tropical Bananaquit by Biaggi (1955). In all of these species, only the female incubates; but in the Black-headed Grosbeak (*Pheucticus melanocephalus*), in which both sexes cover the eggs, Weston (1947) found that continuous incubation began with the laying of the next-to-last egg. These and other birds show relatively slight daily changes in attentiveness after the completion of their set; and the fluctuations in constancy which occur in the course of the incubation period are likely to reflect variations in temperature or other environmental factors rather than growing attachment to the eggs.

Since many birds begin to sit in at least a desultory fashion on the day they lay their first egg and each succeeding day increase their time on the nest, we might expect that the larger the set, and the greater the number of days required to complete it, the more closely they would approach full constancy on the day the last egg is laid and we begin to measure the incubation period. Hence northern birds which lay large sets would reach normal constancy in incubation by the time they have finished laying, but tropical birds with smaller sets would require a few days longer. Although this consideration will help us to understand some of the observed divergences, it will not apply in all cases. Pigeons lay small sets yet begin at once to incubate continuously;

bushtits and anis produce sets twice as large yet require a number of additional days to warm up to their task of incubation. And in the Netherlands, the Great Tit (*Parus major*), despite its set of ten eggs, failed to incubate in the mornings of the two days following the laying of the last, not reaching high constancy until the third day. This was for first broods, but with second broods full constancy was attained by the time the set was complete (Kluijver, 1950).

It is a common observation that, as the day of hatching approaches, birds cling more steadfastly to their nests when we come near them, and are more likely to permit us to touch them than at earlier stages of the nesting. This increased attachment leads us to suspect that they devote a greater part of the day to sitting; but careful watching from concealment, or mechanical recording, usually fails to confirm this. One of the Ovenbirds (*Seiurus aurocapillus*) studied by Hann (1937) showed increased constancy in incubation as the date of hatching approached in 1936, but in the preceding year this same bird (No. 15, Table 2) failed to increase her total time on the nest as the days passed. A female Bananaquit watched for 102 hours by Biaggi (1955) sat less constantly during the last four days of incubation than during the seven preceding days, although some of these days had been just as warm. One of the Marbled Wood-quails (*Odontophorus gujanensis*) that I studied showed a tendency to shorten her morning outing toward the end of the incubation period, but the other quail did not.

The majority of studies fail to demonstrate an increase in attentiveness to the eggs as they approach the point of hatching, and we must conclude that, on the whole, the greater stanchness of the sitting parent in the face of apparent danger is not an indication of more constant incubation. After a bird has reached its normal attentiveness, which it generally does a few days after laying the last egg if not by the time the set is complete, it maintains this degree of constancy, often with irregular daily fluctuations, to the end of incubation, with rarely a definite increase as the chicks begin to chip their shells. As soon as the young escape and require food, the parent's constancy in sitting typically enters a period of steady decline, especially if only one parent incubates and broods. But if the male begins to bring food very soon after the nestlings hatch, he may in an initial spurt of activity fetch more than the little ones can eat. The female profits by this, and sometimes she is able to cover newly hatched young more constantly than she incubated her eggs (Skutch, 1953).

Rain.—The effect of rain on the length of the sessions and recesses of incubating birds may vary considerably according to whether it comes in the form of a short, swift shower or a long-continued downpour. The sudden, hard rainstorm sends birds to their nests and often keeps them there, shielding their eggs or nestlings. But if the rain is of long duration, it may make food more difficult to find, and so lengthen the bird's absences from the nest.

A sudden, hard shower may cause a bird to go to her nest to protect her eggs even before she has completed her set and begun to incubate, as I once witnessed at a nest of the Bellicose Elaenia. During a violent afternoon rainstorm, she covered her single egg in the wind-tossed open cup; but not until the second day following did she lay her second egg and begin regular incubation. At the other end of the nesting cycle, I once saw a female Yellow-green Vireo brood her three well-feathered nestlings in a hard downpour. Otherwise she had quite ceased to cover them by day or by night, and the following morning they left the nest.

The longest diurnal sessions of incubating birds are frequently taken during storms and showers. Nice (1937:124) reported of the Song Sparrow: "Two of K2's very long periods on—63 and 68 minutes—were both during storms, while the longest—71 minutes—occurred on a bleak and windy afternoon." Moreau (1940) said of the African Rough-wing Bank-Martin: "Very few spells of incubation by the Rough-wings exceeded 30 minutes. The longest, which lasted 50 minutes, was while rain was falling at nearly the rate of 1 mm a minute. There is no other indication of rain affecting brooding spells." The two longest sessions which the same author (1939) recorded for the Wire-tailed Swallow, lasting 23 and 61 minutes, were both associated with periods of rain. These long spells on the nest are the more significant when we recall that about 70 per cent of the sessions of this restless swallow lasted seven minutes or less.

In my own experience, too, several birds have taken their longest recorded sessions while rain fell. In 12 hours of watching, I timed 42 sessions of a Bellicose Elaenia, only two of which exceeded 27 minutes; these lasted 32 and 60 minutes, respectively, and were taken while rain fell. An Orange-billed Nightingale-Thrush sat continuously for 56 minutes beneath a slow rain in the late afternoon, although in ten hours of rainless weather her longest session was 21 minutes. A Streaked Saltator incubated for 65 minutes continuously in the rain, but her longest session otherwise was only 31 minutes. A Golden-masked Tanager sat for 51 minutes in a heavy shower; in rainless weather the longest session that I recorded for her was 27 minutes. A Silver-throated Tanager took a session of 43 minutes beneath the light rain that followed a torrential downpour. Her next longest session, in drier weather, lasted only 33 minutes. Although she sat in a closed nest, a Rose-throated Becard increased the lengths of both her sessions and her recesses during a hard rain in the afternoon. Other birds, however, have failed to lengthen their sessions while I watched them in the rain; but they were not exposed to the hardest downpours.

It is more revealing to consider, not the longest single session, but the general change in the character of incubation which rain, especially if long-continued, may effect. In the Guatemalan highlands at an altitude of 8,500 feet, I devoted a day to watching a nest of the White-breasted Blue Mockingbird which, unlike most passerines of the region, nests chiefly in the wet season. The morning was cloudy with a disagreeable chill in the air, but the rainfall was generally light and came in little showers of brief duration. In the afternoon, cold rain fell strongly and steadily. For the morning period (until 2 PM) the mockingbird's sessions on her eggs ranged from 12 to 42 minutes and averaged 20.6 minutes. Her recesses varied from 3 to 23 and averaged 9.2 minutes. During the afternoon of hard rain, her sessions ranged from 8 to 42 and averaged 21.2 minutes; her recesses ranged from 1 to 7 and averaged 3.7 minutes. Accordingly the rain caused scarcely any change in the average length of her sessions, but a marked reduction in that of her recesses. It brought her back sooner to her exposed and chilling eggs.

On a more heavily wooded part of the same mountain slope, a Slate-throated Redstart had her covered nest. An afternoon of hard rain affected her mode of sitting in a manner just the reverse of that of her neighbor the mockingbird. During 2½ hours of hard rain, her two sessions lasted 42 and 49 minutes, her two recesses 37 and 35 minutes. The average length of her sessions during the first eight hours of the day, when no rain fell, had been 35.9 minutes, the average of her recesses 14.6 minutes. The rain caused her to increase her sessions by about 25 per cent; but her recesses more than doubled in length.

I believe that we can account for the difference in the effect of hard rain upon these two birds by a consideration of their modes of finding food. The redstart breeds chiefly in the dry season and was caught in the midst of her nesting by the first hard rains of the year. She found in the air and amidst the foliage the small insects on which she chiefly subsisted. By washing and beating these to the ground, the rain made it more difficult for her to satisfy her appetite, hence her far longer absences from her eggs. The mockingbird, a wet-season nester, nourished herself principally with berries and small creatures she picked up from the ground. The rain hardly affected the abundance of the berries, and possibly even made her terrestrial prey more available by bringing the small invertebrates out from beneath the ground litter where there they lurked. Hence the mockingbird could eat her fill in a few minutes and return promptly to her rain-splashed eggs.

During a rainy afternoon, both the sessions and recesses of a Highland Wood Wren were shorter than on a sunny morning. While the sun shone, eight sessions averaged 19.0 minutes and eight recesses 20.1 minutes. On the rainy afternoon, seven sessions averaged 13.4 minutes and six recesses 12.3 minutes. This bird dwelt upon an excessively wet mountain, where cold, long-continued rains were of common occurrence, and she should have been adept at finding her food in the rain.

Very different behavior was exhibited by a Piratic Flycatcher incubating in a nest she had stolen from a Gray-capped Flycatcher. During a rainless morning she had taken sessions varying from 20 to 49 minutes, and recesses ranging from 5 to 18 minutes. But on an afternoon of slow, intermittent rain, I found her in the nest at 2:35; and she sat without interruption until nightfall. Such a radical change in the mode of incubation of a small bird, accustomed to taking short sessions and frequent recesses, is almost without parallel in my experience. She did not even take advantage of the lulls in the rain to sally forth for food, and she was not fed by her mate.

Temperature.—The relation between constancy of incubation and the temperature of the outer air has been discussed by Nice and Thomas (1948) and Kendeigh (1952). There is now available a considerable mass of observations showing that with passerine birds of a number of species the proportion of the day spent on the eggs drops as temperature increases. Birds tend to cover their eggs more continuously in cool weather than in warm, thereby compensating for the more rapid chilling of exposed eggs when temperatures are low. Such an adjustment might be achieved in three ways: by shortening the absences, by lengthening the sessions, or by both augmenting the sessions and reducing the recesses—which last would have the most pronounced effect.

Although the inverse correlation of temperature and attentiveness appears to be fairly general, at least in the passerines, the method by which this adjustment is effected varies from species to species and even within a species. Perhaps the most common method is the simultaneous shortening of sessions and lengthening of recesses as the temperature rises. This is shown clearly by Kendeigh's (1952) records for the Barn Swallow (*Hirundo rustica*), which by this double shift effected great changes in constancy with varying temperature, incubating 80.5 per cent of the time when the thermometer stood below 70 F (21.1 C), 72.4 per cent between 70 F and 75 F, 58.6 per cent between 75 F and 80 F, 38.0 per cent between 80 and 85 F, and 31.6 per cent above 85 F (29.4 C). A similar but less pronounced reaction to changes in temperature is suggested by Kendeigh's records for the Eastern Bluebird and the Chipping Sparrow (*Spizella passerina*). In the House Wren, the sessions became much shorter as the temperature rose, although the recesses first diminished, then increased slightly in length. In the Robin, the sessions were likewise abbreviated with rising temperature, although no consistent change in the length of the recesses was evident; and the percentage of the daytime spent on the nest fell from 78.1 per cent at 58 F (14.4 C) to 60.7 at 83 F (28.3 C). In the Catbird (*Dumetella carolinensis*) the recesses also changed little with variations in temperature, but the sessions first lengthened, then became shorter, as the thermometer rose from 63 F to 79 F. Unlike the other birds reported on by Kendeigh, the Wood Pewee (*Contopus virens*) took the longest sessions on the warmest days, her recesses remaining about the same.

The Great Tits studied in the Netherlands by Kluijver (1950) showed the double adjustment very clearly, reducing their sessions and prolonging their recesses as the temperature rose. Kluijver calculated that for first broods a rise of 1 C caused a reduction of eight minutes per day in the time spent on the eggs; but for second broods there was a reduction of 15 minutes per day for each additional degree of temperature. Although all nests showed lower constancy of incubation with higher temperature, the actual falling-off varied somewhat with the individual bird. In the Pied Flycatcher, experimental increases in the temperature of the nest box caused shortening of the female's sessions on the eggs, while her recesses remained the same (von Haartman, 1956).

In the nonpasserines, little attention appears to have been given to the influence of temperature on constancy of incubation. In the Redhead (*Aythya americana*), Low (1945) found that a female incubating in a replacement nest left her eggs more often and spent fewer hours on them than did females with first layings, and he attributed this lower constancy to the higher temperature prevailing when the duck renested. Stoddard (1946) stated that the single daily recess of the incubating Bobwhite varied in length from an hour or two when the weather was cool and showery to as much as seven hours on fine, warm days.

These variations in the constancy of sitting are not always evident when we compare records of the same bird made on two days which differ considerably in temperature. Thus, in the Rufous-sided Towhee (*Pipilo erythophthalmus*), Davis (1960) found no consistent correlation between constancy of incubation and temperature; two females who were watched for many hours responded to fluctuations in daily temperature in diametrically opposite ways. Temperature is only one of the factors which affect the constancy of attendance, and it is sometimes necessary to have a considerable mass of data in order to demonstrate the temperature effect.

The influence of temperature on incubation is shown not only by the different constancy of sitting on colder or warmer days, but likewise by hourly variations on the same day. Many birds spend more time on their eggs in the cool of the morning and evening than in the middle of the day when the air is usually warmest, although this daily march of attentiveness is by no means universal. I have noticed the decline in constancy as the morning grows older especially in small flycatchers; but it is difficult to decide whether this is a direct effect on the birds of the rising temperature, or whether they sit less constantly after the sun is high because insects become more active and fly-catching yields higher returns. At these times, an insect which blunders temptingly close entices them from the nest to snatch it up. In very warm weather, however, birds may remain away from their eggs, especially if these are in a box or hollow tree heated by the sun, although they do nothing but loaf in a cooler spot.

In unseasonably cool weather, which increases the bird's need of nourishment at the same time that it makes insects harder to find, the normal relation between temperature and constancy of sitting may break down completely, for the parent neglects the eggs for long periods while it searches for food. This effect of cold and wet or snowy weather is especially noticeable in small insectivorous birds like swallows and flycatchers. Among the latter, the Eastern Phoebe (*Sayornis phoebe*) will sometimes permit its early sets of eggs to chill in a late snowstorm, which scarcely affects the incubation of hardier birds that are sustained on their nests by their mates, like siskins and jays.

THE RHYTHM OF INCUBATION

The comings and goings of some incubating birds are so regular that they almost seem to be governed by the clock. The phrase "rhythm of incubation" aptly describes their movements. Other birds are far more erratic. Possibly this contrast arises from the circumstance that the former enjoy a steady, dependable supply of food, whereas the latter have variable luck in foraging, sometimes satisfying their hunger quickly, at other times taking long to find enough food, often no doubt returning to the nest before they are satisfied, with the result that they fly off to forage again after a session shorter than normal. In other cases, it appears that interference by the male causes irregularities in the lengths of the female's sessions.

As an example of a bird with a remarkably regular rhythm we may take a Collared Redstart (*Myioborus torquatus*) nesting in the Costa Rican highlands, which on the morning of 23 April 1938 incubated in minutes as follows:

Sessions	27	30	28	28	29	29	28	29
Recesses	9	9	7	8	12	9	11	13

A Silver-throated Tanager, whose nest I watched on the morning of 29 May 1943, was almost as regular in her movements. Her record in minutes is:

Sessions	25	25	29	20	17	20	23	22	27	33
Recesses	5	7	5	7	4	7	14	5	11	

As an example of extreme and most unusual irregularity in coming and going, we may take the four-hour record of a Streaked Saltator whose mate was inconsistent in guarding the nest in her absence. Save for the erratic conduct of her partner, there appeared to be no disturbing element in her surroundings. On 29 May 1939 her periods in minutes were:

Sessions	27	108	7	31	
Recesses	7	8	10	16	30

In the regularity of their movements, most of the birds that I have watched during incubation have fallen somewhere between these extreme examples.

THE DURATION OF INCUBATION

We know the normal duration of incubation in all those species of birds of which the incubation period—in the technical sense—has been measured. But the incubation period is determined by the speed of embryonic development, and its termination puts an end to typical incubation behavior by providing other occupations for the parents, who now devote an increasing pro-

TABLE 3

INCUBATION OF INFERTILE OR SPOILED EGGS

Species	Length of attendance in days	Incubation period in days	Authority
*Black-crowned Night Heron (*Nycticorax nycticorax*)	40, 49, 51	22–24	Noble and Wurm, 1942
Wood Duck (*Aix sponsa*)	62	about 30	Leopold, 1951
Bobwhite (*Colinus virginianus*)	56	23	Stoddard, 1946
*Sarus Crane (*Grus antigone*)	70–72	about 32	Walkinshaw, 1947
Smooth-billed Ani (*Crotophaga ani*)	24	13–15	Davis, 1940
Black-chinned Hummingbird (*Archilochus alexandri*)	24	14	Bené, 1946
White-tailed Trogon (*Trogon viridis*)	51	about 17	Original
Yellow-shafted Flicker (*Colaptes auratus*)	30	11–12	Sherman, 1952
Common Crow (*Corvus brachyrhynchos*)	21, 22, 24 26, 28, 32	16–18	Emlen, 1942
Carolina Chickadee (*Parus carolinensis*)	24	12–13	Odum, 1942
Blue Tit (*Parus caeruleus*)	25	13–15	Gibb, 1950
European Wren (*Troglodytes troglodytes*)	25, 26, 51	15–17	Armstrong, 1955
Gray's Thrush (*Turdus grayi*)	17–18, 19	12	Original
European Robin (*Erithacus rubecula*)	35, 48	13–15	Lack, 1953
Eastern Bluebird (*Sialia sialis*)	21, 21, 21	13–14	Laskey, 1940
	33		Thomas, 1946
Chestnut-capped Brush-finch (*Atlapetes brunnei-nucha*)	19	about 15	Original
American Goldfinch (*Spinus tristis*)	23	13	Berger, 1953

* In captivity.

portion of their time to feeding their young. Only when the eggs fail to hatch can the bird's impulse to incubate run its full course and spontaneously exhaust itself. Hence observations on the period that infertile or spoiled eggs are attended provides an index of the duration of the internal drive that expresses itself in sitting in the nest. Table 3 gives a number of instances of this sort that have come to my attention, and additional cases are recorded by Nice (1943:222–223) and Berger (1953). Most birds seem to remain faithful to their eggs for an interval at least 50 per cent longer than is normally required to hatch them, and many continue to incubate for twice the usual period, or even more. Thus the strength of the impulse to incubate provides a wide margin of safety; for if eggs fail to hatch within a few days of the normal time, they scarcely ever produce living chicks.

In sharp contrast to many other kinds of birds, some pigeons will desert their eggs if they fail to hatch in the normal time. They abandon eggs whose hatching is overdue, even if the chicks are already breaking out of the shell and peeping, as can be proved by removing the eggs from the nest for one day, so that they hatch 24 hours late. In these pigeons, the cessation of incubation is caused by the formation of "pigeon milk" in the parents' crop, whereas in other birds the shift from incubation to other parental activities is caused by the actual appearance of the young. Some domestic pigeons, however, have lost this fine adjustment and will continue to attend the eggs longer than the normal incubation period (Heinroth and Heinroth, 1959: 31–32).

Nice (1943:223–224) has collected a number of records of incubation by birds who either had not laid eggs or had lost them. Such behavior is far from common, and only one example of it has come to my attention in the field. In May of 1959, I found a Gray-headed Tanager incubating in an empty nest in a privet hedge in front of my house. She continued to sit by day and by night for at least two weeks—long enough to hatch eggs if they had been present. One morning I watched for five hours, during which she took three sessions, lasting 25, 70, and 61 minutes, and three recesses which continued for 29, 48, and 52 minutes. Her constancy was only slightly less than that of other Gray-headed Tanagers which I watched while they incubated eggs in the normal manner. This erratic female was attended by a mate. Whether she laid and lost eggs or never had any, I do not know.

IS HIGH CONSTANCY IN INCUBATION AN ADVANTAGE?

When we recall that many birds manage to hatch out their eggs by covering them for short stretches and leaving them exposed much of the day, we may well ask why others practice such long and, from the human point of view, tiresome sessions in their nests. What are the advantages of more continuous sitting? We might look for such advantages in two directions: constant sitting might increase the safety of the parents or nest, or of both, or it might accelerate the hatching of the eggs. This reduction of the incubation period should less directly reduce losses by diminishing the time the eggs are exposed to predation. A population of birds whose incubation period is 15 days and which loses 30 per cent of its nests to predators before hatching—not an unusually high mortality in some regions—suffers an average loss of 2 per cent per day; so that a reduction of the incubation period to 12 days should increase its hatching success by about 6 per cent.

In a bird like Leach's Petrel (*Oceanodroma leucorhoa*), which runs the gantlet of the Great Black-backed Gulls (*Larus marinus*) every time it approaches its nesting ground except on moonless nights, the long intervals between changeovers, which reduce the number of the parents' visits to the islands, are an obvious advantage and even necessary for the continued existence of these little birds of the high seas (Gross, 1935). In this instance, it is the parent rather than the egg in its subterranean chamber which is jeopardized by the bird's approach or departure. More often the adult bird incurs no special perils in the vicinity of its nest, although the latter may be betrayed to predators by the revealing movements of its attendants. The avoidance of unnecessary approaches and departures assumes special importance in small, inconspicuous nests exposed to high predation, like those of many antbirds, manakins, and cotingas of the tropical forest. While the dull-colored birds sit motionless on their diminutive nests they are inconspicuous enough, but the movement of coming or going is likely to cancel the value of their cryptic attire. Hence long sessions with infrequent recesses or changeovers seem an integral part of the system of concealment of these forest birds. On the other hand, those flycatchers which hang their pensile nests conspicuously from a dangling twig may come and go as freely as they please; for with them the nest's safety seems to depend upon its inaccessibility rather than its invisibility.

The eggs in these small, inconspicuous nests of the tropical forest frequently require long to hatch, which makes it obvious that short incubation periods depend upon something more than long periods of patient sitting. So many factors conspire to determine the lengths of incubation periods, and the subject is shrouded in such great complexities, that it is only by comparing species rather closely related that we can hope to discover some connection between constancy of sitting and rapidity of embryonic development. Fortunately, certain families provide the materials we need for such a comparison. Among the swallows, the Rough-wing Bank-Martin studied by Moreau (1940) had the exceptionally long incubation period of 19 days and showed the unusually low constancy of 31 to 66 per cent. Since other swallows that incubate more assiduously hatch their eggs in 14 to 16 days, this appears to be an instance of retarded embryonic development caused by inconstant warming. Such a long incubation period is apparently not detrimental to a bird that nests in a burrow. In the thrushes, a number of studies show that species of *Turdus*, including the Robin and Gray's Thrush, incubate more steadily than bluebirds (*Sialia*) and nightingale-thrushes (*Catharus*), and it is perhaps for this reason that the larger eggs of the first-mentioned genus hatch in 12 or 13 days, whereas those of the last two require 13 to 15 days of incubation. I have found two species of wood wrens (*Henicorhina*) inconstant sitters, and their eggs hatch in the remarkably long period of 18 to 20 days. It is noteworthy that in these cases where it seems that exceptionally long incubation periods are the result of inconstant sitting, the birds' constancy falls below 60 per cent. Some of the small American flycatchers with pensile nests have very long incubation periods, up to 18 or even 23 days; and this may be a consequence of their restless sitting; yet other small flycatchers with cuplike nests hatch their eggs in much less time, even if they are scarcely more attentive to them, so that other factors seem to be at work here (Skutch, 1945).

Instances of the acceleration of embryonic development by exceptionally constant sitting are difficult to find. In the Fringillidae, the high constancy of goldfinches, siskins, and other cardueline finches that are supported on the nest by their mates, does not seem to have caused a reduction of incubation periods, which in this group are 11 to 13 days, as in many other finches whose constancy in incubation rarely exceeds 80 per cent. So, too, the eggs of the Black-headed Grosbeak and the Rose-breasted Grosbeak (*Pheucticus ludovicianus*), in which the male and female together keep the nest almost continuously covered, hatch in 12 or 13 days, like those of finches in which only the female sits. Possibly the incubation by the male grosbeaks fails to be effective because they lack bare brood patches. In the wood warblers, for which a generous amount of information has become available, I can detect no certain correlation between the attentiveness of the incubating female and the length of the incubation period. But Stoddard (1946) stated that when eggs of the Bobwhite are incubated by bantam hens, which take a daily recess of about an hour instead of the quail's several hours, they hatch in 22 to 23 days (average 22½) instead of 23 to 23½ days, as when they are attended by the Bobwhites themselves.

To sum up, there is some evidence that when the constancy of sitting falls below 60 per cent it retards hatching, but it does not appear that an increase of constancy above 70 or 80 per cent abridges the incubation period, at least in passerines and in the milder weather when most birds nest. In this connection, it is of great interest that the shortest incubation period recorded by Kendeigh (1952:44) for a House Wren whose constancy in incubation was known, one of 12 days (13 days by the more usual method of reckoning), was achieved by a bird which incubated only 43.6 per cent of the day, but in a box exposed throughout the day to the full glare of the sun, which sometimes raised the temperature of the interior to 100 F in the middle of the day. Thirty-two other incubation periods were one to three days longer, by House Wrens which sat approximately 58 per cent of the daytime, but at lower average air temperatures. It may be significant that with constant heat in an incubator the eggs of the Skylark (*Alauda arvensis*) hatched in 13 to 14 days, although with the less constant heating that they receive from the female lark they hatch in 11 or 12 days (Jourdain *in* Bent, 1942:317). Perhaps in the incubator the humidity was less favorable. On the whole, it does not appear that the more constant incubation which might be achieved by many passerine birds if the male shared in this occupation, or fed his mate liberally while she sat, would significantly accelerate hatching. In this respect, as in others that were considered earlier, incubation or non-incubation by the male appears to be largely indifferent to the welfare of many species, so that we may regard this as a non-adaptive character, resulting from chance mutations, and not closely controlled by natural selection.

SUMMARY

The terms "sessions" and "recesses" are suggested as the least cumbersome designations of a bird's periods on and off the nest. Methods of computing the percentage of time devoted to incubation are discussed. In those species in which a single parent incubates, most individuals keep the eggs covered from 60 to 80 per cent of their period of diurnal activity; and this may be regarded as average or normal constancy. Constancy above 80 per cent is shown chiefly by birds well nourished on the nest by attendants and by those which enjoy exceptional advantages in finding food during their recesses. Constancy below 60 per cent is shown chiefly by small birds, such as American flycatchers, which subsist largely on small volitant insects. Nidicolous birds which fast on the nest for several days together require correspondingly long periods for foraging and recuperation, so that with them such protracted sitting is feasible only when the sexes alternate on the eggs. But nidifugous birds, which provide for their chicks with less strenuous exertion, so that it is less imperative for them to pass through the period of incubation without loss of vital reserves, may fast throughout this period. Sometimes, however, their attempt to do so causes their exhaustion and consequent abandonment of the eggs.

Other factors which influence the constancy or rhythm of sitting are the size of the birds, the number which share incubation at the same nest, the behavior of the male when he does not incubate, the type of the nest (whether open or covered, etc.), the bird's temperament, rainfall, and the temperature of the air. Although there may be a slight or, in some species, a pronounced increase in attentiveness during the first few days after the completion of the set, the stage of incubation has on the whole little influence on constancy of sitting.

When their eggs fail to hatch, most birds continue to incubate them at least 50 per cent longer than is normally required to hatch them, and they may continue for twice or even three times the normal period. An outstanding exception is provided by pigeons, some of which fail to incubate even a day beyond the usual time of hatching.

In species of birds whose constancy of incubation falls below 60 per cent, the incubation period is sometimes longer than in related species which sit more assiduously. Those exceptional birds which nest amid snow and ice must keep their eggs constantly covered lest they freeze. But in the milder weather when most birds breed, it does not appear that a constancy above the 60–80 per cent range, which might readily be effected if the male shared incubation or fed his mate liberally on the nest, would materially reduce the length of the incubation period, thus diminishing losses to predators by decreasing the time the eggs are available to them. In this respect, as in several others, incubation or non-incubation by the male appears largely indifferent to the welfare of the species, especially in passerine birds.

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