CLUTCH SIZE AND FLEDGING SUCCESS IN THE TURQUOISE-BROWED MOTMOT

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ABSTRACT.—Clutches of 4 eggs accounted for 64–73% of all clutches laid in 3 yr by a population of Turquoise-browed Motmots (*Eumomota superciliosa*) in Yucatán, Mexico. The consistently high frequency of 4-egg clutches was associated with only a slight advantage in fledging success relative to clutches of 3 eggs, which ranged in frequency from 11% to 33%. Differences in number of young fledged and proportion of hatchlings fledged were not statistically significant over 3 yr or in any particular year. Clutches of 4 yielded more surviving young in 2 of 3 yr, averaging 2.02 compared to 1.71 for clutches of 3. The proportion of hatchlings that fledged was higher in broods of 3 (overall = 0.67) than in broods of 4 (overall = 0.55) in 2 of 3 yr. The proportion of hatchlings fledged from clutches of 5 (0.36) was lower over 3 yr than that fledged from clutches of 4 or 3. Approximately 40% of nestling mortality in nests that escaped predation was due to starvation. Other known causes included falls from nests and parasitism by maggots. *Received 12 July 1984, accepted 9 April 1985.*

IN summarizing 2 yr of study of Turquoise-browed Motmot (*Eumomota superciliosa*) breeding biology (Scott and Martin 1983), we reported that most females laid clutches of 4 eggs and that in nearly all successful nests 1 or more nestlings died. The poor fledging success observed raised the question: Would birds laying clutches of 3 normally fledge as many young as the parents of clutches of 4, and thereby obtain a higher return on their energetic investment in offspring? We now compare the productivity of natural clutches of 3, 4, and 5 eggs, incorporating the results of a third year of study in which 3-egg clutches were relatively common. We focus on egg hatchability and the number and proportion of young fledged as measures of productivity.

STUDY AREA AND METHODS

The study population consisted of approximately 45 pairs of motmots nesting in holes in the interior chamber walls of structures at 5 Mayan archaeological sites (Uxmal, Kabah, Sayil, Xlapak, Labná) in the Puuc Hills region of the state of Yucatán, Mexico (Scott and Martin 1983). The nest cavities used by motmots appear to have been built into the masonry as beam-support recesses. Most were >2 m above the chamber floor, >1 m in length, and approximately

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10 × 10 cm in cross-section. Nest cavities were inspected at least twice weekly throughout the nesting period (May–August) in 1980, 1982, and 1983 by use of ladder, flashlight, and extensible mirror. In 1982 and 1983, 7–10 nests in which contents could be reached by hand were visited daily or more frequently during oviposition and hatching periods. Eggs and chicks were marked and weighed with 10-g and 100-g Pesola scales (to the nearest 0.1 g when <10 g, to the nearest 0.5 g when >10 g). Marked nestlings were weighed at intervals of 2 or 3 days. The significance level for rejection of null hypotheses was <0.05. Pairwise comparisons (Mann-Whitney U-tests) were two-tailed.

RESULTS

Breeding phenology and rainfall patterns.—*Eumomota superciliosa* pairs attempted to raise one brood annually in the first half of the 5–6-month rainy season. The nest period (from clutch initiation to fledging) lasted approximately 8 weeks. Nestlings were fed mainly insects, especially beetles, cicadas, and orthopterans (see Orejuela 1977).

The rainy season in the Puuc Hills usually began within 2 weeks after the sun passed directly overhead (21 May at Uxmal) and continued through October. Mean annual rainfall at a weather station 5 km northeast of Uxmal during the period 1969–1982 was 1,086 mm, with a standard deviation of 114 mm (data courtesy of División Hidrométrica, Secretaría de Agricultura y Recursos Hidráulicos). Eighty to ninety percent of the annual rain usually fell

TABLE 1. Distribution of clutch sizes of Turquoise-browed Motmots in 1980, 1982, and 1983.

	1980	1982	1983	Total
Number of clutches	37	45	39	121
Clutch size				
2	0	2	1	3
3	9	5	13	27
4	24	33	25	82
5	4	4	0	8
6	0	1	0	1
$\bar{x}$	3.86	3.93	3.61	3.81

TABLE 2. Hatchability of motmot clutches in 1983.

	Clutch size		Total
	3	4	
Number of clutches	10	23	33
Number of clutches in which all eggs hatched	5	15	20
Number of eggs	30	91[a]	121
Number hatched	24	83	107
Percent hatched	80.0	91.2	88.4

[a] One egg in one clutch of 4 disappeared several days before hatching and is excluded from calculations of hatchability.

between May and October. The dry season of 1982–1983 was interrupted by rainfall in February (114 mm), March (74 mm), and April (105 mm) that in each case exceeded the highest monthly totals previously recorded (63, 67, and 64 mm). Rainfall totals in May (0 mm) and June (255 mm) were within the ranges observed in recent years; the 282 mm that fell in July exceeded the previous maximum of 198 mm. The departure from normal rainfall patterns may have been a distant effect of the El Niño current that developed in the Pacific Ocean beginning in June 1982 (Schreiber and Schreiber 1983). At Uxmal the forest surrounding the archaeological site remained green throughout the "dry season" months. In other years, it usually was leafless, except for a few evergreen species, from February until June. Many motmots nested a few weeks earlier than usual in 1983. More clutches were laid in May in 1983 ($n = 15$) than in 1980 ($n = 8$) or 1982 ($n = 4$) (Scott and Martin 1983). Curiously, clutch size decreased in 1983, and this season proved to be the least productive in our study for birds laying clutches of 4 eggs (see below).

Clutch size.—Four was the most common clutch size in all 3 yr and accounted for 64–73% of all clutches (Table 1). However, clutch size varied among years ($P < 0.05$; adjusted $H = 6.63$, df = 2, Kruskal-Wallis test). Clutch size in 1983 differed significantly from clutch size in 1982 ($P < 0.05$; $U = 1,108$, U-test). In 1983 there was a higher proportion of 3-egg clutches (33%) than in 1982 (11%) or 1980 (24%).

Laying and hatching patterns.—Eggs normally were laid at 2-day intervals (Scott and Martin 1983) in the early afternoon. Nocturnal incubation began the day the third egg was laid in clutches of 4 eggs. The first-laid egg hatched 19 or 20 days after the laying of the third egg

in clutches of 3, 4, and 5. The hatching period spanned 1–1.5 days in clutches of 3 (1983 data, $n = 4$ clutches), 2–3 days in clutches of 4 (Scott and Martin 1983), and 5 days in one clutch of 5.

Each egg was weighed within 24 h of laying in 6 clutches of 3 and 6 clutches of 4. Mean weights ± 1 SD in clutches of 3 were: egg 1, 8.4 ± 0.69; egg 2, 8.1 ± 0.69; egg 3, 7.7 ± 0.63. Eggs within clutches were ranked from lightest to heaviest. There was significant variation among eggs according to position in the laying sequence ($P < 0.01$; $T_2 = 9.68$, Friedman analysis of variance by ranks test). A multiple-comparison test (Conover 1980) indicated that egg 1 and egg 2 each were heavier than egg 3 ($P < 0.05$). No consistent pattern of variation was detected among eggs in clutches of 4 ($P > 0.5$; $T_2 = 0.60$, Friedman test). Weights in clutches of 4 were: egg 1, 8.1 ± 0.67; egg 2, 8.1 ± 0.53; egg 3, 8.1 ± 0.34; egg 4, 8.0 ± 0.52.

In 5 clutches of 3 and 5 clutches of 4 in which all eggs hatched, young were weighed within 24 h after the last egg hatched. In the 4-egg clutches it was known which young came from which egg, and that eggs hatched in the sequence in which they had been laid. In two 3-egg clutches, hatching order of the first 2 eggs was not known. Mean weights in broods of 3 were: heaviest nestling, 11.0 ± 2.84; next-heaviest, 9.3 ± 1.82; last-hatched, 7.0 ± 0.11. In broods of 4, weights after hatching of the last chick were: first-hatched, 14.8 ± 3.49; second-hatched, 11.3 ± 1.04; third-hatched, 9.1 ± 1.30; last-hatched, 6.5 ± 0.47. In one brood of 5, weights were 18, 14, 13.5, 7.7, and 6.5 g.

Hatchability.—Hatchability, the proportion of eggs present at the end of incubation that hatch (Koenig 1982), was determined most reliably in 1983, when the fates of all eggs in 33 clutches

TABLE 3. Numbers of motmot nestlings that died in broods weighed at 2–3-day intervals. Numbers in parentheses denote nestlings that lost weight in the interval prior to death.

	1982	1983	Total
Number of nests	7	9	16
Number hatched	17	28	45
Number died	13 (8)	15 (3)	28 (11)
Location of dead or dying nestlings			
Not found	6 (4)	7 (0)	13 (4)
In nest	5 (3)	0	5 (3)
On ground below nest			
Dead	2 (1)	3ª (0)	5ª (1)
Alive	0	5 (3)	5 (3)

ª Includes one death due to parasitism.

were known (Table 2). Hatchability (overall = 88.4%) was nearly equal for unhandled clutches (88.9%, $n = 23$) and those in which eggs were marked (88.2%, $n = 10$), and was nearly equal to the mean hatchability calculated by Koenig (1982) for a variety of cavity-nesting species (88.7%, $n = 32$ populations). One or more eggs failed to hatch in 39% of the clutches. Seven of 14 unhatched eggs were opened for inspection. One was infertile, and 6 contained dead embryos. Hatchability was lower for eggs from clutches of 3 than for eggs in 4-egg clutches (Table 2); the difference approached significance ($0.05 < P < 0.10$; $\chi^2 = 2.77$, df = 1). No clutches of 5 eggs were laid in 1983. In 1982 all eggs hatched in 4 clutches of 5 eggs, and in 1980 4 eggs hatched in 1 clutch and 5 in another.

Predation and nest failure.—Owls (*Tyto alba*, *Bubo virginianus*) hunted around the ruins and often perched on edifices. They were suspected of predation at 2 nests with large entrances in which adult motmot feathers and scattered or broken eggs were found. Rat snakes (*Elaphe phaescens*) were observed in ruins chambers at all sites, usually in Cave Swallow (*Hirundo fulva*) nests, and were suspected of eating most motmot clutches and broods that disappeared between our visits (Scott and Martin 1983). Nest contents vanished in 30–36% of all nests in each year. Daily survivorship rates of nests containing eggs and nests with nestlings were similar (Scott 1984).

Nestling mortality.—Loss of one or more nestlings during the 4-week nestling period was a very common event even in nests from which at least one young fledged. Factors causing the gradual reduction of broods included starva-

tion, falls from nests, and parasitism. Possibly, nest predators sometimes did not capture the entire brood, although it is unlikely that nestlings of any age could elude a snake that entered the nest cavity. If owls do enter cavities with sufficiently large entrances, it might be possible for a nestling to escape by retreating into narrower recesses of the cavity. Another possible cause of brood reduction, sibling aggression, could not be evaluated because interactions among siblings in the dark cavity could not be observed without disturbing them. No external wounds (except those caused by maggots) were observed on nestlings that were handled.

The relative importance of starvation and falls from nests is not well known. Evidence of starvation could be obtained only from the 16 broods in which marked nestlings were weighed at intervals of 2–3 days (Table 3). If a nestling lost weight between the two visits that preceded its death and was at an age (<16 days) when it should have been gaining weight (Orejuela 1977, Martin and Martin 1985), we attributed its death to starvation. No nestlings aged 1–15 days that lost weight over an interval of 2 or 3 days survived.

Eleven of the 28 dead nestlings in the sample (39%) apparently starved. Three of the 11 that had been losing weight subsequently were found on the floor below the nest still alive, in very weakened condition; the others either were found dead on the room floor, in the nest, or were not found (Table 3). The 11 young belonged to 6 broods (1 brood of 2 young, 1 of 3, 3 of 4, and 1 of 5). The last-hatched young starved in each of the 6 broods. In 4 broods more than 1 nestling starved. In 3 of these, the last-hatched began to lose weight and died before others, and in the fourth, the last-hatched and next-to-last-hatched lost weight simultaneously and died during the same interval. One nestling in the sample was killed by parasitic maggots (see below). Of the remaining 16 nestlings (which had not previously lost weight), 2 were found dead in the nest. The number that died as a result of accidental falls from the nest probably was substantial but could not be estimated, since it is possible that some died in the nest and were removed from the cavity by their parents. Two of the nestlings found dead on the room floor were the first-hatched and heaviest members of their broods, and almost certainly died as a result of accidental falls.

TABLE 4. Numbers of motmots fledged from clutches of 4 and 3 eggs in which all eggs or all but one egg hatched.[a]

	Number hatched	Number of nests	Number fledged					$\bar{x}$	F/H[b]	F/E[c]
			0	1	2	3	4			
4-egg clutches										
1980	4	10	0	1	7	2	0	2.10	0.53	0.53
	3	7	1	3	2	1		1.29	0.48	0.36
	Total	17	1	4	9	3	0	1.82	0.51	0.46
1982	4	14	0	2	3	5	4	2.79	0.70	0.70
	3	4	0	1	1	2		2.25	0.75	0.56
	Total	18	0	3	4	7	4	2.67	0.71	0.67
1983	4	12	0	5	6	1	0	1.67	0.42	0.42
	3	7	1	3	2	1		1.43	0.48	0.36
	Total	19	1	8	8	2	0	1.58	0.43	0.39
All years	4	36	0	8	16	8	4	2.22	0.55	0.55
	3	18	2	7	5	4		1.61	0.54	0.40
	Total	54	2	15	21	12	4	2.02	0.55	0.50
3-egg clutches										
1980	3	2	0	1	1	0		1.50	0.50	0.50
	2	0								
	Total	2	0	1	1	0		1.50	0.50	0.50
1982	3	3	0	0	2	1		2.33	0.78	0.78
	2	1	1					0.00	0.00	0.00
	Total	4	1	0	2	1		1.75	0.64	0.58
1983	3	5	0	1	3	1		2.00	0.67	0.67
	2	3	1	0	2			1.33	0.67	0.44
	Total	8	1	1	5	1		1.75	0.67	0.58
All years	3	10	0	2	6	2		2.00	0.67	0.67
	2	4	2	0	2			1.00	0.50	0.33
	Total	14	2	2	8	2		1.71	0.63	0.57

[a] Only nests not lost to predation are included.
[b] Fledged/hatched = overall proportion of hatchlings that fledged.
[c] Fledged/eggs = overall proportion of eggs yielding fledglings.

Parasitism by dipteran maggots caused the death of 5 nestlings in 3 broods in 1983. (Two of these broods are not included in the frequently visited sample in Table 3.) Three nestlings were killed at <6 days of age by maggots that opened holes in the ear, breast, or wing. Two older nestlings died after conspicuous infestations of 1–2 weeks by maggots that burrowed into the flesh around emerging wing, tail, or spinal tract feathers. In 1980 and 1982, parasitic maggots were observed only twice, each time in an external naris of a nestling. Some instances of parasitism involving young nestlings may have been overlooked in those years.

Fledging success in relation to clutch size.— Analysis of fledging success is restricted to (1) nests whose contents were not lost all at once to predation, (2) clutches of 3, 4, and 5 eggs (97% of the 3-yr total of clutches), and (3)

clutches in which all eggs or all but one egg hatched. All or all but one egg hatched in 88% of clutches of 3 ($n = 16$), 92% of clutches of 4 ($n = 59$), and 100% of clutches of 5 ($n = 6$).

The most common initial brood size (after hatching) was 4 in 1980 and 1982 (Table 4). In 1983 there was an equal number of initial broods of size 4 and 3. There was only one year (1982) in which all young from any broods of 4 were fledged. None of the 5 broods of 5 that escaped predation fledged as many as 4 young. One or more young were lost in 89% of all broods of 4 hatched from clutches of 4 and in 80% of broods of 3 hatched from clutches of 3.

The number of young fledged from clutches of 4 varied significantly among years ($P < 0.01$; adjusted $H = 11.27$, df $= 2$, Kruskal-Wallis test). More young were fledged in 1982 than in 1983 ($P < 0.01$; $U = 269$, U-test) or 1980 ($P < 0.05$; $U = 223.5$, U-test). The productivity of clutches

of 3 did not differ between years ($P > 0.5$; adjusted $H = 0.39$, df = 2, Kruskal-Wallis test).

Average productivity over 3 yr was 1.71 ± 0.914 (SD) for clutches of 3 (Table 4), 2.02 ± 0.981 for clutches of 4 (Table 4), and 1.67 ± 1.211 for clutches of 5. Variation in productivity among the three clutch sizes was not significant ($P > 0.5$; adjusted $H = 0.95$, df = 2, Kruskal-Wallis test). In clutches of 4, more young were fledged when all eggs hatched ($\bar{x} = 2.22 \pm 0.929$) than when only 3 eggs hatched ($\bar{x} = 1.61 \pm 0.979$; $P < 0.05$; $U = 428$, U-test). However, the productivity of broods of 4 was not significantly greater than that of broods of 3 hatched from clutches of 3 ($\bar{x} = 2.00 \pm 0.667$; $P > 0.5$; $U = 200$, U-test). Two was the number of young most frequently fledged in both groups (Table 4). In the year that was most productive overall (1982) more young were fledged in broods of 4, whereas in the least productive year (1983) more young fledged from broods of 3 hatched from clutches of 3 (Table 4). The differences, however, were not statistically significant in either year.

The proportion of hatchlings that fledged over 3 yr (comparing only clutches in which all eggs hatched) was highest in clutches of 3 eggs (0.67) and lowest in clutches of 5 (0.36). Variation among parents of different clutch sizes in proportion fledged approached significance ($0.05 < P < 0.10$; $\chi^2 = 5.47$, df = 2). Parents of 3-egg clutches fledged a higher proportion of hatchlings than parents of 4-egg clutches in 2 of 3 yr.

DISCUSSION

Our expectation that a higher proportion of young might fledge from clutches of 3 than from the modal clutch of 4 was based on the assumption that starvation was the main cause of nestling mortality in nests that escaped predation, and that in years of low food availability fewer young would starve in smaller broods. Unfortunately, we were unable to distinguish causes of mortality in the majority of nests, and we also lacked an independent measure of food availability. Data from the 16 marked broods of various sizes indicated that starvation accounted for approximately 40% of nestling mortality. These data were too limited to indicate whether any particular cause of death, including starvation, varied with clutch or brood size.

Based on proportion and number of young

fledged, it appears that parents of clutches of 3 were at least as capable of rearing young as parents of clutches of 4. Parents of 3-egg clutches fledged a higher proportion of hatchlings than parents of 4-egg clutches in 2 of our 3 years of study, and fledged more young than parents of 4-egg clutches in which only 3 young hatched. Nevertheless, clutches of 4 yielded more surviving young in 2 of the 3 years. None of these differences between clutches of 3 and clutches of 4, however, was statistically significant. Thus, birds laying clutches of 4 had only slightly better season-specific fledging success than birds laying clutches of 3. Parents of 5-egg clutches fledged a lower proportion of hatchlings than birds laying 4- or 3-egg clutches.

Failure of one egg in a clutch to hatch may be a greater disadvantage for birds laying clutches of 3 than those laying clutches of 4. It would be disadvantageous if the food supply was adequate to raise 3 young, and if a nestling in a brood of 2 was just as likely to die of other causes as a nestling in a larger brood.

Hatching was increasingly asynchronous in clutches of 3, 4, and 5 eggs. The weight hierarchy present at the end of hatching apparently was due mainly to differences in amount of feeding time between each young and the next-hatched young. In clutches of 3, the lower initial weight of the third egg also may have contributed to the after-hatching weight hierarchy. In our small sample of marked broods in which starvation occurred, the last-hatched starved first or simultaneously with the next-to-last-hatched while older siblings continued to gain weight. Lack (1947) considered this pattern to be a widespread and adaptive characteristic of asynchronously hatching species. However, it cannot be assumed without experimental evidence that asynchronously hatched clutches yield more surviving young on average than would synchronously hatched clutches of the same size (Clark and Wilson 1981).

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