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Morphological Correlates of Synchronized Nesting in a Tricolored Blackbird Colony

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Our knowledge of the morphological and physiological changes associated with reproductive cycles in female birds has been derived largely from studies of the domestic fowl (Romanoff and Romanoff 1949), several species of domestic doves (Riddle 1916, Lehman 1965), and the domestic canary (Hinde 1965). Few comparable data are available on seasonally breeding wild birds (but see Petersen 1955, Marshall and Coombs 1957).

The Tricolored Blackbird (*Agelaius tricolor*), because of extremely high nest densities in its huge breeding colonies (characteristically several nests per square meter) and, particularly, a remarkable breeding synchrony of colony members (all nests within a local colony unit of several hundred or thousand nests vary around a mean by only one or two days; Neff 1937, Lack and Emlen 1939), provides an unusual opportunity to collect specimen series for correlating reproductive condition with nesting stages.

While performing a study of the breeding behavior of this species (Emlen 1941), I shot 74 breeding females as they circled directly overhead or within 10 m of a typical, densely packed and closely synchronized cluster of Tricolored Blackbird nests in a colony near Davis, California. The specimens, collected at 2-day and later 3-day intervals, were measured and autopsied for data on the condition of reproductive tracts and brood patches. Data on body weights, brood patch condition, and oviduct lengths are summarized in Fig. 1, and data on ovum diameters are summarized in part in Table 1.

Body weights showed a significant downward trend ($P < 0.01$, $\chi^2 = 12.162$, 2×2 contingency test) from a mean of about 50 g at nest building and egg-laying to about 43 g at fledging. The main decline apparently occurred during the nestling stage.

Brood patch indices, based on 4 subjective classes of dermal edema, showed a steep drop from a high during egg-laying and incubation to a low during the nestling and fledgling stages. Defeathering of the

brood patch was apparently nearly complete early in the nest-building stage.

The overall length of the oviduct (including infundibulum and vagina) dropped precipitously from a high during the nest-building and egg-laying stages to the incubation stage, then gradually dropped during the nestling stage to a low in the fledgling stage. I saw no evidence of a recrudescence at the end of the cycle indicative of an oncoming second breeding cycle.

The ovarian indicators of reproductive progress closely paralleled the patterns of reproductive behavior during nest building and egg-laying. In the late afternoon of 16 May, 1-3 days before nests in the colony section received their first egg [stages: NB1(1), NB2(3), NB3(9), NB4(3), E1(0); see Fig. 1], I collected 9 females, all of which were apparently within 1-4 days of laying their first egg (Table 1). Six held single ovulated ova in their oviducts (presumably ready to be laid the next day) and from 1 to 3 appreciably enlarged ova (diameter > 5.0 mm) in their ovaries, numbers appropriate for predicting completion of the usual 3-4-egg clutch of the species (Emlen 1941). In the other 3 birds, the largest ovum diameters suggested that 2 probably would have laid their first egg on the succeeding day and the other on the following day. The slightly enlarged ova (2.5-5.0 mm; see Table 1) can be interpreted either as growing and potentially viable ova or as resorbing ova that had abortively initiated a terminal rapid-growth phase.

Because eggs are laid at 1-day intervals, the step-wise pattern of increasing ovum diameters in the 16 May specimens (Table 1) provides an indication of the growth curve of individual ova, and, combined with similar data from specimens collected before and after that date, a basis for tracing the daily progress of egg production in these birds. As in the domestic fowl (*Gallus gallus*) and the Ringed Turtle-Dove (*Streptopelia risoria*), ova apparently take 4-5 days to

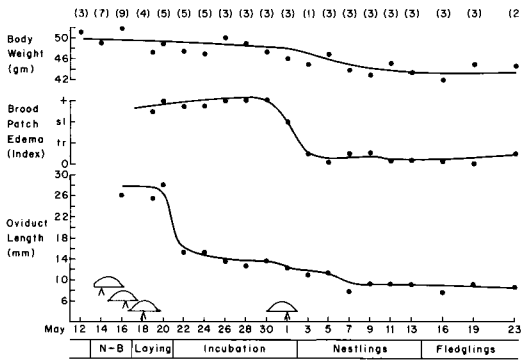


Fig. 1. Trends in body weight, brood patch edema, and oviduct length during the breeding cycle in a closely synchronized colony unit of Tricolored Blackbirds. The small distribution curves near the baseline show the extent of individual variation in nesting progress along the time scale of the breeding cycle; carets indicate when specimens were collected. Figures in parentheses at the top are the number of specimens examined on each date. Brood patches were assigned to one of four classes of dermal edema (0 = none, tr = trace, sl = slight, + = heavy) and indices are simple means.

complete a final rapid-growth phase in the ovary before ovulation, then 1 additional day for oviposition. Several ova beyond the usual clutch of 3 or 4 may initiate this final 5-6-day phase (see specimens 11, 16, and 17 in Table 1) and subsequently regress. In the extended series shown in Fig. 1, ova greater than 5.0 mm in diameter appeared 3 days before the start of nest building and disappeared soon after the completion of laying. On 12 May, 5 days before the first recorded laying, the largest ovum in 3 collected specimens was 8.2 mm, and on 14 May, 8.5 mm. On 19-20 May, shortly after the peak of laying activity, 7 of

the 9 collected birds had the last ovum of their clutches in the oviduct, and all showed regressive (recently discharged) follicles in the ovary. Two days later, on 22 May, the largest ovum in the 5 collected specimens was 3.7 mm; after May, no ova exceeded 2.8 mm.

I conclude that the morphological evidence for close, within-colony synchrony revealed in this series matches the evidence from nest observations, and that the Tricolored Blackbird, a determinate layer, closely resembles the domestic fowl, the Ringed Turtle-Dove, the Common Canary (*Serinus canaria*), and the Bank Swallow (*Riparia riparia*) in the progress of morphological developments that accompany the behavioral stages of female reproductive cycles.

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TABLE 1. Size and location of ova in the reproductive tracts of 9 females collected midway during the nest-building stage of the breeding cycle (see stage distribution curve for 16 May in Fig. 1).

Specimen number	Enlarged ova in ovary					Ovum in oviduct	
	≥2.5 mm diameter					Diameter (mm)	Position
11	2.5	3.2	5.8	8.6	10.0	1	Middle magnum
12	—	—	2.9	6.0	9.6	1	Upper magnum
13	—	—	3.0	3.6	7.2	1	Lower magnum
14	—	3.0	3.6	7.8	9.7	1	Lower magnum
15	—	2.5	2.5	4.9	7.0	—	—
16	2.7	2.8	6.8	8.8	10.2	1	Uterus
17	—	2.6	2.7	3.6	3.9	—	—
18	—	2.8	3.3	3.9	7.8	1?	—
19	2.5	5.1	7.7	9.4	10.3	1	Uterus

* R = ruptured (recently discharged) follicle.

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Food of Breeding Leach's Storm-Petrels (*Oceanodroma leucorhoa*)

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Storm-petrels are strictly surface feeders that obtain their food by pattering (Ashmole 1971). Fish, squid, copepods, euphausiids, and amphipods are recorded as their prey (Palmer 1962), although there is no detailed information on prey composition. I studied the prey and seasonal changes in the diet of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) breeding on Daikoku Island (42°56'N, 144°52'E) from May to September 1982. For a description of the island, see Abe et al. (1972). Leach's Storm-Petrels arrive at the island in late April and lay eggs during June. Chicks hatch in mid-July and fledge in September and early October.

Adult petrels were caught on their nesting grounds by hand or with a swooping net from 2100 to 2300. Their stomach contents were drained as much as possible using a stomach pump with a plastic tube (4.5 mm diameter, 15 cm length; Grubb 1971). Petrels with empty or nearly empty (<0.5 cc) stomachs included parents caught just after exchanging incubation duties or feeding chicks, or birds already sampled. These petrels were excluded from the analysis. Undigested items were fixed in 10% formalin and preserved in 70% ethanol. Almost all could be identified to class. Squid were separated from other items by noting the presence of beaks or eye lenses, and fish by the presence of scales or bones. Fish and squid were so digested that they could not be identified further, but copepods and euphausiids were identified to species level. Amphipods were identified to family level by Y. Kamihira.

Samples were collected from 307 stomachs, of which 178 contained recognizable items and 129 only orange oil. Many samples taken in June but few taken in September contained only orange oil (Table 1). The seasonal change in the proportion of samples containing only orange oil was significant ($\chi^2 = 20.24$, $df = 4$, $P < 0.001$). The stomach oil of petrels is a dietary product (Imber 1976). This suggests that the digestion periods in September are shorter than in earlier months, although seasonal diet changes (see below) also may account for the proportion of orange oil in the samples. Weights of samples varied among the months ($F_{4,302} = 2.53$, $P < 0.05$), but those from June to September were similar ($F_{3,234} = 1.10$, NS; Table 1). Mean weights in August and in September, when many breeders fed chicks, were much lower

than the maximum estimate of a food load of a parent to a chick ($\bar{x} = 8.0$ g, Watanuki 1985). This suggests that the stomach pump did not remove large items (as observed with penguins by Volkman et al. 1980).

The diet composition is given in Tables 1 and 2. Petrels fed on squid, amphipods, euphausiids, and copepods in May and June. Most euphausiids eaten in May were *Tysanoessa longipes* and *T. inermis*. In August and September fish and euphausiids (*Euphausia pacifica*) dominated. Fish eggs occurred in July. The percentages of euphausiids and of fish increased later in the breeding season (euphausiids: $\chi^2 = 10.1$, $df = 4$, $P < 0.05$; fish: $\chi^2 = 21.9$, $df = 4$, $P < 0.01$; Chi-square test for monthly variation), while those of squid and amphipods did not change seasonally (squid: $\chi^2 = 2.9$, $df = 4$, NS; amphipods: $\chi^2 = 2.4$, $df = 4$, NS). Pebbles and plastic were found every month.

When the monthly data were combined, fish, squid, and euphausiids dominated; amphipods, copepods, and fish eggs were the next important; and decapods and isopods were least important. Among euphausiids, *E. pacifica* dominated, while *T. longipes* and *T. inermis* occurred less commonly. *Calanus cristatus* was the only copepod eaten. The mean lower length of squid beaks recovered from stomachs was 2.7 mm ($n = 5$), which corresponds to a weight of about 35-40 g (estimated from Imber 1976: Table 3). The length of the vertebral column of one fish sample was 0.9 mm; the corresponding body length is about 3-6 cm (estimated from Tataru et al. 1962: Table 1). Linton (1978, cited in Brown 1980) found myctophid fish in the diet of Leach's Storm-Petrels, so it is possible that petrels in the northwestern North Pacific also eat lanternfish and fish and squid larvae (Takeuchi 1972).

The dominant prey (euphausiids, squid, and fish) remain deep in the sea during the day and rise to the surface at night (Brinton 1967; Kawaguchi 1969; Roper and Young 1975, cited in Naito et al. 1977), although surface swarming of *E. pacifica* occasionally is observed during the day (Komaki 1967). Less important prey (*C. cristatus* and amphipods) show no such diurnal vertical migration (Sekiguchi 1975, Murano et al. 1976). These facts suggest that the food of the surface-feeding Leach's Storm-Petrels is abundant at night but scarce during the day. The foraging period of the petrels was not determined in this study. Gordon (1955) observed nocturnal activity of Leach's