

external pipping and hatching is a greater percentage of the total incubation period for the smaller eggs. The total water loss during this interval is also a greater percentage of the total water loss over the entire incubation period, in the smaller eggs. These results are a corollary to a previous report that the duration of the pre-pipping phase of incubation, and the water loss during this phase, tend to be relatively less in the smaller procellariiform eggs than in the larger ones (Whittow et al. 1982). Table 2 also reveals that the total water loss over the entire incubation period tends to be relatively greater in the smaller eggs. It is, in fact, likely that the water loss from the Bonin Petrel eggs has been somewhat underestimated because Grant et al. (1982a) did not obtain data for water loss from eggs with a pip-hole. Nevertheless, this consideration should not alter the main conclusion to be drawn from Table 2 viz. that, over a range of egg size of almost eight-fold, the main variation in water loss from the eggs consists of a change in the division of water loss between the pre-pipping period on the one hand, and the period between external pipping (star-fracture of the shell) and hatching, on the other.

Ar and Rahn (1980) reported that the mean paranatal water loss in a variety of species was "about one quarter of the total calculated water loss." They used Visschedijk's (1962) definition of the paranatal period: "between internal pipping . . . and hatching." Ar and Rahn (1980) assumed that "Within this period, external pipping designates the beginning of the hatching process." Unfortunately, this is not the case in the Wedge-tailed Shearwater, or in many other species in which external pipping precedes internal pipping. In addition, Ar and Rahn (1980) calculated paranatal water loss in such a way as to exclude the water loss by simple diffusion during this period. The total water loss during the paranatal period must therefore have been greater than the paranatal water loss as defined by Ar and Rahn (1980).

It is clear from Table 1 that external pipping results in an increased water loss from the egg and that the production of a pip-hole results in a further increase in water loss. Using a value of 7.09 ml/min for the respiratory minute volume of embryos in eggs with pip-holes (Pettit and Whittow 1982; Table 2), a water content of inspired air of 0.017 g/l (air temp. = 36°C; relative humidity = 40%) and a water content of expired air of 0.030 g/l (measured expired air temp. = 30°C; saturated with water vapor), it was calculated that the respiratory water loss, under laboratory conditions, was 0.133 g/day. The total water loss from eggs with pip-holes was 0.858 g/day (Table 1). Therefore the respiratory water loss represented 15.5% of the total water loss. A maximal value for respiratory water loss, assuming expired air to be at 36°C and saturated with water vapor, was calculated to be 29.7% of the total water loss from eggs with pip-holes. Therefore, even at this late

stage of development, most of the water loss from the egg was by way of extrapulmonary pathways.

ACKNOWLEDGMENTS

This work was supported by grants from the National Science Foundation (PCM 76-12351-A01) and the Leahi Trust of Honolulu. We are grateful to M. Seki for technical assistance. We would also like to thank the Division of Forestry and Wildlife, State of Hawaii, and the U.S. Fish and Wildlife Service for granting permits for this study. We are particularly indebted to John L. Sincok of the U.S. Fish and Wildlife Service for providing the eggs used in this study.

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Condor 85:109-111
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VARIATION IN THE EGG MARKINGS OF THE BROWN-HEADED COWBIRD

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Previous studies of the parasitic Brown-headed Cowbird (*Molothrus ater*) have assumed that eggs from individual female cowbirds are consistent in their shape and pigmentation markings (Friedmann 1929, Walkinshaw 1949,

McGeen and McGeen 1968, Elliott 1977). However, it has not been possible to attribute specific eggs to specific females in the wild because of difficulties in observing actual egg-laying (cf. Hann 1941). I collected four pairs of eggs known to have been laid by four different female cowbirds. I determined whether eggs from individual females are consistent in their appearance by testing the ability of human subjects to identify the four pairs from a random arrangement of the eight eggs.

During the breeding season (April-June) of 1981 I captured cowbirds in grain-baited traps on the grounds of the Rockefeller University Field Research Center in Millbrook, New York. The birds were color-banded, and fe-

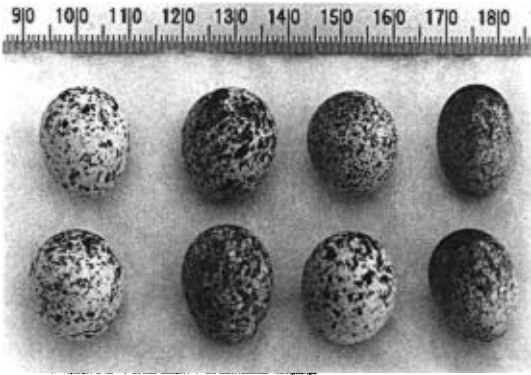


FIGURE 1. The four pairs of Brown-headed Cowbird eggs used in the matching experiment. Eggs from the same female are arranged one above the other.

males were housed until 10:00 the following morning in metal cages (approximately $21 \times 26 \times 22$ cm) with wire mesh (2.54 cm) floors. The cages were elevated 5–6 cm above pieces of foam rubber. If a female laid an egg it fell through the mesh onto the foam rubber, out of her reach. Captive female cowbirds often eat their eggs if this precaution is not taken (pers. observ.). Food and water were available at all times.

I obtained two eggs from each of three females and seven eggs from a fourth. One egg of the latter was severely damaged as it fell through the wire mesh and was discarded. Of the remaining eggs of these females, two were damaged at their narrow ends, but their blunt ends, where most of the pigmentation markings occur, were unharmed; two others were cracked but were otherwise undamaged. The average measurement of 12 eggs for which both length and width could be measured accurately was 21.3×16.6 mm. These dimensions are similar to those reported in Bent (1958), where 127 cowbird eggs had average measurements of 21.45×16.42 mm.

I presented two eggs from each of the four females (Fig. 1) in a random arrangement to each of 10 people. The two eggs used from the clutch of six were chosen at random. I instructed the subjects to group the eggs into four pairs, and to pay particular attention to shell pigmentation in so doing. The shape of the eggs probably also provided salient cues, but since some eggs were cracked or dented, I did not emphasize egg shape in the instructions.

Three of the subjects correctly matched all four pairs, six subjects matched two pairs (it is not possible to make three correct and one incorrect match), and one individual matched one pair, for a total of 25 correct. I calculated the expected number of correct matches under the null hypothesis of random matching as follows. The expected number of matches obtained by making two correct and two incorrect matches is the probability of making two correct matches ($1/7 \times 1/5 \times 2/3 \times 1 = 2/105$) multiplied first by 2, the number of correct matches produced, and then by 6, the number of possible combinations of two correct and two incorrect matches ($2/105 \times 2 \times 6 = 24/105$). Similarly, the expected number of correct matches obtained by making one correct and three incorrect matches is $1/7 \times 4/5 \times 2/3 \times 1 \times 1 \times 4 = 32/105$, and the expected number of correct matches obtained by correctly matching all four pairs is $1/7 \times 1/5 \times 1/3 \times 1 \times 4 \times 1 = 4/105$. The sum of these values is 0.57, the expected number of correct matches per trial under the null hypothesis. Over 10 trials the expected number of correct matches is 5.7. The expected and observed results are significantly different ($\chi^2 = 62.00$, Yates' correction employed, $P < 0.001$), indicating that eggs from the same female resemble

one another more than they do the eggs from another female.

My results indicate that a female cowbird's eggs have consistent features that are recognized by humans. Whether the cowbirds can make similar distinctions remains unknown. Egg recognition has been demonstrated in some species (e.g., Victoria 1972, Buckley and Buckley 1972, Rothstein 1974, 1975, 1978), although it is absent in others (e.g., Noble and Lehrman 1940, Allen and Mangels 1940).

The possible adaptive value to cowbirds of producing eggs with consistent characteristics is unclear. One possibility is that consistent egg markings result from selective pressure by hosts on cowbirds to produce mimetic eggs. Some female cowbirds may lay their first egg nonrandomly (Preston 1948, Elliott 1977), but there is little evidence for host specialization by individual females (but see Walkinshaw 1949). Alternatively, the resemblance of two eggs from the same female may have no adaptive significance, and may be the inevitable result of being formed in the same oviduct. Support for this position comes from Dawson (1972), who showed that the egg characteristics of successive clutches of an individual female of a non-parasitic species (House Sparrow, *Passer domesticus*) are less variable than those of clutches laid by different females. Similarly, Nolan (1978:176) and Nice (1937:111) indicated that the eggs of an individual female are more similar to each other than to eggs of different females in the Prairie Warbler (*Dendroica discolor*) and the Song Sparrow (*Melospiza melodia*), respectively. In the absence of evidence to the contrary, I feel that the latter, more conservative, explanation must be favored.

Little is known about the laying habits of individual female cowbirds. By collecting sample eggs from marked females, as described above, investigators may be able to match cowbird eggs discovered in the wild with those of a known sample, thereby determining the breeding locations and host preferences of specific female Brown-headed Cowbirds.

I thank D. Cheney, H. Gouzoules, S. Gouzoules, S. Peters, W. Searcy, M. Searcy, R. Seyfarth, V. Sherman, C. Whitney, and J. Wingfield for serving as subjects. H. Gouzoules, W. Searcy, and R. Seyfarth also aided in statistical computations. S. Rothstein and W. Searcy criticized earlier versions of this manuscript, and C. Clark helped produce the figure. This research was supported by N.I.M.H. grant number PHS MH08458.

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Condor 85:111-113
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SEASONAL VARIATION IN NEST PLACEMENT OF ABERT'S TOWHEES

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Several meteorological variables are known to influence the heat budgets of nesting birds (e.g., Walsberg and King 1978a, b). Such factors include air temperature, incident radiation, wind, and humidity. If the microclimate of the nest is unfavorable, parent birds may become inattentive, exposing eggs or nestlings to excessive heat or cold. They may then desert the nest and their offspring may die. To improve the probability of nesting successfully, many Old World desert birds place their nests so as to receive morning sunlight (Maclean 1976). Several investigators have demonstrated nonrandom orientation of hole entrances of New World cavity-nesting birds (Ricklefs and Hainsworth 1968, Inouye 1976, Inouye et al. 1981), but few have tested for the significance of nonrandom placement or variation in placement between seasons of open nests. Maclean (1976) indicated that larks in the Kalahari Desert oriented their nests to receive shade in summer and sun in winter. Balda and Bateman (1970) predicted that Pinyon Jays (*Gymnorhinus cyanocephalus*) in Arizona may place first nests of the season on the sunny sides of ponderosa pines (*Pinus ponderosa*), but that they may orient later nests more randomly. They showed that these trees in March were 3°C warmer on the south side than on the north side, and that the jays selected nest sites to gain more heat: all jay nests, regardless of season, had a significant southward orientation. I report here a second test of Balda and Bateman's (1970) hypothesis, using data for a bird of hotter climates, the Abert's Towhee (*Pipilo aberti*). This sedentary species inhabits only desert riparian regions of the southwestern United States, whereas the mobile Pinyon Jay occupies a greater elevational and latitudinal range, though breeding chiefly in foothills and lower mountain ranges. Because nests of the Abert's Towhee are typically exposed to higher spring and summer temperatures than those of the Pinyon Jay, a second test of Balda and Bateman's prediction may demonstrate greater seasonal variation in nest placement.

The study was conducted in honey mesquite (*Prosopis glandulosa*) habitat on the Colorado River Indian Reservation 10 km north of Ehrenberg, Arizona. From January to July 1980, I spent 15 h each week (84 5-h searches) looking for nests on, or near a gridded study plot of 20 ha. Field work terminated in July when no new nests were started.

The Abert's Towhees in my study area built their open nests in mesquite, willow (*Salix goodingii*), exotic salt cedar (*Tamarix chinensis*), saltbush (*Atriplex lentiformis*), in-

kweed (*Suaeda torreyana*), arrowweed (*Tessera sericia*), and mistletoe (*Phoradendron californicum*), a parasite of mesquite (Finch 1981a). Nests built in March were constructed of mesquite bark, saltbush, salt cedar and arrowweed leaves, grasses and even newspaper. Later nests were made predominantly of mesquite leaves, which became available in April (Finch 1981a).

Compass direction of the nest with respect to the main trunks of mesquites, willows and salt cedars was recorded for 52 nests. I did not include nests built in small shrubs because compass directions were difficult to determine accurately. Nests were allocated to early and late seasons by dividing in half the number of days of the observed breeding season (118 days from first to last nest initiated). The Rayleigh Z test (Batschelet 1965) was used to test for randomness of nest concentration of early and late nests, and Batschelet's (1965:33) parametric two-sample test applying the F-statistic was used to test for a difference in mean direction between early and late nests. Information on solar paths and prevailing wind directions in the lower Colorado River valley was provided by the Laboratory of Climatology, Arizona State University, Tempe.

The results indicate that the placements of early nests were more concentrated than late nests (Table 1). Their distribution was significantly unimodal with a preferred southeast direction, whereas the distribution of late nests had a nonsignificant northwestward orientation. The mean directions of early and late nests were significantly different ($F_{(1,50)} = 14.82, P < 0.001$). Because the distribution of late nest orientations was nonsignificant, the value of this two-sample test may be lessened. The Rayleigh tests nevertheless confirm the difference in the distributions of nest orientations. The circular distributions of early and late nests are shown in Figure 1.

These results suggest that Abert's Towhees place their nests in response to environmental factors that are important only during the first half of the breeding season. In the lower Colorado River valley, the sun rose at 89° (almost due East) in March 1980 and traversed the south-

TABLE 1. Orientation of Abert's Towhee nests with respect to the main trunk of the tree.

Season	Number of nests	Nest concentration ^a	Rayleigh's Z test ^b	Mean direction ^c
Early	24	0.367	3.23	130° ± 69°
Late	28	0.205	1.18	321° ± 72°

^a A value of 1 indicates all nests were placed in precisely the same direction, and a value of 0 indicates a uniform distribution.

^b Rayleigh's Z test (Batschelet 1965) shows that the distribution of early nests was significantly unimodal ($P < 0.05$), whereas the distribution of late nests was random ($P > 0.05$).

^c Standard deviation is included.