

## WATER-VAPOR PRESSURE IN NESTS OF THE SAN MIGUEL ISLAND SONG SPARROW<sup>1</sup>

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**Abstract.** The water-vapor pressure ( $P_N$ ) in nests of the San Miguel Island race of Song Sparrows (*Melospiza melodia micronyx*) averaged 16 torr, but varied considerably between nests and within individual nests during successive days of incubation. Large daily fluctuations occurred throughout the incubation period and did not parallel concurrent changes in ambient vapor pressure ( $P_i$ ). Daily rates of water loss from nest eggs ( $\dot{M}_{H_2O}$ ) averaged 28 mg day<sup>-1</sup>, but also varied considerably within and between nests and did not correlate with changes in  $P_i$ .  $\dot{M}_{H_2O}$  increased 6–33% after the third day of incubation.  $P_N$  was significantly higher and  $\dot{M}_{H_2O}$  significantly lower in nests located in sheltered gullies than in nests from a windswept slope. These data suggest that Song Sparrows do not regulate  $P_N$  to achieve hatching success.

**Key words:** Egg; mass loss; nest; Song Sparrow; water-vapor pressure.

### INTRODUCTION

Because (1) freshly laid eggs and the chicks which hatch from them tend to be hydrated to the same extent (Ar and Rahn 1980), (2) eggs tend to lose similar relative amounts of water during incubation (Rahn and Ar 1974), (3) differences between the water-vapor pressure within the egg ( $P_A$ ) and in the surrounding nest air ( $P_N$ ) produce such water loss (Wangensteen et al. 1970/71), and (4) humidity levels in commercial incubators significantly affect egg mortality (Landauer 1967), Rahn and his associates (1976, 1977; also see Morgan et al. 1978, Ar and Rahn 1980) postulated that incubating parent birds regulate daily water loss from incubated eggs ( $\dot{M}_{H_2O}$ ) and  $P_N$  to optimize hatching success. Walsberg (1980) questioned this hypothesis and countered that  $P_N$  is neither constant nor regulated and need not be for successful hatching. Evidence exists supporting both views (Manning 1982; Vleck et al. 1983; Walsberg 1983, 1985), although most appear to support Walsberg's position.

One way to test this hypothesis is to measure

$P_N$  in the same nest at daily or shorter intervals throughout incubation. Studies of this design have been done now with domestic fowl (*Gallus domesticus*; Burke 1925, Chattock 1925, Koch and Steinke 1944), several anseriforms (Howey et al. 1984), and Common Canaries (*Serinus canarius*; Kern 1987), but with conflicting results. For fowl, day-to-day variations in  $P_N$  were small (the difference between extreme maximal and extreme minimal measured daily values, a property which we will call  $\Delta P_{max}$ , was only about 4 torr) and paralleled changes in ambient vapor pressure ( $P_i$ ). For swans and geese, variations were more pronounced ( $\Delta P_{max} = 8-9$  torr) and not in step with  $P_i$ . For canaries, they were even larger ( $\Delta P_{max}$  up to 15 torr) and tracked  $P_i$  in some, but not all cases.

In the experiments reported here, we used the same approach to see if  $P_N$  is reasonably constant within and between nests of Song Sparrows (*Melospiza melodia*) during successive days of incubation.

### MATERIALS AND METHODS

#### BIRDS AND STUDY AREA

During March and April 1986, we measured  $P_N$  and  $\dot{M}_{H_2O}$  in nests of Song Sparrows (*M. m. mi-*

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TABLE 1. Water-vapor pressure ( $P_N$ ) in nests of Song Sparrows on San Miguel Island during 2-9 days of incubation.

Nest <sup>1</sup>	Nest site		Clutch size <sup>2</sup>	Period when $P_N$ monitored			Extreme $P_N$ (torr)		Average $P_N$ (torr)
	Slope/gully	Plant <sup>2</sup>		No. of days <sup>3</sup>	Inclusive dates	Days of incubation at onset	Maximal	Minimal	
01-86	S	H	4	9 (3-4-1-1)	15-26 Mar	1	31.5	9.1	15.9 ± 7.1
07-86	S	M	4	4 (4)	22-25 Mar	9	21.9	11.6	14.6 ± 4.9
08-86	S	H	4	7 (7)	18-24 Mar	6	26.0	8.7	15.6 ± 7.1
09-86	S	B-G	4	5 (4-1)	21-26 Mar	3	23.2	16.0	18.4 ± 3.4
18-86	S	G	3	2 (2)	1-2 Apr	7	13.0	10.6	11.8
34-86	S	H	3	8 (8)	19-26 Apr	6	23.8	8.2	15.5 ± 5.6
35-86+	S	H	3	5 (5)	22-26 Apr	?	30.3	8.8	14.1 ± 9.1
43-86+	S	B-G	3	3 (1-2)	24-27 Apr	?	16.2	9.3	13.3 ± 3.6
02-86+	G	G	4	8 (4--4)	11-20 Mar	0	29.1	12.2	19.7 ± 5.9
06-86	G	B	4	8 (5--3)	16-25 Mar	2	31.2	10.1	18.2 ± 8.1
13-86	G	L	4	2 (2)	25-26 Mar	7	23.9	16.9	20.4
All nests	—	—	3-4	2-9	—	0-9	—	—	16.1 ± 2.7

<sup>1</sup> Nests whose numbers are followed by "+" were unsuccessful; two to three eggs hatched in nests not so marked.

<sup>2</sup> B = coyote bush (*Baccharis*), H = *Haplopappus*, G = grass, L = lupin (*Lupinus*), M = horehound mint (*Marrubium vulgare*).

<sup>3</sup> Clutch size includes the egg hygrometer.

<sup>4</sup> Numbers in this column are total days of incubation during which  $P_N$  was monitored. Series of numbers in parentheses indicate how those total days were distributed during the period. For example, for nest 01-86, (3-4-1-1) means that  $P_N$  was recorded on 15-17, 19-22, 24, and 26 March, but not on 18, 23, and 25 March.

*cronyx*) on San Miguel Island (120°W, 34°N), 43 km off the Pacific coast near Santa Barbara, California. Our study site was a 9.2-ha area of tableland on the north-central side of the island between Cuyler Harbor and San Miguel Hill, approximately 400 m NW of the Nidever Canyon ranger station, which served as our field laboratory. The study area sloped toward the ocean and was crossed by several gullies. It had patchy vegetation dominated by *Haplopappus* scrub and grasses and was exposed to strong northwesterly winds that swept south from Point Conception. Ambient temperatures ( $T_a$ ) and  $P_1$ , measured with a hygrothermograph, fluctuated between 4 and 34°C and 4 and 13 torr, respectively. Wind speeds, measured with a hotwire anemometer, ranged between 2 and 20 m sec<sup>-1</sup>. Overcast conditions, heavy morning dew, fog, and rain were common. Song Sparrows nested here in a variety of plants both on the slope and in the gullies (Tables 1, 2).

#### MEASUREMENT OF $P_N$ , $P_1$ , AND $M_{H_2O}$

We measured  $P_N$  in the field with canary and Song Sparrow eggs that had been converted into egg hygrometers. We removed the contents of the eggs through small holes in the shell; rinsed them out with water; allowed them to dry at room temperature (about 20°C); and filled them with crushed silica gel. The holes in the shell were

then closed with silicone adhesive (Permatix, Loctite Corporation). We measured the water-vapor conductance ( $G_{H_2O}$ ) of these hygrometers by keeping them in small sealed containers over water at 29-30°C and weighing them daily for five to six consecutive days, following procedures described by Rahn et al. (1977).

Because the eggs were so small, we could not outfit them with screw-top caps to change the silica gel when it became waterlogged, as Rahn and others (1977) did with larger eggs. We found, however, that we could remove the water from the silica gel within the hygrometers by heating them in an oven for 2-4 hr at temperatures near 200°C, and that their  $G_{H_2O}$  did not change when they were repeatedly oven-dried provided their color (pale blue) did not change (to brown).

Few hygrometers lasted the entire nesting season. Most were broken, destroyed in the nest, or simply disappeared from the nest. Those that did survive were accidentally overheated late in the study, at which time we stopped using them.

Since small egg hygrometers sometimes absorb enough water within 1-2 days to make them unreliable for measuring  $P_N$  (Rahn et al. 1977), ours were not left in a nest, with one exception (48 hr), for more than 24 hr. Because there were only small increases in their mass in the nest, compared with much larger increases over similar periods of time when their  $G_{H_2O}$  was measured,

TABLE 2. Daily rate of water loss from eggs ( $\dot{M}_{H_2O}$ ) in nests of Song Sparrows on San Miguel Island during 3-12 days of incubation.

Nest <sup>1</sup>	Egg no.	Nest site		Clutch size <sup>2</sup>	Period when $\dot{M}_{H_2O}$ monitored			Extreme $\dot{M}_{H_2O}$ <sup>4</sup> (mg day <sup>-1</sup> )		Average $\dot{M}_{H_2O}$ <sup>4</sup> (mg day <sup>-1</sup> )
		Slope/ gully	Plant <sup>2</sup>		No. of days	Inclusive dates	Day of incubation at onset	Maxi- mal	Mini- mal	
24-86+	1	S	H	3	3	10-13 Apr	?	31.9	18.9	27.1 ± 7.1
34-86	1	S	H	3	9	17-26 Apr	4	46.6	23.8	33.1 ± 8.0
	2				9	17-26 Apr	4	38.4	24.8	31.2 ± 5.2
35-86+	1	S	H	3	7	17-24 Apr	?	36.9	18.1	30.7 ± 7.0
	2				10	17-27 Apr	?	31.8	18.1	27.1 ± 5.5
43-86+	2	S	B-G	3	5	23-28 Apr	?	38.0	24.3	28.8 ± 5.3
	3				5	23-28 Apr	?	39.2	22.1	28.0 ± 6.9
29-86	2	G	L-MG	3	12	10-22 Apr	-1	31.2	20.3	25.7 ± 3.7
30-86	1	G	H-E	3	7	10-17 Apr	4	33.0	15.9	25.0 ± 5.3
38-86	1	G	H	4	7	21-28 Apr	1	33.0	26.3	30.1 ± 2.4
	3				7	21-28 Apr	1	29.3	19.7	22.3 ± 3.8
	4				7	21-28 Apr	1	29.8	20.8	23.7 ± 4.0
All eggs	—	—	—	3-4	3-12	—	(-1)-4	—	—	27.7 ± 3.2

<sup>1</sup> (+) = unsuccessful nests. Eggs hatched in nests that are not followed by a "+."

<sup>2</sup> E = yellow yarrow (*Eriophyllum confertiflorum*), MG = morning glory (*Ipomoea purpurea*); for other abbreviations, see footnote 2 of Table 1.

<sup>3</sup> Clutch size includes one egg hygrometer in all nests except 38-86.

<sup>4</sup> Data are extremes of mean  $\dot{M}_{H_2O}$  after day 2 of incubation.

we concluded that the amount of water absorbed by the hygrometers in 1-2 days did not invalidate their use.

We located nests on the study area during periods of nest construction, egg laying, or incubation. When possible, we began to monitor  $P_N$  on day 0 of incubation (= the day on which the last egg in the clutch was laid). But, in several cases, incubation was already in progress when the nest was found and we determined day 0 by extrapolation from the day when the last egg hatched. In four cases, we were unable to determine day of incubation because the nests were abandoned before the eggs hatched. Chicks hatched in the other 11 nests in the study.

To determine the average daily vapor pressures in each nest, we weighed a dehydrated egg hygrometer, placed it in the nest for 24 hr, and then retrieved and reweighed it (Roller-Smith balance, accuracy ± 1.0 mg). Since we knew the hygrometer's  $G_{H_2O}$  and by weighing obtained the increase in its mass during this 24-hr period ( $\dot{M}_{H_2O}$ ), we were able to calculate  $P_N$  for the same period using the equation (Ar et al. 1974)  $G_{H_2O} = \dot{M}_{H_2O} / |P_A - P_N|$ . In this case,  $P_A$ , the water-vapor pressure in the egg, is 0 because the hygrometer was filled with silica gel, and accordingly the equation reduces to  $P_N = \dot{M}_{H_2O} / G_{H_2O}$ .

Hygrometers were wrapped in plastic (Saran

Wrap) and taken to the ranger station for weighing. We ignored the minor effect that this had on the mass of the eggs because unused hygrometers packaged in plastic ( $n = 33$ ) lost an average of only 0.7 mg while being carried to and from the study area for periods lasting several hours. With rare exceptions, the change in mass of these wrapped eggs ranged between -2 and +3 mg, and the average mass loss was only 6.25% of the average mass gained by hygrometers left in the nest for 24 hr.

We tried initially to measure  $P_1$  at each nest site with egg hygrometers suspended in mesh sacs within inverted styrofoam cups. But, heavy fog and dew coupled with low  $T_a$ 's caused water to condense on them (or to condense on the cup and drip onto them) making them unreliable. Consequently, we had to rely on data from a single Cole-Parmer hygrothermograph for information about  $P_1$ . The instrument was calibrated periodically against a sling psychrometer and a centigrade thermometer. Between 13 and 23 March, we put the hygrothermograph in Nidever Canyon near nest 02-86. Between 26 March and 28 April it was on the exposed tableland in the center of the study area. Because Song Sparrow nests are within 1.1 m of the ground on San Miguel Island, because the vegetation on the study site is open and patchy, and because strong

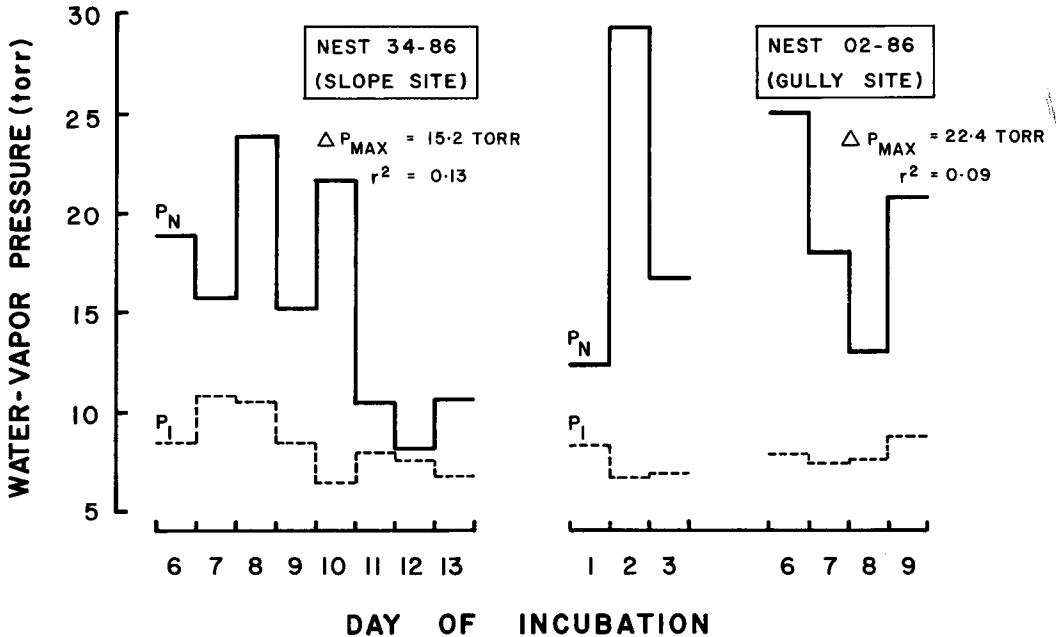


FIGURE 1. Daily changes in nest ( $P_N$ ) and ambient ( $P_I$ ) water-vapor pressure in representative Song Sparrow nests from gully and slope sites on San Miguel Island.  $\Delta P_{\text{MAX}}$  = the difference between extreme measured values (maximal and minimal) of  $P_N$ .  $P_N$  did not correlate with  $P_I$  in either nest as indicated by the small coefficients of determination ( $r^2$ ).

northwesterly winds constantly mix layers of air near the ground, we assumed that  $P_I$  values at this single site were reasonable first approximations of ambient conditions elsewhere on the *slope*; but not in the gullies which were more or less sheltered from wind. Consequently, we limited comparisons of  $P_N$  vs.  $P_I$  to nest 02-86 in the 13–23 March interval and to slope nests in the 26 March–28 April interval. The daily values of  $P_I$  used in our analyses (and appearing in Fig. 1) are averages of values obtained from the hygromograph at 2-hr intervals throughout each 24-hr period.

In April, we also measured  $M_{H_2O}$  of 12 Song Sparrow eggs in seven nests for three to 12 consecutive days of incubation. Eggs were numbered with a felt-tip pen for identification. They were taken from each nest once a day, transported to the laboratory, weighed, and then returned to the nest. They too were wrapped in plastic while in transit.

#### STATISTICAL EVALUATION OF DATA

Data were evaluated by Student  $t$ -tests, paired  $t$ -tests, and correlation analysis (Zar 1974). Values in the text and tables of this paper are means  $\pm 1$  SD.

#### RESULTS

##### WATER-VAPOR PRESSURE IN THE NEST AND ATMOSPHERE

Water-vapor pressure in individual nests averaged 13.3–20.4 torr over periods of 2–9 days of incubation (Table 1). The collective average for all 11 nests was  $16.1 \pm 2.7$  torr. However,  $P_N$  fluctuated widely from one day to another within individual nests (Fig. 1):  $\Delta P_{\text{MAX}}$  averaged 14.6 torr; in the most extreme case (nest 01-86, Table 1), it was 22.4 torr. Meanwhile  $P_I$  varied between 6.4 and 10.8 torr and averaged 8.1 torr (see Fig. 1).  $P_N$  did not track  $P_I$  significantly in the four nests for which we had adequate data for comparison.

Water-vapor levels in nests from the slope ( $14.9 \pm 2.0$  torr,  $n = 8$ ) were significantly ( $P < 0.01$ ,  $t$ -test) lower than in nests from gullies ( $19.4 \pm 1.1$  torr,  $n = 3$ ).

##### DAILY CHANGES IN EGG MASS

$M_{H_2O}$  averaged 22.3–33.1 mg day<sup>-1</sup> in individual nests, and  $27.7 \pm 3.2$  mg day<sup>-1</sup> collectively, over 3–12 days of incubation (Table 2). Rates of mass (= water; Ar and Rahn 1980) loss also varied considerably from day to day within individual

nesses with extreme differences amounting to 6.8–22.7 mg day<sup>-1</sup> (13.8 ± 4.6 mg day<sup>-1</sup> on average for all seven nests).  $\dot{M}_{H_2O}$  and  $P_N$  changed independently in six of seven eggs from four nests; they were significantly correlated for one egg in nest 35-86 ( $r = +0.66$ ,  $P < 0.05$ ,  $df = 10$ ).  $\dot{M}_{H_2O}$  was higher ( $P < 0.05$ ,  $t$ -test) at slope sites (29.4 ± 2.3 mg day<sup>-1</sup>;  $n = 7$  eggs) than at gully sites (25.4 ± 3.0 mg day<sup>-1</sup>;  $n = 5$  eggs).

In the two nests (29-86 and 38-86; four eggs; Table 2) for which we have sufficient data,  $\dot{M}_{H_2O}$  increased 6–33% ( $P < 0.05$ , paired  $t$ -test) after the third day of incubation (25.7 vs. 19.3, 30.1 vs. 28.5, 22.3 vs. 19.5, and 23.7 vs. 19.9 mg day<sup>-1</sup>).

## DISCUSSION

$P_N$  averaged 16 torr (Table 1), well within the range of published values (6–26 torr) for a large number of other avian species (Walsberg 1980). However, there were considerable differences between nests (individual averages between 12 and 20 torr; Table 1) and from day to day within single nests ( $\Delta P_{max}$  values between 2 and 22 torr; Fig. 1). Variations of this magnitude suggest that Song Sparrows do not have a specific optimal  $P_N$  which they attempt to maintain while incubating. Even among waterfowl and pheasants where  $P_N$  was purportedly constant (Rahn et al. 1977),  $\Delta P_{max}$  within individual nests averaged about 6 torr and could well have been higher had  $P_N$  been measured on a daily basis rather than over periods of 2–3 days at a time. In nests of Black Swans (*Cygnus atratus*) and Barnacle Geese (*Branta leucopsis*),  $P_N$  changed as much as 8–9 torr within a single 24-hr period (Howey et al. 1984). Since large variations in  $P_N$  occurred in nests in which the eggs hatched (Table 2), our data, like those of Howey et al. (1984) for anseriforms, are consistent with Walsberg's (1980) model and the experimental work of Simkiss (1980) and Carey (1986) indicating that  $P_N$  would have to change radically to significantly impair hatchability.

Perhaps it is not critical that  $P_N$  be maintained at constant levels throughout the incubation period, but it is only necessary to keep  $P_N$ : (1) *within a fairly broad range*. Our data are consistent with such an hypothesis, as is the high tolerance of developing avian embryos to drastic changes in the egg's water content (Simkiss 1980, Carey 1986). (2) *constant during sensitive periods* in embryonic development like those described for domestic fowl (Snyder and Birchard 1982). Our

data are not consistent with this idea since large daily changes in  $P_N$  occurred during all phases of incubation (Fig. 1). (3) *constant during part of each day* of incubation. This is consistent with the behavior of songbirds which sit tightly on the clutch at night and are on eggs at least 70% of the time during incubation (e.g., Haftorn 1981, Zerba and Morton 1983). However, long periods of constant  $P_N$  are not apparent in data for incubating geese and swans (Howey et al. 1984).

$P_N$  did not correlate significantly with  $P_i$ , although one might expect it to if  $P_N$  depended solely on the ventilating behavior of the incubating bird. Using swans and geese, Howey et al. (1984) showed previously that short-term fluctuations in  $P_N$  bore no relation to ventilating movements of incubating birds.

Using the equation (Rahn and Ar 1974)  $F = \dot{M}_{H_2O} \cdot I/W$  in which  $\dot{M}_{H_2O} = 27.7$  mg day<sup>-1</sup> (Table 2),  $I$  = length of the incubation period (13 days for San Miguel Island Song Sparrows) and  $W$  = fresh egg mass (2.6–3.1 g in San Miguel Island Song Sparrows; unpubl. data of Kern et al. for eggs weighed on the day they were laid), we estimate that the fraction of the egg's initial mass ( $F$ ) that was lost during incubation, under these variable  $P_N$  conditions, was 0.11 to 0.14. These values are within the range (0.10–0.23) reported for other birds (Ar and Rahn 1980), and agree well with the actual mass loss (11%, pipping losses not included) that we recorded at nest 29-86 over 12 days of incubation. So, large variations in  $P_N$  within and among Song Sparrow nests did not produce unusual or markedly different amounts of water loss from the eggs during incubation.

$\dot{M}_{H_2O}$  is often assumed to be constant throughout the incubation period (Rahn et al. 1977). However, it varies in many passerines (Manning 1982), some shorebirds (Vleck et al. 1983), and also apparently in Song Sparrows (Table 2). Fluctuations in our eggs may have been caused by day-to-day variations in egg temperature (Vleck et al. 1983) or changes in the eggshell's  $G_{H_2O}$  (Carey 1979, Hanka et al. 1979, Birchard and Kilgore 1980, Sotherland et al. 1980, Kern 1986). The significant increase in  $\dot{M}_{H_2O}$  of our eggs after 3 days of incubation may indicate that they became more permeable to water at that time.

$\dot{M}_{H_2O}$  also depends on  $P_N$ , but not just  $P_N$  since  $\dot{M}_{H_2O}$  and  $P_N$  were significantly correlated ( $r = -0.81$ ,  $P < 0.05$ ,  $df = 5$ ) in only one of three eggs from two nests in which we measured both during five to seven consecutive days of incu-

bation. Water added to the egg by the brood patch or nest with which it is in contact during incubation, and reductions in the  $\text{GH}_2\text{O}$  of the egg because part of it is in contact with the incubation patch (Handrich 1989), may also influence  $\text{MH}_2\text{O}$ .

Average  $P_N$  was significantly higher and  $\text{MH}_2\text{O}$  significantly lower in gully nests than in nests from the slope of our study area. If such differences are real, rather than a consequence of small sample sizes, they probably reflect different ambient conditions at the two locations since we did not find site-related differences in nest structure and placement or in the attentiveness of Song Sparrows to their clutches. The most conspicuous ambient difference between the two sites was that gullies were more sheltered than the slope. On windy days, e.g., airspeed averaged 6.8 m  $\text{sec}^{-1}$  near nests on the slope, but only 1.6 m  $\text{sec}^{-1}$  near gully nests ( $P < 0.01$ , paired  $t$ -test; Kern et al., unpubl. observ.). Low windspeed may reduce the rate of drying of gully nests, thus conserving nest humidity and reducing the rate of water loss from eggs within them.

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