

# THE REGULATION OF EGG TEMPERATURES AND ATTENTIVENESS PATTERNS IN THE DUSKY FLYCATCHER (*EMPIDONAX OBERHOLSERI*)

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**ABSTRACT.**—Egg temperatures ( $T_{egg}$ ) and attentiveness were measured in *Empidonax oberholseri* breeding at high altitude in the Sierra Nevada of California. Eggs were tended in daytime during the laying period but were above the assumed threshold temperature for development (28°C) for only 17.6% of the time. Mean  $T_{egg}$  increased during the laying period and for the first few days of incubation. This may have been related to brood patch development.

Full-time incubation began at night following the laying of the penultimate (6 cases) or prepenultimate egg (3 cases). Once incubation began, there was little diurnal variation in mean  $T_{egg}$ . Eggs were above developmental threshold for 92.2% of the time during the active day and 99.9% of the time during night rest. Mean  $T_{egg}$  for 5 nests for the full period of incubation was 37.62°C.

Trends in  $T_{egg}$  indicated that body temperature ( $T_b$ ) of incubating females decreased at night when ambient temperature ( $T_a$ ) was between 12°C and 4°C. Shivering thermogenesis probably was employed at  $T_a$ s below 4°C.

During storms, despite heavy hail and rain, females endured on the nest for long periods. If the storm continued, they eventually left to feed, thus exposing eggs to possible damage. When potent thermolytic conditions were coupled with food shortage, as during large storms or prolonged episodes of cold, windy weather, incubating females neglected their eggs in order to extend foraging time. They also allowed eggs to cool at night by withdrawing their brood patch. We assume that this increased their ability to defend  $T_b$ .

Attentiveness varied diurnally, being highest at midday. Duration of foraging trips varied little with time of day or  $T_a$ , but attentive bouts were longest at midday. The rate of foraging bouts was highest at the beginning and end of the active day. Unlike many species, total attentiveness in *E. oberholseri* was correlated positively with  $T_a$ . This may be a general pattern in open-nesting birds at high altitude that has evolved because of the need to protect eggs from damage by solar radiation. Repeated excursions of eggs to low temperatures or outright periods of neglect during cold weather did not seem to affect embryo survival. Received 10 April 1984, accepted 2 October 1984.

STRATEGIES employed by incubating birds must often represent compromises between the embryo's thermal requirements for development and the tending adult's energy balance (White and Kinney 1974, Carey 1980a, Vleck 1981a). It follows that information on egg temperatures and on attentiveness patterns of adults during incubation should elucidate important elements of these coadapted characters, particularly when they are being amplified by stringent environmental conditions.

To learn more about how the scope and mechanisms of adaptation to the environment are expressed during incubation, we studied the Dusky Flycatcher (*Empidonax oberholseri*) at a high-altitude location where periods of inclement weather often occur. This small (11-g) bird builds an open nest, and only the female

incubates. It winters in Mexico and summers in the western United States and far-western Canada (Johnson 1963). In California it generally breeds in montane habitat between elevations of 1,500 and 3,000 m.

## STUDY AREA AND METHODS

Our study area is at about 3,000 m in the eastern Sierra Nevada near Tioga Pass, Mono County, California. The area consists mostly of the upper portions of glaciated valleys that have lakes, wet meadows, willows (*Salix* spp.), and small pines (*Pinus jeffreyi* and *P. contorta*) in their bottoms and quaking aspens (*Populus tremuloides*), tall pines, and talus on their sides. The majority of nests ( $n = 110$ ) were located in willows, aspens, or pines between 1 and 4 m above the ground. Clutches were started during June and July, and clutch size usually was 3 or 4. Freshly laid eggs

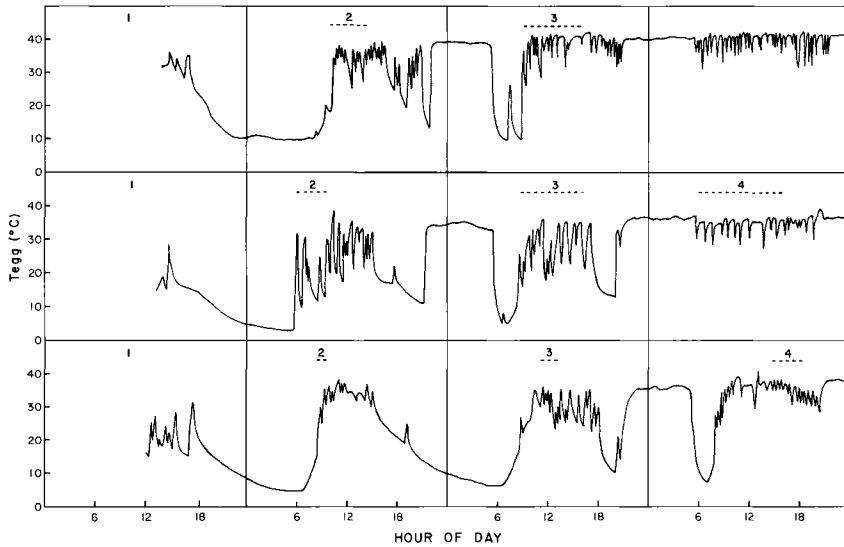


Fig. 1. Egg temperatures in *Empidonax oberholseri* during the laying period in 1 three-egg (top) and 2 four-egg clutches (middle and bottom). Each box is a 24-h period. Recordings were made from a thermocouple inserted into the first egg on the day it was laid. Known boundaries for laying times of subsequent eggs are indicated by dashed lines under the egg's number.

weighed about 1.2 g. Data were gathered during the summers of 1981, 1982, and 1983.

Egg temperature ( $T_{egg}$ ) was measured using a 40-gauge copper-constantan thermocouple that was inserted to the egg center, spot-glued to the shell, threaded through the bottom of the nest, and connected to a Bailey thermometer (Bat-12). An Esterline-Angus strip chart recorder (MS411BB) provided a continuous record. Egg temperatures used in this report were taken from these charts at 3-min intervals. Attentiveness was determined from the same records because sudden temperature changes usually signaled departure or arrival of the incubating female. This was verified by direct observation. Thermocouples were inserted in the first eggs laid in 11 *E. oberholseri* nests. Two of these nests were depredated within 48 h, but data were obtained for the complete laying period on all 9 of the remaining clutches. One of these was lost during incubation, and we report here attentiveness data from the remaining 8 clutches. Temperature calibration difficulties were encountered at times in 3 nests, so  $T_{egg}$  data for the whole incubation period are presented only for 5 nests. Ambient temperature ( $T_a$ ) was recorded with hygrothermographs placed 1–4 m from the nest or from thermocouples placed immediately beneath the bottom of the nest.

Brood-patch temperatures were taken with a custom-built surface probe and thermometer (Bailey, Bat-12). Incubating females were often so docile that they would permit us to slip the probe under them and hold it against their brood patch while they sat on

the nest. Sunrise and sunset times were obtained by direct observation of the sun's appearance and disappearance at the study area. Pacific Daylight Time was used throughout.

We defined night rest as the period between the return of the female to the nest for the last time in the evening until she left the next morning. The active day was the time between periods of night rest. The egg-laying period began with the laying of the first egg and ended with the onset of incubation. Incubation began when the female sat on the eggs continuously at night for the first time.

## RESULTS

*Temperatures during egg-laying.*—Temperature recordings of the first egg in a clutch began on the day it was laid. This provided a record of  $T_{egg}$  and attentiveness for both laying and incubation periods. Data were obtained for the complete laying period in 3 three-egg clutches and 6 four-egg clutches. The development of incubation was similar in all three-egg clutches in that females tended eggs during the day and began nighttime sitting just prior to laying the third egg (Fig. 1, top). Two patterns were observed in four-egg clutches. In 3 nests nighttime sitting began before the third egg was laid (Fig. 1, middle), and in the other 3 it began before the fourth egg was laid (Fig. 1, bottom).

TABLE 1. Mean 24-h egg temperatures ( $^{\circ}\text{C}$ ) in *Empidonax oberholseri* during the laying period and during incubation. Data are from 5 nests.  $n$  refers to individual readings taken at 3-min intervals.

Day	Mean	SD	$n$
Laying			
1	14.7	5.9	928
2	16.3	10.6	1,920
3	20.3	10.7	480
Incubation			
1	34.0	8.6	2,336
2	36.7	4.4	2,100
3	37.8	2.6	2,201
4	37.6	7.2	2,400
5	38.3	6.1	2,400
6	38.8	2.2	2,400
7	38.6	2.2	1,883
8	38.5	2.5	2,160
9	38.2	2.3	2,400
10	37.4	3.8	2,280
11	37.6	3.3	2,220
12	37.7	4.9	2,313
13	37.8	2.5	2,400
14	37.8	2.6	2,325
15	37.7	2.8	1,020

Mean  $T_{\text{egg}}$  rose steadily during the laying period and continued to increase through the first few days of incubation (Table 1).  $T_{\text{egg}}$  was lowest on the first night of incubation and tended to increase slightly but steadily for several consecutive nights thereafter. Mean  $T_{\text{egg}}$  during episodes of constant attentiveness (defined as periods when the female was on for at least 15 min and  $T_{\text{egg}}$  was at equilibrium) rose  $4.0^{\circ}\text{C}$  for active day measurements and  $2.4^{\circ}\text{C}$  for night rest during the first four days of incubation (Table 2). Both increases were significant ( $t$ -test,  $P < 0.01$  in each case) and may be related to brood-patch development. Mean brood-patch temperature of 2 females between days 1 and 4 of incubation was  $41.52^{\circ}\text{C}$  (SD =  $0.56^{\circ}\text{C}$ ,  $n = 5$ ). Mean patch temperature of 3 females taken between days 6 and 15 of incubation was  $42.44^{\circ}\text{C}$  (SD =  $0.52^{\circ}\text{C}$ ,  $n = 10$ ). These means were different ( $t$ -test,  $P < 0.05$ ). Tightness of sit also could be involved in  $T_{\text{egg}}$  changes with progress of incubation, but we have no way to evaluate this possibility.

The first night of incubation, unlike subsequent nights, was bracketed by long inattentive periods in all 9 nests studied (see Fig. 1). Mean duration of the inattentive bout was 58.9 min (SD = 69.4 min) immediately preceding and 89.6 min (SD = 49.5 min) following the first

TABLE 2. Mean egg temperature ( $^{\circ}\text{C}$ ) during constant attentiveness (following 15 min or more of continuous sitting) by day of incubation in *Empidonax oberholseri* during the active day and during night rest. Data are from 5 nests.  $n$  refers to individual readings taken at 3-min intervals.

Day of incubation	Active day			Night rest		
	Mean	SD	$n$	Mean	SD	$n$
1	34.4	8.1	360	36.0	2.9	531
2	37.3	3.4	525	36.9	2.8	804
3	37.8	2.6	479	37.7	2.1	804
4	38.4	2.5	605	38.4	1.7	796
5	38.0	2.4	447	38.0	2.7	829
6	39.0	2.0	592	38.4	2.0	887
7	39.6	1.5	672	39.2	1.6	868
8	39.8	1.5	423	38.7	1.6	690
9	39.7	1.5	458	39.2	1.8	773
10	39.1	1.6	488	38.7	1.9	893
11	38.4	1.7	535	38.4	1.9	856
12	38.4	1.7	504	38.9	1.7	781
13	38.9	2.2	533	38.2	1.8	815
14	38.7	1.7	508	38.0	1.6	890
15	38.7	1.8	530	38.2	1.8	821

night of sitting. These periods off were much longer than those observed before and after all other nights of incubation (before =  $4.4 \pm 1.4$  min, after =  $4.9 \pm 0.6$  min). It appears that females were both anticipating and reacting to the first night of incubation with very long foraging bouts.

Examination of  $T_{\text{egg}}$  records gives the impression that *E. oberholseri* spend considerable time on their nests during the laying period (Fig. 1). Eggs were allowed to assume ambient temperatures at night but from the first egg onward were tended regularly in daytime. Despite the frequent daytime visits of females, however, eggs were not maintained for long periods at temperatures necessary for embryonic growth (Table 3).

We cannot yet report conclusively on the time of day that eggs are laid. We do know that laying can occur anywhere from early morning to midafternoon, and we suspect that the pattern observed in Fig. 1 (bottom) is common, i.e. consecutive eggs are laid at intervals greater than 24 h.

*Temperatures during incubation.*—Upon completion of the clutch, eggs were tended steadily with short interruptions during daylight hours when females left to forage. The duration of foraging bouts varied little unless it was stormy or windy (see below). This rather constant at-

TABLE 3. Percent of time spent by *Empidonax oberholseri* eggs within various temperature intervals during laying and during incubation. Data are from 5 nests.

Temperature interval (°C)	Laying period	Incubation	
		Active day	Night rest
0.0-1.9	0.00	0.19	0.00
2.0-3.9	1.35	0.28	0.00
4.0-5.9	9.90	0.33	0.00
6.0-7.9	11.53	0.59	0.00
8.0-9.9	9.00	0.97	0.00
10.0-11.9	9.72	1.03	0.00
12.0-13.9	8.07	0.80	0.00
14.0-15.9	6.33	0.34	0.00
16.0-17.9	6.66	0.44	0.00
18.0-19.9	4.41	0.43	0.00
20.0-21.9	5.25	0.53	0.01
22.0-23.9	3.09	0.47	0.01
24.0-25.9	3.78	0.70	0.02
26.0-27.9	3.27	0.66	0.04
28.0-29.9	3.33	1.23	0.20
30.0-31.9	3.27	2.44	0.56
32.0-33.9	3.66	5.33	1.60
34.0-35.9	5.13	11.95	4.79
36.0-37.9	1.59	22.01	36.00
38.0-39.9	0.45	23.23	25.54
40.0-41.9	0.12	23.37	30.02
42.0-43.9	0.09	2.60	1.21
44.0-45.9	0.00	0.08	0.00

tention yielded mean values for  $T_{egg}$  that had little diurnal variation. The lowest means occurred in early morning, when foraging coincided with the day's lowest  $T_a$ s (Fig. 2). The grand mean for  $T_{egg}$  measured every 3 min in 5 nests for the full period of incubation was 37.62°C (SD = 3.97°C,  $n = 32,838$ ).

$T_{egg}$  might be expected to vary more in daytime than at night because of foraging trips by tending females and because of greater variability in thermal conditions during daylight hours. This expectation is met when the relative distributions of  $T_{egg}$  during the active day and during night rest are examined (Table 3). Daytime  $T_{egg}$  had a range twice that measured at night. In both time frames, however  $T_{egg}$  was most frequently in the range of 36-42°C (68.6% of the time during the active day and 91.6% during night rest). Eggs were above 28°C for 92.2% of the time in the daytime and 99.9% of the time at night (Table 3).

Large variations did not occur in  $T_{egg}$  during night rest, but a consistent and interesting relationship between nighttime  $T_{egg}$  and  $T_a$  was present nonetheless (Fig. 3). Mean  $T_{egg}$  de-

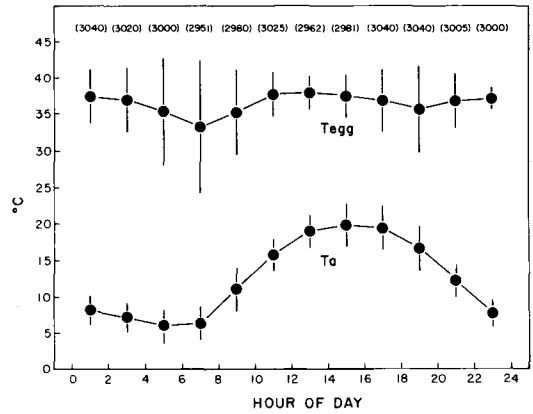


Fig. 2. Mean egg ( $T_{egg}$ ) and air ( $T_a$ ) temperatures per 2-h interval for all days of incubation in *Empidonax oberholseri*. Vertical lines show  $\pm 1$  SD. Sample sizes are in parentheses. Temperatures were taken every 3 min from 5 nests.

creased steadily at  $T_a$ s between 12°C and 4°C, then increased to a level seen at the higher  $T_a$ s. The total change in mean  $T_{egg}$  was only 2.4°C (37.3-39.7°C), but the sample sizes involved were large and all consecutive pairs of means between 0°C and 14°C were significantly different from one another ( $t$ -test,  $P < 0.01$  in every case).

Some of our most informative incubating bird-environment interactions are revealed in individual records obtained during environmental perturbations. In Fig. 4 are plotted 72 consecutive hours of  $T_{egg}$  recordings (direct tracings of the original records, 25-27 July 1982, days 11-13 of incubation) along with concur-

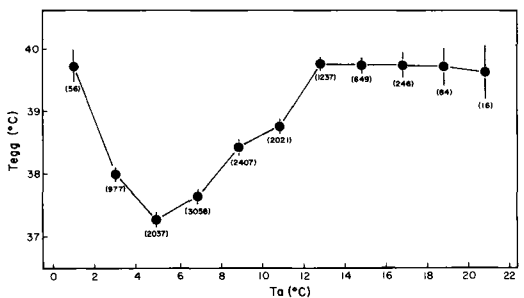


Fig. 3. Relationship of mean egg temperature ( $T_{egg}$ ) to air temperature ( $T_a$ ) during night rest in *Empidonax oberholseri*. Vertical lines show  $\pm 2$  SE. Sample sizes are in parentheses. Temperatures were taken every 3 min from 5 nests.

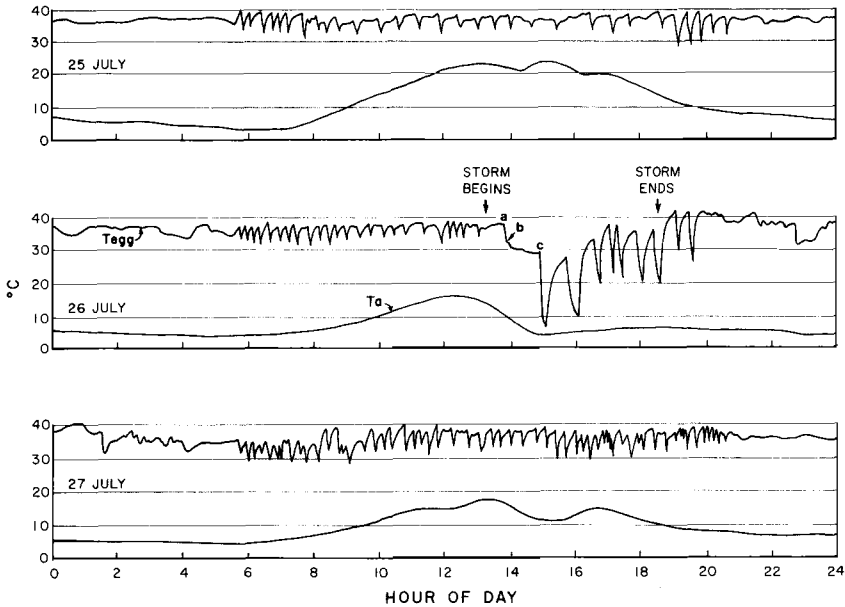


Fig. 4. Egg ( $T_{egg}$ ) and air ( $T_a$ ) temperatures for 3 consecutive days at nest 15. A severe storm, marked by arrows, occurred on 26 July (middle).

rent data on  $T_a$ . This nest (#15) was located 1.5 m above the ground in a willow. It contained 4 eggs, 2 of which were implanted with thermocouples. One of the 2 undisturbed eggs hatched, and the nestling eventually fledged. For all of 25 July (Fig. 4, top) and until about noon on 26 July (Fig. 4, middle) weather conditions were mild, and the patterns of  $T_{egg}$  and attentiveness shown are typical for those of fair weather. The sky then became overcast, and at 1314 a downfall of hail began. Hail and then rain continued until 1830, at which time hailstones were on the ground to a depth of 2 cm. Several *E. oberholseri* and Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) nestlings were killed by this storm, and many *E. oberholseri* eggs were heavily dented by impact from hailstones. This type of damage could occur only if the female left the nest while the storm was in progress. At nest 15 the  $T_{egg}$  record shows (Fig. 4, middle) that the female remained on the nest continuously for the first 31 min of the storm, then got off (point a) for 6 min. She returned (point b) and sat for 62 min before getting off again (point c). Although this was a long attentive period,  $T_{egg}$  was only about 30°C throughout. We think the female was unable to heat the eggs higher than this because hailstones accumulated in the nest during the

interval a-b. At point c she began a series of foraging trips during which  $T_{egg}$  dropped precipitously. Seven such trips were made while the storm was still in progress, and 9 trips were made in all before she began night rest. These trips lasted from 4 to 22 min, with a mean of 9.7 min (SD = 5.3). Eggs took much longer to rewarm than to cool even though they were not always rewarmed completely. Attentive bouts varied between 10 and 39 min (mean = 25.4, SD = 9.9,  $n = 8$ ). Note that the female began night rest about 80 min earlier than was customary for her and that  $T_{egg}$  variation was greater than usual during night rest. The latter probably occurred because the nest was water-soaked.

During the next active day (27 July) this female made 58 foraging bouts, in contrast to only 30 trips made on 25 July. This increased rate of feeding may have been an attempt to compensate for an energy deficit suffered the previous day and/or a reaction to lower than usual  $T_s$  on the 27th.

High winds, particularly when coupled with low  $T_a$ s, are another environmental circumstance with energetic consequences to incubating *E. oberholseri*. A 72-h tracing of temperatures at nest 8 on 7-9 July 1983, days 10-12 of incubation, is illustrative (Fig. 5). This nest was

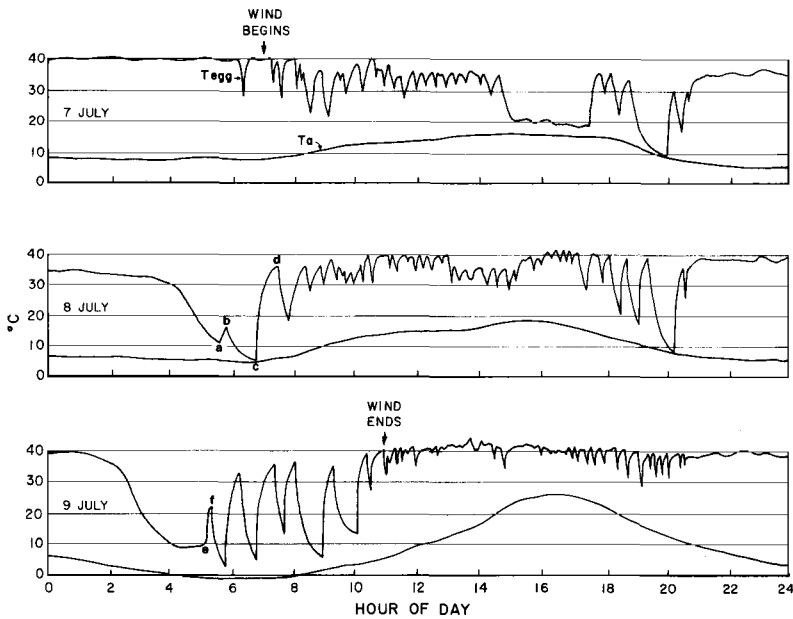


Fig. 5. Egg ( $T_{egg}$ ) and air ( $T_a$ ) temperatures for 3 consecutive days at nest 8. Strong winds began on 7 July (top) and continued until 9 July (bottom).

located 0.6 m above the ground in a stunted aspen on the upper portion of a talus slope. This was an unusually open and exposed nesting site. High winds began blowing on the study area ca. 0700 on 7 July 1983 and continued day and night until ca. 1100 on 9 July. We did not have wind-recording instruments but believe that wind speeds, conservatively, were 10–20 m/s during most of this 52-h span. The female at nest 8 was off her eggs for long periods of time, especially at the beginning and end of the active day.  $T_{egg}$  dropped to near ambient levels (which generally were low) during several of these trips. The longest period off (175 min) occurred in the afternoon of 7 July.  $T_{egg}$  remained 4–5°C above  $T_a$  during this particular bout because the eggs were heated somewhat by the sun. The lowest  $T_{egg}$  recorded during an off bout was 2.8°C at 0550 on 9 July.

In the last hours of night rest on 8 July (Fig. 5, middle),  $T_{egg}$  decreased steadily until at 0536 it reached 11.1°C (point a). During the next 11 min (a–b),  $T_{egg}$  increased to 16.4°C. It then decreased during the next 57 min (b–c) to 5.0°C. Our interpretation of this record is that the female reduced or eliminated contact between her brood patch and eggs during the last hours of night rest. Contact was reestablished briefly (a–

b), whereupon she began the day's first foraging trip. During the first attentive period of the active day (c–d) full contact with eggs occurred, and they were reheated to the usual level.

During the next night (Fig. 5, bottom) this cycle of events was repeated. As before,  $T_{egg}$  decreased rapidly, but it then leveled off and was maintained well above  $T_a$  at between 8.2 and 9.9°C for 71 min. Then between 0512 (point e) and 0523 (point f)  $T_{egg}$  increased from 9.9 to 21.7°C. Again, this female seemed deliberately to reduce heat flow to her eggs. They were allowed to remain cool and were rewarmed (e–f) just before onset (point f) of the day's first foraging trip.

We obtained one additional record from another nest wherein the pattern in  $T_{egg}$  was similar to that observed in nest 8. The only unusual associated environmental circumstances were thundershowers during the two days preceding the response. We can only infer the female's actions from  $T_{egg}$  records in these cases, but similar tracings were obtained from Goldcrests (*Regulus regulus*) standing or roosting over eggs at night during the laying period (Haftorn 1978a). Decreased body temperature ( $T_b$ ) in the female at nest 8 also could have contributed to

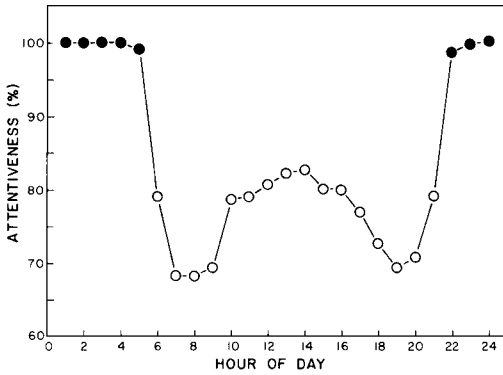


Fig. 6. Relationship of attentiveness to time of day in *Empidonax oberholseri*. Closed circles show data from hours of night rest, open circles from hours of active day. *n* is ca. 1,500 for each data point. Data were taken at 3-min intervals from 8 nests.

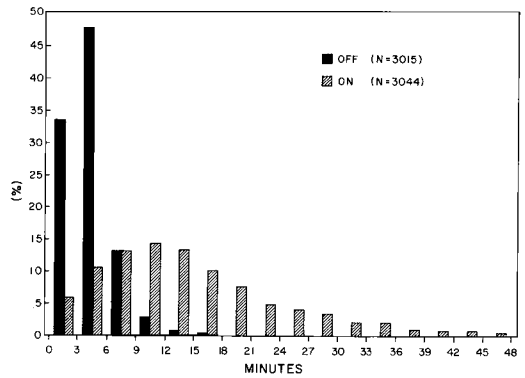


Fig. 8. Frequency (%) of bout durations in incubating *Empidonax oberholseri*. Bout classes encompassing fewer than 1% of cases are not shown.

egg-cooling, but it seems clear that she was not hypothermic at the time eggs were rewarmed. The reheating process began abruptly and proceeded at a rate of 1–2°C/min, which is typical of the records obtained when normothermic *E. oberholseri* came back onto cold eggs. Also, eggs

were only 16.4°C and 21.7°C on 8 and 9 July when the female got off to feed. In contrast, when eggs are warmed during arousal from hypothermia by incubating hummingbirds,  $T_{egg}$  begins to increase gradually, the rate of increase is less than half that observed in *E. oberholseri*, and the female does not leave until  $T_{egg}$  (and her own  $T_b$ ) are well above 30°C (Calder and Booser 1973, Vleck 1981b).

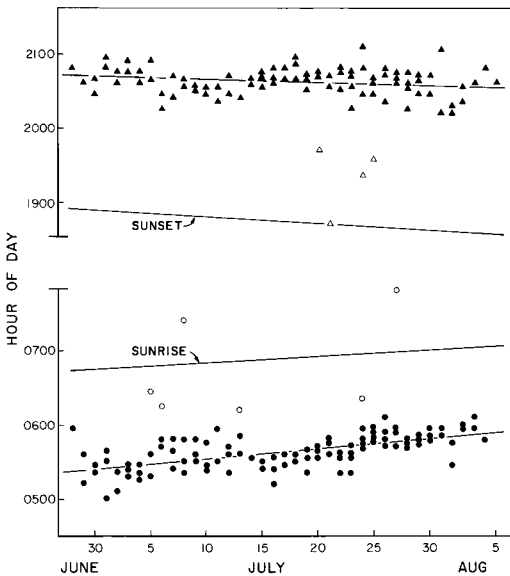


Fig. 7. Times of onset (bottom, circles) and cessation (top, triangles) of active day in *Empidonax oberholseri* throughout the nesting season. Data points shown as open symbols were associated with inclement weather (see text) and were not used in calculations of regression lines.

The data from nest 8 on 9 July (Fig. 5, bottom) are of additional interest in that they illustrate clearly the vagaries of summer weather at high altitude. Only a few hours after freezing  $T_s$ s and high winds, the air became calm and was warmed rapidly by the sun. Eggs then became subject to solar heating, and in the early afternoon the female, now panting at times, had to be on the nest to prevent eggs from overheating.

There were 4 eggs in nest 8. The first 2 laid were implanted with thermocouples; the other 2 hatched and the nestlings fledged. Embryonic development probably was slowed by the spell of cold, windy weather because the incubation period (17 days) in this nest was longer than that usually observed by us in *E. oberholseri* (15 or 16 days) at Tioga Pass.

*Attentiveness patterns during incubation.*—Once full-time incubation began, and in the absence of foul weather, attentiveness in *E. oberholseri* had a predictable daily pattern. During the active day it tended to be below 70% early and late in the day and near or above 80% at midday (Fig. 6). The constancy of incubation (total time on the nest during the active day) for each of

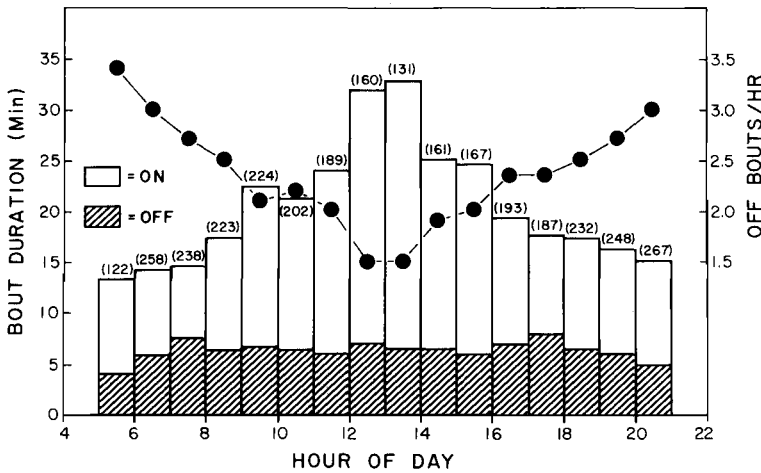


Fig. 9. Mean duration of on and off bouts (histograms, left ordinate) and mean frequency of off bouts (filled circles, right ordinate) with time of day in *Empidonax oberholseri*. Sample sizes are in parentheses.

5 nests for the full period of incubation was 75.1, 73.5, 72.0, 76.3, and 81.9% ( $\bar{x}$  = 75.8%).

The active day began later as the season progressed (Fig. 7, bottom) and ended earlier (Fig. 7, top). Regression lines fitted to the data points by the least-squares method suggest that the trends were probably related to light intensity or photoperiod because they closely paralleled those describing sunrise and sunset. Total seasonal decrease in photoperiod during times of incubation was 40.2 min, whereas decrease in active day for the corresponding period was 42.6 min. Occasionally, females started their active day unusually late or ended it early. In every case the behavior was linked with inclement weather. Mean duration of active day was 891.1 min (SD = 59.2 min, range = 435-1,056 min,  $n$  = 97).

The durations of off (inattentive) and on (attentive) bouts during the active day were quite different in their frequency distributions (Fig. 8). Periods off tended to be brief; 82% were 6 min or less. Periods on were more widely distributed and were nearly 3 times longer in mean duration (19.3 min vs. 6.8 min).

During the active day, periods off changed by only a few minutes (Fig. 9). Attentive periods varied greatly, however, being 2-3 times longer at midday than in early morning and late evening. A corollary, of course, is that the rate of feeding trips changed. Their frequency was 3 or more/h at the onset and end of the active day but only 1.5/h at midday (Fig. 9).

The diurnal rhythm in constancy of incubation (Fig. 6) and in duration of on bouts leads one to ask if attentiveness changed with  $T_a$ . Attentiveness can shift during storms, but these occasions were relatively rare and the effects unpredictable in scope. During mild weather, however, there was a predictable relationship between attentiveness and  $T_a$ . The duration of on bouts, but not off bouts, increased as  $T_a$  increased (Fig. 10), and total attentiveness during

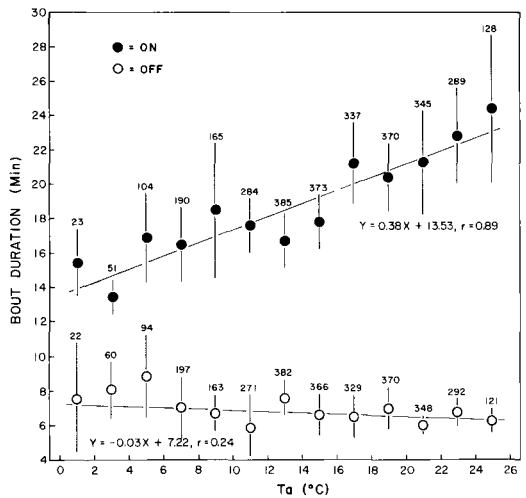


Fig. 10. Duration of on and off bouts with air temperature ( $T_a$ ) in *Empidonax oberholseri*. Means  $\pm$  2 SE (vertical lines) are shown. Sample sizes are above each mean.



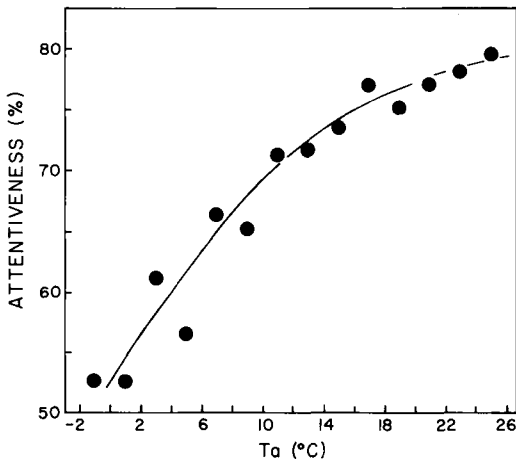


Fig. 11. Attentiveness (% time on nest during active day) vs. air temperature ( $T_a$ ) in *Empidonax oberholseri*. Data are from 8 nests. Curved line was fitted by eye.

the active day increased steadily with  $T_a$  (Fig. 11).

#### DISCUSSION

*Attentiveness and temperature during the egg-laying period.*—A striking aspect of attentiveness was that it consistently occurred during daylight hours prior to clutch completion. We suggest that this behavior is important because eggs were often exposed directly to solar radiation. Regular visits by the female would assure that such exposures would be too brief to be fatal. This is particularly true early in the season when vegetative canopies (leaves) may not yet be fully developed. *Empidonax oberholseri* embryos in the early stages of a clutch were sometimes maintained at temperatures permitting development (Fig. 1). However, if we accept 28°C as the minimum  $T_{egg}$  for embryo development (Drent 1975), we can see that this threshold value was actually exceeded only 17.6% of the time during the laying period (Table 3). A very similar daytime attentiveness pattern during laying was observed in *Z. l. oriantha*, another open-nester, on this same study area (Zerba and Morton 1983a).

Attentiveness at night prior to full clutch completion is not unusual. It seems to occur in all passerines that have been carefully studied and has been previously observed in several *Empidonaces* (King 1955, Davis et al. 1963, Mumford 1964). Haftorn (1978a) pointed out

that this may protect embryos from low temperatures. However, eggs are routinely neglected in many species when it is cold, so the situation remains unclear. To our knowledge, only in the Black-tailed Godwit (*Limosa limosa*, Lind 1961) is there facultative nighttime sitting during the laying period in response to unusually cold weather.

Average  $T_{egg}$ /day was always 34°C or higher once full-time incubation began (Table 1), and  $T_{egg}$  was kept above the developmental threshold (28°C) 92.2% of the time during the active day and 99.9% of the time during night rest (Table 3). This seems remarkable given the frequency at which females foraged, especially because foraging trips occurred most often during the coldest parts of the active day. Maintenance of high mean  $T_{egg}$  was possible because females usually left the nest for short periods. Foraging trip duration was independent of  $T_a$ , and for more than 80% of the time was held to 6 min or less (Fig. 8). This meant that eggs usually cooled only slightly and could be restored quickly to high temperature upon resumption of incubation.

When females were exhibiting constant attentiveness,  $T_{egg}$  was 38°C or higher except during the first few days of incubation (Table 2). This last effect was probably due to changes in brood-patch function because full vascularization of the patch does not occur in many species until incubation is well underway (Drent 1975). Our measurements showing that brood-patch temperature increased as incubation progressed support this interpretation.

Because foraging trips by females coincided with the day's coldest air temperatures (Fig. 2), embryos experienced large and frequent fluctuations in temperature. Tolerant of such oscillations, even when they are prolonged, might be a key adaptation of birds that breed at high altitude. It has been suggested, however, that excursions of this type usually are not a problem and might actually stimulate embryo development (Kendeigh 1940, Lundy 1969), thus compensating for the time that temperatures were below optimum levels.

The regular decrease in  $T_{egg}$  within the  $T_a$  range of 12–4°C during night rest (when females sit continuously) and the reversal of this trend at still colder  $T_a$ s (Fig. 3) points to functionally significant changes in heat flow and heat generation. The total change in mean  $T_{egg}$  was 2.5°C; not a large effect but one that is sta-

tistically significant. If one accepts the view that the eggs and incubating parent function thermally as a unit (see Drent 1972, 1975), these data indicate that core  $T_b$  in females was labile. For a time  $T_b$  apparently decreased as  $T_a$  decreased. Warming of the bird and its eggs at still lower  $T_a$ s (below 4°C) could occur only if females were shivering. This is similar to data obtained on *Z. l. oriantha* (Zerba and Morton 1983a) occupying aerial nests at Tioga Pass except that  $T_a$ s sufficient to induce shivering in *Z. l. oriantha* were about 6°C higher than in *E. oberholseri*. Biebach (1979) found that increases in metabolic rate could be used effectively by European Starlings (*Sturnus vulgaris*) to maintain high  $T_{egg}$ s even at subfreezing  $T_a$ s.

Ettinger and King (1980) found that daily energy expenditure of female *E. traillii* reached a minimum during the incubation phase of the breeding season. This matches well with our observation that incubating *E. oberholseri* had visible subdermal fat stores. These reserves must help to buffer the energetic consequences of cold weather and storms. Typically, summer storms on the study area were violent but brief (under 2 h). In many cases females could probably remain on their eggs and protect them for the storm's full duration. We are certain that eggs need protecting because females that leave the nest during hailstorms sometimes lose their eggs from breakage by hailstones (Pereyra and Morton MS).

We have not evaluated foraging efficiency in *E. oberholseri*. They are primarily sit-and-wait predators that fly out from perches to take prey. We have also observed them gleaning tree bark and foraging on the ground. Whatever their feeding techniques, they usually must be highly efficient. For example, several times we have seen females complete clutches during snowstorms that were severe enough to cause *Z. l. oriantha* to abandon nests entirely.

Skutch (1976) made the often-cited observation that birds hurry to their eggs and cover them when rain begins. He also observed that if the storm is prolonged, the parent will eventually leave to feed, and that in flycatching species foraging time may actually increase during storms because insects become hard to find. This response seems to have occurred during a heavy hail and rainstorm at nest 15 (Fig. 4). A similar pattern was also recorded during rainstorms in *R. regulus* (Haftorn 1978a, b).

During a series of cold and very windy days and nights,  $T_{egg}$  measurements in another nest of *E. oberholseri* (nest 8) indicated that toward the end of two successive periods of night rest, the female stopped applying her brood patch to the eggs (Fig. 5). This caused  $T_{egg}$  to decrease for a time to levels below those required for embryo development, but presumably it also assisted the female in her efforts to maintain normothermia.

Ordinarily, small birds seem able to produce enough heat at low  $T_a$ s to maintain easily both  $T_{egg}$  and  $T_b$  (Biebach 1979, 1981; Vleck 1981a). At nest 8 continuous high winds coupled with low  $T_a$ s probably reduced food availability and greatly increased heat loss from the bird-egg-nest complex. The incubating female, with insufficient energy reserves to fuel appropriate levels of shivering thermogenesis, was able to reduce heat loss from her body core by standing above the eggs instead of applying her patch to them. As pointed out by Drent (1975) for birds in hot environments, the parent's main problem while incubating is to maintain its own  $T_b$  in the face of environmental stresses. The same principle may apply to birds in the cold, particularly when energy reserves are depleted because of food scarcity.

*Attentiveness.*—Incubating females usually began their active day about 75 min before sunrise and ended it about 110 min after sunset. The pattern was seasonally consistent, indicating that it probably was cued by light intensity (Fig. 7). Major deviations did occur, however. The active day was sometimes shortened by as much as 2 h when it was very windy or a storm was in progress. Thus, females sometimes compensated for harsh environmental conditions by increasing their attentiveness.

The mean constancy of incubation in *E. oberholseri* was 75.8%. This is within the range of 60–80% reported by Skutch (1976) for numerous species and similar to that reported for congeners by Davis (1954), Davis et al. (1963), Mumford (1964), and Ettinger and King (1980). We have frequently observed incubating female *E. oberholseri* being fed by their mates both on and off the nest. The effect of this behavior on the female's time and energy budget and its ubiquity among Empidonacines are still open questions, but it could be contributing to an increase in attentiveness.

Foraging bouts by females usually were brief (Fig. 8), and there was little deviation in length

of feeding trips with time of day (Fig. 9) or with  $T_a$  (Fig. 10), although the shortest trips tended to be the first and last ones of the active day (Fig. 11). A notable exception to this occurred before and after the first night of incubation, when off bouts were always very long (Fig. 1).

The frequency of foraging trips, on the other hand, varied diurnally. Off bouts averaged only 1.5/h at midday but occurred at twice that rate at the beginning and end of the active day (Fig. 9). This modification of foraging behavior was linked, naturally, to changes in duration of on bouts, which were longest at midday (Fig. 9). The result was a diurnal pattern wherein attentiveness was greatest from midmorning to mid-afternoon (Fig. 6).

The duration of on bouts correlated positively with  $T_a$  (Fig. 10). Given the constancy of off-bout duration, a strong positive relationship emerged between attentiveness and  $T_a$  (Fig. 11). This was unexpected. Usually, attentiveness decreases in passerines as  $T_a$  increases (see Drent 1972, 1975; White and Kinney 1974; Haftorn 1978a, 1979, 1981). Exceptions to this pattern have been found, however, and even predicted (Drent 1972). Desert birds may come back on at very high  $T_a$ s and incubate constantly to prevent eggs from overheating (Maclean 1967, Russell 1969, Walsberg and Voss-Roberts 1983). Vleck (1981b) found that attentiveness was independent of  $T_a$  in Anna's (*Calypte anna*) and Black-chinned (*Archilochus alexandri*) hummingbirds or that it increased with  $T_a$  in Costa's Hummingbird (*C. costae*). Zerba and Morton (1983b) saw little change in attentiveness in *Z. l. oriantha* until  $T_a$  increased to 20°C; thereafter attentiveness increased rapidly. In *E. difficilis* attendance did not correlate with  $T_a$ , although the longest attentive periods observed (ca. 3 h) did occur on very hot days (Davis et al. 1963).

White and Kinney (1974) formulated a widely accepted model describing the relationship of attentiveness to  $T_a$  in single-sex intermittent incubators. They show that attentiveness decreased as  $T_a$  increased, eventually ceasing altogether when  $T_a$  equaled mean maximum  $T_{egg}$  (ca. 37°C). However valid the model of White and Kinney for the Village Weaver (*Ploceus cucullatus*) and other species that they considered, it is clearly inappropriate for the two species studied at high altitude (Fig. 12). At Tioga Pass both *Z. l. oriantha* (Zerba and Morton 1983b) and *E. oberholseri* (Fig. 10) lengthened their at-

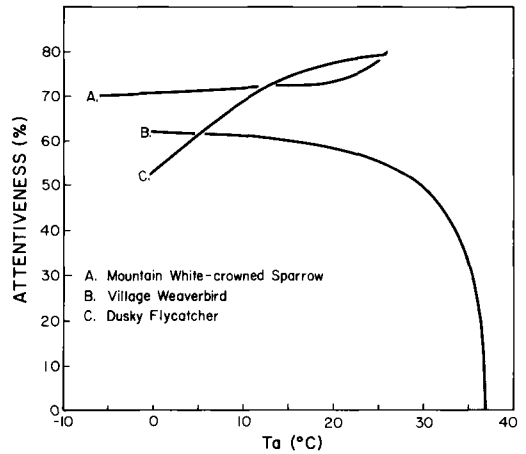


Fig. 12. Attentiveness (% time on nest during active day) vs. air temperature ( $T_a$ ) in three species: Mountain White-crowned Sparrow (Zerba and Morton 1983b), Village Weaver (White and Kinney 1974), and Dusky Flycatcher (this study).

tentive bouts as  $T_a$  increased, exactly opposite to the response predicted by White and Kinney. We suggest that the attentiveness pattern of a species varies in accordance with selective pressures imposed by its environment. At Tioga Pass,  $T_a$  is always well below levels that would be troublesome to embryos. On the other hand, solar radiation can be intense, and eggs within a nest exposed to direct sun are rapidly heated to lethal temperatures (Zerba and Morton 1983b). Given the usual coincidence of high  $T_a$  and insolation, we conclude that *E. oberholseri* exhibits compensatory behavior in anticipation of potentially harmful environmental conditions. Such anticipation is particularly important because damage to eggs from overheating can occur quickly. It is also irreversible and must always be prevented in the first place (Drent 1975). We saw the anticipatory response (long on bouts at high  $T_a$ s) in *E. oberholseri* during the laying period and even in cases where the nest was completely shielded from direct sun. Apparently the most appropriate behavior for females at high altitude is to stay on their nests as much as possible when it is hot. This would eliminate errors in evaluating moment-to-moment exposure of eggs to sun, a situation that can change quickly depending upon time of day and cloud cover. Also, nest exposure often changes greatly as foliage develops seasonally and when nests are relocated upon loss of a clutch.

Additional benefits of long attentive bouts are that they diminish the energetic cost of incubation (Drent 1972, Vleck 1981a), promote faster embryonic development, and maximize the female's ability to protect eggs from predators (Drent 1972, 1975).

As pointed out by Carey (1980b), it is often difficult in cases of environmental adaptation to determine routes of natural selection or even which factor in the environment is the selecting agent. We propose that in *E. oberholseri* attentive behavior evolved in response to both food availability and dangers from solar heating of eggs. The most favorable pattern is for the bird to feed intensively during the early morning and late afternoon hours, when exposure to sun is least likely. This is feasible because they probably are highly adept foragers and because their embryos tolerate rapid cooling, low temperatures, and rapid reheating. The fact that this pattern of attentiveness is followed in both shaded and unshaded nests suggests that insolation is the selecting factor but that  $T_a$  is the environmental cue directing incubation behavior.

Temporary hypothermia of the incubating bird, egg neglect, and feeding of the incubating female by her mate have all been identified as adaptive reactions that could reduce the conflict between attentiveness and foraging time in small, single-sex incubators, thus allowing them to breed in cold regions (Walsberg and King 1978, Carey 1980a). The latter two of these responses, at least, have now been observed in *E. oberholseri*.

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