

ADAPTATIONS OF HORNED LARKS (*EREMOPHILA ALPESTRIS*) TO HOT ENVIRONMENTS

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THE adaptations of similar animals to different environments are of particular evolutionary interest. Only a few of the many studies of the adjustments of vertebrates to rigorous environments have dealt with closely related populations (or species) living in contrasting environments (Salt, 1952; Dawson, 1954; Cade and Bartholomew, 1959; Hudson and Kimzey, 1966; Brown, 1968).

Most small birds are diurnal, and therefore are often exposed to extremes of heat and associated problems of temperature regulation. Consequently a bird may live in an entirely different microclimate than a small nocturnal mammal with which it is sympatric. The Horned Lark (*Eremophila alpestris*) is an excellent subject for study. It is ground-dwelling, diurnal, small (25–40 g), and occupies open country with low or sparse vegetation. It nests in grasslands, arctic and alpine tundra, salt marshes, and deserts. Such exposed habitats offer the lark little protection.

Horned Larks belong to an Old World family, Alaudidae, of which they are the only indigenous New World representative. They are found throughout the Holarctic and an isolated population lives in Colombia. Of the 40 subspecies of Horned Larks recognized, 14 are in the Old World and 26 in the New (Peters, 1960).

This study of behavioral and physiological adaptations of two subspecies of Horned Larks undertakes to compare an inland valley form from a relatively mesic environment (*E. a. actia*) with a desert form (*E. a. ammophila*). The environments in which these subspecies live differ especially with respect to temperature, humidity, and available water.

The inland valley form (*actia*), hereafter called the mesic form, is the more widespread of the two subspecies, occurring from northern California (Humboldt County) south along the entire western half of California to northern Baja California (30° N). This race occurs in many different habitats, and Behle (1942) points out that it is outstanding in its range of ecological tolerances. At various points along the periphery of its range it intergrades with five other subspecies. Also as this race is non-migratory, individuals are subjected to the environmental influences in the same locality the year around. In correlation with these factors, this race is the most variable in color of the eight California subspecies. The least variable and most typical representatives are found from Los Angeles to San Diego (Behle, 1942).

The desert lark (*ammophila*) occurs sporadically in the level areas and valleys of the entire Mojave Desert. The altitude of the desert floor varies from 700 m near Palmdale, to about 1,500 m in the Owen's Valley. The climate is hot in the summer (30° to 50°C) and cold in the winter (-10° to 20°C), with low rainfall and humidity (Jepson, 1925). The predominant plant over much of this lark's range is creosote bush (*Larrea tridentata*), which provides more shade than is present in the habitat of most of the other races. This lark is also nonmigratory, and variation between individuals is almost as pronounced as that in *actia*, with which it intergrades in the southwestern corner of the San Joaquin Valley (Behle, 1942).

MATERIALS AND METHODS

Capture and maintenance.—A total of 30 *actia* and 27 *ammophila* were used in this study. All were caught in 18-m, sand-colored mist nets. Usually several nets were placed in a row. As the Horned Lark subspecies are very similar in appearance, no attempt was made to capture larks in the large, mixed wintering flocks. Instead, all birds were taken on the breeding grounds during the nesting season. The *actia* specimens were caught in a large pasture 5 km west of Warner Springs, San Diego County, California, at an elevation of about 975 m; the *ammophila* came from the Antelope Valley, Los Angeles County, California, about 40 km northwest of Lancaster at about 800 m.

After capture the larks were banded with individual colored leg bands, taken to the campus of the University of California at Los Angeles, and placed in large outdoor flight cages. Larks are gregarious birds, so keeping large numbers together in the flight cages was not difficult. At least a week before they were to be measured, the larks were taken into the laboratory and maintained in a windowless, ventilated room with a controlled photoperiod (lights on from 09:00 to 21:00). The ambient temperature in the room remained constant at about 23°C in the winter and 25°C in the summer. The relative humidity in the room varied between 40 and 60 percent.

The larks were housed in individual Hendrix bird cages measuring 26 × 26 × 24 cm. Paper covered the floor and a small rock in the middle gave the lark a place to stand. Water was provided from inverted 100-ml graduated cylinders, fitted with a stopper and an L-shaped drinking tube inserted through the bars in the cage. The birds were fed a commercial assortment of small bird seeds throughout the study.

Metabolic measurements.—Oxygen consumption was measured in an open flow system using a Beckman G-2 oxygen analyzer coupled to a recording potentiometer that recorded the percent oxygen in the air at consecutive 5-minute intervals from two animal chambers and a blank. The chambers were made from 3.8-l (1 U. S. gal) jars in which a platform of wire mesh (0.6 cm²) was inserted over a layer of mineral oil to collect urine and feces. The lids were fitted with ports for the passage of air into and out of the chamber, and for a thermocouple connected to a Brown strip chart potentiometer for recording ambient temperature (T_A). One of the lids also had a port for a humidity probe which led to an Aminco electric hygrometer, and allowed a continuous record of humidity. The air was dried with silica gel and indicating drierite (CaSO₄) before being metered to the chambers. The effluent air was redried in a U-tube of drierite and then passed to the analyzer. Evaporative water loss was determined gravimetrically after passing expired air through the previously weighed U-tube for 30 minutes. The flow rate was regulated at 700

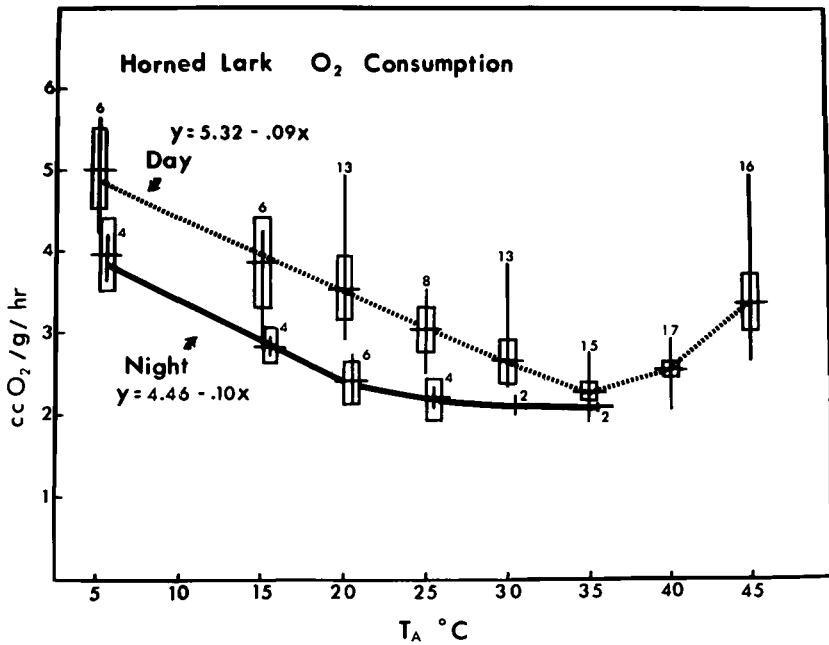


Figure 1. The relation of oxygen consumption to ambient temperature (T_A). The vertical lines represent the ranges; horizontal lines, mean values; rectangles, 95 percent confidence intervals ($\bar{X} \pm tSE$). The numbers are the number of different birds in each sample. The comparative measurements on this and remaining figures were taken at 5° intervals, starting with 5°C, but were displaced for graphic purposes. The equations are for lines fitted to the data by the method of least squares. Both subspecies are included in the figure.

cc/min at T_A 's of 5° to 40°C. At 45°C the flow rate was increased to 1,500 cc/min in order to maintain a low chamber humidity. T_A was regulated within $\pm 0.5^\circ\text{C}$ by placing the animal chambers in a controlled temperature box. Minimal oxygen consumption was determined by averaging the lowest two 5-minute readings after the bird had been in the chamber at a given T_A for at least an hour. Except for the 24-hour runs all daytime and nocturnal measurements were made on postabsorptive birds in the dark, and the oxygen consumption was corrected to standard temperature and pressure. Body temperature (T_B) was measured at the end of each metabolic run by inserting a quick-registering mercury thermometer at least 2 cm into the cloaca. Data from both subspecies were lumped for most of the measurements, and separated only for special consideration.

Water consumption.—In measurements of *ad libitum* water consumption the fluid intake and body weight were recorded daily before the lights came on (09:00). The windowless bird room was used for measurements at $T_A = 23^\circ\text{C}$, and a Modu-Lab, walk in, controlled temperature cabinet was used for $T_A = 33^\circ\text{C}$. The relative humidities varied between 40 and 60 percent at 23°C, and 24 and 39 percent at 33°C. In all cases an extra drinking device was used to correct for evaporation.

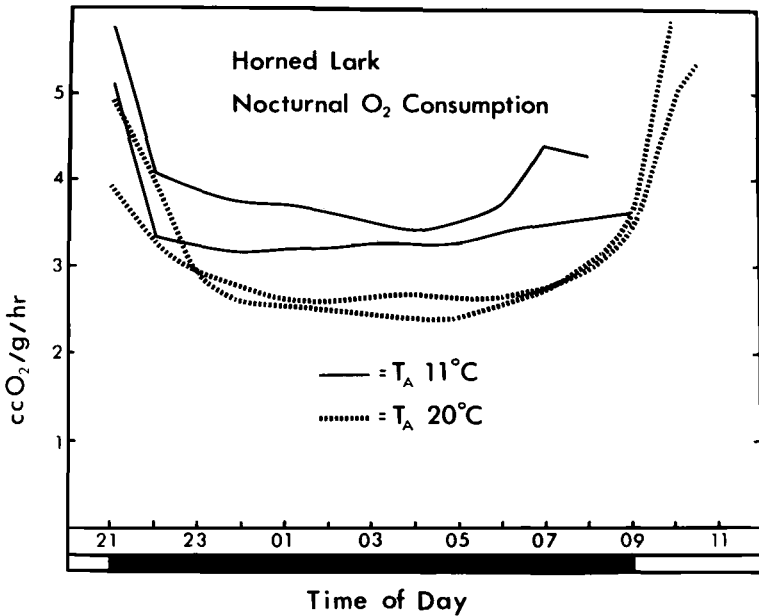


Figure 2. Decrease in oxygen consumption at night in four desert Horned Larks (*E. a. ammophila*) at two ambient temperatures. The dark period is indicated by the black bar between 21:00 and 09:00.

Minimal water consumption was determined by reducing the quantity of water daily until a level was reached below which the animals could no longer maintain weight.

RESULTS

Oxygen consumption.—Oxygen consumption was inversely related to ambient temperature below 35°C (Figure 1). During the daytime thermal neutrality was at about 35°C, whereas at night the thermal neutral zone extended to below 25°C. At any given temperature the oxygen consumption was lower at night than during the day. The minimum oxygen consumption of 2.28 cc O₂/g/hr was about 25 percent lower than that predicted by the equation of Lasiewski and Dawson (1967) for a passerine bird of this size. Between 35° and 40°C the increase in oxygen consumption was accompanied by an increase in T_B (41.0° and 42.5°C, respectively), and had a Q₁₀ of 2.0. At 45°C the mean oxygen consumption increased further to 3.38 cc O₂/g/hr, with a Q₁₀ of 3.1 (T_B increased from 42.5° to 45.0°C).

At night the metabolism of the birds began to drop as soon as they were placed in the darkened chamber (Figure 2). The lowest rates

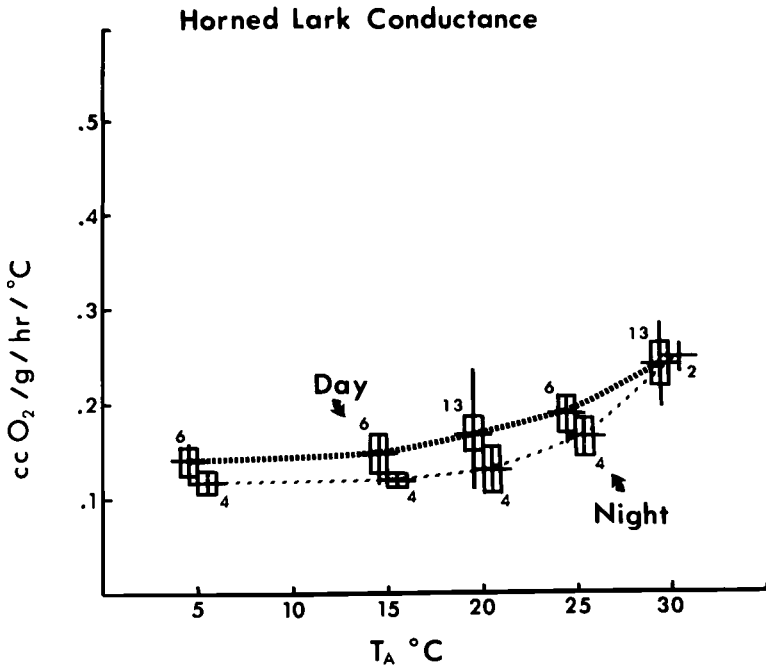


Figure 3. The relation of thermal conductance to ambient temperature. Symbols, numbers, and symbol displacement as in Figure 1.

usually occurred between 23:00 and 05:00, after which the metabolism began to increase as the birds anticipated their usual photoperiod (09:00).

Thermal conductance.—Both the daytime and nocturnal curves of oxygen consumption extrapolated to ambient temperatures above the observed body temperatures, indicating either a change in thermal conductance or a high metabolism caused by excitement (Hudson and Kimsey, 1966). The two regression lines were fitted to the data below thermal neutrality by the method of least squares and each had a correlation coefficient of 0.9. The slopes of the daytime (0.09) and nocturnal (0.10) curves were nearly parallel. The thermal conductance (C) was calculated from the following equation:

$$C = M/T_B - T_A$$

where m is the metabolic rate in cc O_2 /g/hr and $T_B - T_A$ is the difference between body and ambient temperature in $^{\circ}\text{C}$. Both the daytime and nocturnal thermal conductances had a slope not different from zero between 5° and 15°C (Figure 3). The mean thermal conductances were 0.15 and 0.12 cc O_2 /g/hr/ $^{\circ}\text{C}$ for day and night, respectively. Above 15°C

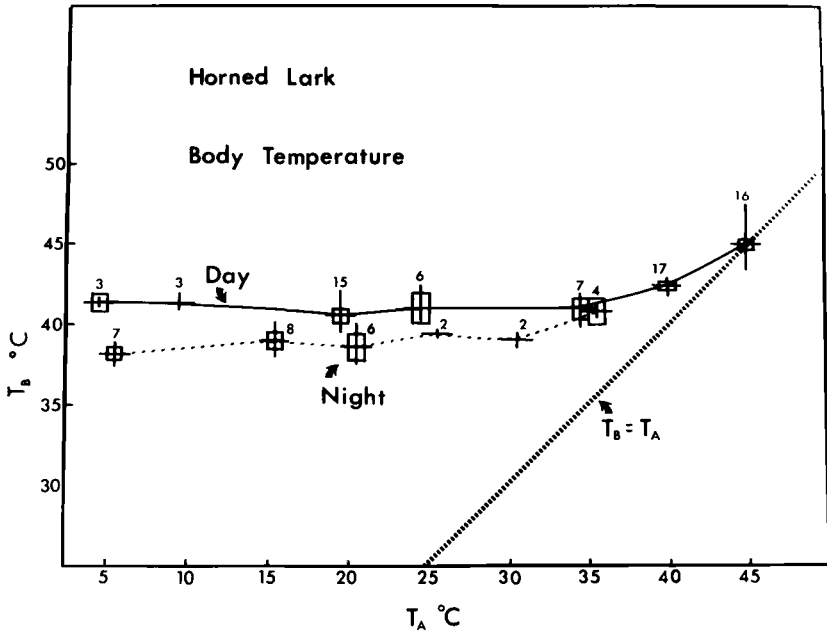


Figure 4. The relation of body temperature (T_B) to ambient temperature (T_A). Symbols, numbers, and symbol displacement as in Figure 1. The dashed line equates body and ambient temperature.

the thermal conductance increased in a curvilinear fashion for both, and the nocturnal values were lower than those during the day at all temperatures except 30°C.

Body temperature.—As the rate of heat production decreased at night and the thermal conductance remained about the same in low ambient temperatures, one would expect a lower body temperature at night (Figure 4). At ambient temperatures from 5° to 30°C, the mean T_B was 2.0° to 2.5°C lower at night than during the day, but at 35°C there was no difference. At 40° and 45°C the larks underwent a marked hyperthermia (mean T_B = 42.5° and 45.0°C, respectively).

Chamber humidity.—The chamber humidity is a result of the amount of water lost by the bird and the flow rate. The humidities measured during the metabolic determinations are presented in Table 1. The absolute humidity during the daytime was constant between 5° and 35°C, and at 40°C it increased threefold. As the flow rate of dry air at 45°C was doubled over that at 40°C, the humidity at 45°C increased only slightly, while the water output of the birds increased greatly. The chamber humidities at night were lower than those during the day at

TABLE 1
ABSOLUTE HUMIDITY¹ IN THE METABOLIC CHAMBER

	5°C	15°C	20°C	25°C	30°C	35°C	40°C	45°C
Daytime								
Mean (\bar{X})	3.22	3.94	2.74	3.69	2.11	2.08	7.64	8.86
Sample size (N)	3	4	6	4	7	9	9	8
Standard error of \bar{X}	0.00	0.27	0.87	1.05	0.46	0.35	1.32	1.21
Night								
Mean (\bar{X})	1.70	1.23	0.75	1.05	1.88	—	—	—
Sample size (N)	2	6	3	2	1	—	—	—
Standard error of \bar{X}	—	0.21	0.06	—	—	—	—	—

¹ g H₂O/m³ air.

comparable temperatures, correlating with the birds' decreased water output at night.

Evaporative water loss.—The daytime evaporative water loss varied between 11 and 15 percent of the body weight per day from 5° to 35°C (Figure 5). The water loss at night (7 to 9 percent of the body weight per day) was lower than during the day at all temperatures between 5°

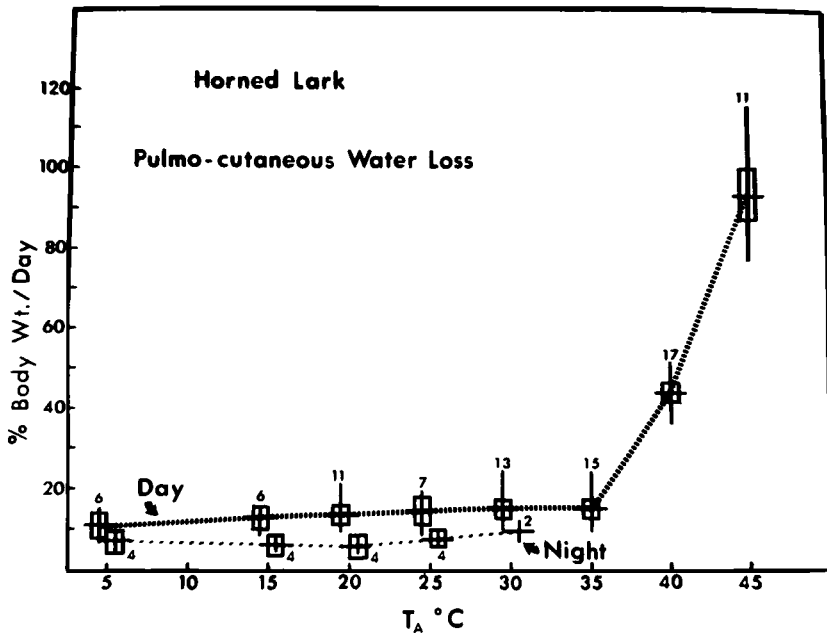


Figure 5. The relation of evaporative water loss to ambient temperature. Symbols, numbers, and symbol displacement as in Figure 1.

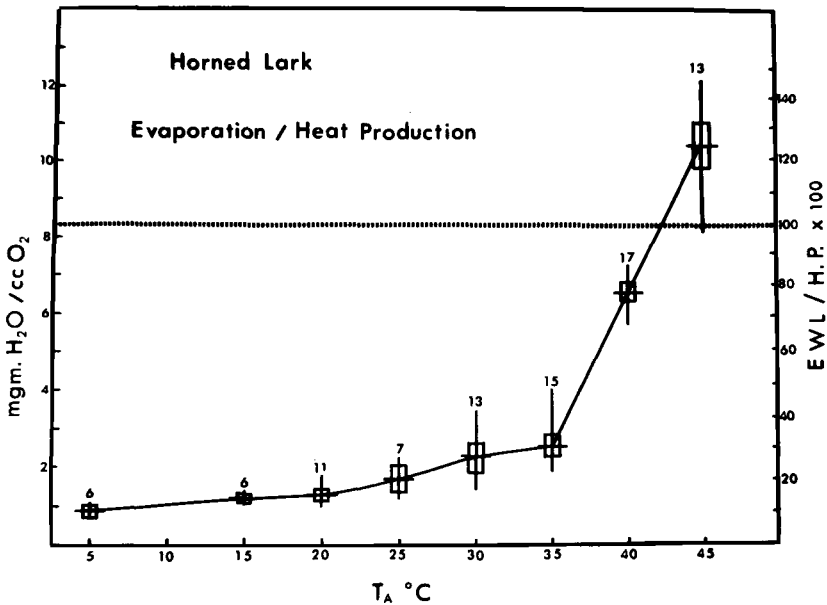


Figure 6. The ratio of heat produced to heat lost by evaporation in relation to ambient temperature. Symbols and numbers as in Figure 1. The dashed line is indicative of the level at which 100 percent of the heat produced is lost by evaporation.

and 30°C. Above 35°C the mean water loss increased markedly to 43 percent at 40°C and 93 percent of the body weight per day at 45°C.

Evaporative heat loss.—The percent of the metabolic heat lost by evaporation was determined by dividing the evaporative heat loss by the heat produced, which was measured indirectly by oxygen consumption (Figure 6). In this calculation it was assumed that each mg of water evaporated removed 0.58 cal at the body temperature of the bird, and each cc of oxygen was equivalent to 4.8 cal. The percent of the heat lost by evaporation gradually increased between 5° and 35°C, and sharply increased at temperatures above 35°C. The increase between 35° and 45°C was essentially linear. At 40°C evaporation accounted for about 80 percent, and at 45°C, about 125 percent of the heat produced.

Dry heat flow.—Using the same conversion factors as for evaporative heat loss, the thermal conductance minus its evaporative heat component (C_D) was calculated (Figure 7). The method was modified from the one presented by Dawson and Schmidt-Nielsen (1966), and the following equation was used:

$$C_D = \frac{M - H_2O}{T_B - T_A}$$

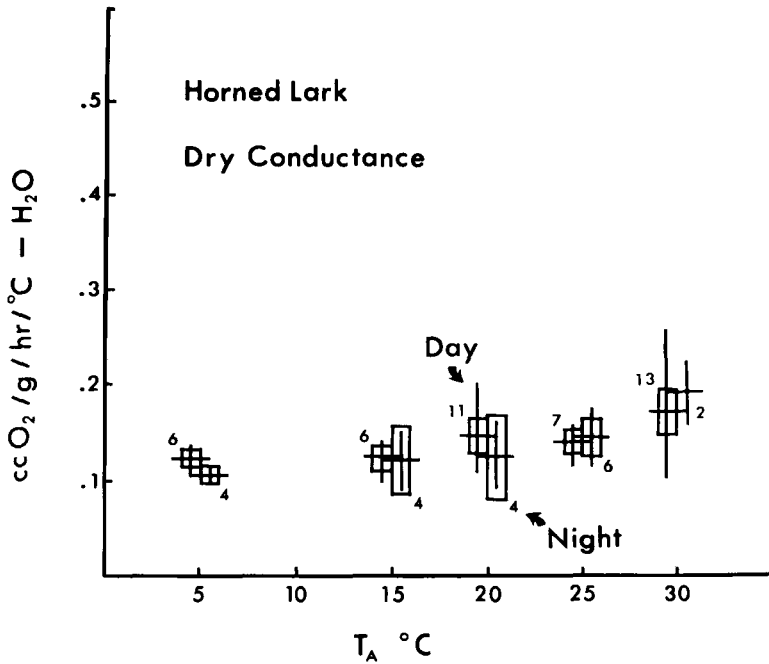


Figure 7. The relation of dry heat flow (thermal conductance minus the evaporative heat loss) to ambient temperature. Symbols, numbers, and symbol displacement as in Figure 1. The nocturnal values are on the right; daytime, left.

where $M - H_2O$ is metabolic rate in calories minus the caloric equivalent of the evaporative heat loss. In order to compare this calculation with Figure 3 the units were reconverted to $cc O_2/g/hr/^\circ C$. When calculated in this manner the differences between the daytime and nocturnal dry heat flow were reduced between 5° and $25^\circ C$, and the zero slope for dry heat flow was extended to $25^\circ C$.

COMPARISON OF MESIC AND DESERT LARKS

Thermoregulation.—High ambient temperatures are one of the main differences between the desert and inland valley habitats, at least during the summer. When exposed to $45^\circ C$ the desert larks (*ammophila*) and the mesic larks (*actia*) behaved differently (Table 2). The oxygen consumption, and thus heat production, of the desert birds was significantly lower ($P < 0.01$) than that of the mesic larks. The Q_{10} of the increase in metabolic rate above that at $40^\circ C$ was 2.4 (T_B from 42.5° to $44.2^\circ C$) in the desert larks and 3.5 (T_B from 42.5° to $45.9^\circ C$) in the mesic larks. The evaporative water loss in the desert larks was significantly lower ($P < 0.05$) than in the mesic larks.

TABLE 2
THERMOREGULATORY RESPONSES OF HORNED LARKS FROM MESIC AND DESERT
HABITATS AT AN AMBIENT TEMPERATURE OF 45°C

	<i>E. a. actia</i> (mesic)			<i>E. a. ammophila</i> (desert)			Significance	
	\bar{X}	N	SE	\bar{X}	N	SE	<i>t</i>	<i>P</i>
Oxygen consumption (cc O ₂ /g/hr)	3.91	7	0.263	2.97	9	0.117	3.52	< 0.01
Body temperature (°C)	45.9	7	0.586	44.2	9	0.208	3.01	< 0.01
Evaporative water loss (% body wt./day)	103.7	5	3.96	87.6	8	3.48	3.05	< 0.05
EWL/HP (cal. H ₂ O/ cal. O ₂)	1.17	5	0.066	1.32	8	0.028	2.40	< 0.05

The desert larks did not become as excited when exposed to 45°C as did the mesic larks. As a result the desert larks lost a larger portion of metabolic heat through evaporation ($P < 0.05$) than did the mesic larks (about 132 and 117 percent of the heat produced, respectively). Correlated with the increased heat loss the desert larks maintained a body temperature almost a degree below the ambient temperature, which the mesic larks were unable to do. The lowest body temperature at which a bird died from heat stress was 45.6°C. The body temperatures were measured from 15 to 30 minutes after the water loss data were collected.

TABLE 3
WATER CONSUMPTION (PER CENT BODY WEIGHT PER DAY) OF HORNED LARKS
FROM MESIC AND DESERT HABITATS IN RESPONSE TO AMBIENT TEMPERATURES
OF 23° AND 33°C

	<i>E. a. actia</i> (mesic)			<i>E. a. ammophila</i> (desert)			Significance	
	\bar{X}	N	SE	\bar{X}	N	SE	<i>t</i>	<i>P</i>
<u>T_A = 23°C</u>								
<i>Ad libitum</i> tap	28.5	10	7.8	20.8	10	2.9	0.876	> 0.05
Minimum tap	2.5	9	0.6	2.6	9	0.4	0.138	> 0.05
Min. distilled	2.3	7	1.0	1.6	9	0.4	0.795	> 0.05
<u>T_A = 33°C</u>								
<i>Ad libitum</i> tap	37.1	9	5.5	50.4	9	8.3	1.308	> 0.05
Minimum tap	7.9	6	1.1	7.1	8	0.7	0.672	> 0.05
Number of days to reach minimum	10.3	6	1.7	7.0	8	0.8	1.938	> 0.05, < 0.10

This probably explains why the mesic larks had an average temperature of 45.9°C, despite the calculation that they lost about 117 percent of the heat they produced. The desert and mesic larks were treated in the same manner.

Water consumption.—The *ad libitum* and minimal water consumption of the desert birds were not significantly different ($P < 0.05$) from those of the mesic at either 23° or 33°C (Table 3), but the desert larks were generally less variable, i.e. smaller standard error of the mean, in their response to the different drinking regimens. Correlated with their more uniform response, the desert larks required fewer days ($P > 0.05, < 0.10$) to reach a minimum level of water consumption at 33°C.

Survival without water.—At the end of the minimum water determination at 23°C water was removed from six larks, and they were weighed daily until they appeared to be severely stressed (Figure 8). It is interesting that at least some larks could survive for 16 and 31 days without water. The three desert birds were no better than the three mesic, and in fact they lost weight more consistently.

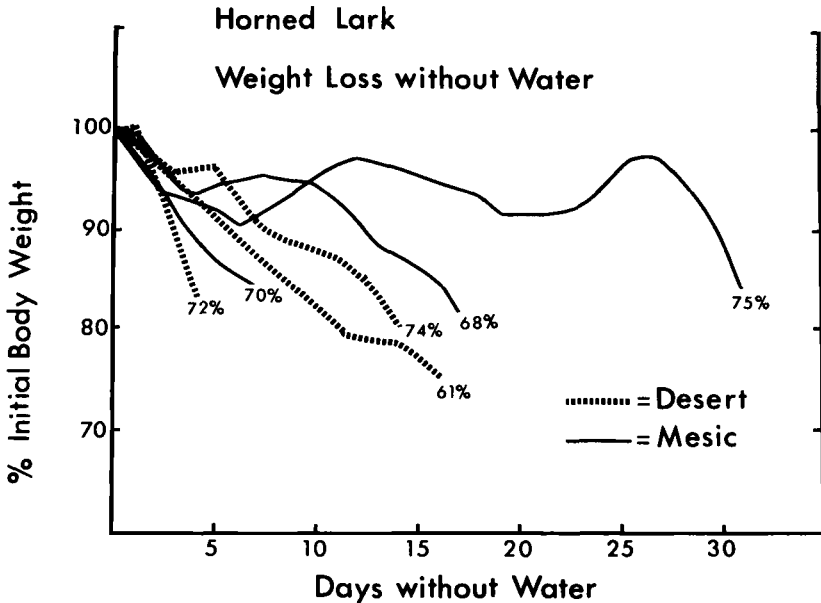


Figure 8. The weight loss per day of three desert (*E. a. ammophila*) and three mesic (*E. a. actia*) Horned Larks without water, but with *ad libitum* food. The numbers under the lines are the percentages of the weights on *ad libitum* water (see text).

TABLE 4
CLIMATES OF THE TWO STUDY AREAS¹

Population	Station, elevation	Length of record, years	Ambient temperature °C				Precipitation, mean annual, cm
			Mean Jan.	Mean July	Min. Jan.	Max. July	
Mesic larks (<i>E. a. actia</i>)	Warner Springs, San Diego County, California, 969 m	28	6.8	22.8	-11.7	42.8	41.15
Desert larks (<i>E. a. ammophila</i>)	Palmdale, Los Angeles County, California, 787 m	28	6.9	27.5	-12.8	44.4	22.61

¹ Data from the U. S. Weather Bureau, 1964.

ENVIRONMENT MEASUREMENTS

Macroclimates.—As Horned Larks are open country birds, the macroclimates of the places where they are found can serve as a useful index to the environmental stresses imposed on them (Table 4). Warner Springs, San Diego County, California, where the mesic specimens were taken, has about the same winter temperature but is not as hot in summer as Palmdale, Los Angeles County, California, near where the desert larks were captured. The rainy season in both regions is in the winter, but Warner Springs receives about twice as much precipitation as Palmdale.

Microclimates.—Even though the macroclimates of open areas are fairly uniform, the larks do not live in the climates recorded at weather stations per se. They select and to a limited extent create a microclimate that may be quite different from the macroclimate. Three of their methods of habitat choice and manipulation are: selection of cooler or warmer parts of the habitat during the daytime, digging and use of roost holes at night, and drinking from man-made water sources.

Almost daily during the late spring and summer the surface of the desert floor becomes very hot, and at these times the larks rarely alight on the ground in the sun. They perch in the wind on top of the abundant creosote bushes, and when they do alight on the ground they fly from the shade of one bush to that of another. This is not to say that larks on the desert are never heat stressed, but they minimize heat stress by using the portion of their environment that is least stressful. At 12:35 on 18 June 1967 in the Mojave Desert below Red Rock Canyon, Kern County, California, the temperature of the ground in the sun was 47°C.



Figure 9. A view of a roost hole. Feces can be seen in the bottom.

At a height of 1.3 m on top of a creosote bush on which a lark had just been perching the temperature was 29.5° to 31°C, and on the ground in the shade of another bush to which the lark flew it was 34° to 39°C, depending on the wind and the amount of sun. This behavioral pattern has been repeatedly observed and appears to be the common response of larks to hot environments.

The alpine environment is in general cold and windy, but on the ground, particularly in sunny areas, the temperatures can be quite moderate. Larks were frequently seen resting in the sun in the shelter of rocks or small bushes. At 2,990 m in Coyote Valley on 12 August 1967, between 11:00 and 15:45 the ground temperature in such a sheltered spot was 37° to 39°C. On a nearby rock just 0.3 m higher the temperature varied between 24° and 30°C, and in the shade it was 25° to 27°C.

A small homeotherm sitting exposed in open country on a cold night is subjected to considerable heat loss from radiation and convection. During cold nights Horned Larks dig roost holes and rest in them (Figure 9). This is apparently a device to reduce their energy loss at night. When larks were placed on a dirt substrate at 10°C in the laboratory they dug roost holes with their bills near the end of their normal photoperiod, but when kept at 25°C they did not dig roost holes. In the field the larks frequently dig the holes behind protective vegetation from the prevailing wind. Larks are usually the only birds present where the holes are found

and were often flushed out of them at night. In hard soil, such as near Warner Springs, the bottom of each hole typically contains from 10 to 15 dry bird droppings, whereas those in the soft soil of the Mojave Desert usually have only 2 or 3. Apparently larks on soft soil dig new holes every night, but in hard soil country they use the holes for longer periods.

The roost holes are just large enough (about $8 \times 5 \times 4$ cm) for a single lark to sit in with its back almost level with the ground surface. In the laboratory three larks placed together in a dirt bottom cage at 10°C dug three separate holes. In the field most of the holes found were only large enough to accommodate one lark, and at one location I found 25 separate holes within a 10-m circle. The only field evidence for communal huddling was a group of five holes placed in a 20-cm wide depression. Perhaps huddling occurs in response to colder ambient temperatures. Even a single lark resting in an isolated hole enjoys a reduction in the amount of exposed surface area, with a concomitant reduction in the radiative and convective heat loss. If the substrate under the lark becomes warmer, the heat loss from conduction also decreases. The roost holes were associated with all the populations studied and appear to be a fine example of how this open country bird adapts to a rigorous environment.

A few larks are scattered throughout the Mojave Desert, but the population is densest near man-made water sources. Miller and Stebbins (1964) report breeding *ammophila* to be scarce local residents in the dry drainage sinks of Joshua Tree National park, but in nearby irrigated areas of the Mojave Desert I found them one of the most abundant birds. On two trips I made to the irrigated alfalfa fields near Red Rock Canyon and Palmdale (Kern and Los Angeles Counties, respectively) during the breeding season on 8 June 1967 and 11 June 1968, I found the larks breeding only within about 6 km on either side of the irrigated land, although the creosote bush habitat here was indistinguishable from that in the outlying desert. During June the larks did not visit these open water sources, and presumably made up their water deficits by eating insects. After the breeding season large flocks of larks converge on water sources daily shortly after dawn. Several flocks of over 100 larks flew to pools of irrigation water between 06:30 and 07:30 on 10 August 1967 in the Antelope Valley west of Palmdale. By 08:00 the incoming flocks numbered only about 25. The larks usually drank for about 5 minutes and departed, although some larks were present all day. The flocks consisted of about 60 percent adult and 40 percent young larks (13 out of 22 captured were adults), and are apparently a post breeding season phenomenon.

DISCUSSION

Oxygen consumption.—Horned Larks are open country, ground-dwelling birds, and temperatures on the ground in the sun are often high, even in the alpine environment. The fact that their standard metabolism is 25 percent less than that predicted for passerine birds by the equation of Lasiewski and Dawson (1967) indicates a reduced metabolic contribution to the total heat load, and should be advantageous to an animal in a hot environment (Figure 1). A low metabolic rate has been reported in several other birds from hot environments (Bartholomew et al., 1962; Hudson and Kimzey, 1966; MacMillen and Trost, 1967a; Lustick, 1968). The Horned Lark also has a narrow thermoneutral zone at 35°C, probably owing to the low metabolic rate; and in this respect is similar to the Inca Dove (*Scardafella inca*), another bird from a hot environment (MacMillen and Trost, 1967a).

At night the larks are quiescent, have a reduced body temperature, and the thermoneutral zone extends downward to near 20°C. In the field these energy saving mechanisms are probably maximized, as a lark resting in a roost hole (Figure 9) loses a minimum of heat by radiation and convection. The values for nocturnal metabolism obtained in the laboratory were gathered from larks sitting on a wire mesh in the metabolic chamber and the freely circulating air doubtless increased heat loss. The nocturnal oxygen consumption in thermoneutrality is almost the same as that during the day at 35°C. The nocturnal rates of many other birds in thermoneutrality are considerably lower than those during the day (Benedict and Riddle, 1929; Irving, 1955; Hudson and Kimzey, 1966; Lustick, 1968). At night the larks reach minimal level of oxygen consumption within 2 hours and maintain it until about 05:00 (Figure 2). After 05:00 the oxygen consumption begins to rise as the larks appear to anticipate their normal photoperiod (09:00). Birds commonly show this anticipation and it probably occurs in the field (Dawson, 1954; Bartholomew and Cade, 1957; MacMillen and Trost, 1967b).

As the daytime metabolic rates below thermoneutrality do not extrapolate to the observed body temperature, the larks do not fit the Newtonian cooling model as proposed by Scholander et al. (1950), but the nocturnal values more closely approximate the model. This suggests that the daytime metabolic rates are elevated by wakefulness or alertness, as Hudson and Kimzey (1966) found in the House Sparrow (*Passer domesticus*).

Thermal conductance.—The constancy of thermal conductance between 5° and 15°C indicates that temperature regulation over this range is maintained by increased thermogenesis, presumably by shivering (Figure 3). The daytime (0.15 cc O₂/g/hr/°C) and nocturnal (0.12) thermal

conductances are slightly below, but not significantly different from that predicted by the equations of Lasiewski et al. (1967) and Herreid and Kessel (1967) for a 26-g bird (0.16 and 0.17 cc O₂/g/hr/°C, respectively). Between 15° and 30°C both daytime and nocturnal thermal conductances are curvilinear, indicating a gradual switch from physical thermoregulation in thermonutrality to chemical thermogenesis at low ambient temperatures. The curvilinear relationship (15° to 30°C) is reminiscent of that in the flying fox (*Syconycteris australis*) (Bartholomew et al., 1964) and probably indicates some peripheral heterothermy and pteromotor activity over this temperature range. The gradual switch from physical to chemical temperature regulation shown by the Horned Lark has also been noted in several other passerines (Dawson and Tordoff, 1959; West, 1962; Veghte, 1964; Lustick, 1968).

The influence of evaporative heat loss is more important with reference to thermal conductance than one would expect from the low and constant evaporative water loss between 5° and 35°C (Figure 5). The dry heat flow (thermal conductance minus its evaporative heat component) (Figure 7) is more constant than thermal conductance between 15° and 25°C. The higher daytime thermal conductance between 5° and 25°C must be mainly due to increased evaporative heat loss during the day, for the daytime and nocturnal dry heat flows are similar and there is less water loss at night.

Body temperature.—Horned Larks are excellent homeotherms and during the day they maintain a constant body temperature of about 41.5°C over an ambient temperature range of 5° and 35°C (Figure 4). This high body temperature is typical for a small passerine (McNab, 1966). Like most small birds when exposed to ambient temperature above 40°C, the larks become hyperthermic ($T_b > 42.0^\circ\text{C}$), which increases the thermal gradient between their shell and the environment. They thereby maximize the heat loss by radiation, convection, and conduction and thus reduce the amount of water required for evaporative cooling. Body and ambient temperatures are equal when the latter is 45°C, and as this is near their upper lethal temperature, body temperature is maintained almost solely by evaporative cooling. At night the body temperature drops 2.0° to 2.5°C over an ambient temperature range of 5° to 30°C. A nocturnal decline of this magnitude saves both energy and water (MacMillen and Trost, 1967b). This phenomenon has been known for many years and is common in most small birds (Simpson and Galbraith, 1905; Baldwin and Kendeigh, 1932; Dawson, 1954).

Water loss.—The daytime evaporative water loss at 25°C (15 percent of the body weight per day) is almost exactly that Bartholomew and Cade (1963) predicted for a 26-g bird (Figure 5). This rate of water

TABLE 5
SUMMARY OF DATA ON MINIMAL WATER CONSUMPTION OF SMALL BIRDS IN THE
ABSENCE OF TEMPERATURE STRESS

Species	Mean body wt. (g)	Minimal water % body wt./day	Source
<i>Scardafella inca</i>	41.0	8.5	MacMillen and Trost, 1966
<i>Columbina passerina</i>	38.0	9.7	Willoughby, 1966
<i>Molothrus ater</i>	33.0	3.4	Lustick, 1968
<i>Melospittacus undulatus</i>	30.0	< 1.0	Cade and Dybas, 1962
<i>Eremophila alpestris</i>	26.0	1.6-2.6	Present study
<i>Carpodacus mexicanus</i>	20.6	10.0	Bartholomew and Cade, 1956
<i>Passerculus sandwichensis</i>	17.0	26.8-45.9	Poulson and Bartholomew, 1962
<i>Amphispiza bilineata</i>	13.5	< 1.0	Smyth and Bartholomew, 1966
<i>Taeniopygia castanotis</i>	11.5	< 1.0	Cade et al., 1965
<i>Sporopipes squamifrons</i>	11.0	< 1.0	Cade, 1965

loss is considerably above the amount obtained from oxidative water (Bartholomew and Cade, 1963). During the breeding season larks eat mainly insects, whereas they eat seeds the rest of the year (McAtee, 1905; Pickwell, 1931). Presumably eating insects during the breeding season lets them make up their water deficit without visiting open water sources. At night the water loss is significantly reduced (7 to 9 percent of the body weight per day) below that during the day. This 40 to 50 percent reduction in water loss is advantageous to a diurnal bird that does not eat or drink during the night (MacMillen and Trost, 1967b). At about 40°C and above the water loss rises sharply as evaporative cooling becomes increasingly important in temperature regulation. More than 100 percent of the heat produced can be dissipated by evaporation at 45°C (Figure 6). This observation is in agreement with the findings of Lasiewski et al. (1966) showing that all birds they measured could lose more than 100 percent of the metabolic heat by evaporation, when measured at high T_a and low humidities.

Water consumption.—In their water requirements Horned Larks appear to have better than average physiological capacities, but as in their thermoregulatory adaptations they must rely on a versatile behavioral repertoire for survival under stressful conditions. Their *ad libitum* water consumption in the absence of heat stress (23°C) falls within the expected range for a 26-g bird (Bartholomew and Cade, 1963) (Table 3). A better indication of their adaptation to water shortage is their minimal water consumption of 1.6 to 2.6 percent of the body weight per day. Although the Horned Lark requires little water, its minimal water consumption is intermediate within a group of small birds for which these data are available (Table 5). The Horned Lark has less effective physi-

ological mechanisms for water conservation than several smaller birds. Both the *ad libitum* and minimal water consumption increase with increasing ambient temperature in the Horned Lark, as is true of many other birds (Seibert, 1949; Dawson, 1954; Bartholomew and Dawson, 1954; Bartholomew and Cade, 1956; Cade and Dybas, 1962; Cade et al., 1965; Willoughby, 1966). In the field the larks, like other birds, compensate for these increased water demands by visiting water sources, eating insects, and remaining inactive in the shade during the hot part of the day.

The *ad libitum* water consumption of the Horned Lark at both 23° and 33°C is greater than the evaporative water loss at those temperatures (Table 3, Figure 5). The minimal water requirements are less than the evaporative water loss of birds that had been on *ad libitum* water prior to the evaporative measurements. Thus larks can reduce their evaporative water loss under conditions of water shortage.

Willoughby (1968) examined the water requirements of two other alaudids from the Namib Desert in South West Africa, the 17-g Grey-backed Finch Lark (*Eremopterix verticalis*) and the 18.5-g Stark's Lark (*Spizocorys starki*). The Horned Lark utilizes more water than either the Finch Lark or the Stark's Lark with respect to evaporative water loss (15.0 compared to 9.6, and 12.0 percent of the body weight per day, respectively) and with respect to *ad libitum* water consumption (20.8–28.5 versus 8.0, and 13.0 percent, respectively). A similar relationship is shown in the mean daily weight loss of the three species of larks when deprived of water; six Horned Larks lost 1.8 percent of the body weight per day, and both the African larks lost less. The Horned Larks did not appear able to maintain weight indefinitely without water, but both the African species could. Apparently these African larks are physiologically more specialized for desert existence, but the Horned Lark is able to exploit many different habitats over a much wider geographic range.

Comparison of desert and mesic larks.—In the laboratory the desert larks respond in a more uniform manner to stressful conditions than do the mesic larks. The water consumption of the desert and mesic larks is not very different, but with the exception of *ad libitum* consumption at 33°C, the desert larks consistently show less variation (smaller standard error of the means) than the mesic larks (Table 3). They also require slightly less water on most of the drinking regimens tested, and require fewer days to reach a minimal level of water consumption. The desert larks are less variable in their weight loss without water and can withstand a slightly greater degree of dehydration than the mesic larks (Figure 8). This greater degree of uniformity, though subtle, may reflect a more stringent selection by climate in the desert.

At ambient temperatures below 45°C the thermoregulatory responses of the two populations are indistinguishable, but at 45°C the responses are very different, and are probably physiological correlates of behavioral differences (Table 2). The desert larks apparently do not become as excited in high ambient temperatures as the mesic larks. The desert birds evaporate an average of 18 percent less water than those from the mesic environment at 45°C (87.6 and 103.7 percent of the body weight per day, respectively), but they also have 32 percent less heat to eliminate than the mesic larks (2.97 and 3.91 cc O₂/g/hr, respectively). Correlated with these differences the desert larks have a higher EWL/HP ratio, and thus a lower body temperature. As the lethal T_B is only slightly above 45°C, the larks cannot survive further hyperthermia. The selective advantages for the proper behavioral and physiological responses at this critical ambient temperature are obvious, both with respect to water conservation in an arid environment and with respect to lethal hyperthermia.

Daytime surface temperatures in areas inhabited by Horned Larks are frequently very warm. Although my data are consistent with the idea that larks have a low metabolic rate, and thus a reduced metabolic contribution to the total heat load in a hot environment, the data do not negate the possibility that a low metabolism may also be an adaptation to food shortage. Lustick (1968) has conclusively demonstrated that the thermoneutral zone of a bird can be shifted to lower ambient temperatures with the application of exogenous heat. A Horned Lark on the ground in the sun would probably utilize radiation and extend thermoneutrality to lower ambient temperatures. In their thermoregulatory responses to hot environments, behavior is just as important as physiology, and when the environment is especially hot, such as on the Mojave Desert, larks select cooler portions of their environment to reduce their heat load further.

Without transplantation experiments, or raising animals in the laboratory, it is not possible to differentiate between genetically and environmentally induced changes between populations. Horned Larks are potentially much more mobile vertebrates than most mammals, and the fact that they seem to rely on slight behavioral modifications rather than physiological adaptations may reflect their relatively recent dispersal onto such environments as the desert.

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SUMMARY

The behavioral and physiological adaptations of two subspecies of Horned Larks are examined and compared. The larks are a desert form (*Eremophila alpestris ammophila*) from the hot and dry Mojave desert and a more mesic form (*E. a. actia*) from the relatively mild inland valleys of California.

Horned Larks have a low standard metabolic rate (2.28 cc O₂/g/hr) and a high thermoneutral zone (ca. 35°C), both of which indicate the larks are well adapted to a warm, open environment. At night the larks have a 2.0° to 2.5°C drop in body temperature, their metabolic rate is reduced, thermoneutrality is extended to near 20°C, and their evaporative water loss is about half the daytime level. All these energy and water saving mechanisms are beneficial to a diurnal bird that does not eat or drink at night. In the field at night behavior supplements physiology when larks select or create a microclimate in a roost hole, which undoubtedly is not so stressful as the macroclimate.

The water requirements of Horned Larks are not exceptionally low for small birds, and the larks must rely on a versatile behavioral repertoire for survival under stressful conditions. The temperature regulation at high ambient temperatures of desert larks is superior to that of larks from a more mesic environment, and is probably a physiological correlate of behavioral differences. The apparent reliance on behavioral, rather than on physiological adaptations is probably a reflection of the recent dispersal of the larks onto the desert.

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