

SEASONAL TIME-ENERGY BUDGETS OF FREE-LIVING CHUKARS IN THE NEGEV DESERT¹

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Abstract. Chukars (*Alectoris chukar*) have a broad Palearctic distribution which includes mesic and semi-arid, but not very hot, arid areas. We studied the seasonal activity patterns of Chukars in the Negev desert highlands of Israel, and examined whether their ability to inhabit hot, dry areas is influenced by limitations imposed on their activities by the physical environment. Daily energy expenditure (DEE) of Chukars (350 to 550 g body mass) was calculated by converting time-activity budgets to time-energy budgets, and by using the operative environmental temperature (T_e) to estimate the Chukar's thermoregulatory requirements. Mean DEE of Chukars was 630 kJ/(kg·day) in summer when they foraged mainly on high energy foods in cultivated fields, and 960 kJ/(kg·day) in winter when they ate mainly natural vegetation of lower energy content. Consequently, Chukars spent twice as much time foraging in winter than in summer (7 to 8 hr/day vs. 3 to 3.5 hr/day). The Chukars' activity pattern during summer was bimodal, characterized by long periods (7 to 8 hr/day) of rest in the shade during the hot part of the day. A significant positive correlation was found between time spent resting and mean daily maximum T_e ($T_{e,max}$) and a significant negative correlation was found between time spent foraging and $T_{e,max}$. We concluded that the geographical distribution of Chukars is limited by a combination of two key factors: the duration of time that Chukars can remain active without risking their heat balance and the amount of time they need to find and eat enough food to meet their daily energy requirements.

Key words: Chukar; *Alectoris*; desert phasianid; time activity budget; time energy budget; temperature; distribution.

INTRODUCTION

Animals that inhabit hot deserts may be exposed to high ambient temperatures, high radiation loads, and seasonally fluctuating food and water supplies. Diurnal, ground-dwelling birds are particularly vulnerable to such conditions.

Chukars, *Alectoris chukar*, are diurnal, primarily granivorous, ground-dwelling phasianids widely distributed in the central and southern Palearctic. Generally, the species inhabits mesic areas and occurs in deserts only at the margins of its range (Cramp and Simmons 1979). In Israel, Chukars are abundant and occupy a variety of natural and modified habitats (Paz 1986). They are, however, not found in extreme hot, arid areas (Pinshow et al. 1983, Paz 1986).

The Negev desert highlands are considered 'arid,' having 250 to 300 biologically dry days per annum and a precipitation:evaporation ratio of less than 0.2 (UNESCO 1977). Unlike Sand Partridges, *Ammoperdix heyi*, with which Chu-

kars are sympatric in the region (Degen et al. 1983, Pinshow et al. 1983), Negev Chukars were not found to have special physiological adaptations associated with desert survival, except for lower than expected standard metabolic rates (Pinshow et al. 1983; Degen et al. 1983, 1984; Alkon et al. 1985; Kleinhaus et al. 1985; Frumkin et al. 1986; Levgorin et al. 1986). Thus, we hypothesized that the physical environment might limit the Chukar's ability to inhabit arid areas through its influence on their activity patterns. We studied time and energy use of free-living Chukars throughout the year, and examined environmental effects on behavior patterns using mechanistic models and the thermodynamic energy balance concept.

METHODS

STUDY AREA

The study was done in an area of 4 km² near Midreshet Sede Boqer in the Negev desert highlands (30°52'N, 34°57'E, 475 m ASL) of southern Israel. The area includes a large canyon (Nahal Zin), a loess covered plateau (Sede Zin), and cultivated areas comprising the Ben-Gurion Me-

¹ Received 3 September 1986. Final acceptance 2 March 1987.

morial Park and fields of nearby Kibbutz Sede Boqer. Rainfall occurs in the winter; the annual average being 105.2 mm with large variations in its temporal and spatial distribution. Average daily air temperature for the hottest (July) and the coldest (January) months are 25.5°C and 9.8°C, respectively. The average maximum daily air temperature for July is 32.4°C and the average minimum daily air temperature for January is 4.8°C. The annual average relative humidity at 14:00 is 39% (Zangvil and Druian 1979, 1983).

Vegetation in Nahal Zin is concentrated along the dry river banks and its tributaries. The major woody herbaceous species are *Tamarix nilotica*, *Retama raetam*, *Hirsuta thymelaea*, and *Atriplex halimus*. The plateau and surrounding slopes support sparse dwarf shrubs such as *Hammada scoparia*, *Artemisia herba-alba*, and *Zygophyllum dumosum*. For further details of the vegetation see Evenari et al. (1982).

METHODS OF OBSERVATION

Chukars were captured from October 1983 to December 1984 using grain-baited 90 × 90 × 60 cm mesh traps with walk-in funnel entrances. Each bird was individually marked with a numbered leg band and, in addition, some were back-tagged (Alkon 1979). A covey of nine Chukars was chosen for the study and all members were tagged and their area of activity was roughly mapped. In January 1984 three individuals were harnessed with radio transmitters (Biotrack, SS-1) to facilitate finding the covey. Transmitter batteries functioned for about 6 months and were replaced when necessary. Transmissions were in the 150–151 MHz range and were monitored with a portable receiver (Telonics, RA-2) and directional antennae (Telonics, RA-2A and RA-4A). Activity within the covey was uniform, i.e., birds foraged, rested, walked, etc., together. Therefore, the time-activity budget of a closely observed individual was assumed to represent that of all members of the covey. Visual observations were made with a pair of binoculars (Lupinus, 7 × 50) and a 20 to 60 × zoom telescope (Swift, Mark II) from January through December 1984.

TIME-ENERGY BUDGET ESTIMATION

To estimate the Chukar's time-energy budget (TEB), activity was divided into 10 categories: (1) pecking while stationary; (2) pecking while walking; (3) walking; (4) flying; (5) daytime rest-

ing; (6) nighttime roosting; (7) social interactions; (8) preening; (9) calling; and (10) standing alert. These activities were then grouped into six broader categories. Foraging was made up of (1) and (2); locomotion consisted of (3) and (4); (5) and (6) were retained as separate categories; (7), (8), (9), and (10) were lumped together as "other activities." Complete 24-hr periods within each month were constructed by combining data from at least 20 spells of observation of no less than 3 hr each that covered all hours of the day during that month.

The metabolic costs of each activity was assessed as follows. The cost of resting was considered equal to the birds' standard metabolic rate (SMR) which is 14.7 kJ/(kg·hr) (Frumkin et al. 1986) and the cost of roosting was considered 20% less (Aschoff and Pohl 1970). The energetic cost of walking was calculated from the equation of Fedak et al. (1974) for the cost of bipedal locomotion in Chukars. Walking speeds of Chukars in the field were determined by measuring the distance travelled during an interval timed by a stopwatch. The cost of social interactions, which consisted mainly of birds chasing one another, was considered equal to the cost of running at 4 km/hr. The cost of pecking while stationary or standing alert was considered to be 1.7 × SMR following Mugaas and King (1981), as were the costs of preening and calling. The cost of flight was assumed to be 11 × SMR (King 1974) which, although high, makes little difference to the total daily energy budget because a negligible fraction of the birds' time was spent flying.

The relation between SMR and ambient temperature for Chukars (Frumkin et al. 1986) was used to calculate the thermoregulatory cost of resting at any operative environmental temperature (T_e , see next section). Lower critical temperature ($T_{lc} = 29^\circ\text{C}$), upper critical temperature ($T_{uc} = 38.5^\circ\text{C}$), and lethal temperature ($T_l = 42.5^\circ\text{C}$) were taken from Frumkin et al. (1986). The cost of thermoregulation during various activities was assumed to be substitutive to the energy cost of those activities when T_e was lower than T_{lc} and additive when T_e exceeded T_{uc} (Paladino and King 1984).

Operative temperature (T_e) was computed according to Robinson et al. (1976) as:

$$T_e = T_a + \frac{R_{\text{abs}} - \epsilon\sigma T_a^4}{\rho C_p(1/r_a + 1/r_s)}$$

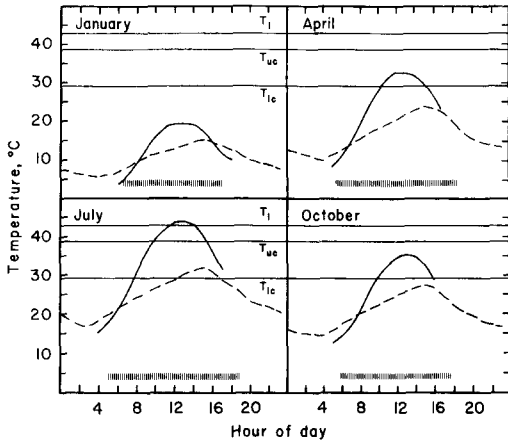


FIGURE 1. Daily thermal environment of Chukars in the Negev desert for winter (January), spring (April), summer (July), and autumn (October). Broken curved line = mean daily air temperature; solid curved line = calculated operative environmental temperature. T_1 = upper lethal temperature, T_{uc} = upper critical temperature, T_{lc} = lower critical temperature. Hatched bars denote day length from sunrise to sunset on the 15th of the month.

where T_a = air temperature ($^{\circ}\text{C}$); R_{abs} = absorbed radiation (W/m^2); ϵ = emissivity (fraction); σ = Stephan-Boltzmann constant [$\text{W}/(\text{m}^2 \cdot \text{K}^4)$]; ρ = density of air (kg/m^3); c_p = specific heat of air [$\text{J}/(\text{kg} \cdot \text{K})$]; r_a = boundary layer resistance (s/m); r_r = resistance to radiative heat transfer (s/m).

Meteorological data for model input were obtained from a weather station located in the center of the study area on Sede Zin where the birds spent most of their time during the day. Data included hourly measurements of global radiation, ground temperature, and wind velocity 3.5 m above the ground. We assumed that wind velocity profiles in the field were the same as at the weather station and we estimated wind velocity at Chukar mid-height of 10 cm (Monteith 1973). Hourly temperatures measured at the ground surface and at 2 m were used to construct continuous temperature profiles (Lowry 1969). Relative humidity and the fraction of the sky covered with clouds were measured at 08:00, 14:00, and 20:00 and daily profiles were constructed by interpolation. Global radiation was measured with a precision spectral pyrometer (Epply), factory calibrated to $\pm 0.5\%$ full scale reading. Wind velocity was measured with a cup anemometer (Lambrecht), factory calibrated to ± 0.2

m/sec. All temperatures were measured with mercury-in-glass thermometers calibrated to $\pm 0.1^{\circ}\text{C}$ against a standard thermometer. Relative humidity was measured with ventilated wet and dry bulb thermometers in a meteorological box at 2 m. Cloud cover was estimated visually (WMO 1956).

Components of absorbed long wave radiation were calculated according to Monteith (1973), and absorbed shortwave radiation was estimated from global radiation. For radiation absorptance of the Chukar's body surface we used values for the similarly colored Northern Bobwhite, *Colinus virginianus* (Gates 1980). Thermal resistances were calculated according to Robinson et al. (1976) and the cube root of body volume was used as the characteristic dimension required for estimating convective heat transfer (Mitchell 1976).

T_e was used to estimate the Chukar's thermoregulatory requirements. Whenever the birds were in shaded areas, i.e., sheltered from the open sky (e.g., while resting during the day or roosting at night), T_e was assumed to equal air temperature.

RESULTS

Of the original nine Chukars in the covey, six were present throughout the study; three were replaced by three new birds that joined the covey. We found the remains and leg bands of two of the three original birds. None of the birds formed breeding pairs during the year of study. Similarly, no pairs were formed in any of four other coveys we observed on a regular basis in the study area.

The relationship of T_e and T_a to time of day for average days during months representing four seasons, i.e., January (winter), April (spring), July (summer), and October (autumn), are presented in Figure 1. On an average winter day, maximum T_e and T_a were, respectively, 9°C and 15°C lower than T_{lc} . On an average summer day, although T_a did not attain T_{uc} , T_e reached 43.8°C and it exceeded T_{uc} for 6 hr of the day. Daily patterns of T_a and T_e were similar in spring and autumn and both were intermediate between those of summer and winter.

Table 1 summarizes, by month, the time allocated by Chukars to each of five major activities in 1984. These data are also presented as percentages of total daily activity time in Figure

TABLE 1. Hours per day allocated by Chukars to different activities during the year. For details of activity category composition, see text.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Foraging	8.64	5.94	8.06	6.35	5.37	3.45	3.03	3.52	3.98	6.40	4.81	7.23
Resting	0.96	1.00	1.96	3.93	5.12	7.78	7.48	6.93	5.79	2.57	3.19	0.73
Locomotion	1.28	2.42	0.86	0.86	1.85	1.14	1.62	0.90	0.90	0.70	0.83	0.99
Other activities	0.87	1.64	2.09	1.86	2.41	1.63	0.62	1.15	1.83	2.08	2.50	2.05
Roosting	12.25	13.03	11.03	11.00	9.25	10.00	11.25	11.50	11.50	12.25	12.67	13.00

2. Time allocated to foraging and daytime resting varied greatly during the year. In January, for example, Chukars devoted more than 8.5 hr per day, or about 36.0% of their time, to foraging, whereas in July they spent only a third as much time foraging (3 hr/day or 12.6%). In July, birds rested for 7 to 8 hr per day (about 31.2%) which is about eightfold the time they spent resting during January (0.96 hr/day or 4.0%). In spring and autumn the times spent at these activities were intermediate between winter and summer.

During daylight hours of all months, most time was spent either foraging or resting. In winter, foraging was intensive and continuous during the day, while at midday this activity was interspersed with short periods of rest. In summer there was a pronounced bimodal pattern of diurnal activity; foraging took place in the early morning and late afternoon, and all birds rested between 09:00 and 15:00. Here again, the values for activity times in spring and autumn fell between those for summer and winter. In winter, Chukars foraged mainly in areas of natural vegetation, whereas in summer they foraged mainly in cultivated areas. Locomotion occurred mainly in the early morning and late afternoon, when the birds moved between their roosting site and foraging areas.

Estimated daily energy expenditure (DEE) for Chukars was lowest in summer and highest in winter. The components of DEE are presented in Table 2, and Figure 3 shows these values as percentages of total DEE. A total of 287.7 kJ/(kg·day) (30.1% of DEE) was expended for foraging in January as opposed to 108.4 kJ/(kg·day) (17.2% of DEE) in July. Furthermore, estimated thermoregulatory requirements were greatest in January and lowest in July: 404.0 kJ/(kg·day) (42.3%) and 150.7 kJ/(kg·day) (24.0%), respectively. Daytime resting required 1.9% of DEE or 17.8 kJ/(kg·day) in winter, whereas in

summer it required 17.6% of DEE or 110.4 kJ/(kg·day).

DISCUSSION

DEE of free-ranging animals is often estimated by converting time-activity budgets (TAB) to time-energy budgets (TEB) using available energetic equivalents (for reviews see King 1974, Kendeigh et al. 1977, Walsberg 1983). A problem associated with this technique is the difficulty in estimating the energetic cost of specific activities (Kendeigh et al. 1977, Weathers et al. 1984). Accuracy of the technique has been examined by comparing TEB values with values estimated from other independent techniques. For example, Weathers et al. (1984) compared energy cost estimates made by concurrently using the TEB and doubly labelled water (DLW) methods. They concluded that accuracy in TEB estimates can be improved by using measured energy equivalents rather than estimations, and by using heat transfer theories such as those based on T_c and thermal resistances for extrapolation

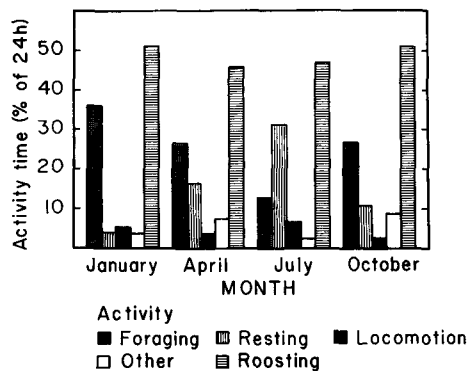


FIGURE 2. Seasonal allocation of time to different activities by Chukars in the Negev desert. Winter (January); spring (April); summer (July); autumn (October).

TABLE 2. Daily energy expenditure (DEE, kJ/(kg·day) of Chukars for each month, and the amount of energy allocated to different activities. For details of activity category composition, see text.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Foraging	287.7	202.7	277.3	225.9	192.9	104.0	108.4	127.2	153.5	204.9	172.1	254.1
Resting	17.8	14.8	19.3	58.2	75.6	114.8	110.4	61.2	85.6	38.0	47.2	10.8
Locomotion	82.5	158.9	57.8	58.0	127.2	78.9	109.2	102.3	61.7	63.8	57.9	65.6
Other activities	20.7	54.2	62.0	47.1	84.8	41.0	16.9	34.7	46.2	52.0	62.6	51.3
Roosting	141.7	153.6	127.1	127.3	109.4	118.3	133.0	135.9	135.9	144.8	149.7	130.0
Thermoregulation	403.9	375.3	303.0	280.6	175.6	173.3	150.9	155.9	171.2	232.8	360.8	450.3
DEE	954.3	959.5	846.5	797.1	765.5	630.3	628.8	617.2	654.1	736.3	850.3	962.1

of laboratory measurements of metabolism to field situations. For the most part, energetic equivalents used in our calculations were measured directly in the laboratory (Fedak et al. 1974, Frumkin et al. 1986) and calculated T_c was used to estimate the Chukar's thermoregulatory requirements.

During March we had an opportunity to compare our TEB values with those obtained using DLW to measure DEE in the same population of Chukars we studied (Kam 1986). Mean DEE using DLW was 814 kJ/(kg·day) which was within 5% of the value we calculated using the TAB-TEB technique, i.e., 856.5 kJ/(kg·day).

DEE for Chukars was highest in winter, but the calculated value was only 80% of that expected for a 425-g (mean body mass of the nine birds in the studied covey) nonpasserine bird according to the allometric equation of Walsberg (1983). The lowest measured value, in summer, was only 52% of that expected. Goldstein and Nagy (1985) also observed low summer DEE in

Gambel's Quail, *Callipepla gambelii*, a desert phasianid of the southwestern United States and northeastern Mexico, i.e., only 34% of the allometrically calculated value. Low summer DEE in Gambel's Quail was attributed to low resting metabolic rates, little time spent flying, long periods spent resting and low thermoregulatory costs. This explanation seems valid in the case of Chukars during the summer as well: SMR was 70% of that expected for a bird of its body mass (Frumkin et al. 1986), they devoted a negligible amount of time to flight, their thermoregulatory requirements in the field were low, and they spent long periods resting.

In winter (January), daily mean T_c (14°C) was below the Chukar's T_{ic} , resulting in increased energy costs for thermoregulation, thereby leading to increased food intake. Moreover, the principle forage available to Chukars in winter, natural green vegetation, has a relatively low fresh-mass energy density (Degen et al. 1984, Alkon et al. 1985); thus, also leading to increased foraging time in that season. Indeed, in winter Chukars foraged more than 8.5 hr/day, as compared to 3 hr in summer.

We assumed that the energy expenditure for activity substituted for that allocated to thermoregulation when $T_c < T_{ic}$. Therefore, being active helped maintain thermal energy balance without increased thermoregulatory costs during cold spells. This assumption was supported by Paladino and King (1984) who reported that the energy expenditure of locomotion and foraging by the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*, at low ambient temperatures was no greater than if the bird sat and shivered in order to produce heat. Further examples were provided by Kendeigh et al. (1977). In addition, Verbeek (1964) noted that foraging time reflected

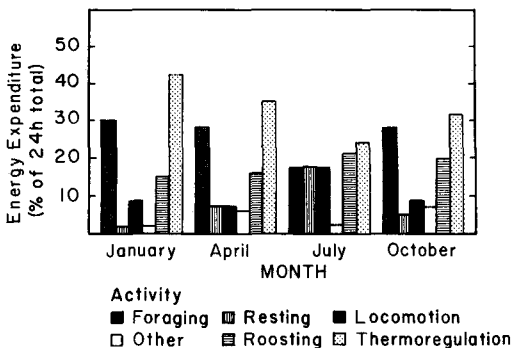


FIGURE 3. Seasonal allocation of energy to different activities by Chukars in the Negev desert. Winter (January); spring (April); summer (July); autumn (October).

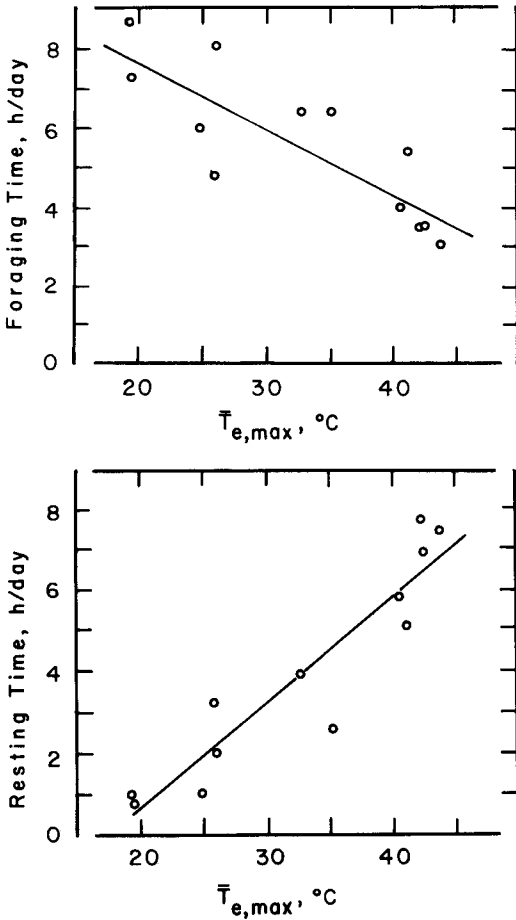


FIGURE 4a (upper), b (lower). Relations between time allocated to different activities (hr/day) by Chukars and monthly means of daily maximum operative temperature ($\bar{T}_{e,max}$, °C). Least-squares linear regression equations for these relations are: 4a. Foraging time = $-0.165 \bar{T}_{e,max} + 10.984$, $n = 12$, $r = 0.828$, $P < 0.001$; 4b. Resting time = $0.261 \bar{T}_{e,max} - 4.619$, $n = 12$, $r = 0.933$, $P < 0.001$; n = number of points, r = correlation coefficient, P = probability that regression is not significant.

the effect of T_a on the thermoregulatory demands of an animal.

In summer, the maximum difference between mean T_a and T_e was greatest, reaching 14°C (Fig. 1). During most of the day $T_a < T_{lc}$, except for 2 to 3 hr at midday when T_a was within the Chukars' thermal neutral zone. However, T_e reached 43.8°C and exceeded T_{lc} for 10 hr and T_{uc} for 6 hr a day. Many species minimize activity during the hours of high T_a which lessens their internal heat load (Dawson and Schmidt-Nielsen 1964, Serventy 1971, Goldstein 1984), and Chu-

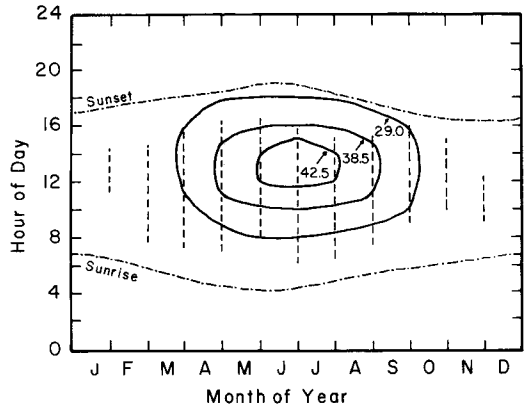


FIGURE 5. Relations between isotherms for operative environmental temperatures of Chukars corresponding to their lower critical temperature (29°C), upper critical temperature (38.5°C) and lethal temperature (42.5°C) and time of day during the year in the Negev highlands. Broken vertical lines represent mean time spent resting in the shade for each month.

kars behaved as expected under such conditions. In summer, during daytime Chukars mainly rested in shade usually after either several hours of foraging or after bouts of intensive locomotion. Birds began to rest after foraging when their crops were presumably full. Internal heat production increases during the process of digestion (Kendeigh 1972, Kleiber 1975) which causes the T_{lc} to decrease (Birkebak 1966). This might be the reason why birds ceased energy demanding activity before T_e exceeded T_{lc} , and renewed it before T_e fell below T_{uc} .

The type of constraint that hot environments impose on Chukars is suggested by the relation between time allocated to their various activities and monthly mean daily maximum operative environmental temperatures ($\bar{T}_{e,max}$). Foraging time was negatively correlated with $\bar{T}_{e,max}$ and resting time positively correlated with $\bar{T}_{e,max}$ (Figs. 4a, b); both correlations being significant. Since on a summer day T_e exceeded T_{uc} for 6 hr (and T_l for at least 2.5 hr), Chukars had to rest for at least 6 hr. Other daily activities, such as preening, locomotion, calling, etc., were not significantly correlated with $\bar{T}_{e,max}$. The time spent on these activities was about 3 hr/day, independent of environmental conditions. Under summer (June to September) conditions in the central Negev highlands, the 6 hr rest and the 3 hr required for activities other than resting and foraging can be serious constraints on the time available for foraging (Fig. 5).

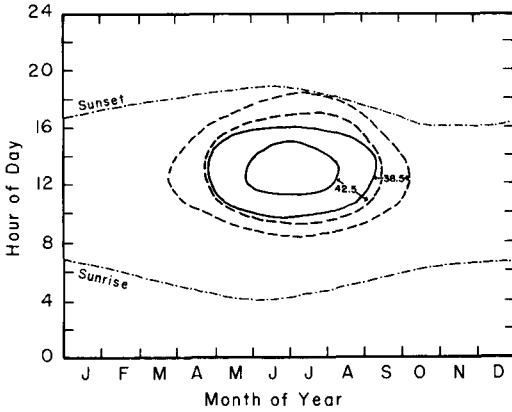


FIGURE 6. Relations between isotherms for operative environmental temperatures of Chukars corresponding to their upper critical temperature (38.5°C) and lethal temperature (42.5°C) and time of day during the year in the Negev highlands (solid lines) and at Eilat in the rift valley (broken lines).

With the above constraints in mind, we used our model to examine the ability of Chukars to inhabit environments hotter and more arid than the central Negev highlands, i.e., the Arava (part of the rift valley), for which meteorological data was available from Eilat, approximately 200 km south of Sede Boqer. At Eilat the daily average $T_{a,max}$ on summer days exceeds that of Sede Boqer by 8°C, and T_e often reaches 50°C (Fig. 6). In July, T_e exceeds T_{uc} beginning 4 hr after sunrise and decreases only after sunset. Therefore, the maximum total time left for activities other than resting before dark is 4 hr. If the time needed by Chukars at Eilat for activities other than feeding and resting is similar to that needed on our study site, they would have only about 1 hr per day for foraging.

Populations of Chukars, however, do occur near Eilat and this may be explained as follows. Chukar habitats in very arid areas in Israel comprise either wadis in which the vegetation is relatively dense, thus containing substantial food in a shaded environment, or modified environments around human settlements in which dense food supplies are available (authors' unpubl. data). In the first habitat, Chukars can fulfill their energy requirements in shaded areas and thus are not exposed to excessive external heat loads. The second habitat supplies concentrated, high quality food which enables Chukars to fulfill their daily energy demands within short periods before rising T_e forces them to shaded resting sites.

It is also conceivable that Chukars make more time available for foraging either by reducing other activities or by combining activities (e.g., preening or calling with resting).

From previous studies it is apparent that Chukars do not possess exemplary physiological adaptations to heat stress (see summary in Frumkin et al. 1986) which might facilitate their living in deserts. Thus, we suggest that the geographical distribution of Chukars in deserts is limited to places where the environmental conditions allow them to be active for sufficient time to obtain their energy requirements without risking their heat balance.

ACKNOWLEDGMENTS

We especially thank Philip Alkon for lending us telemetry equipment, for helpful discussions, and for commenting on a draft of this paper. We thank Avraham Zangvil and Uriel Safriel for helpful discussions, Michael Kam and Mark Goldberg for their assistance, and J. N. Mugaas and an anonymous reviewer for their helpful suggestions. This paper is contribution number 60 of the Mitrani Center for Desert Ecology and was funded by U.S.-Israel Binational Science Foundation grant 2911/82.

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