THE THERMAL ENVIRONMENT AND ITS CONSTRAINT ON ACTIVITY OF DESERT QUAIL IN SUMMER

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ABSTRACT.—I measured the thermal environments experienced by Gambel's Quail (*Callipepla gambelii*) during the summertime in the Colorado Desert by using estimates of standard operative temperature (T_{es}). Simultaneously with these measurements, I monitored the activity patterns of quail. The thermoneutral zone of freshly captured quail extends to 44°C, yet T_{es} in sunlit areas may exceed this upper critical temperature for more than 10 h of a hot day. Even in the shade, T_{es} is at the upper limits of thermoneutrality for much of the day. At these temperatures the birds maintain a body temperature that is very close to their upper lethal limit. The activity pattern of Gambel's Quail on hot summer days is bimodal, with morning and late afternoon foraging separated by a long quiescent period during midday. The time of onset and the duration of this inactive period varies directly with T_{es}, and foraging occurs throughout the day on cool, overcast, summer days. This suggests that the thermal environment constrains midday activity. A bimodal activity pattern during the winter is probably a response to predation pressure from avian raptors. During the summer, however, it is advantageous for growing juvenile quail to maximize foraging, and the thermal environment is the most important factor shaping the activity schedule. *Received 19 August 1983, accepted 15 December 1983.*

LABORATORY studies have demonstrated that when birds are exposed to environments varying in temperature and/or thermal radiation, they often select conditions that minimize thermal stress and its consequent energetic demands (Laudenslager and Hammel 1977, Mahoney and King 1977, DeJong 1979). Presumably, these factors also influence habitat utilization by free-living animals. Numerous investigators have examined the influence of thermal factors on winter roost-site and nest-site selection by birds (e.g. Walsberg and King 1980, and references therein). Yet, our knowledge of the relationship between environmental microclimate variation and patterns of daily activity in birds remains scant (Ricklefs and Hainsworth 1968, Grubb 1978, DeWoskin 1980, Mugaas and King 1981, Alatalo 1982).

Gambel's Quail (*Callipepla gambelii*) is a permanent and abundant resident of the deserts of the southwestern United States. These regions are characterized by extreme summer heat, and it is well known that during these months avian activity declines during midday.

This period of quiescence is generally attributed to avoidance of thermal stress (e.g. Vorhies 1928, Dawson 1954). Beck et al. (1973), however, suggest that quail may pattern their activity primarily in order to avoid predators. In this study I characterized the thermal environments used by *C. gambelii* in their daily foraging and simultaneously observed the activity of the quail. Changes in microhabitat utilization both between and within summer days were examined to test the hypothesis that thermal constraints shape the foraging schedule.

METHODS

STUDY SITE

Research was conducted at the Philip L. Boyd Deep Canyon Desert Research Station in Palm Desert, California. The study site, at 250 m elevation, possesses one permanent water hole and is characterized by Colorado Desert alluvial plain vegetation. Creosote-bush (*Larrea tridentata*), burro bush (*Ambrosia dumosa*), indigo bush (*Dalea schottii*), and *Opuntia* cacti are the dominant plant species (Zabriskie 1979). Palo verdes (*Cercidium floridum*), the most abundant trees used regularly by Gambel's Quail for shade and roosting, occur primarily in the washes, which transect the study area.

STANDARD OPERATIVE TEMPERATURE

The thermal environment was described by standard operative temperature (T_{es}), a direct index of thermal flux for a particular animal in a given environment. A detailed theoretical development of the standard operative temperature concept may be found in Bakken (1976, 1980); the application of T_{es} to field studies of endotherms may be found in Chappell and Bartholomew (1981) and Buttemer (1981). T_{es} is defined as:

$$T_{es} = T_b - (K_e/K_{es})(T_b - T_e), \qquad (1)$$

where T_b is body temperature (°C) and T_e is the operative environmental temperature (°C). The ratio of overall thermal conductance at environmental wind speed (K_e) to overall thermal conductance in standard (free convective) conditions (K_{es}) describes the convective enhancement of heat flux between the animal and its environment.

T_b.—Body temperatures of free-ranging birds were extrapolated from measurements conducted as part of laboratory metabolic studies (Goldstein and Nagy MS). Quail were trapped with Potter walk-in traps either in early morning or evening; all measurements were made within 24 h of capture. Birds were placed in a ventilated Plexiglas chamber and were subjected to temperatures between 27 and 48°C, for at least 40 min at each temperature. Body temperature was measured by inserting a 36-gauge thermocouple at least 2 cm into the cloaca at the start and termination of each experimental period. Chamber-wall temperature, measured with a 36-gauge thermocouple, did not differ from chamber T_a, and there was no forced convection in the Plexiglas chamber. Therefore, $T_a = T_{es}$ in the laboratory chamber, and T_b under field conditions was assigned from measurements of T_{es}. The upper critical temperature (T_{uc}) was also determined from these laboratory experiments.

T_e.—Operative temperature was measured by placing plumage-covered copper models of Gambel's Quail (Bakken and Gates 1975) in microhabitats (open sun, shade, up in bushes) typical of those used by the birds in their daily activity. Skins used for covering the models were obtained from birds captured outside the Boyd Reserve within 5 km of the study area. Six 24-gauge thermocouples attached to the copper body of each model and connected in parallel provided an integrated T_e, which was recorded continuously on a Honeywell multipoint potentiometer.

In open sun, two copper models were placed at right angles to each other. It was not possible continuously to record the orientation of free-living quail with respect to the sun, and so I assigned T_e in the sun for these birds as the average of those measured on the two copper models. I measured T_e of male and female adult quail, as well as of juveniles ranging in mass from 5 to 25 g.

Ambient wind speed was measured with hot-ball anemometers (Buttemer 1981) placed adjacent to the models at a height of 6 cm (quail shoulder height) and was recorded simultaneously with T_e.

K_{es} and K_e.—The convectional changes in conductance (K_{es} and K_e) were measured both on live quail (see Goldstein 1983 for experimental and calculational details) and on heated copper models (Bakken et al. 1981). The copper-model birds were tested in the same wind tunnel as the live quail, at wind speeds of 0.06, 0.78, 1.15, 2.10, and 2.75 m/s. Models were heated so as to maintain a "skin" temperature of 37°C (Dawson and Tordoff 1959) and were positioned facing into the wind. Conductance was calculated as $P/(T_s - T_a)$, where P is the power (watts) needed to heat the model, T_s is model "skin" temperature, and T_a is ambient temperature. Models were tested at ambient temperatures between 6 and 25°C.

I have assumed that the temperature range of the thermoneutral zone is not affected by wind, i.e. that $T_{es} = T_e$ within thermoneutrality. This simplification is adequate at the low wind speeds measured during this study. K_{es} at all temperatures above thermoneutrality is considered to be maximal and equal to 0.12 W/°C (calculated from Weathers 1981).

ACTIVITY SCHEDULE

Concurrent with the micrometeorological recordings, I followed groups of Gambel's Quail and recorded their activity continuously. All observations were made during the summer months of July through early September. During these months quail live in single or combined family groups. The individuals in a covey forage largely in unison, and they may be monitored at a distance of 15–20 m with no apparent effect on behavior. The coveys that were observed during this study were comprised of 6–9 birds, including either 2 or 4 adults and juveniles ranging in mass from 30 to 110 g.

RESULTS

BODY MASS

Adult mass averaged 158 g ($n = 13$, SD = 5.3) for males and 142 g ($n = 14$, SD = 4.7) for females. During the course of trapping birds for physiological measurements, several individuals were captured more than once. Of the 15 birds recaptured during periods of consistently hot summer weather, 13 had either maintained body mass (less than a 2-g, or 1.4%, change) or gained mass.

STANDARD OPERATIVE TEMPERATURE

Body temperature.—Gambel's Quail tolerate high ambient temperatures and body temper-
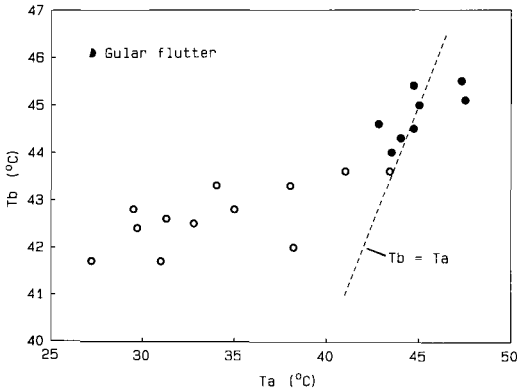
Fig. 1. Body temperature of Gambel's Quail under laboratory conditions as a function of ambient temperature. All measurements were conducted within 24 h of capture during the summer.

TABLE 1. The proportional increase in conductance (K_e/K_{es}) with increasing wind in live and copper model Gambel's Quail.

Wind speed (m/s)	K_e/K_{es}			
	Live bird (10°C)	Live bird (20°C)	Model (MM1)	Model (MM2)
0.06	1.0	1.0	1.0	1.0
0.74	1.17	1.20	1.32	1.36
1.03	1.29	1.28	1.45	1.49
1.74	1.47	1.56	1.72	1.80
2.31	1.66	1.72	1.92	2.04

atures (Lasiewski et al. 1966, Weathers 1981). In the present study on summer-acclimatized birds under laboratory conditions, T_b increased from 42°C to 45.5°C as T_a increased from 27°C to 45°C (Fig. 1). T_b was maintained at or below 45.5°C at T_a's of up to 47.5°C, the highest temperature tested. Most birds were strong and alert at T_b's of 45–45.5°C, but one individual was weak and had trouble flying. A single bird became excited at a T_a of 45°C and died of hyperthermia; its body temperature upon removal from the respirometry chamber was 46.5°C. It therefore appears that the upper lethal body temperature of the quail is near 46°C. The upper critical temperature of these field-acclimatized birds was approximately 44–45°C, and some individuals did not initiate gular flutter until T_a exceeded 45°C (Fig. 1).

Convective heat exchange.—Gambel's Quail became frantic when placed in a wind tunnel respirometry chamber at high temperatures, and so the effect of wind on conductance above the T_{uc} could not be measured directly. Instead, it was estimated from measurements conducted at lower temperatures. Below thermoneutrality, dry thermal conductance of live *C. gambelii* increases linearly with increasing wind speed (Goldstein 1983). Although the actual value of thermal conductance at a given wind speed differs at different temperatures, the proportional increase in conductance (K_e/K_{es}) over the range of wind speeds tested (Table 1) was the same

at both 10 and 20°C (analysis of covariance, $P > 0.05$).

In contrast to the live birds, the convectional increase in conductance of two copper models was best described as a function of wind speed to the 0.85 power (Fig. 2). The thermal conductance of copper models was independent of temperature. Moreover, both the absolute magnitude of conductance (Fig. 2) and the proportional increase of conductance in wind (Table 1) were greater in models than in live birds.

Calculation of T_{es}.—It is evident that copper models responded differently to wind than did live birds. The effect of wind on thermal conductance of *C. gambelii* at high temperatures was therefore not derived from measurements on copper models. Instead, I calculated T_{es} by assuming that the proportional increase in conductance (K_e/K_{es}) of live birds at temperatures below the lower critical temperature (T_{lc}) obtained also above the upper critical temperature (Fig. 3, method a). The T_{es} reported for field conditions was calculated by this procedure (method a).

For comparison, I calculated T_{es} by the method used by Chappell and Bartholomew (1981). They assumed that the absolute increase in thermal conductance (K_e-K_{es}) measured on a heated copper model of *Ammospermophilus leucurus* applied also to live antelope ground squirrels both above and below thermoneutrality. I used a value of 0.12 W/°C for dry thermal conductance of *C. gambelii* above thermoneutrality and added to this the average of the increases in conductance measured on the two copper models as a function of wind speed. This technique (Fig. 3, method b) resulted in T_{es}'s
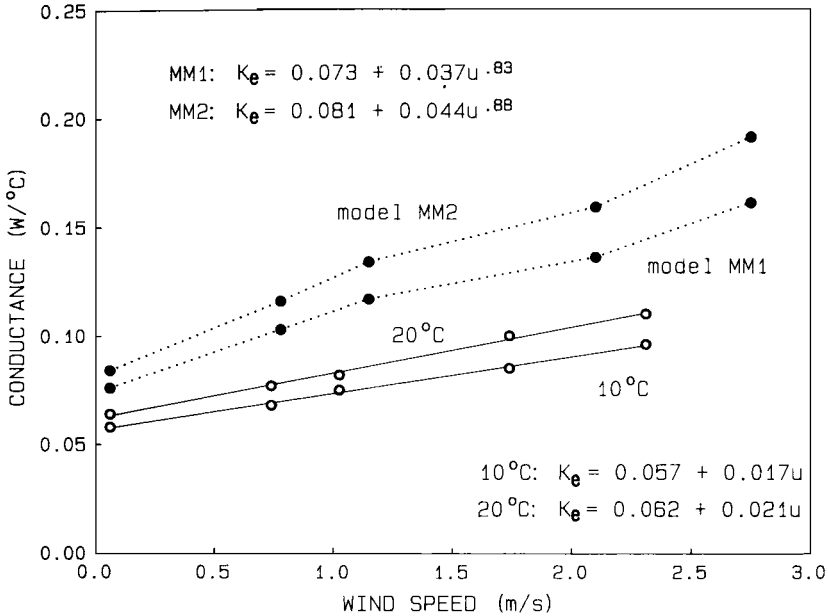
Fig. 2. Overall thermal conductance (K_e) vs. wind speed (u) in live Gambel's Quail at two temperatures (open circles) and in two heated copper models (closed circles). Equations represent best-fit descriptions of the data points. Conductances of copper models are not linear functions of wind speed, and so data points are simply connected by the dotted lines. Solid lines are linear regressions for the data from live birds. Data for live birds and the method of determining best-fit regressions are from Goldstein (1983).

nearly indistinguishable from those determined by method a.

A third procedure for calculating T_{es} rests on the assumption that the proportional increase (K_e/K_{es}) measured on copper models obtains also for live quail above thermoneutrality (Fig. 3, method c). Substituting these values of K_e/K_{es} into equation (1) produced T_{es}'s that were up to 4.11°C higher (at $T_e = 60$°C and wind speed = 2.0 m/s) than those calculated by the other two methods. The difference between T_{es} calculated by method c and that calculated by method a or b increases as wind speed and/or temperature increases.

Field conditions.—There was no difference between the T_e of copper models with male plumage and those with female plumage, and K_e and T_b measured in the laboratory also did not differ between the sexes. Consequently, male and female quail probably experience the same T_{es} in the field. On a sunny, mid-summer day, T_{es} in open areas rose sharply after sunrise, peaked in mid-afternoon, and fell rapidly after sun-

down (Fig. 4a). On a hot day T_{es} in full sun exceeded the T_{uc} of *C. gambelii* for over 10 h. Even in the shade where, because of the low wind speeds, T_{es} approximates T_e, T_{es} may exceed the T_{uc} for several hours of mid-day on unusually hot days. On overcast days I was unable to measure any difference in T_e between open areas and those under or in bushes. T_e's on cloudy summer days remained within the thermoneutral zone of *C. gambelii*; because wind speeds were generally low, T_{es}'s presumably remained within thermoneutrality as well (Fig. 4).

T_e's of both very young downy chicks and of chicks in juvenal plumage did not differ from those of the adults. Conductances were not measured in the juveniles. Because wind speeds and, consequently, convective heat transfer were generally low near ground level where the juveniles spend their time (Figs. 4a and 5), however, T_{es}'s of the juveniles should be similar to those of the adults.
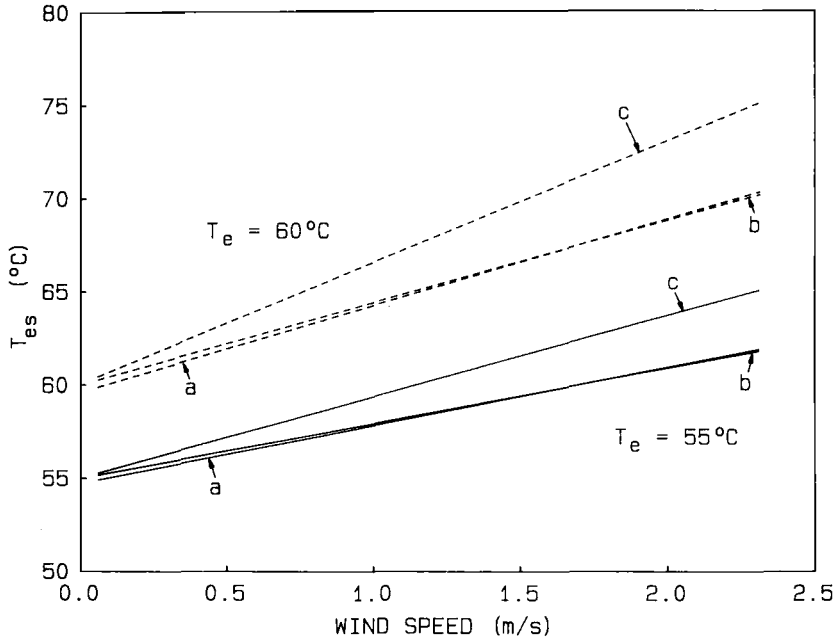
Fig. 3. T_{es} calculated by three procedures as a function of wind speed: (a) assuming conductance increases proportionally the same above thermoneutrality as it does below thermoneutrality in live birds, (b) by the method of Chappell and Bartholomew (1981), and (c) assuming conductance increases proportionally the same in live birds as it does in copper models. See text for details.
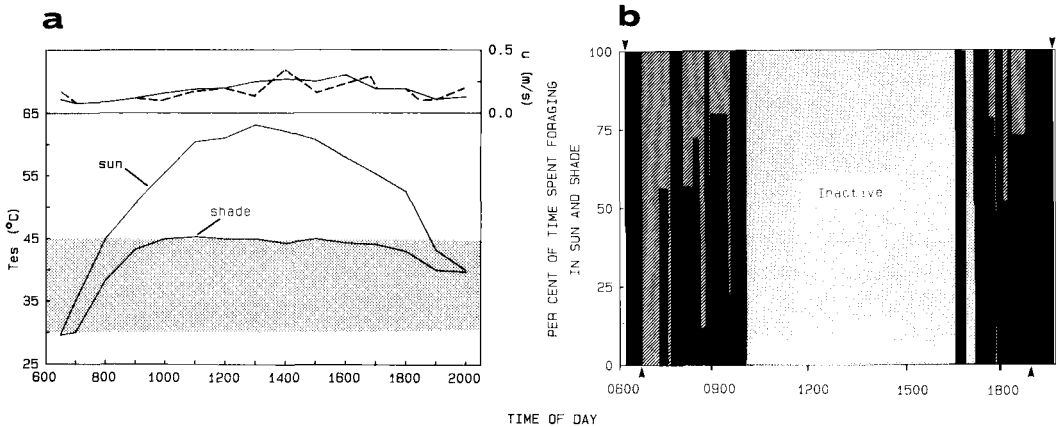

Fig. 4. **a.** Upper graph—wind speed at a height of 6 cm (dashed line = shade, solid line = sun). Lower graph—standard operative temperatures in open sunlit areas and in deep shade under a bush through the course of a typical hot summer day. The stippled area encompasses the thermoneutral zone of Gambel's Quail. **b.** Activity schedule of Gambel's Quail on the hot summer day illustrated in Fig. 4 **a.** Dark shading = foraging in shade; diagonal striping = foraging in sun; light shading = inactivity. Arrows on the upper axis indicate start and end of activity. Arrows on the lower axis represent sunrise and sunset.
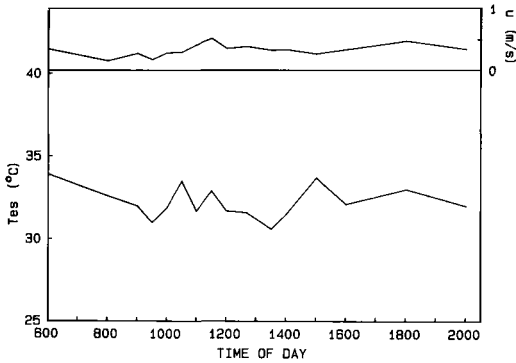
Fig. 5. T_{es} and wind speed on a heavily overcast summer day (15 July 1981).
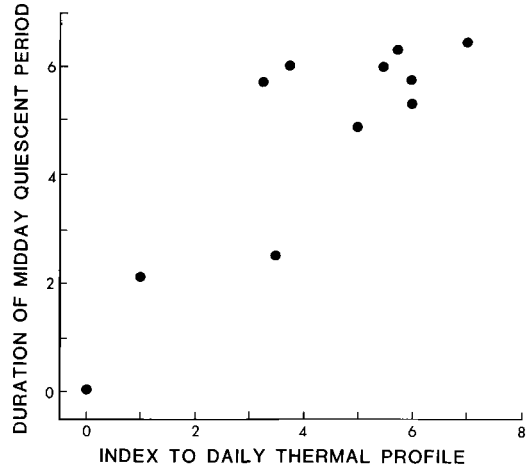

Fig. 6. Duration of mid-day quiescent period as a function of the number of hours during which T_{es} in open sun exceeded 55°C. This independent variable serves as a convenient index to the torridity of the daily thermal profile.

ACTIVITY SCHEDULE

On hot, sunny, summer days, Gambel's Quail had a bimodal activity pattern (Fig. 4b). They started to forage approximately 0.5 h before sunrise and stopped in the evening about 1 h after sundown. In the morning, as T_{es} in the sun and then in the shade successively reached or surpassed the upper limits of their thermoneutral zone, the quail spent progressively less time foraging in sunlit areas. During mid-morning, foraging ceased altogether. The T_{es} in open sun at the cessation of foraging averaged 53.7°C on 8 days of day-long continuous observation of coveys, and T_{es} in the shade averaged 42.2°C. The time at which foraging ceased ranged from 0945 to 1100 and was consistently later on cooler days (Fig. 6).

The quail spent the hours of mid-day resting quietly beneath large trees [either palo verdes or desert willows (*Chilopsis linearis*)] or in the shade of boulders. All birds of a covey shared the same refuge. On several occasions individuals scratched depressions in the dirt in which to rest.

Foraging was resumed between 1600 and 1630. At this time, the average T_{es} had decreased to 56°C in the sun and to 43.5°C in the shade. The pattern of the late afternoon foraging bout was the reverse of that in the morning—foraging became less restricted to shaded areas as temperatures decreased, although the setting sun of course reduced sunlit areas.

On cooler sunny days, when T_{es} in the sun exceeded T_{uc} but T_{es} in the shade did not exceed 40°C and so remained well within their ther-

moneutral zone, quail foraged intermittently throughout the day. As on hot days, the birds restricted themselves almost exclusively to the shade during the mid-day hours. On the cooler days they alternated periods of inactivity with periods of foraging under trees or movement from one shaded area to another. On two completely overcast days quail were active continuously throughout the entire day.

DISCUSSION

T_{es} IN HOT CONDITIONS

Standard operative temperature is a direct index to animal/environment thermal flux and as such is a physiologically meaningful parameter for use in ecological studies. Both the T_{es} index (Bakken 1980) and the use of copper models in its determination (Bakken et al. 1981, Buttemer 1981) have been validated for cold environments. Copper models have also proven useful for measuring the operative temperature (T_e) affecting birds in hot environments (Salzman 1982, Chappell et al. in press). The application of the procedures of standard operative temperature (T_{es}) to temperatures within and above thermoneutrality, however, has not been validated.

In particular, the effect of convection on heat transfer between live animals and the environment at high temperatures has not been studied. In the present study, the estimation of T_{es} at high temperatures was based on assumptions derived from measurements on copper models or on live birds at temperatures below thermoneutrality. It was therefore of interest to compare the values of T_{es} obtained by applying these data in different ways.

The effect of wind on conductance differed both between models and live birds (Bakken et al. 1981; Table 1) and from model to model (Bakken et al. 1981; Fig. 2); this effect also changes from temperature to temperature as the animal alters its conductance (Goldstein 1983). Despite this, a comparison of methods a and b indicates that the calculation of T_{es} from copper models may yield results at high temperatures very similar to those determined using data extrapolated from live animals. Ideally, copper models should be calibrated against live animals; the models can then be used directly to determine T_{es} in the natural environment (Bakken et al. 1981). The proper definition of the assumptions and procedures for calculating T_{es} within and above thermoneutrality must yet await studies of live animals at these temperatures.

An additional assumption of the present analysis is that, in convection at a given temperature above T_{uc}, evaporative heat loss changes only as a response to the enhanced heat load incurred by the increase in dry conductance. Up to 25% of pulmocutaneous evaporative heat loss in birds may take place through the skin at high temperatures, however (Richards 1980), and gaping during bouts of gular flutter exposes the moist lining of the mouth. Convective enhancement of evaporative cooling from the skin and mouth is likely, and this would partially offset the increased heat flux from the environment. For these conditions, the actual standard operative temperature would be lower than I have calculated.

ACTIVITY

Seasonal and daily changes in the activity schedule of Gambel's Quail undoubtedly reflect responses to numerous biotic and abiotic factors. I propose here a scenario that emphasizes the importance of energy procurement, thermal relations, and predator avoidance in shaping these activity patterns.

Gambel's Quail follow a generally bimodal activity schedule in the summertime at Deep Canyon. Beck et al. (1973) suggested that this pattern may be associated with the avoidance of avian raptors at waterholes, which were observed most frequently during the mid-day hours. It is difficult to assess the risk of predation incurred by *C. gambelii* during the different seasons at Deep Canyon. Raptors are well known to time their hunting flights according to the activity schedules of their prey, however, and it is unlikely that quail could avoid raptors by foraging in morning and evening. The two most likely avian predators of Gambel's Quail at the Deep Canyon site are the Cooper's Hawk (*Accipiter cooperii*) and the Prairie Falcon (*Falco mexicanus*). Both of these species hunt primarily from perches, and so they do not rely on mid-day air currents for foraging flights. Even during the nesting season, when food demands are highest, the Prairie Falcon hunts most heavily in the morning and evening and least intensely during mid-afternoon (Haak 1982). Nevertheless, quail are most conspicuous and vulnerable, and least able to watch for predators, when they are foraging. There is presumably selection for these birds to minimize their activity period. Quail are able to fill their large crops in the morning with a supply of food sufficient for the daytime; in the evening foraging bout, they can acquire sufficient energy to last the night. Mid-day is spent resting quietly and inconspicuously.

Despite the probable pressure from predators, the activity of the quail in the summer was not consistently bimodal. The foraging schedule varied in a regular manner with changes in the daily environmental temperature profile. This pattern of protracted foraging on cooler days suggests that quail are constrained in their activity by excessively high mid-day temperatures.

At the high T_{es}'s regularly experienced during the summer in the Colorado Desert, Gambel's Quail exist near the upper limit of their thermal tolerance. Even in the shade for much of a hot day, these birds maintain their body temperatures very close to the upper lethal temperature. Gambel's Quail may dissipate up to 1.4 W by evaporative heat loss at high temperatures (Weathers 1981). If we assume a le-

thal T_b of 46°C, then a 140-g bird, with a T_b of 45.5°C, that left the shade to begin foraging at a T_{es} of 60°C and at a metabolic rate of 2.1 W [the energetic cost of a slow (0.5 m/s) walk, estimated from Fedak et al. (1974)] would experience a fatal hyperthermia in just over 1 min (conductance = 0.12 W/°C, specific heat of tissue = 3.43 j·g^{-1}·°C^{-1}). Active foraging presumably would disrupt gular fluttering, and so the actual time available for foraging through open areas is even less.

The precocial chicks of Gambel's Quail (mass, 4–5 g at hatching) may emerge at any time from May through early July, and they take approximately 4 months to reach full adult mass (Raitt and Ohmart 1966). Consequently, juveniles that are considerably smaller than adults are present through the hot summer months. It is possible that the small chicks may be able to find slightly cooler microhabitats in the shade of rocks or plants that are unavailable to the adults. At any T_{es}, however, the body temperature of a juvenile would change even faster than that of a fully-grown bird. Coveys are therefore extremely limited in their use of sunlit areas during the hot part of the day.

This situation is exacerbated by the absence of any cool retreat in which a temporary heat load may be dumped to the environment. The antelope ground squirrel is another small diurnal endotherm found in the same habitat as Gambel's Quail. It is able to remain sporadically active during hot summer days by shuttling between the surface and cool burrows, where T_b may be reduced by 5°C or more (Hudson 1962, Chappell and Bartholomew 1981). I observed very small juvenile *C. gambelii*, and in one instance an adult, using rodent burrows as refugia from pursuers (see also Dawson 1923). I never saw this behavior used as a means of thermal escape during the summertime, however.

Although the evidence suggests substantial thermal constraints on foraging, repeated trapping of individual quail in the summertime indicated that they are able to maintain weight even on those days during which foraging is curtailed during mid-day. Why, then, do these birds extend their activity period on cooler days? The coveys that I followed contained juvenile as well as adult birds. Whereas the birds may be able to maintain themselves on a short day of foraging, it seems likely that increasing the foraging period permits greater energy accumulation by the juveniles and, hence, more rapid growth. This hypothesis is supported by the observation that in the wintertime, when all birds are fully grown and mid-day temperatures are mild, Gambel's Quail still maintain a bimodal activity schedule and so do not forage for much of the day (Gorsuch 1934, pers. obs.).

Thus, during the summertime in the Colorado Desert, the extreme thermal environment is the most important proximate factor shaping the foraging schedule of Gambel's Quail. It is apparent, however, that a number of factors influence the quail's activity pattern and that these factors change seasonally. During the cooler months adult quail are inactive for much of the day, which probably reduces the risk of predation; foraging bouts in morning and evening are sufficient to supply energy for an entire day. Thermal constraints reinforce this bimodal activity pattern during the summertime; the quail must remain inactive during mid-day to maintain their body temperature at tolerable levels. In contrast, for the juvenile birds it is advantageous to maximize foraging time through the summer and thereby to maximize growth. Yet, the thermal environment places even greater constraints on the juveniles than on the adults, and during the summer months the activity schedule of the covey may be governed largely by the requirements of the young.

Hence, during the winter, quail are able to forage throughout the day, but it is disadvantageous for them to do so. In contrast, during the summer it is advantageous for the quail to forage throughout the day, but they are constrained from doing so. The net result of these conflicting pressures is a relatively uniform activity pattern at the two different seasons.

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