COMPARATIVE TEMPERATURE AND MOISTURE RESPONSES IN GAMBEL AND SCALED QUAIL

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Gambel Quail (*Lophortyx gambelii*) range throughout the desert areas of the extreme southwestern United States and northern México, while Scaled Quail (*Callipepla squamata*) generally inhabit the more mesic semiarid grass plains of the Southwest and much of México. The ranges of the two species overlap in southeastern Arizona and southwestern New Mexico (A.O.U. 1957; Leopold 1959). The habitats of these species are similar in the area of sympatry. The species are also similar in general body size, food habits, and in other parameters of their ecology. Comparative data relating to temperature and water relations would appear to be valuable in understanding these sympatric and closely related species. These data are also important in understanding adaptations of birds to hot, arid climates.

Bartholomew and Cade (1963) reviewed the literature concerning water economy studies of birds. Since 1963 several studies dealing with water and temperature relations have provided additional information on several species of birds, but, to date, published data are lacking on minimum water requirements, metabolism, and evaporative water loss in Gambel and Scaled Quail.

Gullion and Gullion (1964) studied the response of body weight to complete water deprivation in Gambel Quail. Bartholomew and Dawson (1958) studied the effect of various ambient temperatures on body temperature in Gambel Quail. No physiological studies of Scaled Quail appear in the literature.

More physiological studies have been done on California Quail (*Lophortyx californicus*) than on the other two species. Bartholomew and MacMillen (1961) determined the minimum daily water requirement necessary for weight maintenance in California Quail, and Hudson and Brush (1964) and Brush (1965) studied the responses of body temperature, metabolism, and evaporative water loss to various ambient temperatures in the same species. Bartholomew and Dawson (1958) also studied body temperature in California Quail.

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The present study was undertaken to obtain comparative quantitative data on water balance in Gambel and Scaled Quail. Minimum daily water requirements were determined under controlled conditions of temperature and humidity. Evaporative water loss, oxygen consumption, and body temperatures were examined as responses to increasing ambient temperature.

METHODS AND MATERIALS

Quail used in this study were captured near Las Cruces, Doña Ana County, New Mexico, between 15 November 1966 and 15 February 1967. All birds were fully grown and at least eight months old at the onset of experimentation. Scaled Quail had an average body weight of 165.8 g with a range of 143.2–195.4 g; Gambel Quail had an average body weight of 158.1 g with a range of 140.6–187.0 g. Ten quail of each species were used in determining minimum daily water requirements and five of each species were used for the remainder of the tests except oxygen consumption.

Before testing began the birds were retained in individual cages indoors with an artificial photoperiod of 8 hr to insure gonadal inactivity. During this preliminary period they were maintained on ad libitum amounts of tap water and a commercially prepared dry game bird food.

MINIMUM WATER REQUIREMENTS

All quail were kept in individual cages measuring 30.5 × 30.5 × 30.5 cm and were supplied with ad libitum amounts of the dry food. The cages were kept in a controlled environment chamber at 28–29° C and a relative humidity of 37–44 per cent; ambient temperature and relative humidity were recorded continuously. Birds were weighed daily to the nearest 0.1 g at the end of the dark period.

Water was delivered to the birds by means of L-shaped drinking tubes attached to test tubes. Birds were provided with ad libitum amounts of tap water for seven days prior to testing to allow them to get used to the drinking devices. The minimum amount of water necessary for maintenance of body weight was determined by starting with an amount of water approximating the daily ad libitum water intake and progressively decreasing the amount until the point was reached at which body weight could no longer be maintained. The amount of water given daily to each bird was measured to the nearest 0.1 ml. Testing lasted 18 days.

OXYGEN CONSUMPTION, TEMPERATURE, EVAPORATIVE WATER LOSS

Ambient and cloacal temperatures were monitored and recorded simultaneously with evaporative water

The Condor, 73:430–436, 1971

TABLE 1. Minimum daily water requirements for Gambel and Scaled Quail expressed in per cent of current body weight per day.

Species	n	Min. daily ration (% body wt) $\bar{x}$	SD	range
C. squamata	10	2.90	0.517	2.0–4.0
L. gambelii	10	2.70	0.538	2.0–4.0

loss; oxygen consumption readings were taken separately. An open flow method was used for measurement of both evaporative water loss and oxygen consumption.

Birds to be tested were fasted overnight and placed in the respirometer one hour before testing began. A 5.7-liter respirometer, painted black in order to secure measurements on resting birds, was placed in a constant-temperature cabinet. The birds rested on a wire mesh platform 2 cm above a layer of mineral oil covering the bottom of the respirometer. Incurrent air was passed through a drying tube containing Drierite (anhydrous calcium sulfate) to remove atmospheric moisture before it entered the respirometer. Air leaving the respirometer was directed through two U-shaped tubes containing weighed amounts of Drierite. The amount of water lost was determined gravimetrically to the nearest 0.1 mg at the end of each hour at the specified temperature. The flow rate through the respirometer was 3800 ml/min.

The evaporative water loss of each individual was measured at 25, 30, 35, 40, and 45°C; each temperature was maintained for one hour.

At the end of each hour, the temperature was raised to the next higher level and the bird was allowed one hour to adjust to that temperature before any measurements were taken. Two thermistors for obtaining ambient and cloacal temperatures were fitted into the respirometer.

The same respirometer procedure and flow rate were used while measuring oxygen consumption. Excurrent air was passed through a tube containing Drierite, then to a Beckman E-2 paramagnetic oxygen analyzer. Oxygen consumption readings were taken at 10-min intervals for one hour at the specified temperature. The two lowest readings were averaged and taken as the minimum value for each bird at each temperature. Oxygen consumption was determined for four quail of each species at 30 and 40°C. All data were corrected to standard conditions.

RESULTS

MINIMUM WATER REQUIREMENTS

The data in table 1 appear to indicate that Scaled Quail required a higher percentage of water intake per day than did Gambel Quail. The means, however, were not found to be significantly different ($P > 0.05$, t-test).

When all quail had reached the point at which body weight could no longer be maintained, they were again given water ad libitum to rehydrate them in preparation for future testing. All individuals were weighed after 10 days of rehydration; Gambel Quail had regained 98.3 per cent and Scaled Quail 98.2 per cent of their pretest weights.

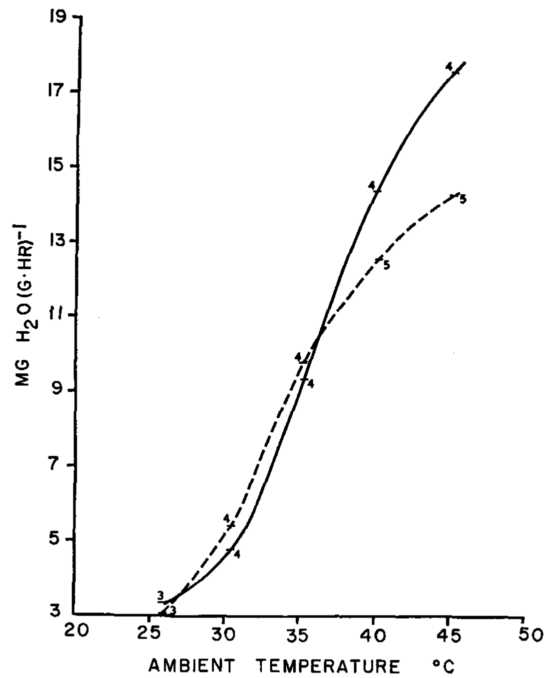

FIGURE 1. Evaporative water loss per gram body weight for Gambel (solid line) and Scaled Quail (dashed line) at various ambient temperatures. Horizontal lines represent means and numerals represent number of birds.

EVAPORATIVE WATER LOSS

Evaporative water loss rates at various ambient temperatures are shown in figure 1. Values for both species were quite similar at 25, 30, and 35°C, but at ambient temperatures above 35°C, values for Gambel Quail were significantly higher ($P < 0.05$, t-test) than those for Scaled Quail. The variability of the water loss values was much greater in Scaled than in Gambel Quail.

The relative humidities of the respirometer chambers were estimated after a method used by Lasiewski et al. (1966a). If complete mixing of the air in the chamber is assumed, the relative humidity can be calculated using the formula: $\%RH = 100 \frac{x/y}{z}$, where x = amount of water lost by the bird in mg/min, y = airflow rate in liter/min, and z = density of saturated steam at that ambient temperature. Lasiewski et al. (1966a) found this estimate to be very close to measured values in the chambers. The small magnitude of these figures (table 2) probably indicates that the

TABLE 2. Per cent relative humidity of respirometer chambers for five Gambel and five Scaled Quail at various ambient temperatures.

T_A (°C)	Scaled $\bar{x}$	Scaled range	Gambel $\bar{x}$	Gambel range
25	9.9	6.8–14.3	9.6	8.7–10.2
30	13.4	10.2–17.0	10.4	8.1–11.7
35	20.3	12.4–29.8	15.1	12.5–17.4
40	18.0	15.1–19.6	17.7	16.2–19.0
45	15.7	13.5–16.9	16.9	15.1–17.5

relative humidities would not greatly lessen the efficiency of evaporative cooling.

TEMPERATURE

The body temperature responses of both species to increasing ambient temperatures were much the same (fig. 2). It appeared that at 25°C, most birds were at or very near the lower limit of the thermoneutral zone as most of the body temperatures were slightly higher than at 30°C. As ambient temperatures exceeded 35°C, all birds became hyperthermic, indicating that the upper limit of thermoneutrality had probably been exceeded.

An average body temperature for Scaled Quail was calculated using all of the values at 25, 30, and 35°C. The temperatures used in this calculation ranged from 40.8 to 42.4°C, with a mean of 41.3°C.

A body temperature of 40–41.5°C has been reported for Gambel Quail by Bartholomew and Dawson (1958). This body temperature was obtained from temperature measurements of the pectoral muscles of one adult Gambel Quail. Data in my study were gathered from four adult Gambel Quail, two males and two females. Temperatures were measured in the cloaca. The wide variability in the body temperatures of these Gambel Quail (fig. 2) cannot be explained; it was not correlated with size, sex, apparent state of health, or the time of day at which the measurements were taken.

Individuals of both species were able to tolerate 40°C without signs of ill effects, with the possible exception of Gambel Quail no. 4. This bird may have been sick as it was unable to stand after two hours at 40°C and was not tested at 45°C. It died approximately 6 hr after exposure to 40°C. This might also explain the unusually low body temperature of Gambel Quail no. 4. Gambel Quail tolerated the 2-hr period at 45°C better than did the Scaled Quail (table 3). All birds that died in the chamber, died near the end of the second hour. Gular fluttering was noted in Gambel Quail when body temperatures exceeded 43°C, but was not observed in Scaled Quail.

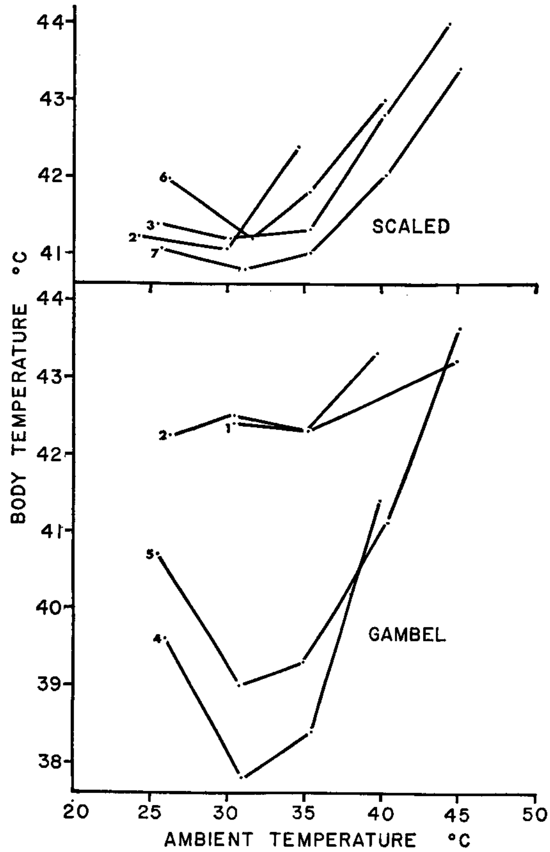

FIGURE 2. Response of body temperatures in Gambel and Scaled Quail to prolonged exposures at various ambient temperatures. Numerals identify individual birds.

OXYGEN CONSUMPTION

Oxygen consumption data, expressed in terms of milliliters of oxygen per gram of body weight per hour, at 30 and 40°C are summarized in figure 3. The mean values plus or minus one standard deviation are: 1.10 ± 0.26

TABLE 3. Fate of Gambel and Scaled Quail when removed from respirometer at 45°C.

Bird	Sex	Wt. (g)	Fate[a]
Gambel 1	♂	144.0	L
Gambel 2	♀	143.8	D
Gambel 5	♂	152.0	L
Scaled 3	♂	159.5	D
Scaled 4	♂	151.2	L
Scaled 5	♂	190.5	D
Scaled 6	♂	176.7	D
Scaled 7	♀	152.8	D

[a] L = live, D = dead when removed from chamber.

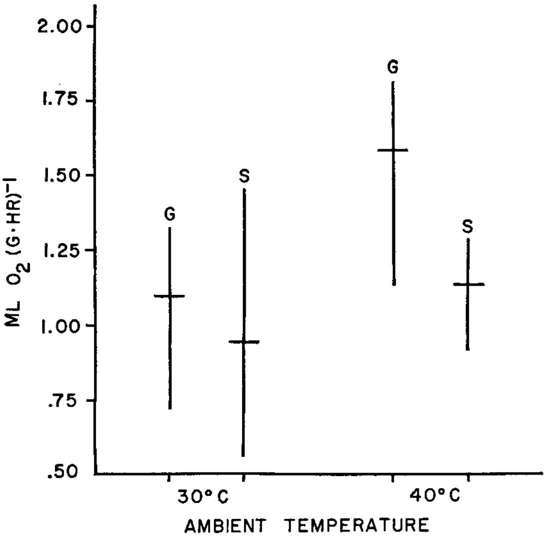

FIGURE 3. Oxygen consumption per gram body weight of Gambel and Scaled Quail at 30 and 40°C. Horizontal lines represent means; vertical lines represent ranges.

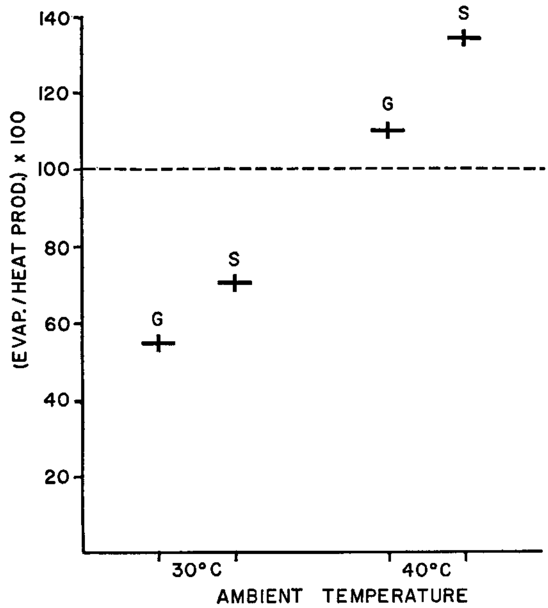

FIGURE 4. Ratio of calories dissipated by evaporation and calories produced ($\times$ 100) at ambient temperatures of 30 and 40°C for Gambel (G) and Scaled (S) Quail. Dashed line represents level at which the two functions are in balance.

at 30°C and 1.58 ± 0.30 at 40°C for Gambel Quail; 0.95 ± 0.38 at 30°C and 1.13 ± 0.16 at 40°C for Scaled Quail. The mean values for oxygen consumption at 30°C did not differ significantly (fig. 3), but at 40°C the Gambel Quail consumed significantly more oxygen ($P < 0.05$, *t*-test). The oxygen consumption values at 30°C probably represent a standard metabolic rate since this temperature appears to fall within the thermoneutral range. The significantly higher consumption for Gambel Quail at 40°C indicates a generally greater metabolic response to elevated temperatures than for Scaled Quail.

Oxygen consumption and evaporative water loss may be used to calculate a measure of relative efficiency of evaporative cooling in metabolic heat dissipation (MacMillen and Trost 1967). To arrive at the relationship expressed in figure 4, it is assumed that 1 cm^3 of oxygen yields 4.8 cal of metabolic heat, and 1 mg of water dissipates 0.58 cal (MacMillen and Trost, op. cit.).

It was not necessary for the birds to dissipate all metabolic heat through evaporative cooling at 30°C since this temperature is below body temperature and heat can be lost passively to the environment. Both species were experiencing hyperthermia at 40°C, and both were able to dissipate heat faster than it was produced (fig. 4, Gambel-109.4 and Scaled-134.5). The higher figure for Scaled Quail at 40°C indicates that they are more efficient in heat dissipation than Gambel Quail, which were able to dissipate all of their heat but at a greater metabolic cost. It is also possible that Scaled Quail simply produce less heat, as indicated by lower oxygen consumption.

DISCUSSION AND CONCLUSIONS

MINIMUM WATER REQUIREMENTS

The minimum daily water requirements of the two species were not significantly different. Although these data appear as minimum water requirements, it is known that Gambel Quail can maintain body weight by the ingestion of succulent plant material when surface water is lacking (Gullion 1960). Bartholomew and MacMillen (1961) found that dehydrated California Quail could regain lost weight and maintain body weight when given shredded cabbage or insect larvae.

I found in a previous study (unpubl. data) that when both species were subjected to complete water deprivation at an ambient temperature of 25 to 29°C, Gambel Quail lost 4.7 per cent (4.3–5.2) of initial body weight per day compared to 5.9 per cent (5.6–6.2) for Scaled Quail. The water deprivation data would indicate that Gambel Quail are better adapted to arid conditions than are Scaled Quail.

McNabb (1969) found during "short-term," minimum water requirement tests that Gambel Quail required 2.1 per cent of body weight per day and the closely related California Quail required 2.0 per cent. The mean relative humidity during McNabb's experiment was 50 per cent, somewhat higher than those encountered during this study. A minimum water requirement of 1.8% of body weight per day was obtained for California Quail by Bartholomew and MacMillen (1961), but these results are not truly comparable to the present ones because the experimental conditions were different. The California Quail were on a 12-hr photoperiod; temperatures varied from 18 to 26°C; and the humidity was not controlled or measured.

In the Las Cruces area, Gambel Quail generally inhabit the valley along the Rio Grande. Their habitat along the river has been described by Raitt and Ohmart (1966). Dense thickets of tall mesquite (*Prosopis juliflora*), screw bean (*Prosopis pubescens*), and tamarisk (*Tamarix pentandra*) afford good cover and roosting sites for the Gambel Quail. An abundance of smaller shrubs and forbs are distributed in the valley.

Scaled Quail are generally found inhabiting the drier "mesa" desert scrub on either side of the valley. The mesa habitat important to desert birds has been described by Raitt and Maze (1968). The principal dominant plant of the entire area is creosotebush (*Larrea divaricata*). Several other species of shrubs and small woody plants are distributed sparsely over the area along with a few species of forbs.

The local distribution of the two species is probably not attributable only to the availability of drinking water. Gambel Quail are known to roost above the ground while Scaled Quail roost on the ground. The vegetation along the river provides a greater amount of cover and more roosting sites than does the desert mesa vegetation. When found on the mesas, Gambel Quail are usually in or along arroyos where the vegetation is more suitable for roosting requirements.

EVAPORATIVE WATER LOSS

The similarites of the water loss rates at 25, 30, and 35°C can be explained by the fact that neither species was experiencing ambient temperatures near or in excess of body temperature. The significantly higher amount of water lost by the Gambel Quail indicates a greater overall cooling capacity as ambient temperatures exceed 35°C.

The higher water loss rates in Gambel Quail may be due to certain specializations for increasing evaporative cooling such as gular fluttering. Gular fluttering has been reported for Gambel Quail by Lasiewski et al. (1966b); gular fluttering was seen in this study when the ambient temperature was 45°C and body temperature exceeded 43°C. Brush (1965) has reported gular fluttering in California Quail beginning as low as 37.5°C, the upper critical temperature in that species. Gular fluttering was not seen in Scaled Quail, but it could have occurred in the darkened chamber during testing. It appears that Scaled Quail, which can dissipate all metabolic heat at an ambient temperature of 40°C, are more efficient in evaporative cooling and water economy without apparent gular fluttering.

It seems rather paradoxical that the desert-inhabiting Gambel Quail lost a greater amount of water per gram body weight than did the Scaled Quail. Probably the total amount of water lost at all five temperatures is not in itself a critical amount. The total amount of water lost during the experimental runs was only about 5 per cent of the initial body weight. Under conditions of complete water deprivation at temperatures between 26 and 32°C, birds of both species lost more than 20 per cent of their initial body weights without signs of ill effects (unpubl. data). Gullion and Gullion (1964) reported similar findings for Gambel Quail undergoing water deprivation; four quail lost 9–18 per cent of body weight and one lost 38 per cent without dying. California Quail, during water denial testing, had lost 48.4–51.9 per cent of body weight at death (Bartholomew and MacMillen 1961).

TEMPERATURES

It is impossible to define the limits of thermoneutrality from the oxygen consumption data obtained during this study, but estimates of them may be made from body temperatures. Considering the temperature and oxygen consumption data at various ambient temperatures, it appears that the thermoneutral zones of the two species are similar, extending approximately from 25 to 35°C. Bartholomew and Dawson (1958) noted a hyperthermic condition in Gambel Quail and California Quail only after ambient temperatures exceeded 40°C. This higher value given by them was for birds subjected to a rapidly warming environment, but quail in this study were subjected to each ambient temperature for a period of 2 hr. It seems possible that the discrepancies between the two sets of data may be explained by a lag in the response of body temperature to a rapidly warming environment or to interpopulational differences.

Brush (1965) reported hyperthermic conditions in California Quail, subjected to the same ambient temperature for 2 hr, when ambient temperature reached 37.5°C.

In Scaled Quail, body temperatures at 25°C were slightly above those at 30°C, indicating that the Scaled Quail were probably just below the lower limit of thermoneutrality, and metabolism was increased to maintain a constant body temperature. It is of some interest to note that the two lowest curves (fig. 2) for Gambel Quail exhibit the widest range of body temperature for either species. With the data available and the observations made, it is impossible to explain the variability observed in Gambel Quail. The data do not indicate any relationship between size or sex and the ability to tolerate an ambient temperature of 45°C.

The death of the four Scaled Quail and one Gambel Quail would suggest that death was a result of heat stress rather than dehydration since only a small percentage of water was lost throughout the entire experiment. Only one Gambel Quail died in the respirometer, pointing to a greater tolerance of elevated temperatures than for Scaled Quail. These data appear to be correlated with the ranges and the usual habitats of the two species since Gambel Quail inhabit the extreme desert areas of the Southwest where temperatures are high and Scaled Quail inhabit semi-arid grasslands of more moderate temperatures. Maximum temperatures in the Las Cruces area do not reach 45°C and rarely exceed 40°C.

OXYGEN CONSUMPTION

At 30°C the oxygen consumption values illustrate the similarity of the apparent standard metabolic rates. From 30 to 40°C Gambel Quail show a significantly greater metabolic response to increasing temperature above the upper limit of thermoneutrality. The Q_{10} for Gambel Quail over this range was 1.44, while that for Scaled Quail was 1.19.

Since the body temperatures were not elevated at 30°C, the birds were unloading all metabolic heat, and the amount of heat not dissipated through evaporation was lost via conduction, convection, and radiation. However, the values at 40°C show that both species were able to dissipate all metabolic heat through evaporative water loss and passive means since the ambient temperature was still below body temperatures. Brush (1965) found that California Quail at temperatures from 37.5 (the upper critical temperature) to 41.5°C were able to dissipate all metabolic heat through evaporative cooling while exhibiting a hyperthermic condition. At 40°C Scaled Quail were more efficient in heat dissipation than Gambel Quail. The fact that Scaled Quail could not survive a prolonged period at 45°C would indicate that metabolic heat production probably rose sharply between 40 and 45°C, exceeding their ability to dissipate it via evaporative cooling. The Scaled Quail probably died because metabolic heat production surpassed evaporative cooling. By the same reasoning, it appears probable that heat production did not exceed evaporative cooling in Gambel Quail since they survived better the 45°C temperature. In summary, Gambel Quail, although not as efficient at lower temperatures, must possess a mechanism which assures their survival at 45°C, while Scaled Quail do not.

ECOLOGICAL IMPLICATIONS

Some ecological inferences have already been made for Gambel and Scaled Quail which can be compared with California Quail. The tolerance of higher ambient temperatures by the Gambel Quail make them better adapted to the extremely high temperatures encountered in some environments of their range. The fact that Gambel and Scaled Quail dissipated all of their metabolic heat while demonstrating hyperthermia at 40°C indicates that they are well suited for the hot, arid, and semi-arid regions which their ranges encompass. California Quail, which are subject to more moderate temperature and moisture conditions along the Pacific Coast, were unable to dissipate metabolic heat by evaporative cooling, even though exhibiting a hyperthermic condition (Brush 1965).

The results of this investigation seem to indicate that in this area of sympatry, where ambient temperatures rarely exceed 40°C, both species are well adapted, and Scaled Quail, because of their lower water loss rate and oxygen consumption, may be even better adapted. The results also seem to indicate that Gambel Quail, even with their greater evaporative water loss and energy expenditure, are, by being more tolerant to higher ambient temperatures, better adapted to those areas of their range where ambient temperatures reach 45°C.

SUMMARY

Various responses to high temperature and low moisture were studied in the laboratory in Gambel Quail (*Lophortyx gambelii*) and Scaled Quail (*Callipepla squamata*).

The minimum daily water requirements of the two species were found not to differ significantly at 28–29°C.

Evaporative water loss rates were similar at 25, 30, and 35°C. At ambient temperatures of 40 and 45°C, Gambel Quail lost significantly higher percentages of water through evaporation than did Scaled Quail.

The response of body temperature to increasing ambient temperatures was, in general, the same for both species, and indicated that the thermoneutral zone was probably between 25 and 35°C. Both species were able to tolerate an ambient temperature of 40°C without ill effects, but at 45°C Gambel Quail survived better than Scaled Quail. Gular fluttering was exhibited by Gambel Quail when body temperature exceeded 43°C, but was not observed in Scaled Quail at any experimental temperature.

Oxygen consumption values were similar at 30°C, but at 40° the values were significantly higher for Gambel Quail. Both species were able to dissipate all metabolic heat while experiencing hyperthermia at 40°C.

These results indicate that Gambel Quail are better adapted, physiologically, to hot, arid environments than are Scaled Quail. This is quite plausible since Gambel Quail inhabit extreme desert areas while Scaled Quail are confined to more mesic areas with more moderate temperatures. Scaled Quail are better adapted with regard to water economy when ambient temperatures do not exceed 40° C. Comparisons were made with the results of other workers on California Quail.

ACKNOWLEDGMENTS

I wish to express my appreciation to Ralph J. Raitt for his advice, assistance, and patience throughout the study, and for critically reviewing the manuscript. I wish to thank Walter G. Whitford for his aid during the study and for reading the manuscript. Richard E. MacMillen critically read the manuscript and offered valuable suggestions.

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Accepted for publication 15 October 1970.