WATER ECONOMY OF GAMBEL QUAIL

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In 1952 the water needs of captive Gambel Quail (*Lophortyx gambelii*) in southern Nevada were investigated experimentally in Boulder City as part of a general study of the management and ecology of this species (cf. Gullion, 1954, 1956, 1958, 1960, 1962). Initially the experiments were designed to explore: (1) the differences in physiological water requirements between "hill" and "valley" quail populations; (2) the derivation of sufficient metabolic water from dry foods to meet water needs; and (3) the effect upon quail of denial of preformed water at varying ambient temperatures.

A primary purpose was to study Gambel Quail under temperature and humidity conditions resembling those prevailing in their normal desert habitats. Boulder City represented a compromise, being hotter but more humid than most desert range or "hill" environments and somewhat cooler and much less humid than most desert valley habitats.

Quail undergoing tests were held in a five-compartment wire poultry laying cage. Each compartment measured 28 × 24 × 18 inches high. This cage was placed 4½ feet off the ground, outdoors, sheltered from westerly winds by a board fence but otherwise exposed to the full effects of the desert climate. A light-weight canvas top on the cage shaded the quail from the sun. A thermometer on the floor of the central of the five compartments provided a record of daily maximum and minimum temperatures.

Three pairs of Gambel Quail taken from a "valley" population near Las Vegas (17 miles northwest of Boulder City and 650 feet lower; cf. Gullion, 1962) on December 12, 1951, and three pairs from a "hill" population, trapped on March 14 and 15, 1952, in the Eldorado Mountains 7 miles northeast of Searchlight (29 miles south of Boulder City and 1200 feet higher in elevation) constituted the original experimental population. Two pairs from each locality were placed in separate compartments in the laying cage and the extra pair from each area was placed in a dirt-floored, 10 × 10 × 6-foot holding pen. The "valley" birds had 61 days to become adjusted to captivity, whereas the "hill" quail were placed in their cages only 27 days before testing commenced.

Another pair of quail (♂780/♀790), wild-trapped in Las Vegas Valley on May 12, 1952, was placed directly in a compartment and began water denial tests one month later.

A pair of "valley" quail (♂684/♀700) was first denied water for 15 days from February 11 to 26 and later for 39 days from April 9 to May 18. During the latter period a pair of "hill" birds (♂852/♀793) went onto an alternating "6–1" program, being denied water for 6 days, then water available for 24 hours, followed by 6 days denial, one day with water, and so forth, until May 31, when water was provided for 24 hours followed by 13 days of denial (fig. 1).

Another "6–1" test series, including both pairs of "hill" quail (♂978/♀800 and 852/793) and two pairs of "valley" quail (684/700 and 780/790) extended from July 6 to September 18, at which time all testing ceased and the surviving birds were moved to the holding pen.

Quail serving as controls had abundant preformed water available at all times, as did all other quail not under denial conditions. Located in the open, the cage was subject to wetting during rainshowers, but rain water did not remain available to quail in the compartments once the showers ceased.

The "A" diet (table 1) was provided all quail until June 22, when the diets of some pairs were changed in preparation for the denial series. These pairs then had 14 to 21 days to adjust to the changed diets before the summer denial series began in the week

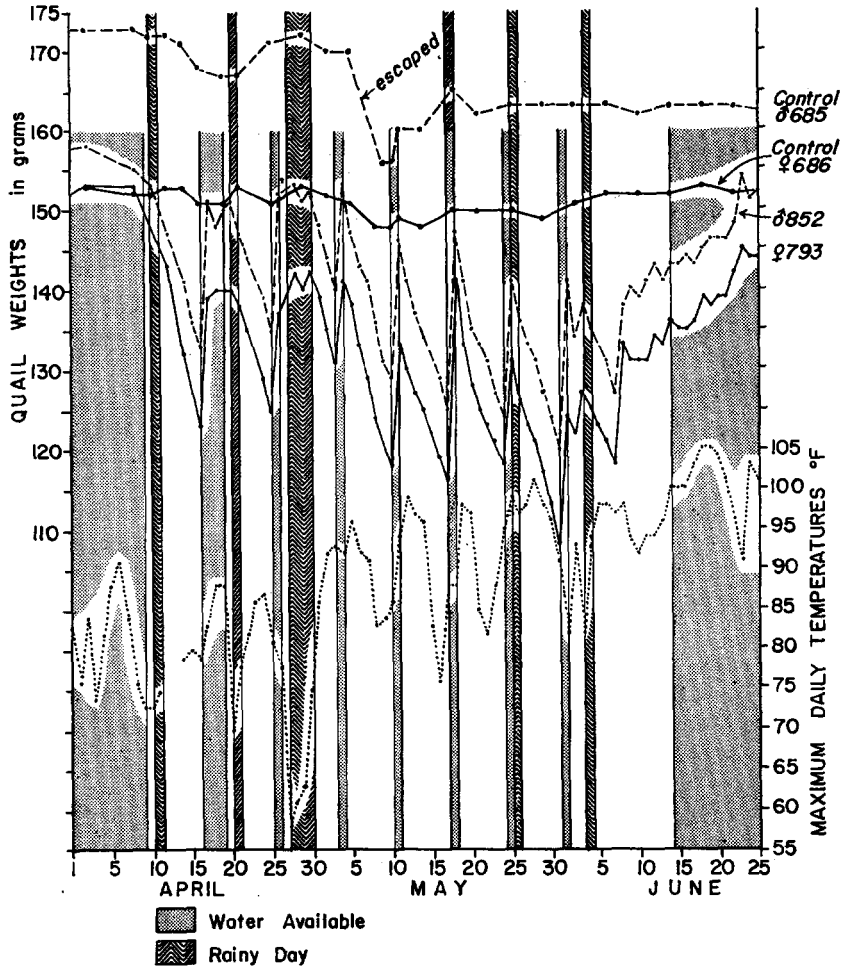

Fig. 1. Weight responses to denial of drinking water in two Gambel Quail (♂852/♀793) from a "hill" population. Birds ♂685 and ♀686 are controls. The dotted line at the bottom indicates maximum daily temperatures experienced by these quail.

of July 6 to 13. Only air-dried seeds were available to these quail. At no time during confinement to the laying cage was green plant material available.

FINDINGS

Condition of control birds.—The quail being held as controls exhibited no abnormal changes during these test series. One pair of "valley" quail was used as a control throughout the experiment, being fed in turn each of the several diets (A, D, F, G, and E–G in sequence) offered quail undergoing tests to determine if diets were affecting weight changes (figs. 1, 2). The hen (♀686) varied only 7 gm. (4.7 per cent) from her lightest to heaviest weight (150 gm. mean weight from April 2 to September 18). Her mate (♂685) escaped twice, each time losing more than 10 gm. (from 182 to 172 gm. and 170 to 156 gm.) before being recaptured less than 24 hours later. However, he exhibited a slow but steady weight gain from his last recapture on May 9, regaining his

TABLE 1

COMPOSITION OF DIETS PROVIDED GAMBEL QUAIL

Item	Percentage composition by volume, Diet* A	C	E	F	G
Triticum aestivum (cracked and whole grain)	45	46	60	44	20
Hordeum vulgare	6	26	....	2	T**
Avena sativa	39	14	5	T	....
Sorghum vulgare	....	5	....	....	....
Zea mays (cracked)	....	6	....	....	....
Echinochloa crusgalli	7	1	26	21	11
Helianthus annuus	3	1	6	....	....
Iva axillaris (flowerheads)	....	....	2	....	....
Rumex acetosella	....	....	1	T	T
Polygonum sp.	....	....	T	....	....
Melilotus officinalis	....	1	T	....	60
Medicago sativa (seeds and pods)	....	....	T	32	9

* Diet "B," 100 per cent cracked corn; diet "D," commercial chick scratch feed, consisting of cracked corn and wheat.

** T = trace.

normal weight of 171 gm. by July 6 and varying within a range of 7 gm. (4.1 per cent) after that date.

The female (♀800) of the "hill" quail kept as a control remained within 5 gm. of her mean captive weight of 152 gm. during her first month in captivity. About April 20 she commenced a weight gain, increasing to 177 gm. during the next 20 days. On May 8 she commenced laying eggs, and laid no less than 23 eggs in the next 60 days. By July 13 her weight had declined to her prelaying mean level of about 152 gm. During this same period her mate (♂978) showed a decline, dropping from about 170 to about 160 gm. during the 20 days his mate was gaining her weight. His weight then remained relatively constant at about 160 gm. for the next 90 days (see Gullion and Gullion, 1961). This pair began denial tests on July 13.

Response to water denial.—Evaluation of the effects of water denial upon individual quail is based upon daily weight changes expressed as percentages of the mean captive pre-test weight of each bird. The differences in mean weight losses between paired males and females from the same populations and undergoing identical tests proved to be statistically insignificant, so data for pairs were treated as identical samples.

During periods of water denial while maximum daily temperatures remained below 102°F. (38.9°C.) there was a highly significant difference ($t=4.840$, $N=166$) between the daily mean weight loss of the "valley" quail pair 684/700 and pair 852/793 from a "hill" population, losing 2.5 and 3.6 gm. per day, respectively, while on grain diet "A."

However, when daily maximum temperatures exceeded 102°F. the differences in weight losses became insignificant when the mean daily loss of 7.0 gm./day for two pairs of "valley" quail is compared to the daily mean loss of 7.8 gm./day for two pairs of "hill" quail.

Rates of weight loss increased abruptly when periods of water denial coincided with daily temperatures exceeding 102° F. The mean daily weight losses (3.3 gm./day) for both pairs of "valley" and "hill" quail while undergoing denial at temperatures of 102°F. or lower are significantly less ($t=9.926$, $N=223$) than the weight losses (7.4 gm. /day) suffered by these quail when daily temperatures exceeded 102°F.

Pair 852/793 provided an exception to the pattern of weight loss in mid-June (fig. 1), when during the last 7 days of a 13-day denial period these two quail abruptly gained weight and maintained a mean daily gain of 1.5 and 1.7 per cent, respectively, to the end of the test period. Mean maximum temperature for this period was 95.0°F. or 35.0°C.

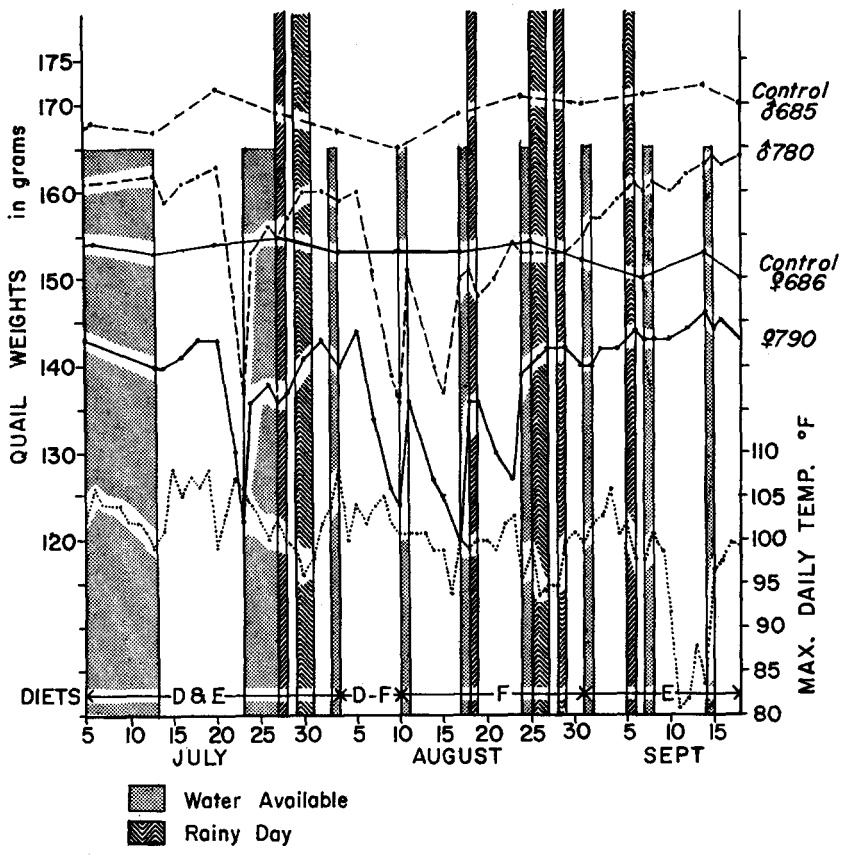

Fig. 2. Weight responses to water denial in two Gambel Quail (♂780/♀790) from a "valley" population. Birds ♂685 and ♀686 are controls. Maximum daily temperatures are indicated by the dotted line at the bottom.

Another exception to the general pattern during the July to September test series was pair 780/790 (fig. 2). These two birds from Las Vegas Valley showed generally persistent weight gains during denial periods as long as maximum temperatures remained below the 102°F. (38.9°C.) level. During the "6–1" series commencing August 18 and lasting for a month, including 27 days of denial, ♂780 gained 13 gm. by the end of the series, weighing 3 gm. more than his mean pre-test weight, and only 2 gm. under his wild weight at trapping. His mate, ♀790, was a little more erratic in her gains but ended the series 7 gm. heavier, with a fairly consistent gain for the last 26 days of the test. Her final weight was 6 gm. below her pre-test mean and 29 gm. lower than her wild weight.

However, when temperatures exceeded 102°F., these two birds lost weight also. In one 10-day period of high temperatures 780/790 held or gained weight for the first 7 days but then lost weight quickly the last 3 days, ♂780 losing 26 gm. or 16 per cent of his weight, and ♀790 losing 23 gm. or 16 per cent of her weight in this period. In a second 7-day denial period, 780/790 gained weight for 2 days in spite of temperatures over 102°F. but then declined during the last 5 days just as before.

Significant additional information was obtained by watching the quail kept in the larger holding pen as replacements for birds which might escape from the experimental cage. The number of birds in this pen varied between 4 and 7 from March 12 to September 18. From March until early July, 1952, green, growing plants were generally available as a source of succulence, but these quail were not provided with drinking water. After early July they had neither green plants nor preformed drinking water available. These quail survived the summer without evident loss of vigor; twenty-five days of rainfall or high humidity occurred in this interval. On September 18 the experimental phase ended and the 10 quail in the laying cage were moved to the holding pen to be held for release in March, 1953. Thereafter a total of 17 quail were in this pen without water or green feed until November 11. On this date a female showing a considerable weight loss died in the pen. Immediately five other birds were weighed and an average weight loss of about 14 gm. among four birds over a 54-day period was shown, dropping to 82 to 91 per cent of their mean pre-test weights. The fifth quail, however, had lost 65 gm. during this period, dropping to 62 per cent of its mean pre-test weight, and was approaching a critical emaciated condition.

Water was placed in the pen and maintained thereafter and 70 days later these same five quail had regained their lost weight, to levels at or above those held at the time of being placed in the holding pen. No further difficulty was experienced in holding these birds, and prior to their release on March 20, 1953, the five had regained or exceeded the weights recorded at the time of original capture.

Response to water restoration.—Within 24 hours after the restoration of preformed water each quail made a gain of from 11 to 22 gm., or about 10 to 14 per cent of pre-test weight. If water remained available beyond 24 hours the quail maintained a steady but much slower weight gain. Two "hill" birds (852/973), after an initial 24-hour gain of 11 and 15 gm., regained their pre-test weights (157 and 152 gm.) in 30 days, a mean gain of 0.6 gm. per day. Two "valley" birds (684/700), after initial 24-hour gains of 18 and 21 gm., also increased at an average of 0.6 gm. per day to regain their pre-test weights (163 and 153 gm.) over a period of 45 days.

In both of these instances the hens eventually increased to higher weights than their mates, suggesting that both hens were following the pattern of the control hen (♀800) and progressing into egg laying (cf. Gullion and Gullion, 1961).

In spite of the continued 6 days denial alternating with 24 hours of water, the peak weights for five quail (♂♂978, 852 and 684; ♀♀800 and 700) increased steadily from mid-August on, indicating a progressively improving physical condition of these birds. During this period mean maximum daily temperatures remained in the 98° to 100°F. (36.7°–37.8°C.) range. Gains in peak weights (the weights attained after being on water for 24 hours) during this period of from 20 to 35 days averaged from 2.4 to 5.8 gm. between subsequent peak periods.

Rainstorms or very humid days occurred several times during periods of water denial. These, of course, represented conditions encountered naturally. In 21 of 36 instances of rain or high humidity during denial periods, the quail showed an immediate weight gain or stabilization. Generally weight gains did not equal those resulting when

preformed water was placed in the cages, but they did show definite reversals of the denial decline.

Food relationships.—There was some evidence that "valley" quail living on low-protein diets (with few or no legume seeds, A, C, D, and E, see table 1) suffered less weight loss under denial conditions than when subsisting on diets rich in protein (F and G). Under similar temperature conditions the daily mean weight loss of 1.4 gm. per day exhibited by the two pairs of "valley" quail is significantly different ($t=3.665, N=165$) from the mean loss of 2.1 gm. per day while dependent upon a diet rich in legumes. The two pairs of "hill" quail showed no significant differences in weight losses while feeding on the different diets during periods of water denial.

DISCUSSION

Several general relationships are suggested by these data. First, most Gambel Quail cannot maintain their body weight on a dry seed diet unless they have additional sources of moisture available. Under moderate environmental temperatures (60° to 102°F.) body weight loss averages about 1.6 per cent per day for males and 2.1 per cent per day for females. This is somewhat less than the daily respiratory water losses Bartholomew and Dawson (1953:164) have recorded for the similar California Quail (*Lophortyx californicus*) in a stable environment at 77°F. (25°C.) and at a relative humidity of 60 per cent. For California Quail the weight loss ranged from 3.1 to 4.1 per cent, for a mean of 3.5 per cent per day. The denial loss rate recorded for Gambel Quail agrees generally with a figure of 1.6 ± 0.4 per cent weight loss per day calculated by Bartholomew and MacMillen (1961:506) for a group of California Quail on a prolonged water denial test.

When environmental temperatures approached normal body temperatures of Gambel Quail the mean rate of weight loss during periods of water denial increased 2- to 3-fold. Bartholomew and Dawson (1958) show a diurnal range in body temperature of from 104° to 106.7° F. (40°–41.5°C.) for this species. Ambient temperatures over 102°F. are above the range of thermal neutrality for these quail, and Bartholomew and Dawson (*ibid.*, fig. 4) show that a hyperthermic condition commenced as ambient temperatures exceeded 102.2°F. in their experimental work. Sturkie (1954:130) points out that hyperthermia produces a tripling of the rate of respiratory water loss in domestic chickens, and the greatly increased weight loss among our experimental quail probably represents a similar response to hyperthermia.

Although Bartholomew and Dawson (1958) did not observe panting when environmental temperatures were raised to 111°F. (44°C.) and the body temperature of the quail reached 110.3°F. (43.5°C.), we have observed panting in free-living Gambel Quail on the desert in southern Nevada at ambient temperatures of about 104° to 106°F. These quail decrease activity and persistently seek shade on the desert when ambient temperatures rise much above 106°F.

When environmental temperatures exceed the upper limits of their thermal neutrality, Gambel Quail in both "valley" and "hill" populations become very dependent upon external sources of moisture to maintain body weight. In desert valley habitats this need can be met by feeding on leaves of many succulent plants, and also the humidity in mesquite bosques and in agricultural areas is much higher than on the desert ranges, thus reducing the moisture deficit. On the upland desert areas preformed water becomes a prime necessity of life during these periods when maximum daily temperatures persistently exceed 102°F. Even though this period lasts for only a few weeks in late June and through July, lack of readily available water becomes a limiting factor in the existence of quail on these areas.

Quail provided water showed no definite response to ambient air temperatures between 102° and 108°F. (the latter being the highest recorded). From July 6 to 27, 1952, maximum daily temperatures in the cage reached or exceeded 102°F. on 17 of 22 days, with temperatures in excess of 105°F. on 7 occasions. Yet, in spite of environmental conditions which must have caused hyperthermia among these birds, those recovering from denial losses continued constant weight increases and the control birds maintained stable weight levels.

In addition to differing rates of weight loss during water denial under different ambient temperatures, there was some difference of loss rates according to the diet available to the quail. Some birds living on a diet consisting largely of grass seeds had a somewhat lower rate of weight loss than when fed a diet containing a high percentage of legume seeds (contradicting an earlier belief, cf. Gullion, 1960:528). Leopold, *et al.* (1961:96–98) point to the increased problems of water conservation faced by desert mammals living on high protein diets. The importance of this to birds excreting uric acid is not known, according to Schmidt-Nielsen (*in litt.*). King and McClure (1944: 40–41) show legume seeds generally to be 3 to 4 times as rich in protein as the seeds of many common grasses.

The water economy of the Gambel Quail is well enough adjusted to the desert enviment that the difference between water loss through respiration and excretion and that gained from metabolism of dry seeds is normally slight. When environmental temperatures remain below the upper limits of thermal neutrality, supplemental water needs can be readily met by the intake of comparatively little succulent food material. Even high environmental humidity tips the balance strongly in favor of these birds.

During heavy rainstorms little, if any, water became directly available to the birds in cages undergoing water denial, yet in nearly two-thirds of the instances when this occurred weight declines were reversed. The high humidity undoubtedly affected the moisture content of the dry seeds being consumed by these quail. In addition, with a high level of atmospheric moisture normal respiratory water losses must have declined proportionately, and it seems possible that these birds were able to obtain at least part of their needed moisture through respiration. In four instances weight increases during denial periods actually occurred during the 24 hours preceding a rainstorm. Also, the weight response to a rainstorm providing only a trace of precipitation was often as great as the response to a storm depositing more than one-half inch of rain.

Perhaps the high noctural humidity which normally occurs on the desert (Schwab, unpublished data) provided additional moisture almost nightly, partly accounting for daily weight losses somewhat less than those to be expected from respiratory water losses alone in a stable environment. Undoubtedly, also, humidity in the environment of Boulder City, with its lawns and shade trees, was somewhat higher than on the surrounding desert, but certainly it was not as high as in the mesquite bosques of Las Vegas Valley.

Apparently a lack of sufficient moisture interferes with the food intake of these quail, and the effect of water denial is at least partly one of starvation. This is indicated by the constant rate of weight decline, which was as great during the first 24 hours of water denial as during the last 24 hours. Persistent denial of water resulted in birds reaching a "nadir of wretchedness" (Leopold, 1933:263) from starvation.

When water was restored food intake increased greatly, with weight increases varying from 10 to 15 per cent during the 24 hours following restoration of water, and with continued availability of water, pre-test weights were regained without any apparent

physiological damage. Two hens, after undergoing extended periods of water denial in April and May showed a pattern of weight recovery during June and early July which strongly suggested the approach of egg formation.

The record of the quail in the large pen, although not so well documented as for the birds in the laying cages, provides an additional basis for understanding the water economy of these birds on the desert. Apparently, these quail were able to find enough other sources of moisture to carry them through the summer, even though their diet was one of dry seeds and no succulence was available. We suspect insects associated with human habitation in a hot climate provided most of this moisture.

Whatever the source of this moisture, the quantity sufficient for 4 to 7 quail on 100 square feet of ground was not sufficient for 18 quail, and the "carrying capacity" of the pen was exceeded, with subsequent loss of one bird and moderate to severe weight losses in others over a 54-day period before an adequate water supply was provided.

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SUMMARY

Weight variations of four pairs of Gambel Quail undergoing varying periods of water denial were studied and related to environmental temperatures and humidity, diet, and origin of the quail. Significant differences were detected under some conditions between weight losses experienced by quail from valley habitats as compared to quail from upland desert situations.

Quail from valley situations were less able to maintain body weight on a diet high in legumes than on a diet of grass and weed seeds. This may be related to the increased water losses required to handle metabolic wastes produced by a diet high in protein. Quail from hill situations lost weight at the same rate while living on either a grain or legume diet.

Environmental temperatures approaching the body temperature of these quail resulted in weight losses double or triple those experienced at temperatures below 102°F.; apparently this increase resulted from increased respiratory water loss to counteract hyperthermia.

Weight recovery was rapid when water became available, and high atmospheric humidity or rain showers reversed the weight decline under denial conditions.

When living in situations where succulent vegetation, or perhaps insects, are readily available, these quail can maintain normal weight and thrive without drinking water. Where this succulence is lacking and they must persist on dry seeds alone, especially legume seeds, drinking water is a necessity. This is particularly true for the short period in the summer when environmental temperatures approach or exceed the body temperatures of these quail.

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