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SEASONAL WATER TURNOVER RATES AND BODY WATER VOLUMES IN DESERT CHUKARS

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ABSTRACT.—Tritiated water was used to estimate water turnover rates and total body water volumes (TBW) in free-living Chukars (*Alectoris chukar*) in the Negev Desert of Israel during late autumn and winter. Water turnover rates varied widely, ranging from 66.8 to 420.1 $ml \cdot kg^{-1} \cdot day^{-1}$ ($n = 25$). They were lowest before winter rains, averaging 15.0% (SD = 1.0; $n = 17$) of TBW in the dry autumn and early winter, and 45.3% (SD = 10.9; $n = 8$) in late winter. This seasonal increase in water turnover rate may reflect a dietary shift from dry foods to succulent green vegetation, the growth of which was induced by winter rains. Water turnover was much more variable among wild Chukars than in captive birds from the same population kept in a controlled environment. TBW averaged 68.5% (SD = 4.1; $n = 58$) of body mass in free-living birds and was significantly elevated during cold, wet weather.

Birds and other homeotherms inhabiting deserts face behavioral and physiological challenges in maintaining favorable water balances under severe and widely fluctuating environmental regimes (Bartholomew and Cade 1963, Bartholomew 1972). Two physiological variables that are sensitive to environmental fluctuations and that are, therefore, useful for examining animal adaptations to extreme environments are the rate of water turnover and total body water volume (TBW). These variables have received increasing attention because of their biological importance and because they can be readily estimated using tritiated water (TOH; Nagy and Costa 1980). Indeed, TOH measurements made under similar ambient conditions demonstrate that xeric mammals generally have lower water turnover rates than species in mesic and humid regions (Macfarlane and Howard 1972, Nicol 1978). Fewer data are available for birds, but a recent comparison suggests that a similar relationship exists in 14 avian species (Degen et al. 1982).

Water turnover rate is sensitive to short-term fluctuations in ambient meteorological conditions, amounts and kinds of food, and available drinking water (Degen 1977, Grubbs 1980, Withers et al. 1980). TBW responds to environmental stresses also, and is considered a useful indicator of body condition. Specifically, elevated TBWs may reflect a loss of body solids (principally fat) and thus indicate poor body condition (e.g., Campbell and Leatherland 1980).

To date, the TOH method has rarely been used in studies of free-living birds. In the present study we employed TOH to measure the rate of water turnover and TOH space (as an estimate of TBW) of wild Chukars (*Alectoris chukar*) in the Negev highlands of southern Israel. Measurements were made before, during, and after winter rains. Our aim was to determine if seasonal fluctuations in the birds' water content corresponded with major changes in climate and phenological patterns.

STUDY SPECIES

The Chukar has an extensive natural distribution in the southern and central Palearctic region and has been successfully introduced in North America and elsewhere (Bohl 1971). Although it is considered typical of semiarid regions (Cramp and Simmons 1980), it occupies relatively mesic and arid areas as well. In Israel, for example, Chukars occur in Mediterranean, steppe, and desert biomes, and utilize a wide variety of natural and agricultural habitats (Dor 1975). Two subspecies are endemic to the country: *A. c. cypriotes* in northern, Mediterranean zones; and the smaller, paler *A. c. sinaica* of more arid regions, including the Negev desert (Nissani 1974).

Given its wide range and broad habitat affinities, the Chukar may serve as an instructive example of behavioral and physiological adaptations of populations of an ecological generalist to desert environments. Some aspects of its thermoregulatory physiology have been investigated (Bernstein 1976, Krausz et al. 1977, Laudenslager and Hammel 1978a, b); and we have reported the water turnover rates and TBW of birds (from the same population as the present study) in controlled environments (Degen et al. 1982). Other studies of the water relationships of Chukars exist, but they concern the response of birds on game farms to water deprivation (Greenhalgh 1955, as reported by Bohl 1957), and the dependence of wild birds on drinking water, (e.g., Bump 1953, Galbreath and Moreland 1953, Christensen 1970). To our knowledge, no one has done quantitative studies of water relationships in wild Chukars.

STUDY AREA

The study was conducted during the autumn and winter of 1980–1981 in the central Negev highlands near Sede Boqer (30°52′N, 34°47′E). Bioclimatically, this region is an "accentuated subdesert," having 250–300 "biologically dry days" per year (UNESCO 1963). Rain occurs during the winter and, at Sede Boqer, averages 90 mm per year, with large annual differences in total precipitation and in its temporal and spatial distribution (Evenari 1981). Relative humidity (RH) averages 58%, and dew occurs on about 190 nights annually (Zangvil and Druian 1980). Ambient temperatures (T_a) are highest during summer, with a daily mean of 25.3°C in August, and are lowest in winter, with a daily mean of 9.7°C in January (Desert Meteorology Unit, J. Blaustein Institute for Desert Research).

The major surge of plant growth occurs in winter and early spring, i.e., about mid-January to mid-April, and most herbaceous vegetation is dormant by late May. The onset of germination and the growth of annual and perennial plants is linked to the timing of winter rain, and the extent of plant production is largely determined by the amount and distribution of precipitation. Large annual variations in primary productivity, especially of annual plants, are characteristic of the region (Evenari 1981).

We captured Chukars at two places: on Sede Zin, a loess-covered plain; and in Wadi Zin, an adjacent large canyon. Sede Zin supports a sparse natural vegetation dominated by shrubs and semi-shrubs (e.g., *Hammada scoparia, Zygophyllum dumosum, Atriplex halimus,* and *Artemesia herba-alba*), although many kinds of herbs and geophytes are also present. The plateau also features cultivated fields of a neighboring agricultural settlement, and an open garbage dump at which Chukars feed and where one of our trapping stations was established. Wadi Zin has lush vegetation near the main river bed and its tributaries, and sparse vegetation on the surrounding flood plain and adjacent slopes. Open water was present throughout the year at several locations in Wadi Zin, especially after winter rains. No open water was present on Sede Zin, but birds we captured there travelled daily to Wadi Zin where they presumably drank.

METHODS

CAPTURE AND HANDLING OF BIRDS

We captured Chukars between 6 November 1980 and 4 February 1981, using baited traps and a recoilless rocket net (Winco Model S-200). Birds were taken to our laboratory (within 15-min driving time of capture sites), weighed to the nearest 0.1 g, and examined for sex and age (based on criteria modified after Campbell and Tomlinson 1962, Weaver and Haskell 1968, Alkon 1974). Standard morphometric measurements were also made. Birds were marked with individually identifiable backtabs (Alkon 1974), and with aluminum and colored plastic leg bands. They were examined and marked during the interval allowed for TOH equilibration (see below), and released again at capture sites within 4 h.

MEASUREMENT OF WATER TURNOVER RATE AND TOH SPACE

Our protocol followed the general procedures of Nagy and Costa (1980) incorporating the assumptions for birds described by Degen et al. (1981). Procedural details and formulae used to calculate water turnover rate and TOH space are given in Degen et al. (1981).

After the initial weighing, we collected a blood sample from the basilic vein of each bird in order to measure background TOH activity. We then injected the bird intramuscularly with 0.1 m Ci/kg body mass of TOH (Radiochemical Center, Amersham, England) in 1.0 ml sterile avian saline solution (0.75% NaCl). After allowing 1–2 h for the TOH to equilibrate with body fluids, we removed a second blood sample in order to measure TOH space (i.e., estimated TBW), and reweighed the bird. For subsequent calculations, we used the mean of the two measurements of body mass. Blood samples were centrifuged immediately, and the specific activity of tritium in duplicate sera samples was measured in a liquid scintillation counter (Packard Tri-Carb Model PLD).

Determinations of water turnover rate were based on the decline of specific activity of tritium in blood samples taken from TOH-injected birds following their recapture in the field at a later time. We did not calculate water turnover rates for samples in which the specific activity of tritium was less than 4× background levels. Birds recaptured after intervals of more than six days in the field were reinjected with TOH. We assumed that birds captured after shorter intervals had the same per-

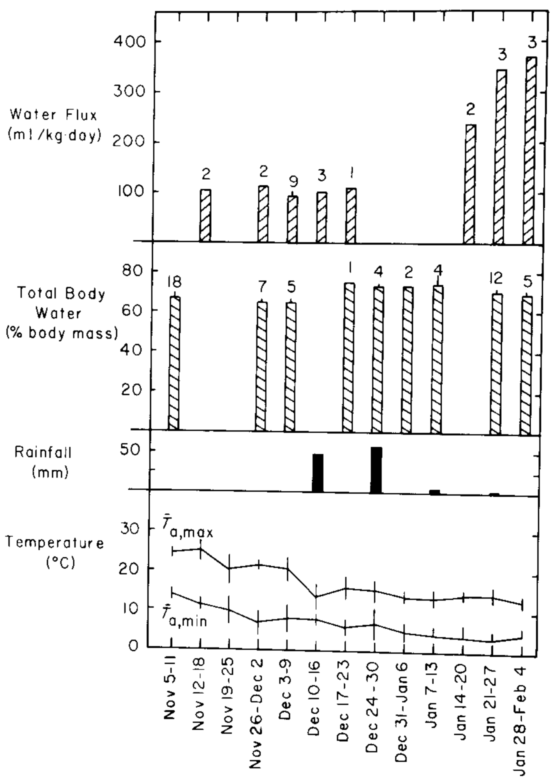

FIGURE 1. Weekly changes in water turnover rates and total body water (TBW) of Chukars and in meteorological conditions at Sede Boqer during the autumn and winter of 1980–1981. For water turnover rates and TBW: bars represent mean values; vertical lines are ±SD; numbers above bars are sample sizes. For temperature: vertical lines are ±SD; $\bar{T}_{a,max}$ = maximum ambient temperature; $\bar{T}_{a,min}$ = minimum ambient temperature.

cent TOH space that was initially measured, and that changes in their TOH spaces were linear with time. Because uniform times and methods of capture were maintained during the study, we assumed that changes in TBW reflected changes in body solids. We recognize, however, that changes in TBW may be partially due to variations in the water content of foods contained in the birds' guts.

We employed analysis of variance with Scheffe's system of multiple comparisons to evaluate the data (Snedecor and Cochran 1973), and chose $P < 0.05$ as the minimal level of significance. Data are expressed as means ± 1 SD.

RESULTS

WEATHER AND PHENOLOGY

During the autumn and winter of 1980–1981, maximum daily temperatures (T_{max}) ranged from 31.7°C to 10.5°C, and minimum daily temperatures (T_{min}) ranged from 18.5°C to 0.5°C (Fig. 1). T_a declined noticeably in late November and in early January, and T_{min} averaged less than 5°C during January and early February. Daily temperature ranges (T_{max} minus T_{min}) were at least 8.5°C in all but one week of the study. Major rainfalls occurred on Dec. 10–11 (47 mm) and on Dec. 25–26 (53.7 mm). Moderate amounts of rain fell on Dec. 29–30 (3.7 mm) and on Jan. 11–12 (3.5 mm). Total rainfall during the study was 110.7 mm. We observed a noticeable development of green vegetation beginning in mid-January.

WATER TURNOVER RATES AND TBW

We measured 25 water turnover rates in 15 individual birds (Table 1). The sample comprised six measurements on males and 19 on females; 24 were on birds of the year (hatched in the 1980 breeding season) and one on an adult (hatched in 1979 or earlier). We also made 58 estimates of TBW using 51 individuals (Table 1) of which 22 were from males and 36 from females; 51 from birds of the year and 7 from adults. All birds had adult plumage and were considered fully grown at the time of study.

A wide range of water turnover rates and TBWs was found (Table 1). The difference between minimum and maximum water turnover rates was more than six-fold. Absolute water turnover rates ranged from 27.5 to 186.3 ml/day, and averaged 73.7 (±52.4) ml/day. Daily water turnover adjusted for body mass ranged from 66.8 to 420.1 ml/kg with a mean of 172.9 (±115.3) ml/kg. TBW estimates ranged from 230.4 to 385.0 ml, and from 61.7 to 81.1% of total body mass (Table 1). Mean values were 302.4 (±35.1) ml and 68.6 (±4.1) % of body mass.

There were no significant differences in water turnover rates or TBW as a fraction of body mass by age class or sex at points in the study where numbers were large enough for statistical analysis; accordingly, we pooled data to examine seasonal changes in them. On a weekly basis, water turnover rates were relatively low and stable from November through late December, increased sharply by mid-January, and continued to rise thereafter until the conclusion of study in the first week of February (Fig. 1). In contrast, TBW as a fraction of body mass remained low from early November through the first week of December, was high from mid-December to mid-January, and low again in late January.

Seasonal differences were examined further by dividing the study period into three meteorological/phenological phases, as follows:

Pre-rain period (Nov. 5 to Dec. 9). Before winter rains; high maximum temperatures and

TABLE 1. Body mass, water turnover rates, and total body water volumes of Chukars during autumn and winter of 1980–1981. Values in the table are $\bar{x} \pm$ SD (n).

Sex	Body mass (g)	Water turnover rate (ml/kg·day)	Total body water (% body mass)
Males	490.0 ± 41.5 (22)[a]	144.1 ± 92.6 (6)[c]	67.8 ± 3.3 (22)[a]
Females	412.7 ± 29.2 (36)[b]	182.0 ± 117.1 (19)[d]	69.0 ± 4.4 (36)[b]
Both (combined)	442.0 ± 50.9 (58)	172.9 ± 112.9 (25)	68.6 ± 4.1 (58)

[a] Two adults and 20 juveniles. See text for definition of age classes.
[b] Four adults and 32 juveniles.
[c] One adult and five juveniles.
[d] Nineteen juveniles.

high-to-moderate minimum ground temperatures; vegetation dormant.

Rainy period (Dec. 10 to Jan. 13). Substantial winter rain; low maximum daily temperatures and moderate-to-low ground temperature; vegetation largely dormant.

Post-rain period (Jan. 14 to Feb. 4). Little rain; continued low temperatures; much growth of green vegetation.

We anticipated that dividing the study period in this manner would reveal the effects of weather on the water regime of the birds. (The names assigned to the periods are for convenience and are not intended to imply that rainfall was the sole basis for this division.)

Water turnover rates did not differ between the Pre-rain and Rainy periods, but increased significantly in the Post-rain period (Table 2). We also examined results from seven birds on which water turnover rate was measured more than once (in no case did measurements for an individual encompass either the Pre-rain or Rainy period, on the one hand, and the Post-rain period, on the other). Two birds were measured in the Pre-rain and Rainy periods; their mean water turnover rates were 108.0 vs. 102.1 and 78.5 vs. 100.3 ml/kg·day for the two periods, respectively. In one bird, water turnover rate increased from 99.6 to 109.3 ml/kg·day at two points during the Rainy period; and in another, the water turnover rate was 204.6, 385.8, and 420.1 ml/kg·day at successive points during the Post-rain period. Water turnover rates for three birds measured twice during the Pre-rain period were 105.3 and 102.6 ml/kg·day; 99.4 and 85.7 ml/kg·day; and 110.7 and 86.5 ml/kg·day.

TBW, as a fraction of body mass, was significantly higher in the Rainy period than in the Pre-rain period (Table 2). The mean value declined during the Post-rain period, but did not differ significantly from either the Pre-rain or Rainy periods. Similar trends were present in four Chukars for which TBW was measured in more than one period. In three of them, Pre-rain and Rainy period measurements (as percent of body mass) were respectively: 64.5 vs. 69.8%; 69.5 and 66.0 vs. 74.9%; and 64.1 vs. 74.9%. In the fourth bird, TBW declined from 76.9% in the Rainy period to 72.8 and 69.2% at two points in the Post-rain period.

We estimated total body solids by subtracting TOH space (i.e., TBW) from total body mass. Because males were significantly heavier than females, seasonal changes in estimated body solids were examined separately for each sex. There were no significant differences in total body mass or in estimated body solids between periods (Table 3). However, the data for both sexes suggest ($P < 0.1$) a decrease in total body mass and body solids during the Rainy period, and an increase during the Post-rain period.

DISCUSSION

COMPARISONS WITH CAPTIVE CHUKARS AND OTHER SPECIES

Seasonal fluctuations in the rate of water turnover and in TBW of wild birds were greater than those observed previously in captive Chukars from the same population and kept under uniform environmental conditions (i.e., at T = 27 ± 1°C; RH = 42 ± 2%; and a daily photoperiod of 12 h). Water turnover rates in the controlled environment were 70.7 ml/kg·day (±15.3; n = 5) for birds offered a dry ration and tap water ad libitum; and 90.5 ml/kg·day (±25.0; n = 5) for birds whose diet was supplemented with succulent vegetation (Degen et al. 1982). The daily water turnovers amounted to 10.3% (±2.5) and 12.0% (±3.5) of the TBW of birds on the two diets, respectively. In contrast, the mean water turn-

TABLE 2. Seasonal changes in water turnover rates and total body water volumes of Chukars during autumn and winter of 1980–1981. Values in the table are $\bar{x} \pm$ SD (n).

Period	Water turnover rate (ml/kg·day)	Total body water (% body mass)
Pre-rain	98.7 ± 14.4 (13) a	65.9 ± 2.8 (30) a
Rainy	102.8 ± 4.4 (4) a	73.6 ± 3.8 (11) b
Post-rain	328.5 ± 67.1 (8) b	70.0 ± 1.9 (17) ab

Values followed by the same letter in each column are *not* significantly different ($P > 0.05$); others differ significantly ($P < 0.05$; analysis of variance and Scheffe's system for multiple comparisons).

TABLE 3. Seasonal changes in the mass and estimated total body solids of Chukars during autumn and winter of 1980–1981. Values in the table are $\bar{x} \pm$ SD.

Period	Males			Females		
	n	Total body mass (g)	Body solids (g)	n	Total body mass (g)	Body solids (g)
Pre-rain	14	486.7 ± 37.6	165.2 ± 22.7	16	411.0 ± 32.6	142.8 ± 18.1
Rainy	3	466.8 ± 50.2	135.7 ± 27.1	8	405.7 ± 32.3	103.5 ± 18.2
Post-rain	5	513.1 ± 50.3	151.2 ± 21.3	12	419.7 ± 24.0	127.3 ± 13.2

There are no significant seasonal differences in the body mass or estimated body solids of males or females ($P > 0.05$, analysis of variance and Scheffe's system for multiple comparisons).

over of free-living Chukars was 172.9 ml/kg·day (±115.3; $r = 25$), or 28.0% (±16.8) of the TBW. Chukars in the wild also showed greater ranges in TBW (62.1 to 81.1%) than captive birds (66.0 to 79.7%).

We conclude that water turnover rates measured in uniform environments are useful for interspecific comparisons, but that they do not adequately reflect conditions in free-living birds. Similar cautions regarding the extrapolation of physiological data from captive animals to their free-living counterparts have been expressed by other workers (Bligh 1970, Borut et al. 1979, Hewitt et al. 1981).

To our knowledge, TOH has been used in only two other published studies of free-living birds. Stephenson (1974) found that daily water turnovers in wild Song Sparrows (*Melospiza melodia*) were significantly higher than in birds held in an outdoor aviary. The difference was attributed to the more moist diet (high proportion of insects) of the free-living birds. Weathers and Nagy (1980) found that the water turnover rate in one free-living Phainopepla (*Phainopepla nitens*) was within the range of values for birds from the same population held in an outdoor aviary. The wild and the captive Phainopeplas were assumed to have identical diets.

SEASONAL TRENDS

Increased water turnover rate in late winter coincided with the appearance of green vegetation induced by winter rains, and probably reflects a shift in the diet of Chukars from seeds and other dry foods to succulent plant material. We did not analyze the birds' feeding habits in this study, but examination of several crops and observations of the birds' feeding behavior in the field indicate that they readily consumed seedlings and other greens in late winter. Previous studies reveal that seeds comprise a principal part of the Chukar's diet, but that succulent plant material is eaten in large amounts when seasonally available (e.g., Galbreath and Moreland 1953, Christensen 1954, Harper et al. 1958). Data concerning the relationship between water turnover rate and the consumption of moist foods in mammals (Brown and Lynch 1972, Degen 1977) and birds (Stephenson 1974) support our suggestion; as does the finding that captive Chukars had higher water fluxes when offered succulent vegetation in addition to dry food and water (Degen et al. 1982). Increased water intake in birds has also been related to high T_a (Stephenson 1974), but in our study the largest water turnover rates occurred during the coldest period.

Increases in water turnover at times of year when succulent vegetation is available probably reflect the Chukars' energy and nutrient requirements rather than their water needs, especially since open water was present in the study area throughout the year. Because many nutrients are less concentrated in green vegetation than in dry foods such as seeds, Chukars must consume large amounts of green plant biomass in order to meet their energetic and nutrient requirements if seeds are scarce. Coincidentally, they also drink more water than needed for their physiological requirements. Thus, the high water turnover rate of Chukars in late winter may be the unavoidable consequence of a diet consisting primarily of succulent vegetation.

The Rainy period was characterized by a significant increase in TBW (as a fraction of body mass) and indicated decreases ($P < 0.1$) in total body mass and in estimated body solids, suggesting a decline in the physical condition of the birds from the Pre-rain period. This coincided with the onset of cold, wet weather but before the extensive development of green vegetation. With the onset of vegetation growth in the Post-rain period, these trends were reversed (i.e., TBW decreased, and total body mass and estimated body solids increased, all at $P < 0.10$), suggesting an improvement in the birds' condition. We suspect that meteorological conditions and the status of food resources exerted important influences on the condition of Chukars during the winter of 1980–1981. The Negev highlands are an area of low primary productivity with large spatial and temporal variations in plant biomass. We hypothesize that natural Chukar habitats in the area are of marginal quality and that the birds may be especially sensitive to changes in the physical environment. Our observations of marked birds in the study revealed that they foraged exclusively in natural habitats and did not consume vegetation in cultivated fields.

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