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SUMMER WATER TURNOVER RATES IN FREE-LIVING CHUKARS AND SAND PARTRIDGES IN THE NEGEV DESERT

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ABSTRACT.—The Chukar (*Alectoris chukar*) and the Sand Partridge (*Ammoperdix heyi*) are permanent residents of the Negev desert, Israel. They are sympatric between the 200 and 90 mm isohyets, with only Sand Partridges occurring in more arid areas. During the dry season, we measured total body water volume (TBW; as tritiated water space) and total water turnover rate, and estimated dry matter intake and components of water turnover in free-living birds of both species. Mean body mass (m_b) of 40 Chukars was 460.8 g and of 42 Sand Partridges was 176.6 g. TBW, as a percentage of m_b, was lower in Chukars than in Sand Partridges (67.4% vs. 69.8%; $P < 0.05$). Mean water turnover was 44.1 ml/day for Chukars ($n = 29$), and 20.8 ml/day for Sand Partridges ($n = 39$). The mass-specific water turnover rate was higher in Sand Partridges than in Chukars (122.5 ml kg^{-1} day^{-1} vs. 100.6 ml kg^{-1} day^{-1}; $P < 0.05$). However, when compared allometrically, per kg$^{0.75}$, water turnover rates were similar (81.7 ml kg$^{-0.75}$ day^{-1} for Chukars vs. 78.5 ml kg$^{-0.75}$ day^{-1} for Sand Partridges). Assuming a diet of seeds, we calculated that drinking water amounted to about 70% of water turnover in both Chukars and Sand Partridges and we concluded that both species must drink water when only dry forage is available.

Two phasianids are permanent residents of the Negev desert in Israel, the Chukar (*Alectoris chukar*) and the Sand Partridge (*Ammoperdix heyi*). Chukars have a wide southern Palearctic distribution and inhabit deserts at the margins of their range (Cramp and Simmons 1980). They are common throughout Israel where two subspecies are present: *A. c. cypriotes* in the Mediterranean zone; and the smaller, paler *A. c. sinaica* in arid regions, including the Negev (Nissani 1974). By contrast, Sand Partridges are wholly restricted to xeric habitats in southwestern Asia and northeastern Africa. In Israel, they occur principally in the Negev, the Arava (Rift Valley), and the Judean Desert (Dor 1975). The two species are sympatric over much of their desert ranges in Israel within the area approximately bounded by the 200 and 90 mm isohyets.

Given the difference in their geographical distributions, we supposed that the two species might differ in total water intake, compared allometrically, as reflected by water turnover rates. Desert species generally have lower water turnover rates than species inhabiting mesic and humid environments; this has been used as a criterion for defining the distribution of some mammalian (Macfarlane and Howard 1972, Nicol 1978) and avian (Degen et al. 1982, Thomas 1982) species.

We compared summer water turnover rates of free-living Chukars and Sand Partridges in order to examine whether this variable could account for their different distribution patterns. We reasoned that interspecific differences in water turnover rates would be especially evident during summer and early autumn when vegetation is mainly dry and dormant. In addition, this is the period of highest ambient temperatures and solar radiation and lowest water vapor pressures.

STUDY AREA

We captured birds from June to October 1981 in Nahal Zin, a large canyon in the central Negev highlands near Sede Boqer (30°2′N, 34°7′E). This area is an "accentuated sub-desert" with up to 300 biologically dry days per year (UNESCO 1963). Rain occurs in winter, and averages 90 mm annually, with large fluctuations in total rainfall and in its temporal and spatial distribution (Evenari 1981). Dew occurs on about 190 nights per year (Zangvil and Druian 1980). Summer and autumn are characterized by intense solar radiation and high air temperatures. During this study, mean maximum daily air temperatures were 31.3°C in June, 32.2° in July, 32.1° in August, 30.9° in September and 28.0° in October. Mean minimum daily air temperatures were 15.6°C in June, 18.9° in July, 18.5° in August, 18.1° in September and 14.9° in October (Desert Meteorology Unit, Blaustein Institute for Desert Research). Vegetation was dry and dormant; however, surface water was available throughout the study.

METHODS

CAPTURE AND HANDLING OF BIRDS

Chukars and Sand Partridges were captured in sorghum-baited, wire mesh traps (90 × 90 × 60 cm) having funnel entrances. Traps were checked twice daily (between 07:00 and 08:00 and between 16:00 and 17:00; shortly after we observed birds to be most active), and captured birds were brought to our laboratory, a 15-min drive from trapping sites. The birds were marked with leg bands and individually identifiable numbered back tabs (Alkon 1974). Only fully grown birds having adult plumage were used.

Methods used to estimate total body water (TBW) and water turnover rate were described by Degen et al. (1981). Birds were weighed (to the nearest 0.1 g), and injected intramuscularly with 0.1 mCi/kg body mass of tritiated water (TOH) in 1.0 ml (weighed to the nearest 0.1 mg) sterile avian saline solution for Chukars and 0.4 ml for Sand Partridges. After allowing 45 to 60 min for TOH equilibration with body fluids, birds were weighed again, and a blood sample was taken from the basilic vein to estimate TBW (as TOH space). The mean of the two body masses was used for subsequent calculations. The birds were then released at the capture sites. In order to estimate water turnover rates, based on the decline in specific activity of tritium over time, blood samples were collected from birds that were recaptured at least two days after TOH injection. On occasion, blood sampling and weighing of recaptured birds were done in the field. We assumed that TOH space remained a constant fraction of total body mass during the capture–recapture interval, and that any change in TOH space was linear with time.

Blood samples were centrifuged and sera removed. To measure specific activity of tritium, 0.05-ml serum samples were added to 5 ml of Bray's solution. Duplicate samples were counted for 10 min in a liquid scintillation counter (Packard Tri-Carb, model PLD) and counts were corrected for 6% serum dry matter content and for quenching. Serum samples from three non-labelled birds were used to measure background counts.

ESTIMATION OF FOOD INTAKE AND COMPONENTS OF WATER INTAKE

We estimated food intake and the components of water intake using two methods. Method I was based on the birds' energy requirements. From analysis of crop contents, it appears that seeds were the principal dry season food of both species. Existence energy (EE), as defined by Kendeigh (1970), for birds on a dry mash or seed diet was calculated as approximately 210 kJ/day for a 450-g Chukar and 105 kJ/day for a 175-g Sand Partridge (Pinshow et al. 1983). Assuming a 50% increase in energy intake over EE during field activity (West 1967, Robel et al. 1974), and that 1 g of feed (mixed graminaceous seeds) contains 0.106 g of preformed water, and that 1 g of dry matter (DM) has an energy density of 15.4 kJ and yields 0.5 g of metabolic water (Thomas and Maclean 1982), we calculated the DM intake and total water obtained from food for both species.

Method II was based on the ratio of DM intake to water turnover rate. We assumed a constant ratio of DM intake of dry forage to water turnover as has been reported for various domestic mammals (e.g., Benjamin et al. 1977). DM intake for caged Chukars and Sand Partridges fed a dry ration and tap water ad libitum was 0.50 and 0.59 g per ml water turnover, respectively. Using these ratios, DM intake was estimated for both species from their water turnover rates, and preformed and metabolic water intakes were calculated as in method I. In both methods water drunk was calculated as the difference between total water turnover and water intake from food.

DATA ANALYSIS

For interspecific comparisons between Chukars and Sand Partridges, we expressed water turnover rates per unit body mass$^{0.75}$ according to the allometric equation of Pinshow et al. (1983). Means (expressed ± SD) were compared using Student's *t*-test, and statistical methods followed Sokal and Rohlf (1973).

RESULTS

Mean body mass (m_b) for 40 Chukars was 460.8 ± 56.0 g, and for 42 Sand Partridges was 176.6 ± 21.4 g. Mean TBW, as percentage m_b, was lower in Chukars than in Sand Partridges (67.4% vs. 69.8%, $P < 0.05$; Table 1). Mean water turnover rate was 44.1 ± 6.7 ml/day for Chukars, based on 29 measurements (m_b = 444.5 ± 52.2 g) in 21 individuals, and was 20.8 ± 4.1 ml/day for Sand Partridges, based on 39 measurements (m_b = 173.1 ± 21.9 g) in 31 individuals. Water turnover per day amounted to 10.1% of m_b, or 14.7% of TBW for Chukars and 12.3% of m_b, or 17.2% TBW for Sand Partridges. Mean water turnover rates per kg$^{0.75}$ were similar for the two species; 82.3 ml/day for Chukars and 80.3 ml/day for Sand Partridges.

From method I, we estimated DM intake as

TABLE 1. Body mass, tritiated water (TOH) space and water turnover rates of free-living Chukars and Sand Partridges in the Negev desert, July to October, 1981. Values are means ± SD.

	Chukars	Sand Partridges	Significance[a]
TOH space			
Sample size	40	42	
Body mass (g)	460.8 ± 56.0	176.6 ± 21.4	*
TOH space (ml)	310.1 ± 39.9	123.1 ± 15.1	*
(% body mass)	67.4 ± 2.5	69.8 ± 4.0	*
Water turnover rate			
Sample size	29[b]	39[c]	
Body mass (g)	444.5 ± 52.2	173.1 ± 21.9	*
Water turnover			
(ml day^{-1})	44.1 ± 6.7	20.8 ± 4.1	*
(ml kg^{-1} day^{-1})	100.6 ± 19.8	122.5 ± 31.9	*
(ml $kg^{-0.75}$ day^{-1})	81.7 ± 14.0	78.5 ± 18.4	ns

[a] * = $P < 0.05$; ns = non-significant.
[b] Based on 21 individuals.
[c] Based on 31 individuals.

TABLE 2. Estimated dry matter intake and components of total water turnover for free-living Chukars and Sand Partridges. Method I is based on energy requirements and method II on dry matter intake to water intake ratio. Values are means and, in parentheses, percentages of total water turnover.

	Chukars	Sand Partridges
Method I		
Dry matter intake (g/day)	20.4	10.2
Water turnover (ml/day)	44.1 (100)	20.8 (100)
Total water from food (ml/day)	12.6 (29)	6.3 (30)
Preformed water (ml/day)	2.4 (6)	1.2 (6)
Metabolic water (ml/day)	10.2 (23)	5.1 (24)
Water drunk (ml/day)	31.5 (71)	14.5 (70)
Method II		
Dry matter intake (g/day)	22.1	12.3
Water turnover (ml/day)	44.1 (100)	20.8 (100)
Total water from food (ml/day)	13.7 (31)	7.6 (37)
Preformed water (ml/day)	2.6 (6)	1.4 (7)
Metabolic water (ml/day)	11.1 (25)	6.2 (30)
Water drunk (ml/day)	30.4 (69)	13.2 (63)

20.4 g/day for Chukars and 10.2 g/day for Sand Partridges; from method II, equivalent values were 22.1 and 12.3 g/day (Table 2). Using the DM values estimated by method I, we calculated water drunk as 31.5 ml/day for Chukars and 14.5 ml/day for Sand Partridges; these values amounted to 71% of the total water turnover in Chukars and 70% in Sand Partridges. Based on method II, Chukars drank 30.4 ml/day or 69% of their total water turnover and Sand Partridges drank 13.2 ml/day or 63% of their total water turnover.

DISCUSSION

Studies of mammals (Macfarlane and Howard 1972, Nicol 1978) and birds (Degen et al. 1982, Thomas 1982) suggest that desert endotherms may have lower water turnover rates than their mesic and humid-zone counterparts. Thus, it might be expected that the Sand Partridge, a bird inhabiting only arid and very arid environments would have a relatively lower water turnover rate than the Chukar, a bird of wide mesic and semi-arid distribution. However, we found that dry season water turnover rates, allometrically compared per $kg^{0.75}$, were similar for free-ranging birds of the two species.

This similarity indicates that the Chukar subspecies, *A. c. sinaica,* can inhabit the same areas as Sand Partridges; however, Sand Partridges do inhabit extremely arid areas (i.e., the Arava) where Chukars are absent. This may be due to interpopulation differences in the water economies of the Sand Partridges we studied and those inhabiting more xeric environments. However, we suspect that physiological variables other than water turnover rate, as well as behavioral differences between Chukars and Sand Partridges may be important determinants of their distributions. For example, free water was available to the birds studied throughout the dry season, perhaps thereby obscuring interspecific differences in minimal water requirements that might be apparent in water-scarce habitats. It is also conceivable that Sand Partridges can more readily satisfy their water requirements from preformed water contained in summer forage than can Chukars, and so occupy areas where surface water is scarce.

We observed birds of both species drinking in the wild. Previous reports revealed that Chukars concentrated at open water sources during the summer (Alcorn and Richardson 1951, Christenson 1958, Alkon 1974), and inferred that they depended on free water when succulent forage was not available (Bump 1953, Christenson 1954, McLean 1955, Harper et al. 1958). Little information is available on the dependence of wild Sand Partridges on free water. Meinertzhagen (1954) reported that Sand Partridges occurred only near open water, but recent observations in the Negev indicate that Sand Partridges inhabit areas where surface water may not be available (G. Illani, pers. comm.).

Assuming that the birds fed only on seeds, we calculated that drinking water comprised about 70% of daily water intake in both species. Because of the low moisture content of the diet, large errors in DM intake would cause relatively small errors in estimates of water drunk. In Sand Partridges, for example, the two meth-

TABLE 3. Estimated daily intakes of dry forage and green vegetation required to fulfill energy and water requirements in free living Chukars and Sand Partridges. See text for details.

	Dry forage (D)	Green vegetation	Total intake (T)	D/T
Chukars				
Fresh matter (g)	13.76	40.50	54.3	0.25
Dry matter (g)	13.34	8.10	21.4	0.62
Water, preformed plus metabolic (g)	7.67	36.45	44.1	0.17
Energy (kJ)	205.44	124.74	330.2	0.62
Sand Partridges				
Fresh matter (g)	8.53	17.84	26.4	0.32
Dry matter (g)	7.63	3.57	11.2	0.68
Water, preformed plus metabolic (g)	4.74	16.16	20.8	0.23
Energy (kJ)	117.50	54.98	172.5	0.68

ods used to estimate DM intake yielded energy intakes of 150 and 193% of existence energy; yet the calculated values for water drunk were similar, i.e., 13.2 and 14.5 ml/day.

The apparent dependence of wild Chukars and Sand Partridges on drinking water when only dry forage is available was supported by our laboratory studies. When offered a dry ration under caged conditions, both species required drinking water in order to maintain body mass (Pinshow et al. 1983). However, at least Chukars are able to maintain body mass with no free water when succulent vegetation is available in addition to dry food (unpubl. data). This has also been found for a number of quail species (see review by Bartholomew and Cade 1963).

During this study crop contents were collected from Chukars from the same wild populations as those birds used for experiments. Analysis of these crops revealed that birds were eating almost exclusively dry food. However, during the other seasons we found both dry seeds and green vegetation in crops. Green vegetation contained 80% water (unpubl. observ.), and we assumed that it had an energy content of 15.4 kJ and a metabolic water production of 0.5 g per gram dry matter. Using these values and the values for dry seeds, we calculated the approximate ratio of dry forage (i.e., seeds) to green vegetation that Chukars must consume in order to obtain 44.1 g of water and 330.2 kJ (mean of values calculated using methods I and II) of energy per day, which would allow them to maintain energy balance and not have to rely on drinking water.

The volume of preformed water in a unit mass of dry forage (D) equals $0.106 \times D$, and the volume of metabolic water equals $0.5 \times 0.896 \times D$. The volumes of preformed and metabolic water in a unit mass of green vegetation (G) equal $0.8 \times G$ and $0.5 \times 0.2 \times G$ respectively. Therefore:

$$0.556D + 0.9G = 44.1 \text{ (g } H_2O\text{)}.$$

The energy content of dry seeds equals $15.4 \times 0.896 \times D$ (kJ), and of the vegetation equals $15.4 \times 0.2 \times G$ (kJ). Therefore:

$$13.768D + 3.08G = 330.2 \text{ (kJ)}.$$

Solving for D and G, we calculate that if Chukars obtain at least 38% of their dry matter from greens, and are above their minimal water requirements, they do not require drinking water (Table 3). A similar calculation for Sand Partridges shows that if they obtain at least 32% of their dry matter from green vegetation they do not need to drink.

Fractions of greens similar or larger than the above calculated minimal intakes have been found in Chukar crops in winter and early spring (unpubl. data). It is, therefore, likely that Chukars and Sand Partridges must drink during the hot summers, but do not need to do so if an adequate supply of green vegetation is available. The smaller proportion of vegetation required by Sand Partridges to maintain positive water balance in absence of drinking water might explain, in part, the ability of this species to penetrate very arid areas where Chukars are absent.

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