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REVIEW

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Water turnover among human populations: Effects of environment and lifestyle

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Abstract

Objectives: To discuss the environmental and lifestyle determinants of water balance in humans and identify the gaps in current research regarding water use across populations. Methods: We investigated intraspecific variation in water turnover by comparing data derived from a large number of human populations measured using either dietary survey or isotope tracking. We also used published data from a broad sample of mammalian species to identify the interspecific relationship between body mass and water turnover.

Results: Water facilitates nearly all physiological tasks and water turnover is strongly related to body size among mammals (r2=0.90). Within humans, however, the effect of body size is small. Instead, water intake and turnover vary with lifestyle and environmental conditions. Notably, despite living physically active lives in conditions that should increase water demands, the available measures of water intake and turnover among small-scale farming and pastoralist communities are broadly similar to those in less active, industrialized populations.

Conclusions: More work is required to better understand the environmental, behavioral, and cultural determinants of water turnover in humans living across a variety of ecosystems and lifestyles. The results of such work are made more vital by the climate crisis, which threatens the water security of millions around the globe.

1 | INTRODUCTION

Water is the most important nutrient for life. It provides structure and transport throughout the body, facilitates digestion and metabolic reactions, and aids in our ability to thermoregulate (Sawka, Cheuvront, & Carter, 2005). Constituting over half of our body mass, water is by far the largest component of the human body (Shimamoto & Komiya, 2000). Deprived of water, humans experience rapid declines in muscular and cognitive function. Prolonged dehydration is associated with a number of chronic diseases, including urolithiasis, urinary tract infection, kidney disease, and cancers of the bladder and colon (Institute of Medicine [IOM], 2004; Manz & Wentz, 2005; Roncal-Jimenez, Lanaspa, Jensen, Sanchez-Lozada, & Johnson, 2015; Sawka et al., 2005).

Despite the importance of water, there have been few studies of water turnover in nonindustrialized farming or foraging societies. The IOM (2004) has established adequate intakes (AI) with data derived from numerous studies, but the supporting research has focused disproportionately on water turnover in industrialized, economically developed settings. Daily life in small-scale foraging and farming communities is often characterized by high levels of physical activity, exposure to the weather, and scarcity of safe water. Furthermore, cultural practices and dietary differences can affect water intake. The effects of temperature, physical activity, and altitude have been investigated (IOM, 2004), but most of this work has been done with Westerners in experimental studies or expedition conditions (eg, high altitude trekking or military operations). Conversely, research on water turnover during daily life has often neglected to integrate environmental and behavioral factors.

In this article, we review the physiology and allometry of water turnover in humans and examine its anthropometric, ecological, and cultural determinants. Our objective is to review established determinants of water turnover, discuss what is known regarding water turnover in small-scale foraging and farming societies, and identify remaining gaps in our understanding of human water turnover.

2 | PHYSIOLOGY OF WATER

Water serves a variety of essential physiological roles in humans. Functionally, water provides structure, lubrication, and transport, aids in thermoregulation, and serves as a primary medium for chemical reactions, without which nearly all the systems of the body cannot properly function (Häussinger, 1996; Kleiner, 1999). Water ingestion is also necessary to digest food (Adolph, 1933; Engell, 1988). Water restriction in humans and other animals leads to a corresponding reduction in food intake (Engell, 1988), and prolong restriction can result in negative energy balance and weight loss (Burgos, Senn, Sutter, Kreuzer, & Langhans, 2001).

The body water pool can be divided into two components, intracellular fluid (ICF), which constitutes about two-thirds of total body water, and extracellular fluid (ECF), which constitutes about one-third (Sawka et al., 2005). ECF can be further segregated into its constituent parts, which include interstitial fluid, intravascular fluid, and transcellular fluid (Jéquier & Constant, 2010). Together, ICF and ECF facilitate key physiological functions, such as providing structure for cells and tissues throughout the body, as water is by far the largest component of cellular fluid (Shimamoto & Komiya, 2000). Cell hydration provided though ICF maintains necessary volumes for cells to function properly and survive. Importantly, variations in cell volumes of certain tissues can also provide important signaling to metabolism and gene expression. For example, variation in the rate of liver cell swelling can produce a wide variety of effects, such as protein and glucose synthesis, lactate uptake, urea synthesis, and others (Häussinger, 1996).

ECF also provides critical structure for the body. The primary components of ECF, interstitial fluid and plasma, provide support and vascular volume to the circulatory system and organ systems. Structurally, the water in ECF also serves to provide lubrication at joints and within the digestive and respiratory tracts, and shock absorption for the brain and spinal cord through cerebrospinal fluid (Jéquier & Constant, 2010).

While ICF aids in signaling cellular chemical reactions through volumetric change, water also serves as an essential medium for chemical reactions in the body, with all chemical reactions occurring in the ICF (Shimamoto & Komiya, 2000). Water is also an important reactant and resultant of metabolic processes. For example, the citric acid cycle (Krebs cycle), which is essential to nutrient catabolism and energy production, requires water in order to produce energy in the form of ATP (adenosine triphosphate). The citric acid cycle also produces NADH (nicotinamide adenine dinucleotide) and hydrogen ions required for the main process of energy production, oxidative phosphorylation. As a final step of oxidative phosphorylation via electron transport chain, oxygen receives electrons, forming "metabolic water" (Widmaier, Raff, & Kevin, 2008). Due to the nature of water as an excellent solvent (it is sometimes referred to as the *universal solvent*), water is an important component in the hydrolysis of macronutrients, which allows for the breakdown of carbohydrates, proteins, and lipids into digestible components (Jéquier & Constant, 2010).

Body water, particularly ECF, serves as the primary medium through which nutrients and waste products are transported throughout the body, which maintains homeostatic conditions within cells (Jéquier & Constant, 2010). Blood plasma, a type of ECF that is mostly made up of water, transports oxygen required for metabolism from the lungs, and the byproduct of that metabolic process, carbon dioxide, to the lungs for exhalation. Blood plasma also serves as transport for hormones, glucose, and other nutrients, while transporting waste to the liver and kidneys for processing and excretion, as well (Shimamoto & Komiya, 2000).

The ability to maintain body temperatures within a homeostatic range in a variety of environments is enabled both by a number of physiological mechanisms involving body water and its high heat capacity (Jéquier & Constant, 2010). This high heat capacity buffers the body against internal temperature changes when in hot or cold environments. The high heat capacity of water makes vasodilation and vasoconstriction effective physiological strategies for thermoregulation by changing rate of conductive heat transfer with the external environment (Widmaier et al., 2008).

In many primates and other mammals, water is also used for thermoregulation via sweating, which is one of the most effective mechanisms by which the body can cool itself (IOM, 2004). Humans have evolved a far greater capacity to sweat than other primates, with eccrine sweat gland densities that are 10 times higher than those of chimpanzees and macaques (Carrier, 1984; Kamberov et al., 2018; Lieberman, 2015). The remarkable human capacity to sweat is thought to reflect selection for thermoregulation in hot climates and when engaging in high levels of physical activity (Carrier, 1984; IOM, 2004; Kamberov et al., 2018; Lieberman, 2015; Popkin, D'Anci, & Rosenberg, 2010). When sweat is secreted onto the skin and is vaporized it transfers heat from the body to the environment through evaporative cooling (Jéquier & Constant, 2010; Lieberman, 2015; Sawka, 1992). The heat of vaporization of a single gram of sweat at 30°C is 2.43 kJ, which results in a substantial thermal change at the skin (Wenger, 1972). The ability to cool the body through sweating is mediated, in part, by environmental variables like temperature and humidity. Both can affect the evaporation rates, with hotter climates eliciting higher rates of sweating to cool the body, and higher humidity eliciting higher rates of sweating as water vapor in the air can stymy evaporation and its cooling effect (IOM, 2004). These phenomena are can be observed in the sweating rates of humans exercising in hot, humid environments vs cool, dry environments (Figure 1) (Sawka, 1992).

3 | WATER BALANCE

Given the importance of water across a number of physiological tasks, prevention of dehydration through the regulation of body water is incredibly important for daily functioning and survival. In adult humans and other mammals, body water is tightly maintained near 73% of fat free mass, which generally corresponds to ~60% of total body mass in humans (Wang et al., 1999). The water content of fat free mass is somewhat higher in children; it can exceed 75% in newborns and steadily declines through childhood and adolescence to adult values (IOM, 2004). Maintaining the body water pool requires balancing water gain (influx) and loss (efflux) each day. The movement of water through the body is variably known as water turnover, water flux, or water turnover. In humans, most water gain comes from food and drink. Water is also formed in aerobic respiration, adding to water gain, and a negligible amount of water is absorbed through the skin (transcutaneous influx) or inhaled (inspired influx; Figure 2). Most water is lost via urine and "insensible" water loss, the water vapor exhaled or lost from the skin without sweating. Fecal loss is generally small. Sweat production is a minor avenue of water loss for sedentary populations in temperate or climate-controlled settings but can be significant in hot climates and with high levels of physical activity (Lieberman, 2015).

Homeostatic control of water and mineral balance results from intracellular and extracellular mechanisms that regulate physiological thirst and urine production in response to water deficits. As body water is lost, osmotic pressure causes water to move from intracellular spaces into extracellular spaces. This exchange results in a decrease of cellular volumes that triggers a neuroendocrine thirst response. Water deficits also increase production of the hormone vasopressin, which increases water permeability in the renal collecting ducts to recoup water and reduce urine volume (European Food Safety Authority Panel on Dietic Products, Nutrition, and Allergies, 2010; Widmaier et al., 2008). Lower urine volume results in higher concentration of solutes. Consequently, hydration status can be assessed through the measurement of urine osmolality, which is a measure of the concentration of dissolved particles in solution, or urine specific gravity, which is a measure of the density of urine relative to water.

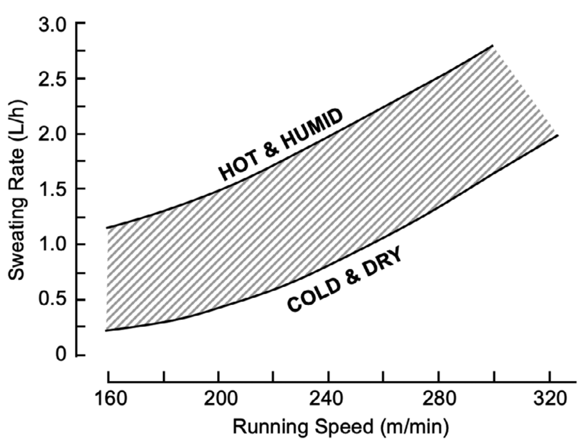

FIGURE 1 Approximate sweating rates under varying activity levels and environmental conditions. Adapted from Sawka (1992)

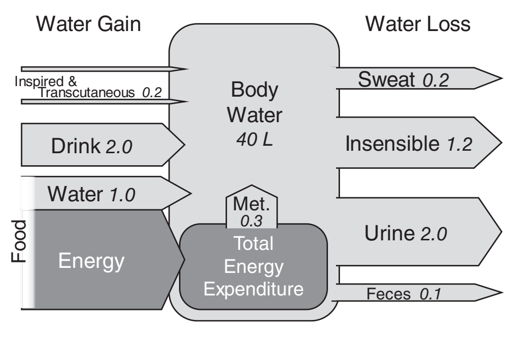

FIGURE 2 Schematic of water balance for an adult human in an industrialized population. Body water is 73% of fat free mass, or 40 L for the 55 kg fat free mass adult depicted here. Approximate water gains and losses (L/d) are given in italics (see Raman et al., 2004). Met. refers to metabolic water produced from aerobic respiration

Usually, body water volume is tightly controlled. When water balance cannot be regulated properly, the resulting overhydration or dehydration can lead to serious adverse effects. Overhydration, also called hyperhydration or water toxemia, can lead to dangerously low concentrations of salt and electrolytes in the ECF, a potentially fatal condition known as hyponatremia (Hoorn & Zietse, 2017). Dehydration is far more common, and its effects vary with the severity of water loss. Mild dehydration is defined by a 1%-2% decrease in body weight due to fluid loss (Kleiner, 1999). This level of dehydration can result in slight impairments to cognitive functioning and physical performance (IOM, 2004; Jéquier & Constant, 2010; Shimamoto & Komiya, 2000; Popkin et al., 2010; Manz, Johner, Wentz, Boeing, & Remer, 2012). Severe dehydration, defined as a >3% loss in body weight due to fluid loss by Kleiner (1999), can result in further deficits in physical and cognitive ability, as well as heat exhaustion, which can be life threatening without proper treatment. Prolonged periods of even mild dehydration can detrimentally affect metabolism and may increase the risk of chronic disease (Armstrong & Johnson, 2018).

Despite previous work demonstrating negative physical effects of even modest dehydration, some work has reported high levels of body water loss among elite athletes during competition (Beis, Wright-Whyte, Fudge, Noakes, & Pitsiladis, 2012; Goulet, 2012). Beis et al. (2012) found an average body mass loss of 8.8% ± 2.1%, ranging between 6.6% and 11.7%, among 10 marathon runners across 13 marathons. Faster runners often had more severe dehydration; the winner of the 2009 Dubai marathon lost 9.8% of his body mass (Beis et al., 2012). These findings run counter to those of Cheuvront and others (eg, Cheuvront & Montain, 2017; Cheuvront, Montain, & Sawka, 2007; King, Cooke, Carroll, & O'Hara, 2008; Maughan, Shirreffs, & Leiper, 2007), who have pointed out that changes in body mass during competition reflect fuel oxidation as well as water loss. Thus, body mass changes during competition will overestimate water loss unless one accounts explicitly for energy expenditure (Cheuvront & Montain, 2017). Isotope tracking techniques provide an alternative method for measuring water turnover during competition and other intense activity (eg, Ruby et al., 2015), and may be preferable to calculating water loss from mass changes alone.

4 | METHODS FOR MEASURING WATER TURNOVER

There are two general approaches for measuring 24-hours water turnover in human populations. The most common method is 24-hour dietary recall surveys or interviews, in which the subject lists the types and quantities of food and beverage consumed over the recall period (Athanasatou, Malisova, Kandyliari, & Kapsokefalou, 2016; Berti & Leonard, 1998; Kant, Graubard, & Atchison, 2009; Laksmi et al., 2018; Manz et al., 2012; Rosinger & Tanner, 2015; Tani et al., 2015; Wutich, Rosinger, Stoler, Jepson, & Brewis, 2019). Several instruments are available for this purpose. The advantage of surveys and interviews is that they are inexpensive and can be implemented in large samples with relative ease. For example, the US NHANES survey regularly collects 24-hour recall data on thousands of adults that can be used to calculate water turnover (eg, Rosinger, Lawman, Akinbami, & Ogden, 2016). The main limitation of dietary recall is the potential for error and bias, particularly underreporting of intake, in completing the surveys (Johansson, Wikman, Åhrén, Hallmans, & Johansson, 2001; Orcholski et al., 2015). However, multipass methods have been shown to reduce these errors (Conway, Ingwersen, & Moshfegh, 2004).

Isotope tracking provides a more direct measure of water turnover in free-living subjects. Subjects drink a dose (typically ~5-10 mL, depending on body size) of water in which the hydrogen atom is in the form of the isotope deuterium. This deuterated water quickly diffuses throughout the body water pool. The isotope enrichment of the body water pool is highest after dosing, then depletes as enriched water is excreted and replenished with unenriched water from the diet. The rate of isotope depletion in the body water thus gives the rate of water loss. Subjects provide two or more body water samples (urine, blood, or saliva) over the subsequent 7 to 14 days, and the change in deuterium enrichment in the samples over time is used to calculate the rate of water loss (L/d) from body water pool. Deuterium tracking is considered the gold standard for measuring water turnover precisely and accurately (IAEA, 2009), and the method is relatively easy to deploy in field settings (eg, Christopher et al., 2019; Kashiwazaki et al., 2009; Raman et al., 2004), but it is considerably more expensive than surveys or interviews. Further, water turnover calculated from deuterium depletion includes all sources of water gain and loss, and thus cannot distinguish, for example, water gained through food, drink, or metabolic water formation.

Using two isotopic tracers, deuterium and oxygen-18, an approach known as the doubly labeled water (DLW) method, enables researchers to calculate daily energy expenditure (kcal/d) as well as water turnover (IAEA, 2009). The measure of daily energy expenditure provided by DLW can be used to calculate metabolic water production (eg, Johnson et al., 2017; Raman et al., 2004). Daily energy expenditure can also be used to calculate the amount of food eaten and, if the composition of the diet is known, to estimate water consumed as food. Water intake through beverages can then be estimated by subtracting metabolic water and the water from food from total water turnover. Johnson et al. (2017) have used this approach to validate a 7-day fluid intake survey. Like deuterium tracking, the DLW method is relatively easy to use in the field (eg, Christopher et al., 2019; Kashiwazaki et al., 2009; Pontzer et al., 2015). However, it is more expensive than using deuterium alone due to the considerable expense of oxygen-18 enriched water.

5 | INTERSPECIFIC COMPARISON

Interspecific comparisons of water turnover provide a comparative, evolutionary framework for understanding human water physiology. Indeed, a number of ecological changes throughout hominin evolution, including persistent hunting and life in a savannah environment, are thought to have shaped human water physiology (eg, Carrier, 1984; Lieberman, 2015; Wheeler, 1992). We compared water turnover measured via isotope depletion in n = 458 US adults (Raman et al., 2004) to water turnovers measured in other mammals using similar methods (Haggarty et al., 1998; Munn et al., 2012; Nagy et al., 1990; Riek et al., 2007; Williams et al., 2001). On a log-log plot of water turnover against body mass, humans (both men and women) fall very near the allometric trendline (Figure 3). Human water turnover is unremarkable for a mammal of our body size. This result is somewhat surprising given physiological adaptations, like our increased ability to thermoregulate via the evaporative cooling of sweating and oronasal breathing during intense physical activity (Lieberman, 2015), that might be expected to increase human water requirements.

Body mass is a strong predictor of water turnover across a broad size range of mammalian species. This relationship collapses when comparing water use among people and populations, however. For example, in the study of US adults by Raman et al. (2004), body mass was correlated with water turnover in men but not women. Rosinger et al. (2016), using a much larger (n = 9601) sample of US adults, reported higher self-reported water intake (but poorer hydration status) in men and women with greater body mass and body mass index. However, the effect of body mass on water turnover was relatively small: mean body mass for the obese cohort was 59% more than the underweight/normal weight cohort but their mean water intake was only 8% greater (Rosinger et al., 2016). Due to the weak effect of body size on turnover, other factors predominate in comparisons across populations. For example, for the cohorts with available body masses in the top portion of Table 1 (excluding special cases such as athletic competition), mean body mass is not correlated with water turnover (df = 15, r^2 = 0.08, P = .76, ordinary least squares regression for all adults). Results are similar ($r^2 < 0.01$) when male and female cohorts in Table 1 are analyzed separately. The poor predictive power of body size in estimating water turnover

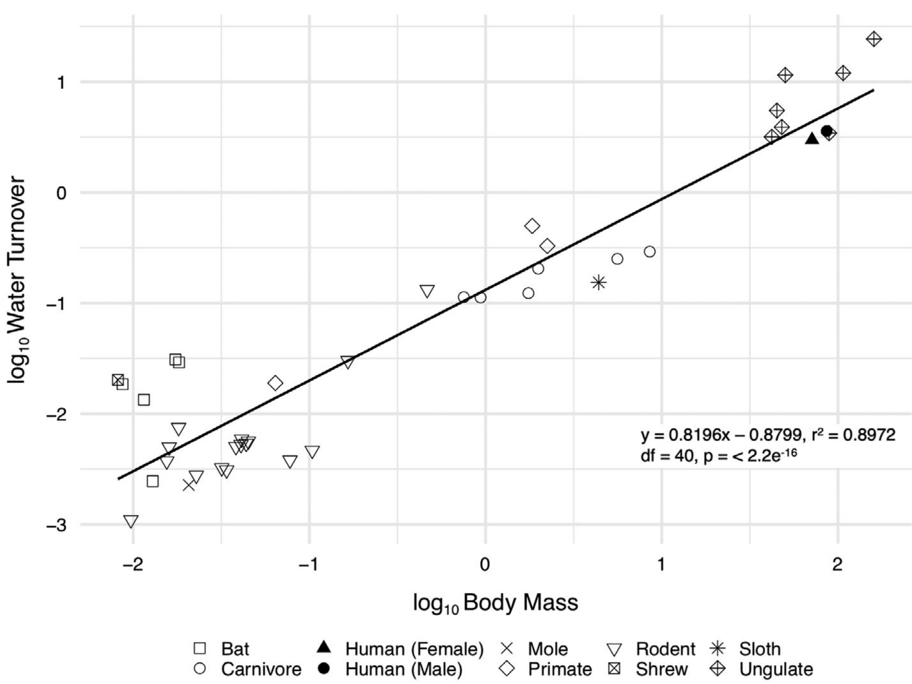

FIGURE 3 Water throughput (L/d) as a function of body mass (kg) among mammals. Humans (female, red, n = 207; male, blue, n = 251) fall very near the allometric scaling for mammals. Human values derived from Raman et al. (2004). Nonhuman mammal values derived from Munn et al. (2012), Williams et al. (2001), Riek et al. (2007), Nagy et al. (1990), and Haggarty et al. (1998)

TABLE 1 Water turnover in human study as measured by dietary recall and deuterium depletion across various lifestyles

Population	Sex	n	Method	Age	Mass (kg)	Fat free mass (kg)	Environment	Lifestyle	Water turnover/ intake (L/d)	Reference
Tsimane	Male	22	Dietary recall	39.5 ± 19.3	61.9 ± 6.9	-	Bolivia: Lowland	Forager-horticulturalist	4.95 ± 1.74	Rosinger and Tanner (2015)
	Female	23	Dietary recall	36.4 ± 15.3	61.4 ± 12.7	-	Bolivia: Lowland	Forager-horticulturalist	4.43 ± 1.32	
Shuar	Male	7	Deuterium	35 ± 15.3	76.7 ± 9.5	60.7 ± 7.1	Ecuador: Amazonian	Forager-horticulturalist	9.37 ± 2.3	Christopher et al. (2019)
	Female	8	Deuterium	34 ± 14.9	59 ± 8.2	41.7 ± 3.5	Ecuador: Amazonian	Forager-horticulturalist	4.76 ± 0.4	
Aymara	Male	9	Deuterium	55.8 ± 20.3	55.2 ± 6.1	45.4 ± 3.1	Bolivian Andes	Agropoastoralist	3.52 ± 0.48	Kashiwazaki et al. (2009)
	Female	11	Deuterium	45.9 ± 25.9	46.1 ± 14.3	32.7 ± 7.3	Bolivian Andes	Agropoastoralist	2.93 ± 0.48	
Kenya	Female	18	Deuterium	24.1 ± 5.2	56.2 ± 11.4	38.8 ± 6.2	Narok County: Tropical	Urban	3.1 ± 0.6	Keino, van den Borne, and Plasqui (2014)
	Female	10	Deuterium	26.7 ± 7.6	58.4 ± 11.0	39.0 ± 4.6	Narok County: Tropical	Rural	3.3 ± 1.2	
Indonesia	Male	1256	Dietary recall	18-65	-	-	Indonesia: Tropical	Rural/urban	2.68 ± 1.17	Laksmi et al. (2018)
	Female	1522	Dietary recall	18-65	-	-	Indonesia: Tropical	Rural/urban	2.76 ± 1.21	
Mestizo	Male	50	Dietary recall	≥20	-	-	Ecuador: Highland	Rural	2.61 ± 0.64	Berti and Leonard (1998)
	Female	51	Dietary recall	≥20	-	-	Ecuador: Highland	Rural	2.41 ± 0.63	
Greece	Male	532	Dietary recall	18-75	81.2 ± 11.5	-	Mediterranean	Industrialized	3.40 ± 1.61	Athanasatou et al. (2016)
	Female	575	Dietary recall	18-75	63.6 ± 12.0	-	Mediterranean	Industrialized	3.12 ± 1.44	
Japan	Male	121	Dietary recall	52.4 ± 12.2	66.4 ± 10.4	-	Temperate	Industrialized	2.42 ± 0.55	Tani et al. (2015)
	Female	121	Dietary recall	49.6 ± 11.3	53.0 ± 18.2	-	Temperate	Industrialized	2.04 ± 0.46	
US	Male	17	Deuterium	25.4 ± 4.0	71.8 ± 6.6	-	Temperate	Industrialized	3.4	Schloerb, Friis-Hansen, Edelman, Solomon, and Moore (1950)
	Female	11	Deuterium	24.7 ± 3.3	58.2 ± 8.9	-	Temperate	Industrialized	2.3	

(Continues)

TABLE 1 (Continued)

Population	Sex	n	Method	Age	Mass (kg)	Fat free mass (kg)	Environment	Lifestyle	Water turnover/ intake (L/d)	Reference
US	Male	251	Deuterium	40-79	86.25	-	Temperate	Industrialized	3.59 ± 0.96	Raman et al. (2004)
	Female	207	Deuterium	40-79	71.25	-	Temperate	Industrialized	2.99 ± 0.72	
US - NHANES	Male	4112[a]	Dietary recall	≥20	-	-	Temperate	Industrialized	3.47 ± 0.79	Kant et al. (2009)
	Female		Dietary recall	≥20	-	-	Temperate	Industrialized	2.90 ± 0.72	
Germany	Male	639	Dietary recall	18-88	80 ± 12	-	Temperate	Industrialized	2.59 ± 0.72	Manz et al. (2012)
	Female	889	Dietary recall	18-88	66 ± 12	-	Temperate	Industrialized	2.12 ± 0.58	
France	Male	8	Deuterium	28.0 ± 2.3	74.9 ± 8.2	-	Temperate	Industrialized	3.5 ± 0.57	Blanc et al. (1998)
	Male	8	Deuterium	28.0 ± 0.8	74.9 ± 2.9	-	Temperate	Industrialized (head down rest)	3.2 ± 0.57	
Special cases										
US	Male	13	Deuterium	43.5 ± 4.8	77.4 ± 6.3	57.5 ± 4.8	Ground Study	Astronaut	3.77 ± 0.51	Lane et al. (1997)
	Male	13	Deuterium	43.5 ± 4.8	77.4 ± 6.3	57.5 ± 4.8	Space Study	Astronaut	2.73 ± 0.61	
US	Male	8	Deuterium	24.5 ± 1.8	74.6 ± 6.4	-	Wildfire	Active firefighter	7.34 ± 1.24	Ruby et al. (2002)
	Female	9	Deuterium	25.0 ± 1.3	65.2 ± 8.0	-	Wildfire	Active firefighter	6.69 ± 1.98	
US	Male & Female	13	Deuterium	41.1 ± 11.6	70.4 ± 7.2	-	Kona Ironman	Ultra-endurance athletes	10.8 ± 2.5[b]	Ruby et al. (2015)
	Male & Female	10	Deuterium	42.9 ± 7.6	71.4 ± 11.7	-	WS 100 Ultra	Ultra-endurance athletes	8.7 ± 1.8[b]	Ruby et al. (2015)
	Male & Female	14	Deuterium	46.6 ± 7.5	77.0 ± 10.0	-	Badwater Ultra	Ultra-endurance athletes	13.0 ± 2.5[b]	
Japan	Male	8	Deuterium	21.6 ± 2.5	63.9 ± 7.5	49.9 ± 5.5	Sedentary	Industrialized	3.43 ± 0.53	Shimamoto and Komiya (2003)
	Male	8	Deuterium	20.8 ± 1.9	57.8 ± 2.5	48.4 ± 2.6	Active	Industrialized	4.25 ± 0.66	
US	Male	6	Deuterium	42 ± 7	71.3 ± 10.9	-	Sedentary	Industrialized	3.3	Leiper, Carnie, and Maughan (1996)
	Male	6	Deuterium	41 ± 6	63.8 ± 7.3	-	Active	Industrialized	4.7	
US	Male	6	Deuterium	38	67.0	-	Sedentary	Industrialized	2.3	Leiper, Pitsiladis, and Maughan (2001)
	Male	6	Deuterium	36	77.6	-	Active	Competitive cyclists	3.5	

Note: Special cases indicate studies involving specialized populations (ie, astronauts, firefighters, athletes) and comparative studies of the effect of physical activity on water throughput variation.
[a]Sample size of male and female cohorts combined.
[b]Measured as L/12 h.

underscores the importance of understanding ecological, behavioral, and cultural influences on human water use.

6 | POPULATION VARIATION

Environmental factors (ie, temperature, humidity, seasonal variability, and altitude), as well as behavioral factors such as the type, intensity, and duration of physical activity, can alter water turnover (Anand & Chandrashekhar, 1996; Fusch et al., 1996; IOM, 2004; Shimamoto & Komiya, 2000). Few studies have attempted to include all of these factors in an analysis of water turnover. Instead, most studies have focused on one or two contributing variables. For example, studies investigating the effects of temperature have shown 50% to 100% greater water turnover for individuals living in hot, tropical climates (Singh et al., 1989). Tani et al. (2015) analyzed dietary records for n = 242 Japanese adults and found daily water intake was 9% higher in the summer, an effect they attributed to higher temperatures (humidity had no effect in their models). Cold, dry air can also increase insensible water loss (Freund & Young, 1996) and thus may contribute to greater water demands.

Physical activity increases water turnover, particularly when sweating to thermoregulate (Leiper et al., 1996, 2001; Ruby et al., 2003; Sawka et al., 2005; Shimamoto & Komiya, 2003). Sweating rates can exceed 3 L/h during strenuous activity in hot conditions (Figure 1, IOM, 2004; Lieberman, 2015; Sawka, 1992). Leiper and colleagues have found water turnovers to be ~1.2 L/d higher for physically active men (Table 1) compared to sedentary men (Leiper et al., 1996, 2001). These findings are consistent with comparisons of age-matched endurance runners and sedentary men, which found that the endurance runners had an increased water turnover of ~1 L/d (Shimamoto & Komiya, 2003). In a study by Ruby et al. (2003), water turnovers were calculated from eight male and nine female wildfire firefighters involved in firefighting activities. The extreme conditions and high physical demands resulted in water turnovers that were ~2 times greater than what has been reported for a US reference population (Raman et al., 2004; Ruby et al., 2003).

While the individual effects of activity, heat, and humidity on water turnover are known (IOM, 2004), the potential interaction of anthropometrics, environment, and behavior on water physiology hinder our ability to model human water needs reliably across populations that vary in ecological, behavioral, and dietary factors. Our ability to predict water turnover during daily life for diverse populations globally is further constrained by a lack of diversity among the populations sampled. Most data on human water intake or turnover come from studies of US or European populations. Two of the largest studies on water turnover come from the US (n = 251 men, n = 207 women) (Raman et al., 2004) and Germany (n = 639 men, n = 889 women) (Manz et al., 2012). By contrast, relatively few studies have collected water turnover or intake data from small-scale, nonindustrialized populations. The list of small-scale populations for whom water turnover data has been collected includes the Shuar forager-horticulturalists of Amazonian Ecuador, the Tsimane forager-horticulturalists of lowland Bolivia, the Aymara agropastoralists of the Bolivian highlands, and a community of Mestizo peoples living in the highlands of Ecuador (Figure 4; Table 1). Data from

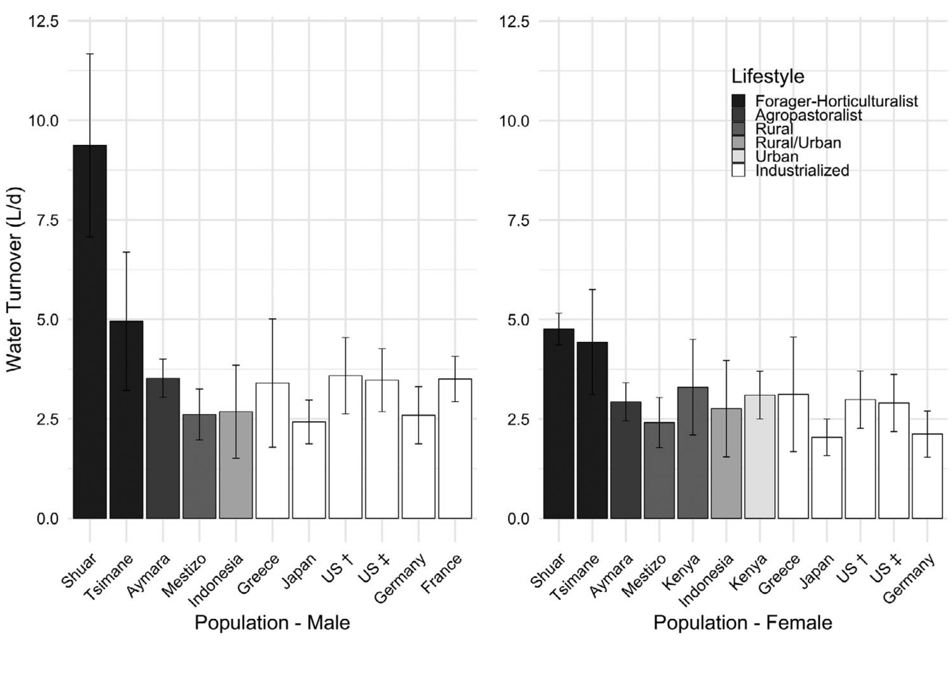

FIGURE 4 Mean daily water turnovers for men and women across small-scale and industrialized populations. US measures were derived from two studies: †Raman et al. (2004) and ‡Kant et al. (2009). Measures for the Shuar (Christopher et al., 2019), Aymara (Kashiwazaki et al., 2009), Kenya (Keino et al., 2014), US† (Raman et al., 2004), and France (Blanc et al., 1998) were calculated using the deuterium depletion method. Tsimane (Rosinger & Tanner, 2015), Mestizo (Berti & Leonard, 1998), Indonesia (Laksmi et al., 2018), Greece (Athanasatou et al., 2016), Japan (Tani et al., 2015), Germany (Manz et al., 2012), and US‡ (Kant et al., 2009) data were collected via nutritional survey. Error bars indicate ±1 SD

developing regions include a sample of rural and urban women living in Kenya, and a large-scale fluid intake study of several Indonesian populations (Keino et al., 2014; Laksmi et al., 2018).

Large-scale studies of industrialized populations provide information on the water requirements for mostly sedentary individuals living in temperate climates with access to climate control and abundant sources of clean water. Mean values of water turnover for industrialized populations, such as those in the United States and Germany, typically lie near the AI values set by the U.S. IOM (2004), which suggest intakes of 3.7 and 2.7 L/d for men and women, respectively. Water throughout varies widely for individuals within these populations. In the large US sample by Raman et al. (2004), water turnover ranged from 1.4 to 7.7 L/day for men and 1.2 to 4.6 L/day for women. Greater requirements would be expected for physically active individuals or those living in hot or high-altitude environments that elicit higher rates of water turnover (IOM, 2004).

The limited data available from small-scale societies indicates that water turnover in these populations is often more similar to industrialized populations than expected. For example, average water turnovers among Kenyan women living in both urban and rural settings and physically active Aymara men and women are within the range of those measured across a number of industrialized study populations (Table 1) (Berti & Leonard, 1998; Kant et al., 2009; Kashiwazaki et al., 2009; Keino et al., 2014; Manz et al., 2012; Raman et al., 2004). Similarly, a large-scale study in Indonesia, a hot, tropical environment, found water intakes similar to industrialized populations in temperate climates (Table 1) (Laksmi et al., 2018).

Cultural practices, particularly diet, can have a larger effect than activity or environment on water turnover. Foods that are high in water content or dependence on culturally important beverages can raise water intake. For example, Shuar adults have the highest mean water turnovers recorded during normal daily life among human populations to date (9.37 ± 2.3 L/d for men, 4.47 ± 0.4 L/d for women), much greater than those of Tsimane men and women who live in a similar ecological context and have broadly similar subsistence and dietary practices (Christopher et al., 2019; Rosinger & Tanner, 2015). Water turnover in both populations is likely influenced by environmental variables and physical activity, but the high turnovers evident in the Shuar clearly reflect the consumption of large quantities of chicha, a traditional fermented beverage made from manioc (Christopher et al., 2019). Indeed, cultural dietary differences can affect not only the amount of water intake, but also the proportion of water intake from different beverages and foods (Athanasatou et al., 2016; Morin et al., 2018; Tani et al., 2015). For example, Morin et al. (2018) found considerable differences between countries (Argentina, Brazil, China, Indonesia, Mexico, and Uruguay) in both the volume of fluid intake and the proportions from sugar-sweetened beverages, dairy, and water among children and adolescents.

Variation in water security, which is often overlooked as an environmental predictor of water turnover, may explain similarities between water turnover and intake values across industrialized and small-scale populations. In most developed populations, clean potable water is consistently available. Safe water is not always readily available in many foraging and farming populations, and poor water quality places many small-scale populations at increased risk of potential lethal water-borne illnesses (Rosinger, 2015a, 2015b). Regions that are arid or prone to drought heighten these challenges. These social and environmental pressures may constrain water consumption behavior and, in turn, affect water balance physiology. Consequently, broad similarities in water turnover among small-scale and industrialized populations (Table 1, Figure 4) may mask differences in hydration-related health. It is unclear at present whether the similar water intakes among populations reflect similar needs, or if needs for small-scale societies are greater but are chronically unmet. Work by Rosinger (2015a, 2015b) suggests water scarcity and dehydration may be common in small-scale societies. Developing better accurate guidelines for water intake in small-scale populations will require more investigation into the environmental and social determinants of water turnover in small-scale societies and their impacts on hydration physiology and health.

7 | CLIMATE CHANGE

The need for a more fully realized cross-cultural understanding of water turnover is amplified by the impending threats of the climate crisis, which are likely to produce significant environmental disruptions that will directly affect water availability. Water scarcity can manifest in two ways, as "physical scarcity" that results from insufficient environmental supply, and "economic scarcity" that occurs when there is a lack of necessary water infrastructure to supply a population (International Water Management Institute, 2007; UNESCO, 2019). Population growth and its related economic changes (increased urbanization, agricultural demand, and pollution) are important drivers of both physical and economic water scarcity (Food and Agriculture Organization of the United Nations [FAO], 2012; Guppy & Anderson, 2017). These economic demands for water and a lack of adequate supply have already led to widespread water scarcity, with over a quarter of the world's population living without access to safe water (UNESCO, 2019). The increased water requirements of growing populations, and their agricultural and industrial needs, are compounded by shrinking of temperate regions and subsequent expansion of hot arid zones around the world, exacerbating issues of water insecurity in developing nations (Intergovernmental Panel on Climate Change [IPCC], 2017; Stringer et al., 2009). Though much work has focused on understanding the complex relationships between water demand and supply, without adequate understanding of variation in water turnover and water requirements across populations living in different environments, large number of people may continue to face a growing risk of water insecurity (DeNicola, Aburizaiza, Siddique, Khwaja, & Carpenter, 2015; Organization for Economic Co-operation and Development, 2012; UNESCO, 2019).

As the world continues to warm and the global population increases, the effects of climate change are predicted to affect nonindustrialized nations disproportionately, with indigenous peoples of those countries being some of the most vulnerable (Levy & Patz, 2015; Moore & Diaz, 2015). Like the asymmetrical distribution of global temperature rise, severe changes in rainfall patterns that result in physical water scarcity are a growing concern for countries already dealing with economic water scarcity (Dettinger, Udall, & Georgakakos, 2015; FAO, 2012; Kaushal, Gold, & Mayer, 2017). These concerns are aggravated by climate models that suggest the likelihood of increased climatic variability (Folland, Karl, & Salinger, 2002; IPCC, 2017). Climate variability can lead to prolonged periods of drought and water stress, specifically in regions that already experience frequent drought condition (Ayoub & Alward, 1996). Consequently, while overall global precipitation is predicted to increase, water stress and dehydration remains a growing threat for many.

Over the past 50 years countries in Asia and Africa have seen the largest increase in population, and current population growth among the 49 least developed nations is nearly double that of developed countries (United Nations, 2010). Of the 25 countries with the highest rates of population growth, 23 are located in the Middle East or Africa (Department of Economic and Social Affairs, Population Division, United Nations [DESA], 2017). Yet, while the importance of environmental and lifestyle effects on water turnover are widely acknowledged (DESA, 2017; IOM, 2004), the preponderance of data on water turnover and hydration requirements come from populations with little cultural, behavioral, and environmental relevance to a large portion of the global population. This combination of underrepresentation in the literature and increased ecological and economic threat leaves small-scale populations around the world at greater threat of water insecurity. A more accurate understanding of the environmental and behavioral variables that can affect water turnover is vital to address this threat.

8 | NEW DIRECTIONS

As this review has described, the factors influencing daily water requirements are myriad, and a better understanding of the diversity of human hydration is needed. Specifically, more research into the water requirements and physiology of small-scale societies and other nonindustrialized populations is essential if we are to develop a comprehensive understanding of human water needs. Water turnover data for children in these populations is of particular importance, not only to increase the cross-cultural representation, but also to help protect those who may be the most vulnerable to water stress.

With more measures of water use across a greater diversity of lifestyle and ecology, the effects of behavioral and environmental factors might come into better focus, advancing current models of water turnovers for humans. These efforts will require researchers in the field to expand current nutritional surveys to include measures of water use. More widespread use of isotope tracking methods would also improve the precision of these measures. The impending threat of increased water stress across the globe due to climate change and increasing economic disparity heightens the importance of understanding human water requirements. It has long been known that water is essential for life. It is past time for our deep understanding of this vital nutrient to reflect its physiological, cultural, and ecological importance.

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