

Current Biology

Evolution of water conservation in humans

Highlights

- Humans have evolved to use less water per day than other ape species
- Human drinking regulation apparently targets lower water/dietary energy ratio
- Water-conserving mechanisms in humans are unclear but may include the external nose
- Zoo apes may benefit from diets that match dietary water/energy ratios in the wild

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In brief

Pontzer et al. use isotope depletion to show that humans have evolved to use less water per day. Apes in zoos and sanctuaries adjust their drinking to obtain a similar ratio of dietary water/energy as wild ape diets. Humans across diverse lifestyles, including hunter-gatherers, habitually consume a lower water/energy ratio than apes.

Report

Evolution of water conservation in humans

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SUMMARY

To sustain life, humans and other terrestrial animals must maintain a tight balance of water gain and water loss each day.^{1–3} However, the evolution of human water balance physiology is poorly understood due to the absence of comparative measures from other hominoids. While humans drink daily to maintain water balance, rainforest-living great apes typically obtain adequate water from their food and can go days or weeks without drinking^{4–6}. Here, we compare isotope-depletion measures of water turnover (L/d) in zoo- and rainforest-sanctuary-housed apes (chimpanzees, bonobos, gorillas, and orangutans) with 5 diverse human populations, including a hunter-gatherer community in a semi-arid savannah. Across the entire sample, water turnover was strongly related to total energy expenditure (TEE, kcal/d), physical activity, climate (ambient temperature and humidity), and fat free mass. In analyses controlling for those factors, water turnover was 30% to 50% lower in humans than in other apes despite humans' greater sweating capacity. Water turnover in zoo and sanctuary apes was similar to estimated turnover in wild populations, as was the ratio of water intake to dietary energy intake (~2.8 mL/kcal). However, zoo and sanctuary apes ingested a greater ratio of water to dry matter of food, which might contribute to digestive problems in captivity. Compared to apes, humans appear to target a lower ratio of water/energy intake (~1.5 mL/kcal). Water stress due to changes in climate, diet, and behavior apparently led to previously unknown water conservation adaptations in hominin physiology.

RESULTS

Total energy expenditure (TEE), fat free mass, temperature, and relative humidity were positively associated with water turnover among apes and humans in multivariate general linear models (Figure 1; Table S2). Stepwise regression with Akaike's Information Criterion identified TEE, fat free mass, mean daily temperature, mean relative humidity, genus, and lifestyle, but neither sex nor age, as significant factors for water turnover. Sex and age were therefore dropped from subsequent multivariate analyses. Accounting for TEE, fat free mass, temperature, humidity, and

lifestyle using general linear models, all ape genera had greater water turnover than humans (Tables 1, S1, and S2; Figure 2). Analyzing water turnover using linear mixed effects models with site of data collection as a random effect produced similar results (STAR methods; Table S2). Among apes, water turnover was greatest for *Pan* (chimpanzees and bonobos; scaled $\beta = 2.25 \pm 0.15$, $p < 0.001$), lowest for *Gorilla* (scaled $\beta = 1.82 \pm 0.26$, $p < 0.001$), and lower for apes in sanctuaries (scaled $\beta = -1.80 \pm 0.23$, $p < 0.001$) than in zoos in general models with fat free mass, TEE, temperature, and humidity as covariates (Figure 2; Table S2).

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Humans consumed water (food and drink) at ratios of 1.52 ± 0.42 mL/kcal of metabolized energy and 6.79 ± 2.01 mL/g of dry food matter eaten (Figure 2; Table 1). These ratios are much higher than the foods in industrialized and hunter-gatherer diets, and, correspondingly, humans drank more than 2 L/d, on average, across lifestyles (Figure 2; Tables 1 and S3). Still, the human ratios of water/energy and water/grams dry matter were lower than in other hominoids ($p < 0.001$, Welch's t test, both comparisons; Figures 2D and 2F). Apes in zoos and sanctuaries consumed water at ratios of 2.79 ± 0.97 mL/kcal and 9.95 ± 3.47 mL/g (Table 1; Figure 2D; Supplemental information). Apes in range-country sanctuaries, located in species' native habitats, were fed diets primarily of fruits, vegetables, and leaves, and they could meet their water needs without drinking (Figure 2C). Apes in zoos in the United States, with much drier diets (Table S4), drank an average of 2 to 5 L/d (Figure 2C).

The ratio of water/energy in wild ape diets (~ 2.5 mL/kcal; Tables S3 and S4) is similar to the ratio of water/energy intake observed among captive apes in our dataset (Figure 2D). Thus, for a given TEE and daily energy intake, the estimated daily water intake and water turnover for wild apes are similar to those of apes in zoos and sanctuaries (Figure 3, Figure S1). Indeed, it is notable that despite large differences in the water content of their food, apes in zoos and sanctuaries, across genera, voluntarily adjusted their drinking such that they converged on a water/energy ratio that matches wild ape diets (Figure 2D). By contrast, the ratio of water/grams of dry matter ingested for zoo and sanctuary apes was elevated compared to the wild (Figure 2F).

DISCUSSION

Results here shed new light on water balance regulation in humans and other apes. In the wild, great apes in rainforests typically obtain the water they need from their food, and can go several days—even several weeks—without drinking,^{4–6} although water stress during dry seasons and for savannah-living

chimpanzees is more acute.⁷ Forest-dwelling early hominins, subsisting on plant foods,⁸ would have presumably been similar to forest-living great apes in their water balance physiology. Maintaining water balance would have become much more challenging as hominins expanded into hotter and more arid environments, evolved prodigious sweating capabilities to cope with heat stress,⁹ and expanded the diet to include more meat and, later, cooked foods. However, prior to this study, it was unknown whether humans differ from other apes in daily water turnover.

Compared to other apes, humans in this study had substantially lower water turnover and consumed less water per unit of metabolized food energy, suggesting evolution in the hominin lineage to reduce water intake with food. In mammals, eating activates neurons that stimulate thirst,¹⁰ and thus, eating leads to drinking.^{11,12} Experimental manipulations of food energy density (kcal/g) have shown that rats will adjust their drinking to maintain a relatively constant ratio of ~ 0.7 mL water per kcal metabolized energy, letting the ingested ratio of water/grams dry matter vary.¹¹ Similarly, water turnover measurements here suggest apes in zoos and sanctuaries, with *ad libitum* access to water and diets of differing energy density, adjust their water intake to maintain a water/energy ratio (~ 2.8 mL/kcal) similar to wild ape diets while letting water/gram dry matter ratios rise above those in the wild (Figures 2D and 2F). In contrast, humans appear to target a lower water/energy ratio (~ 1.5 mL/kcal).

The low water/energy ratio in humans (Figure 3D) was consistent across populations, with cohort means ranging from 1.24 ± 0.50 to 1.92 ± 0.31 mL/kcal (Table S6). Even recent measures from a small sample of adults in the Shuar population,¹³ a forager-farmer society in rural Ecuador with cultural drinking practices that result in remarkably high daily water turnover (men: 9.37 ± 2.3 L/d, $n = 7$; women: 4.76 ± 0.4 L/d, $n = 8$), show a similar ratio of water/energy (men: 2.1 ± 0.4 ; women: 1.7 ± 0.2) to the human cohorts in this study. Notably, the water/energy ratio of human breast milk (1.5 ± 0.2 mL/kcal) is identical to the intake ratio determined here for adults, and it is $\sim 25\%$

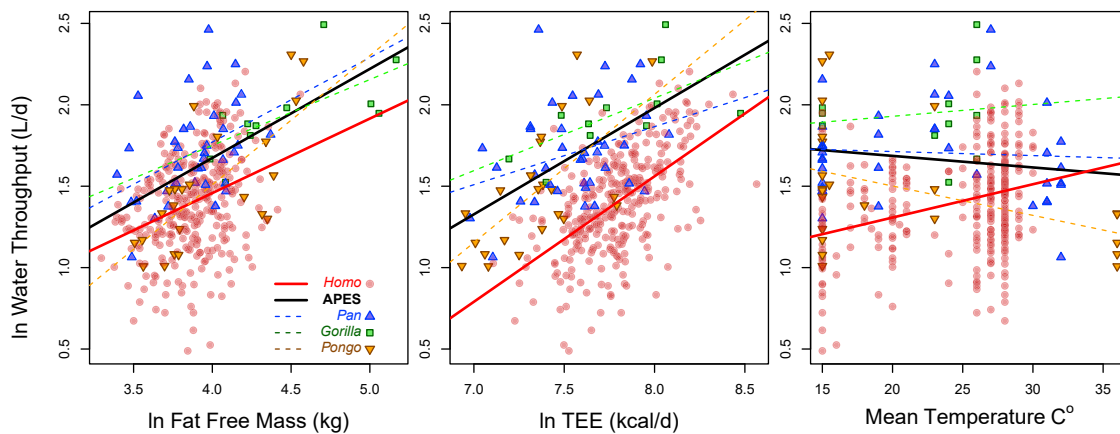


Figure 1. Water turnover in humans and other apes plotted against fat free mass, TEE, and mean daily temperature.

All data points shown. Lines indicate least-squares regressions unadjusted for other factors. See text and [Table S2](#) for full model. Note that temperatures <15°C are pooled.

lower than breast milk in other apes ([Figure S3](#)). Food manipulation experiments in humans and apes are needed to confirm whether human thirst response and water balance physiology is tuned to target a lower ratio of water/energy. Further, more work is needed to assess the ontogeny of water balance physiology and test whether the pattern of water turnover in apes here are consistent across species (e.g., mountain gorillas) and biomes (e.g., semi-arid habitats⁷) not included in these analyses.

Whether drinking behavior in captive apes is influenced by the ratio of water/energy or some other physiological target, their daily water intake combined with their relatively energy-dense, low-bulk diets led to much higher water intake per gram of dry matter ingested compared to wild apes ([Figure 2F](#)). Water/gram

intake must be balanced by water/gram absorption in the intestines and water/gram excretion in the feces. Since fecal moisture in zoo apes is similar to that in wild populations ([STAR methods](#)), the high water/gram intake in captivity requires greater intestinal water absorption ([Figure 3](#); [Table S1](#)). Greater intestinal water absorption in captivity is also evident in lower urine-specific gravities (which indicate greater 24 h urine production) in zoo and sanctuary apes compared to wild populations ([Figure S2](#)), as increased water absorption into the bloodstream must induce increased urine production in order to maintain blood osmolality homeostasis. The physiological challenge of greater intestinal water absorption in captive apes could contribute to the prevalence of digestive problems, and associated atypical behaviors

Table 1. Key characteristics for human and ape cohorts

Genus	lifestyle	sex	N	Mass (kg)		TEE (kcal/d)		Water Turnover (L/d)		Water/Energy (mL/kcal)		Water/DM Food (mL/g)	
				mean	SD.	mean	SD.	mean	SD.	mean	SD.	mean	SD.
<i>Homo</i>	Sedentary	F	70	80.3	19.5	2,196	354	3.32	0.84	1.33	0.43	6.36	2.04
	Labor	F	68	75.1	18.8	2,284	437	4.24	1.13	1.63	0.35	7.77	1.69
	HG	F	22	69.7	6.4	1,849	355	3.77	0.60	1.87	0.34	5.83	1.08
<i>Pan</i>	Zoo	F	15	48.0	7.8	1,770	364	5.66	1.99	3.15	1.42	11.26	5.08
	Sanctuary	F	3	41.7	9.3	1,600	393	4.86	0.73	2.87	0.78	10.26	2.77
<i>Gorilla</i>	Zoo	F	7	78.6	14.7	2,005	491	6.18	0.94	2.97	0.57	10.61	2.03
<i>Pongo</i>	Zoo	F	8	60.4	6.1	1,613	386	4.06	1.06	2.38	0.65	8.49	2.30
	Sanctuary	F	3	47.1	1.9	1,113	71	3.23	0.53	2.67	0.66	9.52	2.36
<i>Homo</i>	Sedentary	M	53	76.8	14.9	2,818	560	4.67	1.32	1.46	0.46	6.97	2.18
	Labor	M	70	73.5	22.1	2,862	577	4.92	1.60	1.51	0.41	7.17	1.97
	HG	M	26	50.4	5.1	2,504	370	4.38	0.59	1.57	0.33	4.90	1.03
<i>Pan</i>	Zoo	M	12	65.9	11.2	2,391	499	6.78	1.69	2.74	0.83	9.79	2.96
	Sanctuary	M	8	49.8	11.3	1,866	448	4.75	1.38	2.36	0.83	8.43	2.96
<i>Gorilla</i>	Zoo	M	4	166.4	42.5	3,521	854	9.07	2.34	2.52	0.98	9.00	3.51
<i>Pongo</i>	Zoo	M	10	88.1	31.3	1,859	514	6.08	2.46	3.09	1.01	11.02	3.61
	Sanctuary	M	2	70.1	27.9	1,458	413	3.36	0.58	2.08	0.27	7.43	0.95

Additional variables and statistical analyses are listed in [Tables S1](#) and [S2](#). Sed, sedentary; Labor, manual labor; HG, hunter-gatherer; Sanct, sanctuary. See [Table S1](#). DM Food, dry matter of food intake.

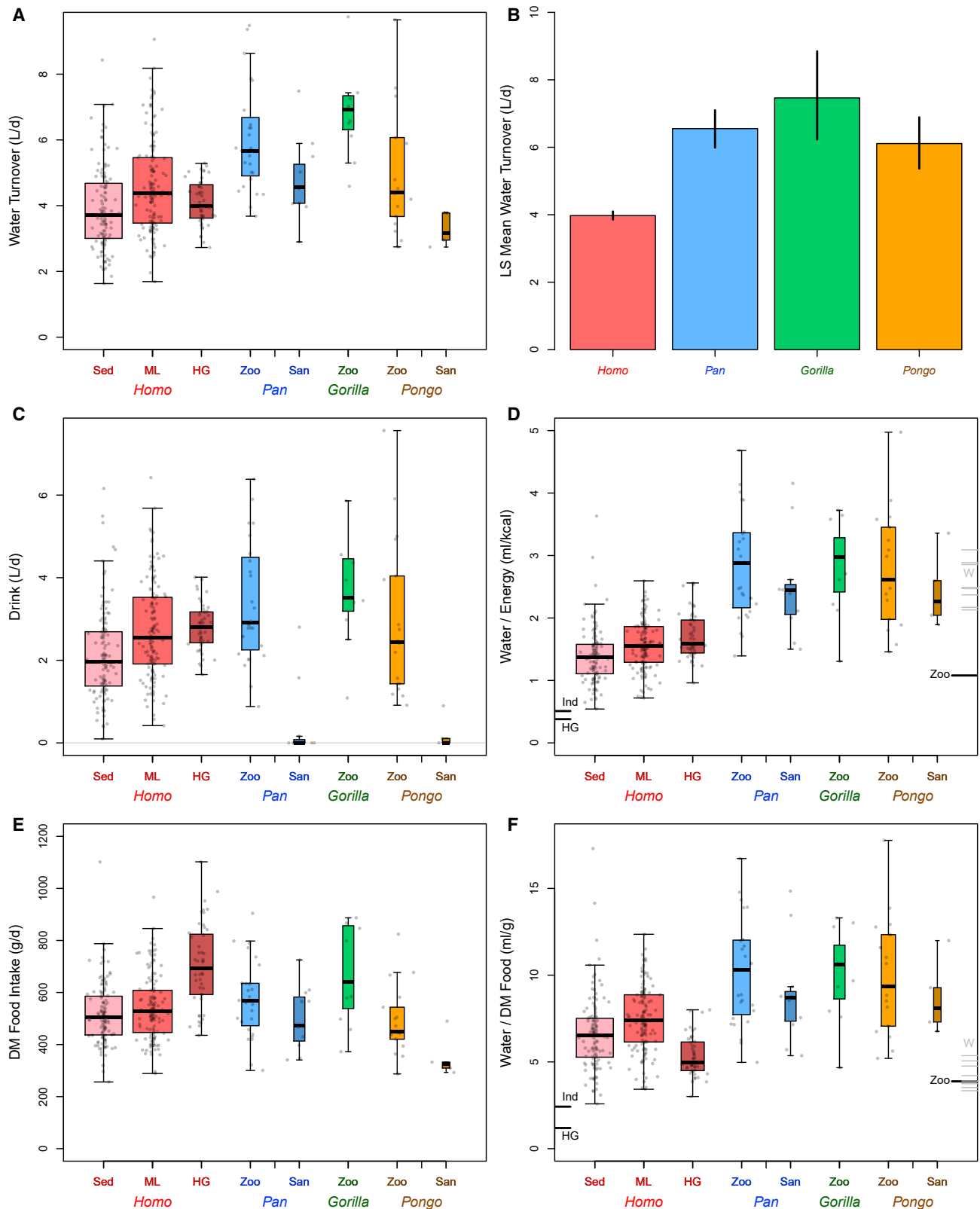


Figure 2. Water turnover for humans (sedentary, manual labor, and hunter-gatherer) and apes (zoo and sanctuary)

All data points shown. Boxes indicate median and quartiles; whiskers indicate range excluding outliers. Box width corresponds to sample size.

(A) Daily water turnover (L/d).

(legend continued on next page)

such as regurgitation and re-ingestion, in these populations. Indeed, provisioning with browse, which increases food bulk and fiber ingestion and thus fecal water loss (and therefore decreases demand for intestinal water absorption), has been shown to reduce regurgitation and re-ingestion behaviors in zoo-living chimpanzees, gorillas, and orangutans.^{14–16}

Humans' derived sweating physiology^{9,17} was apparent in the effects of physical activity and temperature on water turnover. Humans' high number of eccrine glands enables sweat production in excess of 2 L/h during heat stress, 4–10 times the rate of chimpanzees,^{9,17} and both sweating and insensible water loss are greater with increased physical activity in hot, dry climates.¹ In the human sample, Hadza hunter-gatherers, the population with the most physical activity in this sample¹⁸ had the highest water turnover in analyses accounting for effects of TEE, climate, and fat free mass (Figure 1; Table S2). Manual laborers' water turnover was higher than sedentary humans' but lower than hunter-gatherers' (Figure 2; Table S2). Mean daily temperature was also correlated strongly with water turnover in humans, likely reflecting increased loss via sweat (Figure 1; Table S2). By contrast, among non-human apes, cohorts in sanctuaries, which were the hottest settings, had lower water turnover than those in zoos (Figure 2; Table S2).

Lower water turnover and water/energy ratio in humans suggest strong selection to conserve water in the hominin lineage. Dietary changes with the advent of hunting and gathering, particularly cooking (other than boiling), increased the caloric density and reduced the water content of hominin foods relative to other primates¹⁹. These changes are evident among living populations today: compared to the diets of forest-living wild apes, modern hunter-gatherer diets have ~80% more energy per gram of dry matter and hold ~80% less water per kcal; diets of industrialized human populations are equally dry (Tables S3 and S4). With such low water content in their foods, hominins became obligate drinkers (Figure 3). Expansion into drier environments, along with increased physical activity in the heat of the day, would have exacerbated water loss and water stress for Pleistocene *Homo*.^{9,17} Natural selection, in turn, appears to have favored anatomical and physiological changes that reduced water turnover, enabling hominins to range further from lakes and streams and reducing their exposure to predators in those environments.

Hominin water conservation adaptations remain to be determined and characterized. Intriguingly, external noses, which reduce insensible water loss²⁰ and have been proposed as water conservation adaptations,²¹ first appear in the hominin fossil record with *Homo habilis* ~2 million years ago and continue to develop thereafter.^{9,21} Anatomical and functional variation in the hominoid kidney warrants further study, but we note that human kidney size is similar to that of other primates (including chimpanzees) and that urine-concentrating abilities appear to be similar among humans and other apes (Figure S2).

The ecological impact of reduced water turnover in the hominin lineage warrants further investigation, including a broader comparative analysis of water turnover in other primates. Some evolutionary reconstructions place Plio-Pleistocene hominins in riparian habitats with constant access to water,²² which would presumably eliminate selection to reduce water needs. Reduced water turnover in humans strongly challenges this view, suggesting selection for behavioral and physiological adaptations to limit dependence on open water for drinking. For baboons living in semi-arid savanna habitats, dependence on water sources for drinking acts as an ecological tether, constraining daily travel.²³ Chimpanzee communities in semi-arid savanna habitats appear to be similarly constrained by access to water.^{7,24} Adaptations to reduce water demands may have been essential in enabling early *Homo* to venture farther from open water sources and pursue a physically demanding foraging strategy as the hunting and gathering ecological regime emerged and developed throughout the Pleistocene.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2021.02.045>.

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(B) Least square mean water turnover (\pm confidence intervals) calculated at a constant TEE, fat free mass, temperature, and relative humidity.

(C) Estimated water drunk per day.

(D) The ratio of water ingested (food and drink) per kilocalorie of metabolized energy. Black lines along panel margins indicate ratios of diets (food only) in industrial (Ind), hunter-gatherer (HG), and zoo populations; gray lines (W) indicate ratios for forest-living wild apes (shown in Tables S3 and S4).

(E) Dry matter (DM) food intake per day.

(F) Ratio of water per DM food ingested. Black and gray lines along margins reflect diets as in (D).

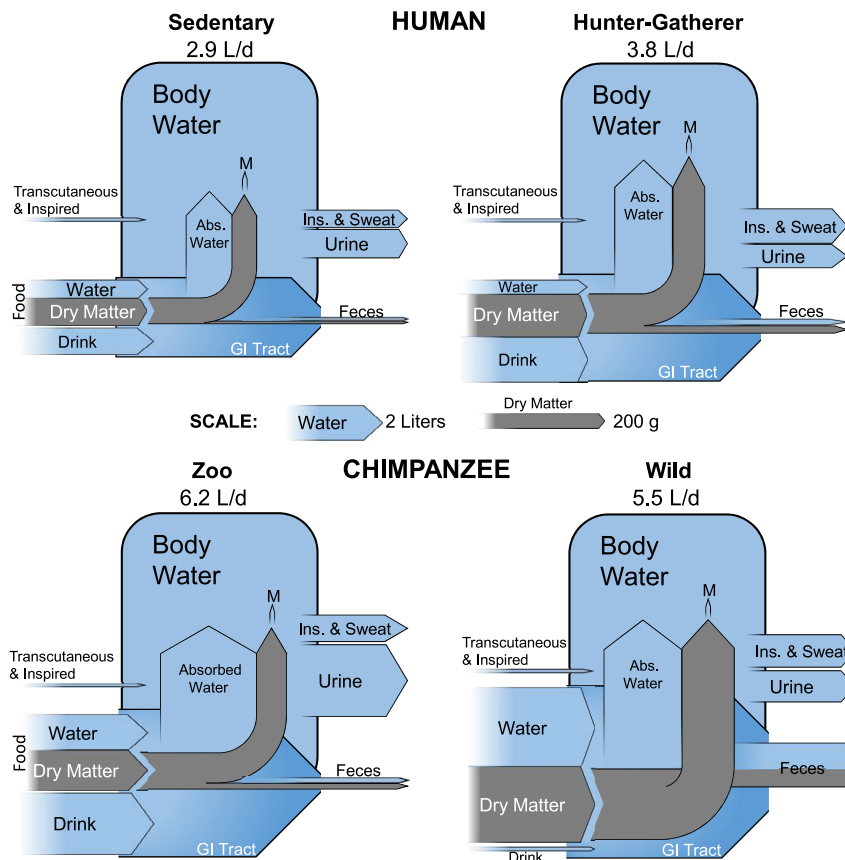


Figure 3. Modeled water turnover for humans and chimpanzees with similar fat free mass and body water pools (calculations in Table S5)

Influx (gain) and efflux (loss) pathways are shown to scale. Water (blue) and grams dry matter (gray) intake from food are estimated from dietary water and energy content (shown in Tables S3 and S4). Among humans, physically active hunter-gatherers subsisting on wild-food diets have greater estimated sweat and fecal water loss than sedentary humans. In zoo apes, net water absorption in the gastrointestinal tract is much greater than observed in wild apes or in any human populations. M, metabolic water production.

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AUTHOR CONTRIBUTIONS

H.P. designed the study; H.P., M.H.B., B.M.W., A.Z.P.M., J.H., D.A.R., H.D., B.H., K.W., A.L., L.R.D., J.P.R., P.B., T.E.F., R.W.S., J.M.R., E.V., F.S., S.A., D.R., and S.R.R. collected data; H.P., M.E.T., S.S.U., J.M.R., and D.S. analyzed data. All authors contributed to writing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing financial interests.

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REFERENCES

- Cheuvront, S.N., Kenefick, R.W., Montain, S.J., and Sawka, M.N. (2010). Mechanisms of aerobic performance impairment with heat stress and dehydration. *J Appl Physiol* 109, 1989–1995.
- Armstrong, L.E., and Johnson, E.C. (2018). Water Intake, Water Balance, and the Elusive Daily Water Requirement. *Nutrients* 10, 1928.
- Popkin, B.M., D'Anci, K.E., and Rosenberg, I.H. (2010). Water, hydration, and health. *Nutr. Rev.* 68, 439–458.
- Wrangham, R.W. (1977). Feeding behavior of chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes*, T.H. Clutton-Brock, ed. (Academic Press), pp. 503–538.
- Ashbury, A.M., Posa, M.R., Dunkel, L.P., Spillmann, B., Atmoko, S.S., van Schaik, C.P., et al. (2015). Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan. *Am. J. Primatol.* 77, 1216–1229.
- Rothman, J.M., Dierenfeld, E.S., Hintz, H.F., and Pell, A.N. (2008). Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia* 155, 111–122.

7. Wessling, E.G., Kühl, H.S., Mundry, R., Deschner, T., and Pruetz, J.D. (2018). The costs of living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees. *J. Hum. Evol.* *121*, 1–11.
8. Su, D.F. (2013). The earliest hominins: *Sahelanthropus*, *Orrorin*, and *Ardipithecus*. *Nature Education Knowledge* *4*, 11.
9. Lieberman, D.E. (2015). Human locomotion and heat loss: an evolutionary perspective. *Compr. Physiol.* *5*, 99–117.
10. Zimmerman, C.A., Lin, Y.C., Leib, D.E., Guo, L., Huey, E.L., Daly, G.E., Chen, Y., and Knight, Z.A. (2016). Thirst neurons anticipate the homeostatic consequences of eating and drinking. *Nature* *537*, 680–684.
11. Adolph, E.F. (1947). Urges to eat and drink in rats. *Am. J. Physiol.* *151*, 110–125.
12. Engell, D. (1988). Interdependency of food and water intake in humans. *Appetite* *10*, 133–141.
13. Christopher, L., Madimenos, F.C., Bribiescas, R.G., Urlacher, S.S., Snodgrass, J.J., Sugiyama, L.S., and Pontzer, H. (2019). High energy requirements and water throughput of adult Shuar forager-horticulturalists of Amazonian Ecuador. *Am. J. Hum. Biol.* e23223.
14. Fuller, G., Murray, A., Thume, M., McGuire, M., Vonk, J., and Allard, S. (2018). Behavioral and hormonal responses to the availability of forage material in Western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biol.* *37*, 23–34.
15. Cassella, C.M., Mills, A., and Lukas, K.E. (2012). Prevalence of regurgitation and reingestion in orangutans housed in North American zoos and an examination of factors influencing its occurrence in a single group of Bornean orangutans. *Zoo Biol.* *31*, 609–620.
16. Struck, K., Videan, E.N., Fritz, J., and Murphy, J. (2007). Attempting to reduce regurgitation and reingestion in a captive chimpanzee through increased feeding opportunities: a case study. *Lab Anim. (NY)* *36*, 35–38.
17. Kamberov, Y.G., Guhan, S.M., DeMarchis, A., Jiang, J., Wright, S.S., Morgan, B.A., Sabeti, P.C., Tabin, C.J., and Lieberman, D.E. (2018). Comparative evidence for the independent evolution of hair and sweat gland traits in primates. *J. Hum. Evol.* *125*, 99–105.
18. Raichlen, D.A., Pontzer, H., Harris, J.A., Mabulla, A.Z., Marlowe, F.W., Josh Snodgrass, J., Eick, G., Colette Berbesque, J., Sancilio, A., and Wood, B.M. (2017). Physical activity patterns and biomarkers of cardiovascular disease risk in hunter-gatherers. *Am. J. Hum. Biol.* *29*, <https://doi.org/10.1002/ajhb.22919>.
19. Simmen, B., Pasquet, P., Masi, S., Koppert, G.J.A., Wells, J.C.K., and Hladik, C.M. (2017). Primate energy input and the evolutionary transition to energy-dense diets in humans. *Proc. Biol. Sci.* *284*, 20170577.
20. Svensson, S., Olin, A.C., and Hellgren, J. (2006). Increased net water loss by oral compared to nasal expiration in healthy subjects. *Rhinology* *44*, 74–77.
21. Franciscus, R.G., and Trinkaus, E. (1988). Nasal morphology and the emergence of *Homo erectus*. *Am. J. Phys. Anthropol.* *75*, 517–527.
22. Vanechoutte, M., Kuliukas, A.V., and Verhaegen, M. (2011). In Was Man More Aquatic In The Past? Fifty Years After Alister Hardy - Waterside Hypotheses Of Human Evolution, G.W. Atta-ur-Rahman, M. Caldwell, A. Vanechoutte, B.A. Kuliukas, Springer, and M. Verhaegen, eds. (Bentham Science Publishers).
23. Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W., and Simpson, A.J. (1992). Habitat use and resource availability in baboons. *Anim. Behav.* *43*, 831–844.
24. Pruetz, J.D., and Bertolani, P. (2009). Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: Implications for hominin adaptations to open habitats. *Paleoanthropology* *2009*, 252–262.
25. Team, R.C. (2020). R: A language and environment for statistical computing (R Foundation for Statistical Computing).
26. Pontzer, H., Brown, M.H., Raichlen, D.A., Dunsworth, H., Hare, B., Walker, K., Luke, A., Dugas, L.R., Durazo-Arvizu, R., Schoeller, D., et al. (2016). Metabolic acceleration and the evolution of human brain size and life history. *Nature* *533*, 390–392.
27. Pontzer, H., Durazo-Arvizu, R., Dugas, L.R., Plange-Rhule, J., Bovet, P., Forrester, T.E., et al. (2016). Constrained total energy expenditure and metabolic adaptation to physical activity in adult humans. *Curr. Biol.* *26*, 410–417.
28. Pontzer, H., Wood, B.M., and Raichlen, D.A. (2018). Hunter-gatherers as models in public health. *Obes. Rev.* *19 (Suppl 1)*, 24–35.
29. Speakman, J.R. (1997). *Doubly Labelled Water: Theory and Practice* (Chapman and Hall).
30. IAEA (2009). *Assessment of Body Composition and Total Energy Expenditure in Humans Using Stable Isotope Techniques* (International Atomic Energy Agency).
31. Rothman, J.M., Chapman, C.A., and Van Soest, P.J. (2012). Methods in primate nutritional ecology: a user's guide. *Int. J. Primatol.* *33*, 542–566.
32. Raman, A., Schoeller, D.A., Subar, A.F., Troiano, R.P., Schatzkin, A., Harris, T., Bauer, D., Bingham, S.A., Everhart, J.E., Newman, A.B., and Tylavsky, F.A. (2004). Water turnover in 458 American adults 40–79 yr of age. *Am. J. Physiol. Renal Physiol.* *286*, F394–F401.
33. Benedict, F.G. (1916). A photographic method for measuring the surface area of the human body. *American Journal of Physiology-Legacy Content* *41*, 275–291.
34. Bruhn, J.M., and Benedict, F.G. (1936). The respiratory metabolism of the chimpanzee. *Proc. Am. Acad. Arts Sci.* *71*, 259–326.
35. Morrison, S.D. (1953). A method for the calculation of metabolic water. *J. Physiol.* *122*, 399–402.
36. Besenbacher, S., Hvilsom, C., Marques-Bonet, T., Mailund, T., and Schierup, M.H. (2019). Direct estimation of mutations in great apes reconciles phylogenetic dating. *Nat. Ecol. Evol.* *3*, 286–292.
37. Schoeller, D.A. (1983). Energy expenditure from doubly labeled water: some fundamental considerations in humans. *Am. J. Clin. Nutr.* *38*, 999–1005.
38. Fjeld, C.R., Brown, K.H., and Schoeller, D.A. (1988). Validation of the deuterium oxide method for measuring average daily milk intake in infants. *Am. J. Clin. Nutr.* *48*, 671–679.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Chemicals		
Doubly labeled water (6% $^2\text{H}_2\text{O}$, 10% H_2^{18}O)	Sigma Aldrich	Q37135-CONF
Software and Algorithms		
R	25	N/A
Other		
Published isotope measures of Ape TEE	26	N/A
Published isotope measures of Human TEE	27	N/A
Published isotope measures of Human TEE	28	N/A

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources and data should be directed to and will be fulfilled by the Lead Contact, Herman Pontzer (herman.pontzer@duke.edu).

Materials Availability

This study did not generate new unique materials.

Data and Code Availability

The datasets and code generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. There are some restrictions to the availability of human data due to confidentiality and privacy concerns as well as the legal requirements of participating institutions regarding the sharing of human data.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Humans

All human subjects in this study were included in previous studies of TEE^{26–28} and are secondary analyses of those data. Human subjects research permissions were obtained from participating U.S. institutions (Loyola Medical School, Hunter College of the City University of New York, Yale University, University of Arizona) and countries and cognizant regional governments in which the measurements took place (Seychelles, Ghana, Tanzania, and Jamaica). All subjects provided informed consent prior to participation, and all were adults (18+ years). All human subjects were adults 18 years or older with no known health issues that would affect energy expenditure or water turnover. Age, gender, weight, and other details are listed in [Tables 1](#) and [S1](#).

Non-Human Apes

For the ape sample, research permissions were obtained from IACUC and other institutional ethics boards at participating institutions (Houston Zoo, Indianapolis Zoo, Jacksonville Zoo, Lincoln Park Zoo, Milwaukee County Zoo, North Carolina Zoo, Oklahoma City Zoo, Oregon Zoo, Zoo Atlanta, Woodland Park Zoo, Dallas Zoo, Brookfield Zoo and Columbus Zoo, Tchimpounga, Lola ya Bonobo, Nyaru Menteng) prior to data collection. Most ape subjects in this study were included in a previous study of ape energy expenditure.²⁶ The dataset in the present study includes new measures for 3 F chimpanzees, 4 M and 3 F orangutans, and 1 F gorilla from U.S. zoos that were completed after the original study on ape energetics.²⁶ We also include a new sample of orangutans from the Nyaru Menteng sanctuary in Indonesia (3F, 2M). These sanctuary orangutans were born in the wild but were rescued from unsafe situations (e.g., logging) and housed in large enclosures with outdoor access during preparations for return to the wild. Methods for the new apes in this sample followed protocols described previously.²⁶ All apes in this analysis were 10+ years old at the time of measurement. We note that the range country sanctuaries included in this study are located in rainforest habitats.

A small number of females were pregnant or nursing (humans: Hadza hunter-gatherers, $n = 7$ nursing, $n = 1$ pregnant; apes: bonobos, $n = 2$ nursing; gorillas, $n = 2$ nursing). We ran all analyses with these subjects excluded and the pattern of results was unchanged. Thus, we included them in analyses in the present analyses. We note that the ape sample was limited by the composition of ape populations at their home facilities, the cooperation of individual apes in participation, and the interest and capacity of institutions in participating. As a result, the size and characteristics of samples varied among species ([Table S1](#)).

METHOD DETAILS

Water Turnover, TEE, and Fat Free Mass

Water turnover, energy expenditure, and body composition were measured using the doubly labeled water method.^{29,30} Measures in this study are largely secondary analyses from our previous studies of energy expenditure in humans and apes,^{26–28} and methods are also described in those papers. Adult humans (18+ years) and apes (10+ years) with no apparent health problems ingested doses of doubly labeled water (6% $^2\text{H}_2\text{O}$, 10% $\text{H}_2\text{-}^{18}\text{O}$; Sigma Aldrich) to achieve adequate enrichment in their body water for a 7 to 12 day measurement. Doses ranged from 30 to 120 g and were tailored to body size following Speakman.²⁹ Human participants drank the dose directly from the bottle, taking care to avoid spills. The bottle was then rinsed three times with tap water, and the rinse water also consumed, to ensure the entire dose was ingested. For apes, zoo or sanctuary staff mixed the dose with fruit juice and the doses were given as a treat. As for human participants, these containers were rinsed and the rinse water ingested.

Urine samples (5 ml) were collected once prior to dosing and then 2–5 times post-dose. For humans, urine samples were collected by the participants themselves using clean urine collection cups, and then transferred to cryovials and frozen (-20°C) until analysis. For apes, urine samples were collected using collection cups (for trained subjects) or from clean, dry trays placed on enclosure floors and then transferred to cryovials and frozen (-20°C) until analysis. Isotope enrichments in each urine sample were measured via mass-spectrometry to calculate the dilution spaces (liters) of ^2H and ^{18}O in each subject's body (N_{D} and N_{O} , respectively) as well as the rates of ^2H and ^{18}O depletion (k_{D} and k_{O} , respectively; percent per day). Mass spectrometry for the samples in this study was carried out at three dedicated doubly labeled water labs (Baylor University, University of Wisconsin, or Hunter College-City University of New York). We tested for lab effects in previous analyses of TEE and found no differences between labs.²⁶ Isotope measures were used to calculate the rate of water turnover (L/d) as

$$\text{Water Turnover(L/d)} = N_{\text{D}}k_{\text{D}} \quad (\text{Equation 1})$$

Total body water (TBW) was calculated from dilution spaces N_{D} and N_{O} following³⁰ as

$$\text{TBW} = 0.5(N_{\text{D}} / 1.041 + N_{\text{O}} / 1.007) \quad (\text{Equation 2})$$

Fat free mass was then calculated by assuming a hydration coefficient of 73.2%. TEE was calculated from the rate of CO_2 production ($r\text{CO}_2$), which was calculated using Equation 6.6 in³⁰ as

$$r\text{CO}_2 = 0.455 \times \text{TBW}(1.007k_{\text{O}} - 1.041k_{\text{D}}) \quad (\text{Equation 3})$$

The rate of CO_2 production was converted to kilocalories per day using the modified Weir equation, following Equation 6.7 in.³⁰

$$\text{TEE(kcal / d)} = 22.4 \times r\text{CO}_2 \times (1.10 + 3.90 / \text{RQ}) \quad (\text{Equation 4})$$

where RQ is the respiratory quotient. RQ values were calculated from dietary macronutrient composition as reported in previous studies.^{26–28}

Temperature and Relative Humidity

Mean daily temperature and mean daily relative humidity were collected from publicly available weather station records (www.wunderground.com). For each subject, weather records from the weather station nearest them (distance varied; all were within 20 km) were analyzed for the days of their doubly labeled water measurement. Average daily temperatures and average daily relative humidity during those days were used to calculate mean temperature and mean relative humidity. Since cool and mild temperatures are not expected to evoke sweating, we pooled all temperatures at or below 15°C for analyses (see [Figure 2](#)) to provide a better estimate of the effect of temperature on water turnover (e.g., [Table S2](#)). The pattern of results reported here are unchanged when unpooled temperatures are used.

Dietary Energy, Water Content, and Dry Matter

Dietary macronutrient, dry matter content, metabolizable energy, and water content were compiled from published studies, zoo records, and new analyses. First, the most common foods in the diet, representing >90% of calories consumed, were identified. Next, the macronutrient and water content of each food was determined from published records ([Table S3](#), [S4](#)), with the exception of water contents for wild gorilla and orangutan foods. For those foods, previously unpublished nutritional analyses from JMR and EV were used; nutrient analyses followed standard methods.³¹ Metabolizable energy was determined from dry matter as follows:³¹ carbohydrate: 4 kcal/g, protein: 4 kcal/g, fat: 9 kcal/g, soluble fiber: 0.543 kcal/g. Finally, the content of each food or food type was weighted by its percentage contribution to the diet to calculate a weighted mean water and macronutrient concentration for each human and ape cohort ([Tables S3](#) and [S4](#)).

Components of Water Influx

For individuals in water balance, as our subjects were, total water influx per day (L/d) is equal to measured water turnover. To model the components of water influx, we calculated water gained from transcutaneous absorption and inspired water vapor following.³² Briefly, transcutaneous water absorption was calculated as

$$\text{Transcut. Influx(L / d)} = 0.18(\text{Absolute Humidity} / 21.7) \times 1.44(\text{BSA} / 1,000) \quad (\text{Equation 5})$$

where 0.18 is the grams of water absorbed per square meter in air that is completely saturated (21.7 mg/L) and BSA is body surface area (m²). Absolute humidity was calculated from mean relative humidity and mean daily temperature. Body surface area (m²) estimated from body mass using Meeh's formula, $12.3 \times (\text{body mass})^{0.67}$, has been shown to approximate BSA values for humans and chimpanzees.^{33,34} This approach will impart some analytical error due to variation in the ratio of surface area to body mass both within and between species. However, given the small amount of water absorbed transcutaneously (~20 – 40 mL/day; [Table S1](#)) these analytical errors are negligible. Water influx through inspired air was calculated from the rate of CO₂ production.³² Using the modified Weir equation and assuming the CO₂ content of expired air is 3.5%, the total volume of air inspired per day is

$$\text{Inspired Air(L / d)} = [\text{TEE} / (1.1 + 3.9\text{FQ})] / 0.035 \quad (\text{Equation 6})$$

where FQ is the food quotient (apes: 0.95; Hadza hunter-gatherers: 0.92; sedentary and manual labor: 0.88). The mass of inspired water is given as

$$\text{Inspired Influx(L / d)} = \text{Inspired Air} \times \text{Absolute Humidity} / 1,000,000 \quad (\text{Equation 7})$$

Values for inspired influx are shown in [Table S1](#). Metabolic water production was calculated from TEE as

$$\text{Metabolic Water(L / d)} = 0.00014 \text{ TEE} \quad (\text{Equation 8})$$

This equation was used for all species. The precise ratio of metabolic water formed per kilocalorie of TEE will depend on the ratio of fats, proteins, and carbohydrate used for aerobic respiration.³⁵ Our approach simplifies this calculation by using a fixed ratio for all cohorts, ignoring variation in fuel utilization. However, the error imparted by this simplification is small, $\pm 5\%$ over the range of physiological plausible variation in RQ,³⁵ and does not affect the results of our analyses.

Ingested water from food and drink was calculated by subtracting transcutaneous influx, inspired influx, and metabolic water production from total water turnover

$$\text{Ingested Water(L / d)} = \text{Water Turn.} - \text{Transcut. Influx} - \text{Inspired Influx} - \text{Metab. Water} \quad (\text{Equation 9})$$

Drinking (L/d) was calculated by subtracting the water ingested as food moisture from total ingested water. The water ingested via food was estimated from the ratio of water per kilocalorie energy calculated for each diet (sedentary and manual labor: 0.51 mL/kcal; Hadza hunter-gatherers: 0.38 mL/kcal; zoo apes: 1.08 mL/kcal; sanctuary apes: 2.5 mL/kcal; [Tables S3](#) and [S4](#)). Multiplying these ratios by TEE for each subject gives the total water ingested via food. Drinking intake was then calculated as

$$\text{Drinking(L / d)} = \text{Ingested Water} - \text{Food Water} \quad (\text{Equation 10})$$

For some sanctuary apes, estimated food water intake exceeded calculated total water ingestion, due to overestimating the water content of their food. In these cases, drinking was set equal to 0.

Dry Matter Food Intakes and Water / DM Food Ratios

Dry matter (DM) of food intake ([Figure 3](#); [Table 1](#) and [S1](#)) was calculated for each subject by multiplying TEE by the ratio of grams / kilocalorie for their diet. Dietary g / kcal ratios for sedentary, manual labor, and hunter-gatherer human cohorts, and for zoo and sanctuary ape cohorts, are given in [Tables S3](#) and [S4](#). The ratio of water ingested per DM grams of food eaten were calculated for each subject by dividing Ingested Water by DM food intake.

Estimating Water Intake and Water Turnover in Wild Apes

To compare dietary water intake and water turnover in captive apes in this study to populations in the wild, we estimated water influx (water from food, transcutaneous and inspired water, and metabolic water production) for wild apes with the same TEE and body size as the captive apes in our sample. First, for each ape genus-sex-lifestyle cohort in [Table 1](#), we multiplied mean TEE and the water/energy ratio of from available data for diets in forest-living wild ape populations (*Pan*: 2.54 mL/kcal, *Gorilla*: 2.79 mL/kcal, *Pongo*: 2.17 mL/kcal; [Table S4](#)) to estimate food water intake for a wild ape cohort with the same TEE. This estimate of water intake via food for wild apes corresponded well with water intake from food and drink in the captive sample ([Figure S1](#)), with estimated water intake and water turnover in wild populations falling within 1 standard deviation of the means for each cohort in our ape sample.

Total water turnover for wild apes was estimated by adding inspired and transcutaneous water gain and metabolic water production to food water intake. Estimates for inspired and transcutaneous water gain and metabolic water production are calculated from TEE and body mass ([Star methods](#)). Thus, because our approach compared wild and captive apes at the same TEE and body size, these estimated values for wild apes were identical to those of their corresponding captive cohorts in [Table S1](#). Water turnover for wild ape cohorts corresponded well with measured water turnovers for captive cohorts ([Figure S1](#)).

Modeling Water Turnover

To compare water turnover and its components across species and lifestyles, we modeled these values for humans in industrialized and hunter-gatherer populations and chimpanzees in zoo and wild populations. Given the effects of body size and composition, TEE, temperature, and humidity on water turnover ([Table S2](#)), we modeled water turnover at TEE = 2000 kcal/d, temperature = 20°C, and

humidity = 70%, values within the observed ranges for humans and chimpanzees in our dataset (Table S1). Humans have a higher TEE for a given fat free mass than other hominoids,²⁶ and thus one can compare humans and chimpanzees at either a common TEE or fat free mass, but not both. TEE had a substantially stronger effect on water turnover in our analyses (Table S2), and so we modeled water turnovers at a common TEE. However, we note that our approach implies that the chimpanzees in our model will have marginally greater fat free mass than the humans in our model. This issue grows larger when modeling and comparing human values with gorillas and orangutans, which have even lower TEE for a given fat free mass ratios than do chimpanzees, and thus we do not include gorillas or orangutans in our model. Nonetheless, we note that one of the primary findings of the model, that wild and captive apes have equivalent water turnover, can also be derived solely from the water/energy ratios of wild apes diets (Figure S1).

Water Influx: For humans (industrial and hunter-gatherer) and zoo chimpanzees, water turnover (L/d) was predicted from a general linear model that included TEE, genus, lifestyle, temperature, and humidity as factors. Food intake (kg/d dry matter, L/d water) was calculated from dietary energy content (g/kcal), water content (mL/kcal), and TEE (2000 kcal/d) (see Tables S3–S4). For wild chimpanzees, water turnover (L/d) was estimated from food intake and drinking, assuming a minimal amount of drinking per day (100 mL/d) based on observations in the wild.² For all groups, transcutaneous and inspired water influx were set at 150 mL/d for all groups based on average values for humans and chimpanzees (Table S1). Metabolic water production was calculated from TEE (Star Methods). For humans and zoo chimpanzees, drinking was calculated by subtracting food water intake, transcutaneous and inspired water, and metabolic water from total water turnover.

Water Efflux: For all groups, urine production (L/d) was calculated from mean urine specific gravity for each group (Figure S1) using the relationship between urinary specific gravity and 24 h urine production published in.³ Fecal water loss (L/d) was calculated from dry matter of fecal production (g/d) and fecal moisture. Fecal moistures were taken from published values for humans and for wild chimpanzees in Kibale National Park, Uganda⁴ as well as new data from $n = 10$ samples from healthy chimpanzees at Lincoln Park Zoo (SRR) (mean: 76%, std. dev. $\pm 4\%$; Table S5). Fecal dry matter production was calculated as the undigestible fraction of food intake, feces = daily food intake (g/d) – 2000 (kcal/d) \times Diet nutrient density (g/kcal). Insensible and sweat water loss (L/d) was calculated by subtracting urine and fecal water loss from total water turnover.

Intestinal absorption: Dry matter of absorbed nutrients was calculated from dietary macronutrient content and the energy/g values²⁹ of carbohydrate: 4 kcal/g, protein: 4 kcal/g, fat: 9 kcal/g, soluble fiber: 0.543 kcal/g. Humans macronutrient ratios were based on published values for industrial (United States) and hunter-gatherer (Hadza) populations⁵ (industrial: 12% protein, 46% carbohydrate, 42% fat; hunter-gatherer: 24% protein, 65% carbohydrate, 11% fat). However, we modified the contribution of carbohydrate for hunter-gatherers, who consume a high fiber diet,⁵ so that 2% of their energy is derived from soluble fiber and 63% from carbohydrate. We used dietary data from zoo apes (Table S3) to calculate macronutrient contributions: 15% protein, 75% carbohydrate, 10% fat. For wild chimpanzees, we used nutrient analyses of fruits eaten by wild chimpanzees Kibale National Park, Uganda⁶ and with nutrient content of leaves eaten primarily by gorillas in Bwindi Impenetrable National Park, Uganda,⁷ along with the proportion of fruit and leaves in the wild chimpanzee diet (Table S4) to establish macronutrient contributions: 12% fiber, 20% protein, 62% carbohydrate, 6% fat. Intestinal water absorption (L/d) by subtracting fecal water loss from total water turnover.

Multiplying the kcal/g value of each nutrient by its percentage contribution to daily energy use and taking its reciprocal gives the mean density of absorbed nutrients (g/kcal, Table S5) for each modeled group. Multiplying this value by TEE gives the estimated dry matter absorbed per day. The remaining, unabsorbed grams dry matter of food ingested per day must be excreted in the feces. Fecal moisture values (% water; Table S5) were then used to calculate fecal water loss (L/d). We calculated net intestinal absorption (L/d, Table S5) by subtracting fecal water loss from combined food and drinking water intake.

As a check on our modeling approach for intestinal absorption and fecal loss, we compared daily fecal production from our model to published values for industrial and hunter-gatherer human populations and wild chimpanzees to published values. Industrial population humans in our model produce 141 g of feces per day (wet mass), similar to the mean value reported for high-income countries (149 g/d, std.dev. ± 95 g/d).⁸ Modeled hunter-gatherer fecal production (411 g/d) fell within the range expected for populations with high fiber intakes ($\sim 300 - 500$ g/d, see Figure 2 in⁸). Fecal production modeled for wild chimpanzees (1380 g/d) was $\sim 60\%$ greater than reported fecal production for chimpanzees in the Kanyawara community of Kibale National Park, Uganda (~ 7 defecations per day $\times 120$ g/defecation = ~ 840 g/d⁹). However, a chimpanzee with TEE of 2000 kcal/d would have a body mass of ~ 55 kg,¹ which is $\sim 40\%$ larger than estimated body weights for Kanyawara adults (females: 37kg, males: 43 kg),¹⁰ and thus consistent with greater fecal production. While further work on water and nutrient absorption is certainly warranted, modeled fecal production, and by extension, intestinal absorption, is consistent with observed values (Figure 3; Table S5).

QUANTIFICATION AND STATISTICAL ANALYSIS

Following our previous work on hominoid energetics,²⁶ we analyzed differences among genera (*Homo*, *Pan*, *Gorilla*, and *Pongo*), pooling data from chimpanzees and bonobos. This approach helps to mitigate the effect of phylogenetic relatedness, as the divergence dates for *Homo-Pan* (~ 11 million years), *Homo-Gorilla* (13 million years), and *Pan-Gorilla* (13 million years) are similar.³⁶ The divergence dates for *Homo/Gorilla/Pan-Pongo* (~ 24 million years) are somewhat greater,³⁶ which should be considered in interpreting differences between orangutans and other hominoids in this sample. Established methods to control for phylogenetic relatedness typically examine species (or other grouping variable) means along a phylogenetic tree, which makes it difficult to assess the effects of within-species variation in the outcome of interest (in this case, water turnover and its components). Given the strong effects of fat free mass, TEE, and other covariates and the degree of within-genus variation in water turnover (Figures 1 and 2) and the broad

similarity in divergence times, we believe it is preferable to analyze subject-level data using multivariate models rather than collapsing measures to single species or population means for standard phylogenetic analyses.

All analyses were conducted in R²⁵ using generalized linear models and other parametric tests. All tests were 2-tailed. Residuals of \ln -transformed water turnover from the full general linear model (Table S2) were normally distributed ($W = 0.99$, $p = 0.07$, Shapiro-Wilk normality test). We also included an analysis of water turnover using a linear mixed effects model (nlme package in R) with “site” (the place of data collection) as a random factor; results were essentially unchanged (Table S2). Details of each test are provided in the text.

Sensitivity Analyses

We examined the potential effects of measurement and analytical errors on our results concerning 1) the determination of water turnover from isotope depletion and 2) the estimation of the relative magnitudes of water turnover components.

Measurement error in the determination of water turnover will be dictated primarily by the accuracy and precision of isotope enrichment in urine samples. Measurement error in the determination of TEE, which requires the measurement of two isotopes (oxygen-18 and deuterium), is generally less than 10%.³⁷ Measurement error in the determination of water turnover, which requires the measurement of one isotope (deuterium), has not been assessed in many studies but is approximately half that of TEE, less than 5%.³⁸ These measurement errors are bidirectional, random errors, and we have no reason to expect that they would bias water turnover or water/energy ratios for humans or non-human apes in a particular direction, although further validation work, particularly in non-human apes, would be welcome. The magnitude of differences between humans and other hominoids in this study, including differences in the water/energy ratio, are considerably larger than 10% (Figure 2). Thus, random measurement error in the determination of water turnover is unlikely to influence the pattern of results in this study.

Error in the determination of water turnover components will affect the modeling and water influx and efflux (Figure 3). Estimated transcutaneous and inspired water influx are based on estimates of body surface area and pulmonary water absorption and must be considered first approximations. However, these components combined account for ~2 to 5% of total influx (Table S1; Figure 3), and thus even if our estimates are in error by 50% it will have negligible effect on other components. Metabolic water production, as described in STAR methods, is estimated from TEE and is expected to vary $\pm 5\%$ about the true value, dependent on the ratio of macronutrients used in respiration. Even if metabolic water production is in error by 10% and transcutaneous and inspired influx are in error by 50%, the combined effect on the estimation of water ingested via food and drink (which is calculated by subtracting transcutaneous, inspired, and metabolic water influx from water turnover) is less than 5%. Thus, even considering measurement error in the determination of water turnover, estimates of water ingestion (food + drink) are expected to have an error of <10%. However, the proportion of water from food versus drink is prone to substantially greater error due to our reliance on estimated food moistures. In human populations and zoo apes, moisture from food is estimated to account for ~20 to 40% of ingested water; water from food is ~90% or more of estimated water ingestion in sanctuary ape populations (Table S1). Thus, if our estimates of food moisture err by 25%, our estimates of food moisture intake will vary by a similar amount and estimated drinking will vary by roughly 5 to 10% for humans and zoo apes. Estimates of drinking water ingestion in sanctuary ape populations, where drinking volumes appear to be quite low (Table S1), are particularly sensitive to estimated food water content.

Components of water efflux, which are modeled for human and chimpanzee populations in Figure 3, must be considered first approximations. We do not have 24 h urine or feces collections for any population in this study, and thus urinary output and daily fecal water loss are estimated from urinary specific gravity and estimated daily stool production, respectively. Studies testing the relationships between urine production and urinary specific gravity, and between stool production and diet, are needed.